

UNIVERSITAT DE BARCELONA



# 23-28 August 1999

- Basel 87 - Rome 89 - Debrecen 91 - Montpellier 93 - Edinburgh 95 - Arnhem 97 - Barcelona 99 - Aachus 01 SEVENTH CONGRESS of the

# **EUROPEAN SOCIETY**

# for

# **EVOLUTIONARY BIOLOGY**

# **BARCELONA, SPAIN**

# 23-28 AUGUST 1999

# **Organising Committee**

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# WELCOME TO THE VIITH CONGRESS OF THE EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY

The European Society for Evolutionary Biology organises every other year an international congress that brings together evolutionists from all over the world to present and discuss topics of the many disciplines that constitute the science of Evolution. The present event has gathered more than 800 evolutionists that will communicate their work through talks and posters included in 26 symposia. In addition, there will be 7 plenary lectures, six by senior scientists and one by the junior scientist that won the John Maynard Smith (JMS) prize.

The organising comittee wishes you a pleasant and profitable stay. Those that choose to be lodged at the Bellaterra campus facilities of the Universitat Autònoma de Barcelona, will find a friendly and charming environment in "Vila Universitaria" and the "Hotel Campus" surroundings, with facilities including restaurants, bars, swimming pool, bank offices, first-aid clinics, supermarkets, etc. that will help to make your life easy during the congress. The conference rooms at the hotel will host all the talks. Poster rooms will be either at the hotel building or at the restaurant building. Poster room locations will be clearly indicated upon arrival. It is very easy to get oriented inside the main hotel building, each conference room has a sign with its name and there are signals at the halls leading you to the rooms.

In this book (pages I8-I13) you may find a general outline of the congress time schedule, distributed by days and rooms. If you wish to find a specific speaker, you must look at the presenter's index where the pages of his/her performance are given. Abstracts are in alphabetical order by presenting authors. The general outline is similar for each day. There is an opening plenary lecture by an invited keynote speaker, followed by up to 13 oral presentations at each of 5 parallel symposia per day. On tuesday there are two additional evening plenary sessions, one is the Presidential Address, the other is a lecture by the JMS prize winner. At three days (tuesday, thursday and friday) there is an afterlunch plenary poster session (I, II and III).

Wednesday is a special day because sessions end earlier due to the excursion. This day is dedicated to ease the tight schedule of the congress and provide some free time to enjoy the countryside at the vineyard area of Sant Sadurni d'Anoia, that we are going to visit. This area, only 30 km far from Bellaterra, is known over the world for producing *cava*, a kind of wine, produced by the "champagnoise" technique, that is highly appreciated. In addition to the beauty of the Anoia region, with spacious vineyards and large catalan country-houses, the vineries are built in artistic mansions in modernist architectural style, a version of the art nouveau, that flourished in Catalonia at the turn of the century. A reception buffet will be offered with catalan food and wine.

On the evening of friday 27 there is a banquet at the Castell de Sant Marçal, close to the Bellaterra campus, for those that have registered. Buses will be provided for transportation.

#### INSTRUCTIONS FOR CONTRIBUTORS

*Talks*: The complete list of talks by symposia are depicted in pages I17-I43. Check your scheduled time, prepare and preview (if necessary) your slides. The speakers are requested to prepare their slides in advance: those speaking in the morning session should prepare slides in the previous evening and those speaking in the afternoon session should make their preparations the same day. This must be done at Marie Curie room, where preview facilities and technical assistance (i.e. trays for slides, etc.) are provided. This room will be open every day from 12 to 16 in the afternoon, and from 18 to 22 in the evening, starting the evening of monday 23. Do not forget to collect your slides at the next break following your talk! Please, follow always the chairperson advise in your presentation. Allow three minutes of discussion for all talks.

**Posters:** Posters must be fixed at several rooms which location will be announced upon arrival. Those presenting their posters at session I (tuesday 24) are requested to fix posters on arrival (monday evening). Those presenting posters at sessions II and III (thursday 26 and friday 27, respectively) should fix posters as soon as possible. Posters must be ready, at least, the day before the presenting session. Each poster is identified by an S followed by the symposium number, a Roman numeral (identifying the session: I, II or III), and by the poster number within the symposium. Thus, poster S1-I-18 indicates poster 18 of symposium 1 scheduled for the poster session I. Consequently, each poster can be exhibited, practically, for the whole congress, although authors are only obliged to be present during poster presentation times (see congress program, pages I8-I13). Please, find your poster identification at the poster list in this book (pages I45-I67) and fix your poster on the board that shows the same identification label. Technical assistance will be provided at the poster rooms.

Poster sessions include the following symposium numbers, as follows:

Poster Session I (Tuesday 24): S1, S7, S12

Poster Session II (Thursday 26): S2, S4, S6, S8, S11, S13, S14, S17, S18, S19, S20, S23, S24, S25.

Poster Session III (Friday 27): S3, S5, S9, S10, S15, S16, S21, S22, S26,

Presenter's names are underlined in abstracts (part II)

#### INSTRUCTIONS FOR CHAIRPERSONS

Chairpersons are required to follow the schedule times, allowing three minutes for discussion.

# DISPLAYS

In the hotel hall you will find displays by:

Blackwell Science Oxford University Press Cambridge University Press

# FINAL RECOMMENDATIONS

The organisers are very satisfied by the great demand that this congress has elicited among evolutionists. Our expectations of attendance have been largely surpassed, not only in numbers but also in diversity of topics. This represents a very positive fact. First, because it shows the great health of the state of the art of evolution, and, second, because it demonstrates that our society is an adequate forum to socialise science. Yet, this overflow of participants imposes some sacrifices to both, organisers and participants. These comprise less available space, less personalised attention, some putative time restrictions, etc. and, above all, the compromise that we must follow sometimes tight rules and ordinances. Some of these rules are stated above and some others will appear at the congress board continuously. We, the organisers, are confident that attendants will follow these rules, and we hope that you will not hesitate to ask any question that you find necessary to make your stay pleasant among us. Members of the crew of the RACC (Reial Automòbil Club de Catalunya) organisation will be ready to attend all your demands. Please, address to these accredited persons to solve all organisational problems you encounter.

# ACKNOWLEDGEMENTS

The organising committee recognises the help received by Universitat Autònoma de Barcelona, Universitat de Barcelona, Ministerio de Educación y Cultura (Spain), Generalitat de Catalunya, European Science Foundation and International Institute for Applied System Analysis (Austria) towards the organisation of this congress. Roche Molecular Biochemicals contributed to some minor expenses and Innogenetics Diagnóstica y Terapeutica, S.A. provided folders for assistants.

# **PROGRAMME OVERVIEW**

| Lecture Room | Arnau de Vilanova          | Lluís Vives I             | Lluís Vives II              | Martí Franqués I              | Martí Franqués II                         |
|--------------|----------------------------|---------------------------|-----------------------------|-------------------------------|---|
|              | 1                          | r                         | 1                           | 1                             |   |
| Tuesday 24   | Plenary Lecture            | Symposium 7               | Symposium 12                | Symposium 11<br>Adaptation to | Symposium 18<br>Horizontal gene transfer: |
| Tuesday 24   | Symposium 1                | evolution: non-           | Cincerstanding intress      | environmental stress          | past and present role in                  |
|              | Molecular population       | equilibrium processes and |                             | environmentar suess           | evolution                                 |
|              | genetics                   | adaptive dynamics         |                             |                               | evolution                                 |
|              | Presidential Address       | adaptive dynamics         |                             |                               |   |
|              | Godfrey M. Hewitt          |                           |                             |                               |   |
|              | L.Maynard Smith            |                           |                             |                               |   |
|              | Lecture                    |                           |                             |                               |   |
|              | Nicolas Galtier            |                           |                             |                               |   |
|              | Plenary Lecture            | Symposium 6               | Symposium 13                | Symposium 2                   | Symposium 23                              |
| Wednesday 25 | Juan Luis Arsuaga          | Origin, evolution and     | The role of the inheritance | Early molecular evolution     | Macroevolutionary                         |
|              | Symposium 17               | stability of coevolved    | of acquired variation in    |                               | patterns and dynamics:                    |
|              | Conflicts arising from sex | mutualisms                | evolution                   |                               | 25 years later                            |
|              | and sexes                  |                           |                             |                               |   |
|              | <b>Plenary Lecture</b>     | Symposium 14              | Symposium 4                 | Symposium 19                  | Symposium 20                              |
| Thursday 26  | Chung-I Wu                 | Future directions in      | Neutralism and              | Retrotransposed DNA           | Evolution of RNA                          |
|              | Symposium 8                | evolutionary quantitative | selectionism: the end of a  | elements: homoplasy-free      | viruses                                   |
|              | Evolutionary significance  | genetics                  | debate?                     | characters for                | ESEB Council Meeting                      |
|              | of colonizations           |                           |                             | phylogenetic and              | Symposium 24                              |
|              | Plenary ESEB Business      |                           |                             | population genetics           | Unravelling the origin of                 |
|              | Wieeting                   |                           |                             |                               | Motogoong                                 |
|              | Planary Lacture            | Symposium 15              | Symnosium 3                 | Symnosium 25                  | Symposium 10                              |
| Friday 27    | Carlos M Herrera           | Unravelling the genetics  | Methods for analyzing       | Evolution of species          | Co-evolutionary                           |
| Triday 27    | Symposium 9                | of evolutionary change    | DNA sequence data and       | flocks in east African        | interactions between                      |
|              | Molecular evolutionary     | of evolutionary enange    | constructing phylogenetic   | cichlid fishes                | symbionts                                 |
|              | ecology                    |                           | trees                       | cicilità fisites              | syntoionts                                |
|              | Plenary Lecture            | Symposium 5               | Symposium 16                | Symposium 22                  | Symposium 21                              |
| Saturday 28  | Denis Duboule              | Deleterious mutation:     | Meiotic drive and related   | Morphological                 | Antibiotic resistance:                    |
|              | Symposium 26               | parameter estimation and  | phenomena                   | constraints: a theoretical    | implications for our                      |
|              | Evolution in the sea.      | evolutionary              |                             | perspective                   | understanding of the                      |
|              | Molecular ecology and      | consequences              |                             |                               | population genetics and                   |
|              | paleontological            |                           |                             |                               | molecular biology of                      |
|              | approaches                 |                           |                             |                               | adaptive evolution                        |
|              |                            |                           |                             |                               |   |

# PROGRAMME (DAILY)

| TUESD | AY | 24 | AUG | UST | 1999 |
|-------|----|----|-----|-----|------|
|-------|----|----|-----|-----|------|

| 8:15-9:15    |                                   |                                  | Room: Arnau de Vilanova<br>RICHARD R. HUDSON<br>Plenary lecture    |  |                               |
|--------------|-----------------------------------|----------------------------------|--|--|-------------------------------|
| Lecture Room | Arnau de Vilanova                 | Lluís Vives I                    | Lluís Vives II   | Martí Franqués I                           | Martí Franqués II             |
| 9:20-9:25    | S1: Molecular population genetics | S7: Linking ecology to evolution | S12: Understanding fitness   | S11: Adaptation to<br>environmental stress | S18: Horizontal gene transfer |
| 9:25-9:55    | C.H.Langley                       | B.J.M.Bohannan                   | R.E.Michod   | R.B.Huey                                   | J.R.Brown                     |
| 9:55-10:25   | D.Charlesworth                    | U.Dieckmann                      | M.van Baalen   | P.M.Brakefield                             | J.P.Gogarten                  |
| Coffee break |                                   |                                  |  |  |                               |
| 10:55-11:25  | J.F.Y.Brookfield                  | M.Travisano                      | R.Ferrière   | R.A.Krebs                                  | E.V.Koonin                    |
| 11:25-11:45  | J.Vieira                          | D.Tautz                          | E.Svensson   | J.R.David                                  | R.Gupta                       |
| 11:45-12:05  | C.Segarra                         | E.Rolán-Alvarez                  | O.Tenaillon  | V.Loeschcke                                | M.Syvanen                     |
| 12:05-12:25  | O.Savolainen                      | T.van Dooren                     | I.Suárez   | R.Bijlsma                                  | T.P.Hauser                    |
| Lunch        |                                   |                                  |  |  |                               |
| 14:25-15:45  |                                   | PLE<br>ESEB Editor               | INARY POSTER SESSION<br>ial Board Meeting (Room:                   | N I<br>Jean Piaget)                        |                               |
| Coffee break |                                   |                                  |  |  |                               |
| 16:05-16:25  | B.Desplanque                      | N.Maire                          | F.Rousset  | A.J.Davis                                  | L.H.Rieseberg                 |
| 16:25-16:45  | J.Bertranpetit                    | O.Leimar                         | O.Håstad   | F.Pulido                                   | D.A.Tepfer                    |
| 16:45-17:05  | D.De Lorenzo                      | S.Gavrilets                      | M.Fischer  | S.Edmands                                  | R.Butcher                     |
| 17:05-17:25  | J.C.Garza                         | A.B.Korol                        | C.Damgaard   | P.Armbruster                               | E.Haring                      |
| 17:25-17:45  | P.Kasapidis                       | R.Ferrière                       | L.Witting  | K.I.Jönsson                                | I.Matic                       |
| 17:45-18:05  | D.Liebers                         | R.Law                            | D.W.Coltman  | P.Capy                                     | W.Wackernagel                 |
| 18:05-18:25  | B.Harr                            | G.Meszéna                        |  | L.De Meester                               | A.Tauch                       |
| Dinner       |                                   |                                  |  |  |                               |
| 20:20-21:05  |                                   | PI                               | Room: Arnau de Vilanova<br>RESIDENTIAL ADDRESS<br>GODFREY M.HEWITT | 3  |                               |
| 21:05-21:50  |                                   | Jo                               | hn Maynard Smith Lectur<br>NICOLAS GALTIER                         | e  |                               |

| 8:15-9:15    |  | Ro<br>JU  | oom: Arnau de Vilanova<br>UAN LUIS ARSUAGA                                |                                  |   |
|--------------|--|---|---|----------------------------------|---|
| Lecture Room | Arnau de Vilanova                            | I luís Vives I  | Lluís Vives II  | Martí Franqués I                 | Martí Franqués II   |
| 9:20-9:25    | S17: Conflicts arising<br>from sex and sexes | S6: Origin, evolution and<br>stability of coevolved<br>mutualisms | S13: The role of the<br>inheritance of acquired<br>variation in evolution | S2: Early molecular<br>evolution | S23:<br>Macroevolutionar<br>y patterns and<br>dynamics: 25<br>years later |
| 9:25-9:55    | G.Arnqvist                                   | A.E.Douglas   | R.Holliday  | L.Landweber                      | M.J.Benton  |
| 9:55-10:25   | A.Pomiankowski                               | O.Pellmyr   | L.Hirschbein  | H.Philippe                       | J.Wagensberg  |
| Coffee break |  |   |   |                                  |   |
| 10:45-11:15  | R.Stouthamer                                 | M-C.Anstett   | E.J.Steele  | S.Dabizzi                        | D.M.Alba  |
| 11:15-11:35  | P.I.Ward                                     | E.A.Herre   | G.Damiani   | L.Ribas de Pouplana              | E.Garcia-Vazquez  |
| 11:35-11:55  | N.Wedell                                     | L.Després and J.B.Ferdy   | R.Wenne   | G.Sella                          | D.B.Vizoso  |
| 11:55-12:15  | L.Sundström                                  | C.Brouat  | C.Pál   | J.L.Siefert                      | A.Ø.Mooers  |
| 12:15-12:35  | N.K.Michiels                                 | M.Gauduchon   | M.Lachmann  | N.Tourasse                       |   |
| Lunch        |  | ESEB Officer  | s Meeting (Room: Bertrand   | Russell)                         |   |
| 14:30-14:50  | R.G.Sharpe                                   | P.Baumann   | M.J.Lamb  | P.López-García                   | D.Cohen   |
| 14:50-15:10  | T.Rigaud                                     | T.L.Bultman   | E.Jablonka  | D.Moreira                        | J.Agustí  |
| 15:10-15:30  | F.Vala                                       | A.N.M.Bot   | K.Hora  |                                  |   |
| 15:30-15:50  | A.Kaitala                                    | D.W.Yu  | D.Dor   |                                  |   |
| 15:50-16:10  | D.Ebert                                      | A.Grutter   |   |                                  |   |
| 16:10-16:30  | C.M.Sgrò                                     | M.Doebeli   |   |                                  |   |
| 16:30        |  |   | EXCURSION   |                                  |   |

I-10

| 8:15-9:15    |  |  | Room: Arnau de Vilanova<br>CHUNG-I WU<br>Plenary lecture | a                                       |                                       |                           |
|--------------|--|--|--|---|---------------------------------------|---------------------------|
| Lecture Room | Arnau de Vilanova                                    | Lluís Vives I  | Lluís Vives II   | Martí Franqués I                        | Martí Franq                           | ués II                    |
| 9:20-9:25    | S8: Evolutionary<br>significance of<br>colonisations | S14: Future directions in<br>evolutionary quantitative<br>genetics | S4: Neutralism and selectionism: the end of a debate?    | S19:<br>Retrotransposed<br>DNA elements | S20: Evolution of F                   | RNA viruses               |
| 9:25-9:55    | R.G.Gillespie  | M.Lynch  | T.Ohta   | T.H.Eickbush                            | S.Wain-Hobson                         |                           |
| 9:55-10:25   | C.Ribera   | T.T.Vaughn   | G.Bernardi   | H.A.Wichman                             | F.García-Arenal                       |                           |
| Coffee break |  |  |  |   |                                       |                           |
| 10:55-11:25  | M.A.Arnedo   | D.A.Roff   | T.Gojobori   | N.Okada                                 | C.Escarmís                            |                           |
| 11:25-11:45  | B.C.Emerson  | D.J.Fairbairn  | A.Eyre-Walker  | X.M.Maside                              | P.E.Turner                            |                           |
| 11:45-12:05  | S.Carranza   | T.F.Hansen   | H.Akashi   | P.Deininger                             | E.Baranowski                          |                           |
| 12:05-12:25  | M.L.Heddle   | A.Monteiro   | M.Przeworski   | J.Brosius                               | S.F.Elena                             |                           |
| Lunch        |  |  |  |   |                                       |                           |
| 14:25-15:45  |  | ESEB   | PLENARY POSTER SESSI<br>Council Meeting (Room: Mart      | O <b>N II</b><br>í Franqués II)         |                                       |                           |
| Coffee break |  |  |  |   |                                       |                           |
| 16:05-16:25  | N.Davies   | G.de Jong  | WH.Li  | S.C.Hardies                             | S24: Unravelling the first bilaterian | ne origin of<br>Metazoans |
| 16:25-16:45  | A.Caccone  | O.J.Hardy  | M.W.Nachman  | O.Verneau                               | A. Adoutte                            | 16:10-16:40               |
| 16:45-17:05  | F.Mestres  | S.Van Dongen   | D.Rand   | A.V.Furano                              | S.Conway-Morris                       | 16:40-17:10               |
| 17:05-17:25  | F.Santucci   | W.U.Blanckenhorn   | H.Boriss   | D.Kordiš                                | R.M.Rieger                            | 17:10-17:40               |
| 17:25-17:45  | S.Steinfartz   | T.J.Kawecki  | M.Antezana   | D.A.Kramerov                            | C.Nielsen                             | 17:40-18:00               |
| 17:45-18:05  | B.Milá   | R.V.Alatalo  | S.E.Ptak   | A.M.Shedlock                            | S.Bengtson                            | 18:00-18:20               |
| 18:05-18:25  | G.Reeves   | J.J.Windig   | T.Mourier  | D.A.McClellan                           | M.Riutort                             | 18:20-18:40               |
|              |  |  |  |   | J.García-Fernández                    | 18:40-19:00               |
| Dinner       |  |  |  |   |                                       |                           |
| 20:30-21:15  |  | PI   | Room: Arnau de Vilanov.<br>ENARY ESEB BUSINESS M         | a<br>EETING                             |                                       |                           |

| FRIDA     | Y | 27 A | UGI | UST | 1999 |
|-----------|---|------|-----|-----|------|
| A ANALYIA |   |      |     |     | 1/// |

| 8:15-9:15    |                                       | I   | Room: Arnau de Vilanova                   |                                  | ,                                    |
|--------------|---------------------------------------|---|---|----------------------------------|--------------------------------------|
|              |                                       | (   | Plenary lecture                           |                                  |                                      |
| Lecture Room | Arnau de Vilanova                     | Lluís Vives I                                 | Lluís Vives II                            | Martí Franqués I                 | Martí Franqués II                    |
| 9:20-9:25    | S9: Molecular<br>evolutionary ecology | S15: Unravelling the genetics of evolutionary | S3: Methods for<br>analyzing DNA sequence | S25: Evolution of species flocks | S10: Co-<br>evolutionary             |
|              |                                       | change  | data                                      |                                  | interactions<br>between<br>symbionts |
| 9:25-9:55    | G.Gerlach                             | M.Kearsey                                     | M.Hasegawa                                | A.Meyer                          | U.J.Mueller                          |
| 9:55-10:25   | P.G.Parker                            | P.D.Keightley                                 | WH.Li                                     | O.Seehausen                      | E.A.Herre                            |
| Coffee break |                                       |   |   |                                  |                                      |
| 10:55-11:25  | L.H.Rieseberg                         | J.Gadau                                       | J.Hein                                    | I.Kornfield                      | I.R.Sanders                          |
| 11:25-11:45  | F.Balloux                             | M.Pigliucci                                   | M.Gouy                                    | N.B.Goodwin                      | E.Jousselin                          |
| 11:45-12:05  | K.Schwenk                             | G.Bell  | YX.Fu                                     | M.Taborsky                       | D.Nash                               |
| 12:05-12:25  | C.R.Engel                             | J.Gockel                                      | O.Gascuel                                 | G.Turner                         | M.S.Sánchez                          |
| Lunch        |                                       |   |   | <b>T</b>                         |                                      |
| 14:25-15:45  |                                       | PLEN  | <b>ARY POSTER SESSION II</b>              | I                                |                                      |
| Coffee break |                                       |   |   |                                  |                                      |
| 16:05-16:25  | D.Forcioli                            | W.G.Zijlstra                                  | S.V.Muse                                  | P.W.Shaw                         | B.Sabater /Silva                     |
| 16:25-16:45  | M.Pascual                             | M.Rozowski                                    | A. von Haeseler                           | C.Sturmbauer                     | A.Buckling                           |
| 16:45-17:05  | T.Pastor                              | A.Barbadilla                                  | Z.Yang                                    | L.Rüber                          | M.H.H.Hansen                         |
| 17:05-17:25  | F.González-Candelas                   | A.Westerbergh                                 | T.Gojobori                                | S.Baric                          | A.Biere                              |
| 17:25-17:45  | L.Bargelloni                          | Ð.Ugarkovic                                   | E.C.Holmes                                | K.Takahashi                      | E.J.de Vries                         |
| 17:45-18:05  | P.Bloomer                             | M.Ackermann                                   | J.Thorne                                  | R.Zardoya                        |                                      |
| 18:05-18:25  | E.Willerslev                          | J.M.Gleason                                   | H.Kishino                                 | M.E.Knight                       |                                      |
| 20:30        |                                       | С   | ONFERENCE DINNER                          |                                  |                                      |

I-12

# SATURDAY 28 AUGUST 1999

| 8:15-9:15    |                           | R                        | oom: Arnau de Vilanova<br>DENIS DUBOULE<br>Plenary lecture |                                |                            |
|--------------|---------------------------|--------------------------|--|--------------------------------|----------------------------|
| Room         | Arnau de Vilanova         | Lluís Vives I            | Lluís Vives II   | Martí Franqués I               | Martí Franqués II          |
| 9:20-9:25    | S26: Evolution in the sea | S5: Deleterious mutation | S16: Meiotic drive and related phenomena                   | S22: Morphological constraints | S21: Antibiotic resistance |
| 9:25-9:55    | J.B.C.Jackson             | M.Lynch                  | R.F.Hoekstra   | G.B.Müller                     | B.R.Levin                  |
| 9:55-10:25   | S.R.Palumbi               | R.G.Shaw                 | D.R.Taylor   | M.De Renzi                     | D.I.Anderson               |
| Coffee break |                           |                          |  |                                |                            |
| 10:45-11:15  | D.A.Powers                | D.Houle                  | A.B. Carvalho  | I.Salazar-Ciudad               | A.A.Medeiros               |
| 11:15-11:35  | H.Fortunato               | T.Bataillon              | C.Capillon   | D.Rasskin-Gutman               | HJ.Carius                  |
| 11:35-11:55  | C.Gili                    | A.Caballero              | A.G.Bugrov   | G.J.Eble                       | F.Dionisio                 |
| 11:55-12:15  | T.Collins                 | J.D.Fry                  | D.Durand   | A.Ressayre                     | T.Little                   |
| 12:15-12:35  | S.Planes                  | R.Korona                 | A.Hingle   | A.Rosas                        | C.D.M.Müller-Graf          |
| Lunch        |                           |                          |  |                                |                            |
| 14:30-14:50  | Giacomo Bernardi          | A.D.Peters               | M.Goddard  | A.Casinos                      | D.Ortius                   |
| 14:50-15:10  | H.A.Lessios               | J.Wang                   | J.H.G.v.d.Schulenburg                                      | N.López-Martínez               | C.T.Bergstrom              |
| 15:10-15:30  | E.Bermingham              | L.Loewe                  | F.Jiggins  | A.D.Buscalioni                 | F.Baquero                  |
| 15:30-15:50  | A.Meyer                   | J.R.Peck                 | G.Bernasconi   | D.M.Alba                       |                            |
| 15:50-16:10  | E.Zouros                  | M.Storhas                | F.Mery   |                                |                            |
| 16:10-16:30  | C.Lemaire                 | N.Bierne                 | M.Reuter   |                                |                            |
| 16:30        |                           |                          | FAREWELL   |                                |                            |

# PLENARY LECTURES AND SCIENTIFIC EVENTS

All lectures are in Lecture room Arnau de Vilanova

# **TUESDAY 24 AUGUST**

| 8:15-9:15   | Richard R. Hudson (University of Chicago, USA)<br>What have DNA polymorphism data told us?   |
|-------------|--|
| 20:20-21:05 | Godfrey M. Hewitt (University of East Anglia, Norwich, UK)<br>Presidential Address   |
|             | Colonisation of Europe after the ice age   |
| 21:05-21:50 | Nicolas Galtier (University of Edinburgh, UK and Université Montpellier 2, France)<br>John Maynard Smith Prize winner's lecture<br>Non-stationary models of DNA sequence evolution and ancestral G+C content |

## WEDNESDAY 25 AUGUST

8:15-9:15 Juan Luis Arsuaga (Universidad Complutense de Madrid, Spain) The first Europeans

# **THURSDAY 26 AUGUST**

8:15-9:15 Chung-I Wu (University of Chicago, USA) The molecular and population genetics of speciation and species differentiation

# **FRIDAY 27 AUGUST**

8:15-9:15 Carlos M. Herrera (Estación Biológica de Doñana, Sevilla, Spain) Plant adaptation to insect pollinators: ecological factors and limits to specialization

# SATURDAY 28 AUGUST

8:15-9:15 Denis Duboule (Université de Genève, Switzerland) Morphological evolution and transitionism

# SYMPOSIA: ORAL PRESENTATIONS

# LECTURE ROOM: ARNAU DE VILANOVA

#### Symposium S1: Molecular population genetics

Organisers: Montserrat Aguadé (Barcelona, Spain), Michel Veuille (Paris, France)

#### Chair: Montserrat Aguadé

# 9:20 Introduction

- 9:25 Charles H. Langley (University of California, Davis CA, USA)
- DNA sequence polymorphism in natural populations: causes, associations and implications9:55 Deborah Charlesworth (University of Edinburgh, UK)
- Can we understand why inbreeding plants have less genetic variability than outcrossers?
- 10:55 John F. Y. Brookfield (University of Nottingham, UK)
- What is the impact of transposable elements on host genome variability?

11:25 Jorge Vieira (University of Edinburgh, UK)

- DNA polymorphism studies on the fused gene of Drosophila virilis
- 11:45 Carmen Segarra (Universitat de Barcelona, Spain) Nucleotide variation at the *yellow* gene region in four different chromosomal arrangements of Drosophila subobscura
- 12:05 Outi Savolainen (University of Oulu, Finland) Nucleotide variation at the Adh locus in outcrossing *Arabis petraea/lyrata* compared to selfing *A*. *thaliana*

#### Chair: Michel Veuille

- 16:05 Benoit Desplanque (Université de Lille1, France) cpDNA and mtDNA diversity in beets (*Beta vulgaris* ssp L., Chenopodiaceae) and association between the two organelle genomes
- 16:25 J. Bertranpetit (Universitat Pompeu Fabra, Barcelona, Spain) Differential sexual migration patterns in humans: comparison of mtDNA sequences and Y-chromosome STRs in Central Asia
- 16:45 David De Lorenzo (University of Texas, Houston, USA) The HKA test into the new millennium
- 17:05 John-Carlos Garza (Université de Montpellier II, France) Detection of reduction in population size using data from microsatellites
- 17:25 Panagiotis Kasapidis (University of Crete, Greece) Extreme levels of mitochondrial DNA sequence divergence among the populations of the gecko *Cyrtopodion kotschyi* in the Aegean Archipelago
- 17:45 Dorit Liebers (University of Greifswald, Germany)
- Cryptic species within the herring gull Larus argentatus/cachinnans complex
- 18:05 Bettina Harr (Veterinärmedizinische Universität, Vienna) Mutational behavior of long microsatellites in *D. melanogaster*

**Symposium S7: Linking ecology to evolution: non-equilibrium processes and adaptive dynamics** \* Organisers: Michael Doebeli (Basel, Switzerland), Ulf Dieckmann (Laxenburg, Austria), J.A.J. Metz (Leiden, The Netherlands)

# Chair: Michael Doebeli

- 9:20 Introduction
- 9:25 Brendan J. M. Bohannan (Stanford University, California, USA) Adaptive dynamics in laboratory communities of bacteria and virulent bacteriophage
- 9:55 Ulf Dieckmann (International Institute for Applied Systems Analysis, Austria) Evolutionary branching in sexual populations: a new model for sympatric speciation

# Chair: Ulf Dieckmann

- 10:55 Michael Travisano (University of Houston, Texas, USA) Ecological interactions during adaptive radiation
- 11:25 Diethard Tautz (Universität zu Köln, Germany)
- Sympatric speciation molecular evidence and ecological mechanisms
- 11:45 Emilio Rolán-Alvarez (Universidad de Vigo, Spain) Phenotypic basis of incipient speciation in an intertidal snail
- 12:05 Tom van Dooren (University of Antwerp, Belgium) The evolutionary ecology of dominance-recessivity

#### Chair: J.A.J. Metz

- 16:05 Nicolas Maire (University of Basel, Switzerland) Evolutionary branching and the evolution of anisogamy
- 16:25 Olof Leimar (Stockholm University, Sweden) Adaptive dynamics in multidimensional trait spaces: Darwinian demons and canonical convergence stability
- 16:45 Sergey Gavrilets (University of Tennessee, USA) Dynamics of speciation on holey adaptive landscapes
- 17:05 A.B. Korol (University of Haifa, Israel)
- Genetic interaction between species on TRAIT-FOR-TRAIT basis
- 17:25 Regis Ferrière (Paris, France)
- The adaptive dynamics of dispersal and cooperation
- 17:45 Richard Law (York University, UK)
- On the evolution of cheating in mutualisms
- 18:05 Géza Meszéna (Eötvös University, Budapest, Hungary) Adaptive emergence of reproductive isolation

\* Supported by the European Science Foundation Programme for the Theoretical Biology of Adaptation and by the Adaptive Dynamics Network, International Institute for Applied System Analysis, Laxenburg, Austria

#### Symposium S12: Understanding fitness

Organisers: Rick Michod (University of Arizona, USA), Regis Ferrière (Paris, France)

#### **Chair: Rick Michod**

# 9:20 Introduction

- 9:25 Rick E. Michod (University of Arizona, Arizona)
- Evolution of individuality and new levels of fitness
- 9:55 Minus van Baalen (University of Amsterdam, The Netherlands) The evolution of dangerous liaisons
- 10:55 Regis Ferrière (Paris, France)
- Fitness and adaptive dynamics in non-equilibrium populations
- 11:25 Erik Svensson (University of California, Santa Cruz, USA) Experimental excursions on adaptive landscapes: density-dependent selection on egg size
- 11:45 Olivier Tenaillon (Institut Jacques Monod, Paris, France)
- Mutator, sex and the adaptation of bacterial populations
- 12:05 Inti Suárez (University of Basel, Switzerland) Reassessing fitness: a differential geometry approach

## Chair: Regis Ferrière

- 16:05 Francois Rousset (Laboratoire Génétique et Environnement, Montpellier, France) The theoretical basis of measures of kin selection in subdivided populations
- 16:25 Olle Håstad (Uppsala Universitet, Sweden) Death and dishonesty - a sexual selection model
- 16:45 Markus Fischer (Universität Zürich, Switzerland) Genetic variation in clone characters of *Ranunculus reptans*
- 17:05 C. Damgaard (NERI, Silkeborg, Denmark)

Fitness components and advantageous alleles in partially self-fertilizing populations

- 17:25 Lars Witting (Greenland Institute of Natural Resources, Greenland) Density dependent competitive interactions set limits to Fisher's fundamental theorem of natural selection
- 17:45 David W. Coltman (University of Edinburgh, UK) Environmental variation determines the mode and tempo of natural and sexual selection in a fluctuating population of feral sheep

# LECTURE ROOM: MARTÍ FRANQUÉS I

#### Symposium S11: Adaptation to environmental stress

Organisers: Kuke Bijlsma (Groningen, The Netherlands), V. Loeschcke (Aarhus, Denmark)

#### Chair: Kuke Bijlsma

- 9:20 Presentation
- 9:25 Raymond B. Huey (University of Washington, Washington, USA)
- Rapid evolution of size and thermal sensitivity in Drosophila subobscura in North America
- 9:55 Paul M. Brakefield (Leiden University, The Netherlands)
- Bicyclus butterflies and developmental aspects of stress
- 10:55 Robert A. Krebs (Cleveland State University, Cleveland OH, USA) Physiological and genetic consequences of high temperature stress in *Drosophila*
- 11:25 Jean R. David (CNRS, Gif sur Yvette, France)
- Cold stress tolerance in Drosophila: a major adaptive difference between tropical and temperate species 11:45 Volker Loeschcke (University of Aarhus, Denmark)
- Thermal stress and evolution
- 12:05 R. Bijlsma (University of Groningen, The Netherlands) Interaction between temperature stress and inbreeding in *Drosophila*

# Chair: V. Loeschcke

- 16:05 A. J. Davis (The University of Leeds, UK)
  - Making mistakes in predicting the effects of global warming on species range
- 16:25 Francisco Pulido (Research Centre Ornithology of the Max Planck Society, Germany) Adaptive changes of migratory behaviour in response to global warming: a quantitative genetic study in the blackcap (Sylvia atricapilla)
- 16:45 Suzanne Edmands (University of Southern California, Los Angeles CA, USA) Local adaptation and the effect of environmental stress on interpopulation hybrids of the intertidal copepod *Tigriopus californicus*
- 17:05 Peter Armbruster (Institute of Zoology, London UK) Evolutionary responses to environmental stress by the pitcher-plant mosquito, *Wyeomyia smithii*
- 17:25 K. I. Jönsson (Lund University, Sweden) Evolutionary and life history aspects of cryptobiosis
- 17:45 Pierre Capy (CNRS, Gif sur Yvette, France)

Stress and transposable elements

18:05 Luc De Meester (Katholieke Universiteit Leuven, Belgium) Local adaptation of *Daphnia* populations: some emerging patterns

# LECTURE ROOM: MARTÍ FRANQUÉS II

| Sympos  | sium S18: Horizontal gene transfer: past and present role in evolution  |
|---------|---|
| organia | in the fact by values (Davis, Corr), while a wasternager (Classically, Corring)   |
|         | Chair: Wilfried Wackernagel   |
| 9:20    | Introduction  |
| 9:25    | James R. Brown (SmithKline Beecham Pharmaceuticals, Collegeville, USA)  |
|         | Have lateral gene transfers up-rooted the universal tree of life?   |
| 9:55    | J. Peter Gogarten (University of Connecticut, Storrs, USA)  |
|         | Comparative analysis of the Deinococcus genome indicates infrequent horizontal transfer between the three domains of life     |
| 10:55   | Eugene V. Koonin (National Institutes of Health, Bethesda, USA)   |
|         | Horizontal gene transfer: evidence and role in the evolution of prokaryotes   |
| 11:25   | R. S. Gupta (McMaster University, Hamitlon, Canada)   |
|         | The phylogeny of prokaryotes: does horizontal gene transfer preclude its determination?                                       |
| 11:45   | Michael Syvanen (University of California, Davis CA, USA)   |
|         | Emergence of arginine and tryptophan after the major microbial diversification  |
| 12:05   | Thure P. Hauser (University of Copenhagen, Denmark)   |
|         | Spontaneous introgresion of (trans)genes from crops to wild species   |
|         | Chair: Michael Syvanen  |
| 16:05   | L. H. Rieseberg (Indiana University, Bloomington, USA)  |
|         | Role of hybridization in species formation  |
| 16:25   | D. A. Tepfer (Institut National de la Recherche Agronomique, Versailles, France)  |
|         | Natural genetic transformation of plants by Agrobacterium rhizogenes  |
| 16:45   | Robert Butcher (Dundee University, UK)  |
|         | Are / were parasitoids really <i>in vivo</i> vectors for the horizontal transfer (HT) of <i>Wolbachia</i> amongst arthropods? |
| 17:05   | Elisabeth Haring (Museum of Natural History, Vienna, Austria)   |
|         | A pseudo-control region in the mitochondrial genome of Buteo buteo and its application for                                    |
|         | phylogenetic analyses   |
| 17:25   | Ivan Matic (Institut Jacques Monod, Paris, France)  |
|         | Evolutionary implications of the frequent horizontal transfer of mismatch repair genes  |
| 17:45   | W. Wackernagel (University of Oldenburg, Germany)   |
|         | Natural bacterial transformation as a mechanism for foreign gene acquisition  |
| 18:05   | A. Tauch (University of Bielefeld, Germany)   |
|         | A Corynebacterium plasmid composed of elements from throughout the eubacteria kingdom   |

# LECTURE ROOM: ARNAU DE VILANOVA

Symposium S17: Conflicts arising from sex and sexes

Organisers: Greg Hurst (London, UK), Tracey Chapman (London, UK)

#### Chair: Greg Hurst

- 9:20 Introduction
- 9:25 Goran Arnqvist (University of Umeå, Sweden) Sexual conflict and speciation rates in insects
- 9:55 Andrew Pomiankowski (University College of London, UK)
- Imprinting is for sex not conflict
- 10:45 Richard Stouthamer (Wageningen Agricultural University, The Netherlands): Selfish genetic elements and sex ratios in parasitoid wasps
- 11:15 Paul I. Ward (Zoologisches Museum der Universität Zürich, Switzerland) Variation in female morphology influences male sperm competition success in the yellow dung fly
   11:35 Nina Wedell (University of Stockholm, Sweden)
- Sexual conflict over female remating: the role of non-fertile sperm in butterflies
- 11:55 Liselotte Sundström (University of Helsinki, Finland)
- Facultative sex ratio biasing and male-female conflicts in ants
- 12:15 Nico K. Michiels (Institut für Spezielle Zoologie, Huefferstr, Germany) Penis fencing in marine flatworms: pre-programmed escalation and the thin line between war and peace

#### Chair: Tracey Chapman

- 14:30 Rosie G. Sharpe (University of Leeds, UK)
- The evolution of microsporidian sex ratio distorters
- 14:50 Thierry Rigaud (Université de Poitiers, France) Differences in feminizing patterns produced by *Wolbachia* endosymbionts in woodlice: the result of a Red Queen process?
- 15:10 Filipa Vala (University of Amsterdam, The Netherlands) Effects of *Wolbachia* infections in three species of spider mites of the genus *Tetranychus*
- 15:30 Arja Kaitala (University of Oulu, Finland)
- Helping vs. intraspecific parasitism: egg carrying in the golden egg bug
- 15:50 Dieter Ebert (Universität Basel, Switzerland) Comparative evidence for positive associations between parasitism and plant life-histories, and possibly the degree of plant outcrossing
- 16:10 Carla Maria Sgrò (University College London, UK) Cost of reproduction and ageing

# LECTURE ROOM: LLUÍS VIVES I

Symposium S6: Origin, evolution and stability of coevolved mutualisms Organisers: Martine Hossaert-McKey (Montpellier, France), Olle Pellmyr (Vanderbilt University, USA)

#### **Chair: Martine Hossaert-McKey**

- 9:20 Introduction
- 9:25 Angela E. Douglas (University of York, UK)
- Conflict and co-operation in animal-microbial symbioses
- 9:55 Olle Pellmyr (Vanderbilt University, USA)
- Patterns of diversification in yucca moths 10:45 Marie-Charlotte Anstett (CEFE CNRS Montpellier, France)
- Modelling coevolutionary conflicts in the fig/fig wasp mutualism
- 11:15 Edward Allen Herre (Smithonian Tropical Research Institute, Panama)
   Heritabilities of characters with reciprocal fitness effects in fig-wasp mutualisms
- 11:35 Laurence Després and Jean Baptiste Ferdy (Université J. Fourier, Grenoble, France) An adaptive dynamics model for the coevolution between the globeflower *Trollius europeus* and its pollinator flies (*Chiastocheta* spp.)
- 11:55 Carine Brouat (CEFE CNRS Montpellier, France) Evolution of a specialised ant-plant mutualism in the genus *Leonardoxa* (Caesalpinioideae)
- 12:15 M. Gauduchon (University of Paris VI, France) Asymmetric competition for partners explains the evolutionary stability and diversification of mutualistic associations

#### **Chair: Olle Pellmyr**

- 14:30 Paul Baumann (University of California, Davis CA, USA) Genetic properties and adaptations of *Buchnera* to an endosymbiotic association with aphids
- 14:50 Thomas L. Bultman (Truman State University, Kiksville, USA)
- Factors affecting the stability of an insect-fungus mutualism
- 15:10 Adriane Nicolette M. Bot (University of Aarhus, Denmark) Compatibility between ants and their mutualistic fungi in two sympatric species of Acromyrmex leafcutting ants
- 15:30 Douglas W. Yu (Imperial College at Silwood Park, UK) Parasitic castration, ant-plants and the habitat destruction hypothesis
- 15:50 Alexandra Grutter (University of Queensland, Brisbane, Australia) Parasitic gnatghiid isopods: the key to the evolution of the fish cleaning behaviour
- 16:10 Michael Doebeli (University of Basel, Switzerland) Variable investments and the origin of cooperation and mutualism

# LECTURE ROOM: LLUÍS VIVES II

#### Symposium S13: The role of the inheritance of acquired variation in evolution

Organisers: Eva Jablonka (Tel-Aviv University, Israel), Marion J. Lamb (Tel-Aviv University, Israel)

#### Chair: Marion J. Lamb

| 9.20 Indoduction | 9:20 | Introduction |  |
|------------------|------|--------------|--|
|------------------|------|--------------|--|

- 9:25 Robin Holliday (C.S.I.R.O., Sydney, Australia) The impact of the environment on the epigenotype
- 9:55 Luisa Hirschbein (Institut Curie UMR-CNRS, France)
- Epigenetic inheritance in prokaryots: myth or reality?
- 10:45 Edward J. Steele (University of Wollongong, Canberra, Australia) Lamarckian evolution of antibody variable genes
- 11:15 Giuseppe Damiani (Università di Pavia, Italy)
- Anti-darwinian "intelligent" evolution driven by the MHC system
- 11:35 Roman Wenne (Polish Academy of Sciences, Poland)
- Transmission of mitochondrial DNA variants in the mussel *Mytilus trossulus* from the Baltic Sea 11:55 Csaba Pál (Loránd Eötvös University, Budapest, Hungary)
- Evolution and divergence of dual inheritance systems on the adaptive landscape 12:15 Michael Lachmann (Santa Fe institute, Santa Fe, USA)

The effect of epigenetic inheritance on the evolution of multicellularity

### Chair: Eva Jablonka

- 14:30 Marion J. Lamb (Tel-Aviv University, Israel)
- The life, death, and resurrection of "the inheritance of acquired characters"
- 14:50 Eva Jablonka (Tel-Aviv University, Israel)
- Some evolutionary implications of social learning
   15:10 Katja Hora (University of Amsterdam, The Netherlands) The influence of larval diet on oviposition preference of hybrids of two *Yponomeuta* species: *Y. cagnagellus* and *Y. padellus*
- 15:30 Daniel Dor (Tel-Aviv University, Israel) Towards a meaning-based theory of the evolution of language

# LECTURE ROOM: MARTÍ FRANQUÉS I

#### Symposium S2: Early molecular evolution

Organisers: Renato Fani (Firenze, Italy), Antonio Lazcano (UNAM, Mexico)

# **Chair: Renato Fani**

# 9:20 Presentation

- 9:25 Laura Landweber (Princeton University, New Jersey, USA) Experimental tests of genetic code and ribozyme origins
- 9:55 Hervé Philippe (Université Paris-Sud, France) Where is the root of the universal tree of life?

#### **Chair: Antonio Lazcano**

- 10:45 Sara Dabizzi (Firenze, Italy)
- The origin and evolution of metabolic pathways: a common origin of nif and bch genes
- 11:15 Lluís Ribas de Pouplana (The Scripps Research Institute, La Jolla, USA)
- Aminoacyl-tRNA synthetases as markers of the evolution of the genetic code 11:35 Guy Sella (Stanford University, Stanford CA, USA)

On the evolution of the structures in the standard genetic code as an outcome of code-message coevolution 11:55 Janet L. Siefert (Rice University, Houston, USA)

Reconstructing ribozyme phylogeny: who begat whom?

12:15 Nicolas Tourasse (University of Chicago, Chicago, USA) Variation of evolutionary rate and the universal tree of life

# **Chair: Renato Fani**

- 14:30 Purificación López-García (Université Paris-Sud, France) Syntrophy, massive gene transfer, and the chimeric origin of eukaryotes
- 14:50 David Moreira (Université Paris-Sud, France) Deciphering the early evolution of eukaryotes using new analysis methods

# LECTURE ROOM: MARTÍ FRANQUÉS II

Symposium S23: Macroevolutionary patterns and dynamics: 25 years later

Organisers: Jordi Agustí (Sabadell, Spain), Pascual Rivas (Granada, Spain)

# Chair: Jordi Agustí

- 9:20 Presentation
- 9:25 Michael J. Benton (University of Bristol, Bristol, UK)
- Diversification on land and in the sea: different evolutionary regimes
  9:55 Jorge Wagensberg (Museu de la Ciència de la Fundació "la Caixa", Barcelona, Spain)
  - On the independence against the environment uncertainty: the question of staying alive

#### **Chair: Michael Benton**

- 10:45 David M. Alba (Institut de Paleontologia M. Crusafont, Sabadell, Spain) What is the nature of the history of life? Contingency vs. predictability in evolution
- 11:15 Eva García-Vázquez (Universidad de Oviedo, Spain)
- Evolution of salmonid species. The role of chromosome rearrangements
- 11:35 Dita B. Vizoso (University of Basel, Switzerland)
- Effect of ecosystem dynamics on long-term evolutionary patterns
- 11:55 Arne Ø. Mooers (University of Amsterdam, The Netherlands) Extinction is more than a field of bullets: simulating the loss of evolutionary history due to anthropogenic extinctions

#### **Chair: Pascual Rivas**

- 14:30 Dan Cohen (The Hebrew University, Jerusalem, Israel) Modeling long-term evolution in multi-dimensional multiple-peak interacting fitness and coexistence space
- 14:50 Jordi Agustí (Institut de Paleontologia M. Crusafont, Sabadell, Spain) Punctuated gradualism in Plio-Pleistocene voles from Europe

# LECTURE ROOM: ARNAU DE VILANOVA

#### Symposium S8: Evolutionary significance of colonisations

Organisers: Lluís Serra (Barcelona, Spain), Miguel-Àngel Arnedo (Hawaii, USA), Godfrey M. Hewitt (Norwich, UK), Antonio Fontdevila (Bellaterra, Spain)

# Chair: Godfrey M. Hewitt

- 9:20 Presentation
- 9:25 Rosemary G. Gillespie (University of Hawaii, Honolulu, USA) Evolution of a spider community in the Hawaiian Islands
- 9:55 Carles Ribera (Universitat de Barcelona, Spain) Colonisation patterns and biogeography in the Canary Islands: the emerging picture

#### Chair: Lluís Serra

- 10:55 Miquel-Àngel Arnedo (University of Hawaii, Honolulu, USA) The Prospero effect or what we can learn from comparing patterns and processes in different archipelagoes
- 11:25 Brent C.Emerson (University of East Anglia, Norwich, UK) Recent origin for a speciose fauna: a molecular phylogeographic analysis of the genus *Calathus* (Coleoptera: Carabidae) on the Canary Islands and Madeira
- 11:45 Salvador Carranza (The Natural History Museum, London, UK) Biogeography of the lizards *Gallotia* and *Tarentola* in Macaronesia
- 12:05 Mandy L. Heddle (University of Hawaii, Honolulu, USA) Biogeography and evolution of the genus Scotorythra (Geometridae: Ennominae) in Hawaii

# Chair: Antonio Fontdevila

- 16:05 Neil Davies (University of Hawaii, Honolulu, USA)
- Island sex: speciation and sexual selection on oceanic islands
- 16:25 A.Caccone (Yale University, New Haven, USA) Where do the Galapagos tortoises come from? A phylogeny based on mtDNA data
- 16:45 Francesc Mestres (Universitat de Barcelona, Spain) Spatial and temporal lethal-gene allelism in American colonising populations of *Drosophila subobscura*
- 17:05 Fiammetta Santucci (University of East Anglia, Norwich, UK)
- Postglacial colonisation routes of European hedgehogs
- 17:25 Sebastian Steinfartz (Universität zu Köln, Weyertal, Germany) Mitochondrial sequence analysis of *Salamandra* taxa suggests old splits of major lineages and postglacial recolonisations of central Europe from distinct source populations of *S. salamandra*
- 17:45 Borja Milá (San Francisco State University, San Francisco CA, USA) Genetic evidence for the effects of Pleistocene glaciations on the phylogeography of MacGillivray's warbler, a neotropical migratory bird.
- 18:05 Guy Reeves (Smithsonian Tropical Research Institute, Panama) The mode and tempo of freshwater fish colonisation across the Isthmus of Panama based on molecular markers: which routes were available?

# LECTURE ROOM: LLUÍS VIVES I

Symposium S14: Future directions in evolutionary quantitative genetics

Organisers: Jack J. Windig (Stockholm, Sweden), Derek A. Roff (Montréal, Quebec, Canada)

#### Chair: Jack J. Windig

9:20 Introduction

| 9:25 | M. Lynch (University of Oregon, Eugene OR, USA)                      |
|------|--|
|      | Estimation of quantitative-genetic parameters in natural populations |

- 9:55 Ty T. Vaughn (University of Washington, USA)
- QTL analysis, a highway or a dead end?
- 10:55 Derek A. Roff (McGill University, Montreal, Canada) The evolution of genetic architecture
- 11:25 Daphne J. Fairbairn (Concordia University, Montreal, Canada) Predicting correlated responses in natural populations: changes in JHE activity, fecundity and calling rate in the Bermuda population of the sand cricket
- 11:45 Thomas F. Hansen (Yale University, New Haven CT, USA) Modelling genetic architecture: a multilinear model of gene interaction with applications in quantitative genetics
- 12:05 Antónia Monteiro (Leiden University, The Netherlands) Relating phylogenetic patterns to short term selection experiments on butterfly wing patterns

#### Chair: Derek A. Roff

- 16:05 Gerdien de Jong (Utrecht University, The Netherlands) Unpredictable selection in a structured population and differentiation in evolved reaction norms
- 16:25 Olivier J. Hardy (Université Libre de Bruxelles, Belgium)
   Spatial autocorrelation of quantitative characters and genetic markers within a natural population of *Centaurea jacea* (Asteraceae)
- 16:45 Stefan Van Dongen (University of Antwerp, Wilrijk, Belgium) Quantitative genetics of fluctuating asymmetry
- 17:05 Wolf U. Blanckenhorn (Universität Zürich-Irchel, Zürich, Switzerland) The trade-off between egg size and number in the yellow dung fly in good and bad environments
- 17:25 Tadeusz J. Kawecki (University of Basel, Switzerland)
- The evolution of genetic canalization under fluctuating selection
- 17:45 Rauno V. Alatalo (University of Jyväskylä, Finland)
- Inherited dispersal avoidance in small and isolated populations of the waterstrider *Aquarius naja* 18:05 Jack J. Windig (Kievitstraat 32, Leiderdorp, The Netherlands)

Quantitative genetics of life history and morphological traits in a recently established population of the speckled wood butterfly *Pararge aegeria* 

# LECTURE ROOM: LLUÍS VIVES II

#### Symposium S4: Neutralism and selectionism: the end of a debate? Organisers: Giorgio Bernardi (Napoli, Italy), Tomoko Ohta (Mishima, Japan) Chair: Giorgio Bernardi 9:20 Introduction Tomoko Ohta (National Institute of Genetics, Mishima, Japan) 9:25 Near neutrality in the interactive systems 9:55 Giorgio Bernardi (Stazione Zoologica Anton Dohrn, Napoli, Italy) Selection and random drift in the evolution of the vertebrate genome Takashi Gojobori (National Institute of Genetics, Mishima, Japan) 10:55 A method for detecting positive selection at single amino acid sites A. Eyre-Walker (University of Sussex, UK) 11:25 Is junk DNA neutral? Hiroshi Akashi (University of Kansas, Lawrence KS, USA) 11:45 Determining the contribution of adaptive molecular evolution from within and between species DNA variation in Drosophila M. Przeworski (University of Chicago, Chicago IL, USA) 12:05 A genome-wide departure from the neutral model in natural populations of Drosophila **Chair: Tomoko Ohta** Wen-Hsiung Li (University of Chicago, Chicago IL, USA) 16:05 Adaptive molecular evolution of primate color vision genes Michael W. Nachman (University of Arizona, Tucson AZ, USA) 16:25 Neutral theory and DNA sequence variation in humans David Rand (Brown University, Providence, USA) 16:45 Neutrality, selection, and the evolution of protein-coding DNA: the importance of the distribution of selection coefficient Hinnerk Boriss (Aarhus University, Denmark) 17:05 Negative cooperativity of heterodimers causes heterozygote advantage Marcos Antezana (University of Chicago, Chicago IL, USA) 17:25 Randomization-based biophysical evidence suggests that strong selection on mRNA structure should act against too high and too low codon usage biases S. E. Ptak (Stanford University, Stanford CA, USA) 17:45 The role of balancing selection in the maintenance of single-locus polymorphism Tobias Mourier (University of Copenhagen, Denmark) 18:05 Consistency between vertebrate codon usage and dinucleotide preferences is reduced in (G+C)-rich sequences

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# LECTURE ROOM: MARTÍ FRANQUÉS I

# Symposium S19: Retrotransposed DNA elements: homoplasy-free characters for phylogenetic and population genetics

Organisers: Anthony V. Furano (National Institute of health, Bethesda, USA), Norihiro Okada (Tokyo Institute of Technology, Kanagawa, Japan)

#### **Chair: Anthony V. Furano**

- 9:20 Introduction
- 9:25 Thomas H. Eickbush (University of Rochester, Rochester NY, USA)
- Arthropod R2 elements and the origin, evolution and integration mechanism of non-LTR retrotransposons 9:55 Holly A. Wichman (University of Idaho, Moscow, Idaho, USA)
- Junkyard genetics: transposable elements and hidden treasures in the mammalian genome 10:55 Norihiro Okada (Tokyo Institute of Technology, Kanagawa, Japan)
- Determination of phylogenetic relationships among cetartiodactyls: hippopotamuses are the closest relatives to whales
- 11:25 Xulio M. Maside (University of Edinburgh, UK) Rates of movement of transposable elements in *Drosophila melanogaster*
- 11:45 Prescott Deininger (Tulane University Medical Center, New Orleans LA, USA) The amplification and evolution of mammalian SINEs
- 12:05 Jürgen Brosius (University of Münster, Germany) Retroposons and the creation of novel genes: the novel neuron-specific genes for BC1 and BC200 RNA were recruited from SINEs

### **Chair: Prescott Deininger**

- 16:05 Stephen C. Hardies (Univ. of Texas Health Science Center at San Antonio, USA) Population genetics of mouse LINE-1
- 16:25 Olivier Verneau (Université de Perpignan, France)
   The use of L1 (LINE-1) retrotransposons for resolving and dating phylogenetic events in *Rattus* sensu lato and stricto (Rodentia: Muridae)
- 16:45 Anthony V. Furano (National Institutes of Health, Bethesda MD, USA) The use of L1 DNA for phylogenetic analysis and population studies in primates
- 17:05 Dušan Kordiš (Jozef Stefan Institute, Ljubljana, Slovenia) Molecular evolution of Bov-B LINEs in vertebrates
- 17:25 Dimitri A. Kramerov (Enhelgardt Institute of Molecular Biology, Moscow, Russia) SINE families as markers of mammalian phylogeny
- 17:45 Andrew M. Shedlock (Tokyo Institute of Technology, Tokyo, Japan) Digging for phylogenetic gold in the genomic junkyard: historical retropositional dynamics of SINEs and the evolution of salmonid fishes in the genus *Prosopium*
- 18:05 David A. McClellan (Tokyo Institute of Technology, Tokyo, Japan) The phylogenetic relationships of mysticete whales as revealed by the analysis of SINE alleles

# LECTURE ROOM: MARTÍ FRANQUÉS II

# Symposium S20: Evolution of RNA viruses

Organisers: Andrés Moya (Valencia, Spain), Esteban Domingo (Madrid, Spain)

#### Chair: Andrés Moya

# 9:20 Introduction

- 9:25 Simon Wain-Hobson (Institut Pasteur, Paris, France)
  - RNA viruses, evolving or merely changing?
- 9:55 Fernando García-Arenal (E.T.S.I. Agrónomos, U.P.M., Madrid, Spain) Genetic structure and variability of plant virus populations

# **Chair: Esteban Domingo**

- 10:55 Cristina Escarmís (Centro de Biología Molecular "Severo Ochoa", Madrid, Spain) Evolution of an FMDV clone debilitated by Muller's ratchet
- 11:25 Paul E. Turner (Universitat de València, Spain)
- Prisoner's dilemma in an RNA virus
- 11:45 Eric Baranowski (Centro de Biología Molecular "Severo Ochoa", Madrid, Spain) Dynamics of antigenic variation in RNA viral populations
- 12:05 Santiago F. Elena (Universitat de València, Spain) Clonal interference and the evolution of RNA viruses

# Symposium S24: Unravelling the origin of the first bilaterian Metazoans: what fossils, morphology and molecules tell us

Organisers: Jaume Baguñà (Barcelona, Spain), André Adoutte (Paris, France)

# Chairs: Jaume Baguñà and André Adoutte

- 16:05 Introduction
- 16:10 A. Adoutte (Centre de Génétique Moleculaire du CNRS, France) The global phylogeny of metazoans: inference from genomic data
- 16:40 Simon Conway Morris (University of Cambridge, UK) The Cambrian explosion: artefact or reality?
- 17:10 R. M. Rieger (University of Innsbruck, Austria) What can extant Bilateria tell us about the organization of the bilaterian stem species?
- 17:40 Claus Nielsen (University of Copenhagen, Denmark) Animal bilaterality - once or twice?
- 18:00 Stefan Bengtson (Swedish Museum of Natural History, Sweden) Fossil embryos – a new source of information on animal origins
- 18:20 Marta Riutort (Universitat de Barcelona, Spain) The quest for the first bilaterian from 18S rDNA sequences. Acoel flatworms as the likely earliest bilaterian
- 18:40 Jordi Garcia-Fernández (Universitat de Barcelona, Spain) Hox-like gene duplications at the Cambrian explosion? (if it did exist)

# LECTURE ROOM: ARNAU DE VILANOVA

# Symposium S9: Molecular evolutionary ecology

Organisers: Marta Pascual (Barcelona, Spain), Loren H. Rieseberg (Indiana, USA)

#### Chair: Marta Pascual

- 9:20 Presentation
- 9:25 Gabriele Gerlach (Universität Konstanz, Konstanz)
- Population genetics in wood mice (Apodemus sylvaticus)
- 9:55 Patricia G. Parker (Ohio State University, Columbus OH, USA)
- Galapagos hawks: genetic studies of variation in mating behavior
- 10:55 Loren H. Rieseberg (Indiana University, Bloomington, USA)
- Hybrid zones and the genetic architecture of a barrier to gene flow between two sunflower species 11:25 François Balloux (Université de Lausanne, Switzerland)
- Sex-specific genetic markers suggest complete absence of male gene-flow across a hybrid zone of the common shrew (*Sorex araneus*)
- 11:45 Klaus Schwenk (Netherlands Institute of Ecology, The Netherlands) Interspecific hybridization in Hyalodaphnia: ancient lineages versus contemporary gene flow
- 12:05 C. R. Engel (Université de Lille, Villeneuve d'Ascq, France)
   Population dynamics at a small scale: evolution of the genetic structure of a population of the red haplodiploid alga, *Gracilaria gracilis*

### Chair: Loren H. Rieseberg

- 16:05 Didier Forcioli (Swiss Federal Research Station for Fruit-Growing, Switzerland) High within population polymorphism for a selected insecticide resistance gene in the Western Flower Thrips, Frankliniella occidentalis
- Marta Pascual (Universitat de Barcelona, Spain)
   Microsatellite variation in Paleartic and colonising populations of *Drosophila subobscura*
- 16:45 Teresa Pastor (Universitat de Barcelona, Spain) Low levels of nuclear genetic variability in the endangered Mediterranean monk seal after a population bottleneck
- 17:05 Fernando González-Candelas (Universitat de València, Spain) Molecular and morphometric differentiation in *Limonium dufourii* (Plumbaginaceae), an endangered Mediterranean plant
- 17:25 Luca Bargelloni (Universita' di Padova, Italy) Crossing the Gibraltar strait: discordant phylogeographic patterns in seven Atlantic-Mediterranean fish species (Sparidae, Teleostei)
- 17:45 Paulette Bloomer (University of Pretoria, South Africa) Comparative mitochondrial DNA phylogeography and evolution in *Procavia* and *Heterohyrax* (Mammalia: Hyracoidea) from southern Africa
- 18:05 Eske Willerslev (University of Copenhagen, Denmark) Diversity of Holocene life-forms in fossil glacier ice

# LECTURE ROOM: LLUÍS VIVES I

#### Symposium S15: Unravelling the genetics of evolutionary change

Organisers: Bas J. Zwaan (Leiden, The Netherlands), L. W. Beukeboom (Leiden, The Netherlands)

#### Chair: Bas J. Zwaan

# 9:20 Presentation9:25 M. Kearsey (T)

- 9:25 M. Kearsey (The University of Birmingham, UK) QTL analysis: new solutions to old problems
  9:55 Peter D. Keightley (University of Edinburgh, UK) From QTLs to genes: high resolution QTL mapping in mice
- 10:55 Juergen Gadau (University of California, Davis CA, USA)
- Genome organization and social evolution in Hymenoptera
- 11:25 Massimo Pigliucci (University of Tennessee, Knoxville TN, USA) Evolution and mechanistic bases of phenotypic plasticity in *Arabidopsis thaliana* 11:45 Graham Bell (McGill University, Montreal, Canada)
- Microevolution in an electronic microcosm
- 12:05 Julia Gockel (University College London, UK)
   Clinal morphologic and genetic variation in *Drosophila melanogaster*

#### Chair: L. W. Beukeboom

- 16:05 Wilte G. Zijlstra (Leiden University, The Netherlands)
- Eyespotsize and development time in Bicyclus anynana: never tear us apart?
- 16:25 Marion Rozowski (University Museum of Zoology, Cambridge, UK) The role of Hox genes in establishing segment-specific bristle patterns in the legs of *Drosophila*
- 16:45 Antonio Barbadilla (Universitat Autònoma de Barcelona, Spain) Recombination rate predicts inversion size in Diptera
- 17:05 Anna Westerbergh (Swedish Agricultural University, Uppsala, Sweden) Multiple QTL control species differences in morphology between wild relatives of maize
- 17:25 Durdica Ugarkovic (Ruder Boškovic Institute, Zagreb, Croatia) Diversity of satellite profiles and low rate of satellite DNA sequence change
- 17:45 Martin Ackermann (University of Basel, Switzerland) Senescence in bacteria
- 18:05 Jennifer M. Gleason (University of St. Andrews, UK) Quantitative trait loci for *Drosophila melanogaster* courtship song

# LECTURE ROOM: LLUÍS VIVES II

**Symposium S3: Methods for analyzing DNA sequence data and constructing phylogenetic trees** Organisers: Wen-Hsiung Li (Chicago, USA), Jotun Hein (Aarhus, Denmark)

#### **Chair: Wen-Hsiung Li**

- 9:20 Presentation
- 9:25 Masami Hasegawa (The Institute of Statistical Mathematics, Tokyo, Japan) Power and pitfalls of molecular phylogenetics
  9:55 Wen-Hsiung Li (University of Chicago, Chicago IL, USA)
- Methods for testing the molecular clock hypothesis
- 10:55 Jotun Hein (University of Aarhus, Denmark) Combining stochastic context free grammars with molecular evolution in predicting RNA secondary
- structure
   11:25 Manolo Gouy (Universite Lyon, France)
   Evolutionary relationships between the primary lineages of life: effect of more realistic models of molecular evolution
- 11:45 Yun-Xin Fu (University of Texas-Houston, Houston TX, USA)
- Estimation of the age of the most recent common ancestor of a sample of DNA sequences 12:05 Olivier Gascuel (LIRMM, Montpellier, France)
- About the BIONJ algorithm: principle, topological accuracy and shape effect

#### Chair: Jotun Hein

- 16:05 Spencer V. Muse (North Carolina State University, Raleigh NC, USA) Multilocus molecular evolutionary analyses
- 16:25 Arndt von Haeseler (Max-Planck Institut, Leipzig, Germany) Exploring the tree space with PUZZLE
- 16:45 Zihen Yang (University College London, UK)
- Models of codon substitution and detecting adaptive molecular evolution

17:05 Takashi Gojobori (National Institute of Genetics, Mishima, Japan)

Intragenic variation of synonymous substitutions and its evolutionary implication 17:25 Edward C. Holmes (University of Oxford, UK)

Detecting recombination among gene sequences: methods and applications

- 17:45 Jeff Thorne (North Carolina State University, Raleigh NC, USA)
- Combining protein structure with protein evolution 18:05 Hirohisa Kishino (University of Tokyo, Japan)
  - Statistical problem in topology selection

# LECTURE ROOM: MARTÍ FRANQUÉS I

Symposium S25: Evolution of species flocks in east African cichlid fishes: the challenge of integrating studies on molecular phylogeny, behaviour, morphology and ecology Organisers: Christian Sturmbauer (Innsbruck, Austria), Michael Taborsky (Vienna, Austria)

#### **Chair: Christian Sturmbauer**

- 9:20 Presentation
- 9:25 Axel Meyer (University of Konstanz, Germany)
- Patterns and processes in the evolution of the East African adaptive radiations of cichlid fishes 9:55 Ole Seehausen (University of Leiden, The Netherlands)
- Sympatric speciation by sex ratio selection?
- 10:55 Irv Kornfield (The university of Maine, Maine, USA) Analysis of color pattern variation in the zebra cichlids of Lake Malawi
- 11:25 Nicholas B. Goodwin (University of East Anglia, UK) Evolutionary transitions in parental care in cichlid fish
- 11:45 Michael Taborsky (Austrian Academy of Sciences, Vienna, Austria) The importance of ecology for the evolution of reproductive and social behaviour: case studies from Lake Tanganyika
- 12:05 George Turner (University of Southampton, UK) Explosive speciation of the rocky shore cichlids of Lake Malawi

#### **Chair: Michael Taborsky**

- 16:05 Paul W. Shaw (University of Hull, UK)
- Evolutionary implications of population structure in Lake Malawi pelagic cichlids
- 16:25 Christian Sturmbauer (University of Innsbruck, Austria)
- Lake level fluctuations, population structures and speciation in Lake Tanganyika rock cichlids
- 16:45 L. Rüber (University of Zürich, Switzerland) Comparative phylogeography and population structure in an endemic cichlid lineage from Lake Tanganyika
- 17:05 Sanja Baric (University of Innsbruck, Austria)
- Gene flow among populations of *Tropheus* from the Zambian shore of Lake Tanganyika 17:25 Kazuhiko Takahashi (Tokyo Institute of Technology, Japan)
- Phylogenetic relationships and incomplete lineage sorting among cichlid fishes in Lake Tanganyika an approach from insertion patterns of retroposons
- 17:45 Rafael Zardoya (Museo Nacional de Ciencias Naturales, Madrid, Spain) Phylogenetic relationships of cichlids based on nuclear sequence data: heterogeneity of evolutionary rates among different cichlid groups
- 18:05 Mairi E. Knight (Southampton University, UK) Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites

# LECTURE ROOM: MARTÍ FRANQUÉS II

# Symposium S10: Co-evolutionary interactions between symbionts

Organisers: Jacobus J. Boomsma (Aarhus, Denmark), Steph B.J. Menken (Amsterdam, The Netherlands)

# Chair: Jacobus J. Boomsma

9:20 Presentation

- 9:25 Ulrich J. Mueller (University of Texas, Austin TX, USA)
- The evolution of agriculture in ants
- 9:55 Edward Allen Herre (Smithsonian Tropical Research Institute, Panama)
- Phylogenetic relationships and molecular evolution in parasitic and mutualistic associates of figs 10:55 Ian R. Sanders (University of Basle, Switzerland)
- The mycorrhizal symbiosis: selection pressures and molecular evolution in a 400 million-year old symbiosis
- 11:25 Emmanuelle Jousselin (CEFE-CNRS, Montpellier, France) Active pollination in the fig/pollinator mutualism: who decides which flowers are pollinated?
- 11:45 David Nash (University of Aarhus, Denmark)

Coevolution, or lack of it, between lycaenid butterflies and ants 12:05 María S. Sánchez (University of Georgia, Georgia, USA) Effects of genetic heterogeneity in vertical transmission on symbiont survival and distribution

#### Chair: Steph B.J. Menken

16:05 Beatriz Sabater (Universitat de València, Spain) Evolution of a regulatory domain involved in the synthesis of aromatic amino acids: characterization of this domain in the endosymbiont of aphids *Buchnera aphidicola* 

- 16:25 Angus Buckling (University of Oxford, UK) Bacteria-phage coevolution: the effect on host genetic diversity
- 16:45 Mette H. H. Hansen (University of Aarhus, Denmark) The genetic basis of host control of life history traits in the yellow fever mosquito Aedes aegypti infected with Vavraia culicis microsporidia
- 17:05 Arjen Biere (Netherlands Institute of Ecology, The Netherlands) Effects of inbreeding on pathogen resistance in *Silene latifolia*17:25 Egbert J. de Vries (University of Amsterdam, The Netherlands)
- 17:25 Egbert J. de Vries (University of Amsterdam, The Netherlands) Symbiotic bacteria in Western Flower Thrips (*Frankliniella occidentalis*)

# SATURDAY 28 AUGUST

# LECTURE ROOM: ARNAU DE VILANOVA

Symposium S26: Evolution in the sea. Molecular ecology and paleontological approaches Organisers: Serge Planes (Perpignan, France), Carles Gili (Barcelona, Spain), Giacomo Bernardi (California, USA), Helena Fortunato (Panamá)

#### Chairs: Serge Planes, Giacomo Bernardi

- 9:20 Presentation
- 9:25 J. B. C. Jackson (The University of California, San Diego CA, USA) Pulses of speciation in the sea
- 9:55 S. R. Palumbi (Harvard, USA)

The evolution of developmental mode and diet diversification in cone snails: a study in molecular paleobiology

- 10:45 D. A. Powers (Hopkins Marine Station of Stanford University, Pacific Grove CA, USA) Expression in a teleost fish: *Fundulus heteroclitus*
- 11:15 Helena Fortunato (Smithsonian Tropical Research Institute, Panama) Biogeography and the tempo of speciation in strombinid gastropods
- 11:35 Carles Gili (Universitat de Barcelona, Spain) Relationship between larval ecology and species extinction in gastropods
- 11:55 Timothy Collins (University Park, Miami FL, USA) Molecular, morphological and paleontological perspectives on the radiation of the Gastropoda

12:15 Serge Planes (University of Perpignan, France) Phylogeography of the coral reef fish, *Acanthurus triostegus*, in the Pacific

#### **Chairs: Carles Gili, Helena Fortunato**

- 14:30 Giacomo Bernardi (University of California, Santa Cruz CA, USA)
   Sea of Cortez Pacific Ocean disjunct populations and cryptic species of fishes
- 14:50 H. A. Lessios (Smithsonian Tropical Research Institute, Panamá)

Mitochondrial DNA divergence of transpacific species across the "Eastern Pacific Barrier" 15:10 Eldredge Bermingham (Smithsonian Tropical Research Institute, Panamá)

A molecular assessment of the diversification and community development of neotropical fishes 15:30 Axel Meyer (University of Konstanz, Germany)

Patterns and processes of speciation in fishes from freshwater and marine environments-a preliminary comparison

- 15:50 Eleftherios Zouros (Institute of Marine Biology of Crete, Greece) Doubly uniparental inheritance of mitochondrial DNA: proximal and ultimate causes
- 16:10 Christophe Lemaire (SMEL, Sete, France) Microsatellites and allozymes: two complementary views on the selection between marine and lagoon habitats in the sea bas
#### LECTURE ROOM: LLUÍS VIVES I

**Symposium S5: Deleterious mutation: parameter estimation and evolutionary consequences** Organisers: Armando Caballero (Vigo, Spain), Peter D. Keightley (Edinburgh, Scotland)

### **Chair: Armando Caballero**

9:20 Presentation

| 9:25 N | Aichael | Lynch | (University | of Oregon, | Oregon, | USA) |
|--------|---------|-------|-------------|------------|---------|------|
|--------|---------|-------|-------------|------------|---------|------|

- Spontaneous deleterious mutation: results from worms, water fleas, and microbes
- 9:55 Ruth G. Shaw (University of Minnesota, Minnesota, USA)
- Spontaneous mutation in Arabidopsis morphology and fitness
- 10:45 David Houle (Florida State University, Tallahassee FL, USA)
- Mutation versus natural and sexual selection 11:15 Thomas Bataillon (INRA-SGAP, France)
- 11:15 Thomas Bataillon (INRA-SGAP, France) Multi-generation maximum likelihood analysis applied to mutation accumulation experiments in *Caenorhabditis elegans*
- 11:35 Armando Caballero (Universidad de Vigo, Spain) On the average coefficient of dominance of spontaneous viability mutations
- 11:55 James D. Fry (Utah State University, Logan TU, USA)
   Do life-history traits have higher mutational variances than morphological traits? A comparison of homozygous and heterozygous mutational effects in *Drosophila melanogaster*
- 12:15 Ryszard Korona (Jagiellonian University, Poland) Fitness effects of single and multiple spontaneous mutations in the yeast *Saccharomyces cerevisiae*

#### **Chair: Peter D. Keightley**

- 14:30 Andrew D. Peters (University of Edinburgh, UK)
- A high frequency of cryptic deleterious mutations in C. elegans
- 14:50 Jinliang Wang (University of Edinburgh, UK)
- Inbreeding rate at neutral loci linked to deleterious mutations in selfing and full-sib mating populations 15:10 Laurence Loewe (Technische Universität München, Germany)
- How many beneficial mutations are needed to stop Muller's ratchet?
- 15:30 Joel R. Peck (The University of Sussex, UK)
- Sex and mutation in a competitive world
- 15:50 Martin Storhas (Wilhelms-Universität Münster, Germany) Inheritance of fitness defects from parthenogens to sexuals: flatworm indication for mutation accumulation
- 16:10 Nicolas Bierne (SMEL, Sete, France) An identity-by-descent model of associative overdominance during a population bottleneck

### LECTURE ROOM: LLUÍS VIVES II

Symposium S16: Meiotic drive and related phenomena Organisers: Catherine Montchamp-Moreau (Paris, France), Anne Atlan (Paris, France)

### Chair: Catherine Montchamp-Moreau

| 9.20  | Presentation  |
|-------|---|
| 9.25  | Rolf F. Hoekstra (Wageningen University, The Netherlands)   |
| 1.20  | Spore killing in fungi  |
| 9:55  | Douglas R. Taylor (University of Virginia, Charlottesville VA, USA)   |
|       | The genetics and natural history of the sex ratio polymorphism in <i>Silene latifolia</i> , a dioecious plant           |
| 10:45 | Antonio Bernardo Carvalho (Universidade Federal do Rio de Janeiro, Brasil)  |
|       | Evolutionary genetics of suppressors of "sex-ratio" meiotic drive in Drosophila mediopunctata                           |
| 11:15 | Caroline Capillon (IJM, Paris, France)  |
| 11.35 | X-linked meiotic drive in <i>D. simulans</i> : where does the reduced fertility of <i>sex-ratio</i> males come from?    |
| 11.55 | Evolution of the neo-XY sex determination in grasshoppers of the genus <i>Asiotmethis</i> UV. (Orthoptera, Pamphagidae) |
| 11:55 | Dannie Durand (Princeton University, Princeton NJ, USA)   |
|       | Genetic drift in populations of ultraselfish gene complexes   |
| 12:15 | Andrew Hingle (University College London, UK)   |
|       | Female eyespan and variation in mating preferences in the stalk-eyed fly, Cyrtodiopsis dalmanni                         |
|       | Chair: Anne Atlan   |
| 14:30 | Matthew Goddard (Imperial College at Silwood Park, UK)  |
|       | The ecology and evolution of selfish genes  |
| 14:50 | J. Hinrich G. v. d. Schulenburg (University of Cambridge, UK)   |
|       | The origin and evolution of male-killing Wolbachia  |
| 15:10 | Frank Jiggins (University of Cambridge, UK)   |
|       | Sex ratio distorters and sex role reversal  |
| 15:30 | Giorgina Bernasconi (University of Zurich, Switzerland)   |
|       | Sexy sperm in the red flour beetle  |
| 15:50 | Frédéric Mery (University of Basel, Switzerland)  |
|       | Male-female conflict and the management of giant sperm  |
| 16:10 | Max Reuter (University of Lausanne, Switzerland)  |
|       | Conflict over colony growth in eusocial Hymenoptera   |

### LECTURE ROOM: MARTÍ FRANQUÉS I

#### Symposium S22: Morphological constraints: a theoretical perspective

Organisers: Angela D. Buscalioni (Madrid, Spain), Diego Rasskin-Gutman (Vienna, Austria)

#### Chairs: Angela D. Buscalioni

| 9:20 Introduction |  |
|-------------------|--|
|-------------------|--|

- 9:25 Gerd B. Müller (University of Vienna, Austria)
- Epigenetic constraints in morphological evolution
- 9:55 Miquel De Renzi (Universitat de València, Spain)
- Physics, morphogenesis and evolution
- 10:45 Isaac Salazar-Ciudad (Universitat Politécnica de Catalunya, Barcelona, Spain) Gene network evolution: developmental constraints, entrenchment and flexibility
- 11:15 Diego Rasskin-Gutman (Konrad Lorenz Institut for Evol. and Cog. Research, Austria) Frontera: Conditions for the simulation of boundary pattern evolution
- 11:35 Gunther Jensen Eble (National Museum of Natural History, Washington, USA) Morphospace and disparity approaches to constraint
- 11:55 A. Ressayre (Université Paris XI, France)
- Developmental variations and pollen morphology evolution
- 12:15 Antonio Rosas (Museo N. Ciencias Naturales, Madrid, Spain) Developmental constraints in the evolution of the human face

### Chairs: Diego Rasskin-Gutman

- 14:30 A. Casinos (Universitat de Barcelona, Spain)
- Endochondral ossification constrains minimum fledging time in birds
- 14:50 Nieves Lopéz-Martínez (Universidad Complutense, Madrid, Spain) Morphological transformation and mosaic transition: example of lagomorph teeth
- 15:10 Angela D. Buscalioni (Universidad Autónoma de Madrid, Spain) Modularity and mosaics in organisms: consequence for disparity in evolution
- 15:30 David M. Alba (Institut de Paleontologia M. Crusafont, Sabadell, Spain)
- Oreopithecus, bonobos, heterochrony, and the paradox of form

### LECTURE ROOM: MARTÍ FRANQUÉS II

Symposium S21: Antibiotic resistance: implications for our understanding of the population genetics and molecular biology of adaptive evolution

Organisers: Bruce R. Levin (Atlanta, USA), Fernando Baquero (Madrid, Spain)

### **Chair: Fernando Baquero**

- 9:20 Presentation
- 9:25 B. R. Levin
- 9:55 D. I. Anderson
- 10:45 Antone A. Medeiros (Brown University, Providence IR, USA Molecular evolution of β-lactamases
- 11:15 Hans-Joachim Carius (University of Basel, Switzerland)
- Genetic variation for host susceptibility and parasite infectivity in a *Daphnia* parasite system 11:35 Francisco Dionisio (Institut Jacques Monod, Paris, France)
- Bacterial "ménage à trois"
- 11:55 Tom Little (University of Basel, Switzerland) Rapid parasite-mediated natural selection in *Daphnia*
- 12:15 Christine D. M. Müller-Graf (CNRS Universite Pierre et Marie Curie, Paris, France) Population biology of carried and invasive isolates of *Streptococcus pneumoniae*

#### Chair: Bruce R. Levin

- 14:30 Diethe Ortius (University of Aarhus, Denmark) Investigating the details of a symbiotic interaction: unravelling chemical variation in an antibiotic gland secretion of the leafcutter ant Acromyrmex octospinosus
- 14:50 Carl T. Bergstrom (Emory University, Atlanta GA, USA) Penetrating the penumbra of plasmid persistence: the role of cross-species gene transfer
- 15:10 Fernando Baquero (Hospital Ramón y Cajal, Madrid, Spain) Overlapping of mutagenic and selective activities of antibiotics

# SYMPOSIA: POSTER PRESENTATIONS

### Poster session I Symposium 1

- S1-I-1 <u>S. Ramos-Onsins</u> and M. Aguadé (Universitat de Barcelona, Spain) The birth-and-death process and the evolution of the Cecropin multigene family in *Drosophila* S1-I-2 <u>A. Florin</u> (Uppsala University, Sweden)
- Population differentiation and bottlenecks
- **S1-I-3** <u>Helmi Kuittinen</u> and Montserrat Aguadé (University of Oulu, Finland) Nucleotide variation at the *Chalcone Isomerase* locus in *Arabidopsis thaliana*
- **S1-I-4** <u>Ángel Blanco</u> and Antonio Barbadilla (Universitat Autònoma de Barcelona, Spain) DNA polymorphic sequences in *Drosophila*
- S1-I-5 <u>A.A. de Haan</u>, Ch. Langley, T. Mitchell-Olds, P.H.van Tienderen, O. Savolainen (Institute for Ecology (NIOO-CTO), Heteren, The Netherlands) Comparative genome mapping between *Arabidopsis thaliana* and *Arabis petraea* including the phytochrome gene family
- **S1-I-6** <u>C. Melser</u>, A. Bijleveld and P.G.L. Klinkhamer (Leiden University, The Netherlands) The stronger sex weakened as well? Late-acting inbreeding depression in both male and female function of an hermafroditic plant
- **S1-I-7** <u>V. Dvornik</u>, M. Mikkonen, A. Sirviö and O. Savolainen (University of Oulu, Finland) Sequence variation in *Pinus sylvestris*
- **S1-I-8** <u>A. Civetta</u>, B. Todd, H. Waldrip and A.G. Clark (Pennsylvania State University, USA) Interspecific divergence in a group of Accessory gland protein genes (*Acps*) among species of the *Drosophila melanogaster* group
- S1-I-9 <u>Bernd Hänfling</u> (University of Hull, UK) Gene flow in a river system and its consequences for population fitness: a case study of the river bullhead *Cottus gobio*
- S1-I-10 <u>Tsuneyuki Yamazaki</u> (Kyushu University, Fukuoka, Japan) Genetic Diversity, Population Structures, and Phylogenetical Study of Tree Species in Tropical Forests in South East Asia
- **S1-I-11** <u>Africa Gómez</u> and Gary R. Carvalho (Universitat de València, Spain) Sex, parthenogenesis and the genetic structure of rotifer populations
- S1-I-12 Arcadio Navarro, Antonio Barbadilla and Alfredo Ruiz (University of Edinburgh, UK) Effect of inversion polymorphism on linked nucleotide variability
- **S1-I-13** <u>H. H. Hangelbroek</u> and N. J. Ouborg (Netherlands Institute of Ecology, The Netherlands) Genetic structure of fennel pondweed populations
- S1-I-14 Cagnon C., Lauga B., D'Amico F., Nisser J., Hemery G. and Mouches C. (Université de Pau et des Pays de l'Adour, Pau, France) Assessment of genetic variability in *Hydrobates pelagicus (Aves*; Procellariiformes) along the French Atlantic coast
- S1-I-15 W.F. van Hooft, A.F. Groen and H.H.T. Prins (Wageningen Agricultural University, The Netherlands) Microsatellite analysis of genetic diversity of African buffalo (Syncerus caffer) populations throughout Africa
- **S1-I-16** <u>W. T. Tay</u>, L. Sundström and R. Rosengren (University of Helsinki, Finland) The population structure and mating pattern of *Formica rufa* (Hymenoptera: Formicidae)
- S1-I-17 <u>G. A. Gutiérrez-Espeleta</u>, S. T. Kalinowski and P. W. Hedrick (Arizona State University, Tempe, USA) Genetic variation and population structure in desert bighorn sheep
- S1-I-18 C. Dutech, L. Maggia and H. I Joly (CIRAD-Forêt, Montpellier, France) Chloroplast genetic diversity in a tropical rainforest tree species, *Vouacapoua americana* (AUBL)
- S1-I-19 S. Østergaard (University of Aarhus, Denmark) Genetic differentiation and relationship between geographical and genetic distance based on microsatellites among Danish Brown trout (Salmo trutta)
- S1-I-20 <u>B.Zangerl</u> and Ch. Schlötterer (Universitaet Wien, Vienna, AUSTRIA) Estimating rates for sister chromatid exchange in rDNA genes of *Drosophila melanogaster* – a computer simulation approach
- S1-I-21 G. P. Sætre, T. Moum, J. Haavie, B. C. Sheldon, T. Borge and H. Ellegren (Uppsala University Sweden)

Sex biased introgression in flycatchers revisited - genetic pitfalls

- S1-I-22 À. Navarro-Sabaté and <u>C. Segarra</u> (Universitat de Barcelona, Spain) Nucleotide variation at the Acph-1 gene region in a Tunisian population of Drosophila subobscura
- **S1-I-23** <u>F. Santucci</u>, J. Seddon N. Reeve and G.M. Hewitt (University of East Anglia, Norwich, UK) Postglacial colonisation routes of European hedgehogs
- **S1-I-24** <u>T. H. M. Mes</u>, C.G.M. van der Hulst, P.Kuperus, J. Kirschner, J. Stepanek, P. Oosterveld and J. C. M. den Nijs (University of Amsterdam, The Netherlands) The detection of clonal evolution in *Taraxacum*: a question of scale
- S1-I-25 Y.C. Li, A.B. Korol, T. Fahima, J.H. Peng, M.S. Roder, e. Nevo (University of Haifa, Mt Carmel, Haifa, Israel)
   Pattern of microsatellite variation resulting for interaction of genetic factors and ecological stress in three natural populations of wild emmer wheat
- **S1-I-26** Lauga B., Cthourou-Ghorbal N., Marrackchi M. and Combes D. (Université de PAU et des Pays de l'Adour, France)
- Assessment of genetic variability in *Lathyrus* using molecular markers **S1-I-27** Doris Bachtrog and Christian Schloetterer (Institut für Tierzucht und Genetik, Wien) Microsatellite mutation rates differ between repeat motifs - evidence from *Drosophila melanogaster*
- **S1-I-28** Dmitry A. Filatov (University of Edinburgh, UK)
- ProSeq v. 2.3: A new sequence editor and analyzer
- S1-I-29 L. Kruckenhauser, A.A. Bryant and W. Pinsker (Inst. f. Medical Biology, Vienna, Austria) Comparative study of microsatellite variation in the Alpine marmot (*Marmota marmota*) and in the endangered species *M. vancouverensis*
- S1-I-30 J. M. Ranz and A. Ruiz (Universitat Autònoma de Barcelona, Bellaterra, Spain) Comparative molecular organization of the Muller's element *E* between two distantly related *Drosophila* species: *D. melanogaster* and *D. repleta*
- S1-I-31 J. P. Castro and L. Madi-Ravazzi (IBILCE-UNESP, São José do Rio Preto, Brazil) RAPD specific patterns and their polymorphisms in the *Drosophila buzzatii* cluster
- **S1-I-32** <u>Marianne Imhof</u> and Christian Schlötterer (Universität Wien, Austria) A new approach to infer microsatellite evolution *in vivo*
- **S1-I-33** <u>T. Palomeque</u>, J.A. Carrillo and P. Lorite (Universidad de Jaén, Spain) Conservation of satellite DNA in species from the genus *Messor* (Hymenoptera, Formicidae)
- **S1-I-34** M. A. Koch, <u>B. Haubold</u> and T. Mitchell-Olds (Max-Planck-Institut Jena, Germany) Molecular evolution of *Arabidopsis*, *Arabis* and related genera (Brassicaceae)
- S1-I-35 <u>S.Hanslik</u> (Universität Wien, Austria) Detecting selective sweeps in cattle populations
- **S1-I-36** E. M. Griebeler (University of Mainz, Germany)
- Estimating the effective population size of a single ideal population
- S1-I-37 J. Hagenblad and M. Nordborg (Lund University, Sweden) Patterns of sequence variation in the chromosomal region surrounding a polymorphic locus affecting flowering time in Arabidopsis thaliana
- S1-I-38 M. Cáceres, J. M. Ranz, A. Barbadilla, M. Long and A. Ruiz (Universitat Autònoma de Barcelona, Spain)

A transposable element mediated the generation of a Drosophila widespread chromosomal inversion

- **S1-I-39** <u>Alice Michel</u> and Didier Bouchon (Université de Poitiers, France) Molecular phylogeny and evolution of mitochondrial genes in terrestrial Isopods
- S1-I-40 Peter Arctander, Hans R. Siegismund, Bo T. Simonsen, Silvester Nyakaana, Josephine Birungi, Carsten Johansen, Louise Grau and Marie-Agnes Coutellec-Vreto (University of Copenhagen, Denmark)
  - Comparative phylogeography of 17 species of large African herbivores
- **S1-I-41** <u>E. Haring</u>, W. Pinsker and S. Hagemann (Museum of Natural History, Vienna, Austria) Successive waves of horizontal *P* element transmission in drosophilids
- S1-I-42 M. Carmen Callejas and <u>M. Dolores Ochando</u> (Universidad Complutense Madrid, Spain) Identification and phylogenetic relationships in Spanish *Barbus* species inferred by RAPD-PCR markers
- S1-I-43 M.Dolores Ochando, C. Callejas, D. Segura and M.P. Fernández (Universidad Complutense Madrid, Spain)

Phylogenetic relationships in four species of insect pests

- S1-I-44 Coyer, J.A., Peters, A.F., Olsen, J.L. and Stam, W.T. (University of Groningen, The Netherlands) Population structure of *Fucus sp* in the Skagerrak-Kattegat (Baltic Sea) as determined by microsatellites
- S1-I-45 M. Pempera and R. Wenne (Polish Academy of Sciences, Gdynia, Poland) Transmission of mitochondrial DNA variants in the mussel *Mytilus trossulus* from the Baltic Sea
- **S1-I-46** A.Was and <u>R. Wenne</u> (Sea Fisheries Institute, Gdynia, Poland) Genetic differentiation of the sea trout populations from the Southern Baltic, at the microsatellite level
- S1-I-47 J. Leiter, C. Sturmbauer and R. Rieger (University of Innsbruck, Austria) Phylogeographic analysis of species and populations of the Macrostomida from three major faunal regions
- **S1-I-48** <u>Sylvain Mousset</u>, Frantz Depaulis, Lionel Brazier and Michel Veuille (Université Pierre et Marie Curie, Paris, France)

Evidence for multiple selective sweep effects in association with the In(2L)t inversion in Drosophila melanogaster

- **S1-I-49** <u>A.P.Kryukov</u> and H.Suzuki (Russian Academy of Sciences, Vladivostok, Russia) Relationships between some East Asian vertebrates inferred from cytochrome *b* sequences
- S1-I-50 Gila Kahila Bar-Gal, P. Smith, E. Tchernov and C. Greenblatt (The Hebrew University, Jerusalem, Israel)

From animal domestication to the Dead Sea Scrolls: evolutionary and ecology changes

- **S1-I-51** <u>A.N.Carmichael</u>, Anna-Karin Fridolfsson and Hans Ellegren (Uppsala University, Sweden) Male Biased Mutation Rates in Avian ATP Synthase α-subunit (ATP5A1) Sequences
- **S1-I-52** Hannah Montell, Anna-Karin Fridolfsson and Hans Ellegren (Uppsala University, Sweden) Contrasting levels of nucleotide diversity at the avian Z and W sex chromosomes
- **S1-I-53** Nuria Sanz, José-Luis García-Marín, and Carles Pla (Universitat de Girona, Spain) The evolutionary history of trout (*Salmo trutta*) in the north-western Iberian glacial refuge
- S1-I-54 F. Herger, C. R. Largiadèr, M. Lörtscher, <u>B. Gantenbein</u> and A. Scholl (University of Bern, Switzerland)
   Nuclear and mitochondrial markers reveal a complex phylogeographic structure for *Austropotamobius pallipes* (Decapoda: Astacidae) in the Alpine region
- S1-I-55 J. Zbinden, C. R. Largiadèr, <u>B. Gantenbein</u> and A. Scholl (University of Bern, Switzerland) Genetic data suggests post-glacial colonisation across two major European watersheds by a freshwater fish species (*Cottus gobio*)

 S1-I-56 <u>Silvana Gaudieri</u>, Roger L Dawkins, Kaori Habara, Jerzy K Kulski and Takashi Gojobori (National Institute of Genetics, Mishima, Japan)
 Extensive nucleotide variability within the Major Histocompatibility Complex: association with polymorphic frozen blocks and recombination

S1-I-57 M. A. González Pérez, P. A. Sosa and J. Caujapé-Castells (Universidad de Las Palmas de Gran Canaria, Spain)

Isozyme diversity in Phoenix canariensis and P. dactylifera populations from the Canary Islands

- S1-I-58 F.A.M. Volckaert, B. Hellemans, J. Lievens, H. Verreycken and C. Belpaire (Katholieke Universiteit Leuven, Belgium) Gene flow in a postglacial aquatic coloniser (bullhead, Teleostei) in western Europe
- S1-1-59 F. Sebastiani, R. Meiswinkel, J. Paweska, P. Mellor, L. Gomulski, G. Gasperi (University of Pavia, Italy)

Discrimination of cryptic African *Culicoides* species of the Imicola complex (diptera: Ceratopogonidae), based on arbitrarily primed DNA fingerprinting

S1-1-60 M. Kankare (University of Helsinki, Finland) Genetic variation between alternate-year cohorts of Xestia testa (Lepidoptera: Noctuidae) in Finnish Lapland

- S1-I-61 F. Batista, A. Bañares, J. Caujapé-Castells, E. Carqué, M. Marrero and P. A. Sosa (Universidad de Las Palmas de Gran Canaria, Spain) Isozyme variation in three endemic species of <u>Cistus</u> (Cistaceae) from Canary Islands: implications for species delimitation and conservation
- S1-I-62 M. M. Ribeiro, C. Plomion, R. Petit, G. G. Vendramin and A. E. Szmidt (Department of Forest Genetics and Plant Physiology, Umeå, Sweden) Haplotypic diversity of maritime pine (*Pinus pinaster*) in Portugal revealed by cpSSR

S1-I-63 <u>R. Billeter</u> and N.J. Ouborg (University of Nijmegen, the Netherlands)
 Clonal diversity of wetland *Carex limosa* as a function of population size and isolation: a comparison between Irish and Swiss populations

S1-I-64 L. Uimaniemi and M. Orell (University of Oulu, Finland)

Population genetic structure of three avian species in fragmented habitats of Fennoscandia **S1-I-65** <u>M. Gómez</u>, A. Bueno, R. Alía and G.G. Vendramin (INIA-CIFOR, Madrid, Spain)

Chloroplast microsatellite markers reveal evolutive history of Aleppo pine in Spain

 S1-I-66 L. Parducci, A. E. Szmidt, M. Anzidei, A. Madaghiele and G.G. Vendramin (Swedish University of Agricultural Sciences, Umeå, Sweden)
 Family structure in *Abies nebrodensis* (Lojac.) Mattei and differentiation from related *Abies* species using allozymes and chloroplast microsatellites

- S1-I-67 <u>A. Parmakelis</u>, S. Giokas, M. Mylonas (University of Crete, Greece) Cladistic analysis of morphological and molecular characters of *Mastus* (Gastropoda, Pulmonata, Enidae)
- S1-I-68 S.C. González-Martínez, R. Alia and L. Gil (CIFOR-INIA, Madrid, Spain) Genetic variation along a South-North cline in *Pinus pinaster* Ait.: a comparison of molecular and quantitative traits
- S1-I-69 <u>P. Jiménez</u>, L. Gil and R.J. Petit (ETSI de Montes, Ciudad Universitaria, 28040 Madrid, Spain) Introgression between *Quercus suber* L. and *Quercus ilex* L. assessed by cpDNA polymorphism
- S1-I-70 <u>C. Rhomberg</u> and C. Sturmbauer (University of Innsbruck, Austria)
   Gene flow among populations of the Lake Tanganyika rock cichlid *Ophthalmotilapia ventralis* along a coherent coastline
- S1-I-71 <u>Grainne McGuire</u>, Mike Denham and David Balding (University of Reading, UK) Molecular phylogenies for gene families using unaligned sequences
- S1-I-72 A. Arnaiz-Villena, L. Allende, V. Ruíz-del-Valle, C. García-de-la-Torre, P. Varela,
  S. Ferre, M. Álvarez-Tejado, E. Lowy and J. Martínez-Laso (Universidad Complutense de Madrid, Spain)

A microevolutionary study in canaries (Genus Serinus) shows that the mtDNA molecular clock is different for different genera

- S1-I-73 A. Arnaiz-Villena, L. Allende, V. Ruíz-del-Valle, C. García-de-la-Torre, P. Varela,
   S. Ferre, M. Álvarez-Tejado, E. Lowy and J. Martínez-Laso (Universidad Complutense de Madrid, Spain)
   Phylogeny and rapid Northern and Southern Hemisphere speciation of goldfinches during the Miocene
- and Pliocene Epochs **S1-I-74** <u>S.B. Piertney</u>, A.D.C. MacColl, X. Lambin, R. Moss and J. Dallas (University of Aberdeen, UK) Male versus female mediated gene flow in red grouse (*Lagopus l. scoticus*)
- S1-I-75 Marie-Theres Hauser, Bettina Harr and <u>Christian Schlötterer</u> (Institut für Tierzucht und Genetik, Universität Wien) Molecular analysis of the *GLABROUS1* locus in *Arabidopsis thaliana* indicates the presence of two
- diverged allelic classes which are not associated with the distribution of trichomes **S1-I-76** J. Xu, T. G. Mitchell and R. Vilgalys (Duke University Medical Center, Durham NC, USA) A historical analysis of a human commensal yeast

**S1-I-77** <u>A. Sanchez-Gracia</u> and J. Rozas (Universitat de Barcelona, Spain) Nucleotide variation in the olfactory-specific genes *OS-E* and *OS-F* of *Drosophila melanogaster* and *D. simulans* 

- **S1-I-78** O. Rüppell, J. Heinze and B. Hölldobler (Universität Würzburg, Germany) Queen size dimorphic ants: a life history syndrome with consequences for population structure?
- **S1-I-79** <u>Béatrice Albert</u> and Carole Sellem (Centre de Génétique Moléculaire,Gif-sur-Yvette Cedex, France) Senescence and dynamics of the mitochondrial genome in *Podospora anserina*
- **S1-I-80** <u>P. Lorite</u>, J.A. Carrillo and T. Palomeque (Universidad de Jaén, Spain) Satellite DNA in the ant *Formica cunicularia* (Hymenoptera, Formicidae)
- **S1-I-81** <u>C. P. Vieira</u>, J. Vieira and D. Charlesworth (University of Edinburgh, UK) Nuclear DNA variation in the genera *Antirrhinum* and *Misopates*
- **S1-I-82** <u>C. MacDonald</u>, J. F. Y. Brookfield and T. H. Day (University of Nottingham, UK) Intra- and interspecific molecular variation in the Coelopidae
- S1-I-83 <u>H.E.M. de C. Bicudo</u>, A.S. Lapenta, A.P. Nascimento (Department of Biology, Sao José do Rio Preto, Brazil) Interspecific variation of esterase expression in *Drosophila*

- S1-I-84 C. Billot, S. Rousvoal, B. Kloareg, M. Valero (Université de Lille 1, Villeneuve d'Ascq, France) Population structure of *Laminaria digitata* (Pheophyceae) in the Channel: use of hypervariable markers
- **S1-I-85** <u>M. Bonizzoni</u>, C.R. Guglielmino, A.R. Malacrida, F. Sebastiani, G. Gasperi, and L. Zheng (University of Pavia, Pavia, Italy)
  - Polymorphic microsatellite markers for population anlysis of a tephritid pest species, *Ceratitis capitata*

**S1-I-86** <u>De-Xing Zhang</u>, G.M. Hewitt (University of East Anglia, Norwich, England) Microsatellites with large repeat number: variability and utility as molecular marker

S1-I-87 M. lizuka, K. Shinoda, S. Kanai, H. Toh and T. Nakahashi (Kyushu Dental College, Kitakyushu, Japan)

Mitochondrial DNA polymorphism of an ancient Japanese population in Yayoi period

- **S1-I-88** L. Moreira da Costa, <u>M.J. Collares-Pereira</u>, S. Lusk and P. Rab (Universidade de Lisboa, Portugal) New data on genome size variation of Centro-European Cyprinidae (Pisces, Osteichthyes)
- **S1-I-89** J. Pons, E. Petitpierre and C. Juan (Universitat de les Illes Balears, Spain)
- Gradual or saltatory evolution of satellite DNA in the genus *Pimelia*?
- S1-I-90 J.M. Guillon and C. Raquin (Université Paris-Sud and Muséum National d'Histoire Naturelle, Paris, France)

Strict maternal inheritance of chloroplasts in the horsetail Equisetum variegatum (Schleich)

- S1-I-91 E. Ladoukakis, C. Saavedra, A. Magoulas, E. Zouros (University of Crete, Greece)
   Role-reversal of mitochondrial DNA and the phylogeography of populations of mussels (*Mytilus galloprovincialis*) in the Eastern Mediterranean and the Black Sea
- **S1-I-92** <u>B.E. Stranger</u>, T. Mitchell-Olds (Max Plank Institute of Ecology, Jena, Germany) Intra- and Interspecific DNA sequence variation at Myrosinase loci in *Arabis* and *Arabidopsis* species
- S1-I-93 P. Martin (Royal Belgian Institute of Natural Sciences, Brussels, Belgium) Phylogenetic relationships of leeches (Euhirudinea) and leech-like worms (Acanthobdellida and Brachiobdellida) among the Clitellata (Annelida) derived from 18S rRNA sequences
- **S1-I-94** Philip Awadalla, M. Scheirup, B. Mable, and D. Charlesworth (University of Edinburgh, UK) Molecular Evolution of Self-Incompatibility loci in *Arabis petraea*
- S1-1-95 Diana Alvarez, Mohamed Noor and Manuel Ruiz-Garcia (Universidad Javeriana, Bogotá DC, Colombia) Comparative genetic structutre between populations of Colombian and North-American Drosophila pseudoobscura using five microsatelite loci. Gene flow, time of divergence, and effective numbers of the Colombian Populations
- S1-I-96 Diana Alvarez, and Manuel Ruiz-Garcia (Universidad Javeriana, Bogotá DC, Colombia) Partial phylogenetic analysis of five Colombian species (*Cebus albifrons*, *Cebus apella*, *Saimiri scieureus*, *Lagothrix lagotricha* and *Aloutta seniculus*) and divergence time among species and genera using RFLP's on mtDNA
- S1-I-97 Manuel Ruiz-Garcia, Maria Ignacia Castillo and Diana Alvarez (Universidad Javeriana, Bogotá DC, Colombia)

Reconstruction of the evolution of the AP68 microsatellite locus in 11 Primate Platyrrhine species (*Cebus albifrons, Cebus apella, Saimiri sciureus, Saguinus oedipus, Saguinus geoffroyi, Cebuella pygmaea, Aoutus lemurinus, Alouatta seniculus, Lagothrix lagotricha, Ateles fusciceps* and Ateles belzebuth)

S1-I-98 Manuel Ruiz-Garcia, Maria Ignacia Castillo and Diana Alvarez (Universidad Javeriana, Bogotá DC, Colombia)

Differential phylogenetic results among seven Colombian Primate species using seven microsatellite loci in function of the genetic distances used. The advantages of the delta-mu 2 genetic distance versus other genetic distances for the reconstruction of primate phylogenies and calculation of time of divergence among the seven species

#### Poster session I Symposium 7

- **S7-I-1** <u>Rebecca Timms</u>, Margaret Mackinnon and Andrew F. Read (University of Edinburgh, UK) The impact of within-host genetic diversity on virulence
- S7-I-2 O.-P. Tikkanen and P. Lyytikäinen-Saarenmaa(University of Joens, Finland) Phenological adaptation of a generalist spring-feeding moth, *Operophtera brumata*, to leaf flush of its host plants
- S7-I-3 Z. Redenbach and E. B. Taylor (University of British Columbia, Vancouver, Canada) Natural hybridization between *Salvelinus malma* and *S. confluentus*: reproductive and ecological fates of hybrids
- **S7-I-4** <u>Lars Witting (Greenland Institute of Natural Resources, Greenland)</u> Selection by density dependent competitive interactions explains major life history transitions
- **S7-I-5** <u>A. J. Crawford</u> (University of Chicago, USA) Differentiation among populations and species possessing a common phenotypic polymorphism: evidence for balancing selection?
- S7-I-6 <u>M. J. Clauss</u> (University of Arizona, Tucson AZ, USA) Bet-hedging and the population dynamical consequences of seed germination in fluctuating environments
- S7-I-7 <u>F. Maltagliati</u>, L. Camilli, A. Castelli, and C. Lardicci (Università di Sassari, Italy) Preliminary allozyme study on the genetic divergence in the bivalve *Mytilaster minimus* from a polluted brackish environment and adjacent marine sites
- S7-I-8 D.F.R. Cleary (University of Amsterdam, The Netherlands) The forest fires of Kalimantan: an analysis of the impact of disturbance on the community structur of tropical forest butterflies
- **S7-1-9** André Levy (Stony Brook State University, Stony Brook NY, USA) Resistance and tolerance in rapid cycling *Brassica*
- S7-I-10 M. Michaud, F. Thomas, S. Becheikh, A. Raibaut, J. Shykoff and F. Renaud (Centre IRD de Montpellier, France) Stage-dependent decisions in a parasitic copepod practising environmental sex determination
- S7-I-11 Krisztián Mágori, Géza Meszéna, Beáta Oborny (Eötvös University Budapest, Hungary) Evolution of integration rate of clonal plants
- S7-I-12 Bengt Carlsson and K. Ingemar Jönsson (University of Ronneby, Sweden.) The fate of generous and greedy strategies in the iterated Prisoner's Dilemma and the Chicken Game under noisy conditions
- **S7-I-13** <u>Pierre-Olivier Cheptou</u> and Andrea Mathias (Centre d'Ecologie Fonctionnelle et Evolutive, France) Evolution of self-fertilization under environment-dependent inbreeding depression
- **S7-I-14** <u>Marco Soliva</u> and Alex Widmer (Swiss Federal Institute of Technology Zurich, Switzerland) The evolution of specific pollinator acquisition in the sexual deceptive orchid genus *Ophrys*
- S7-I-15 M. Matos, P. Ferreira, N. Sagueiro, C. Rego, T. Avelar, and M.T. Rocha Pité (Faculdade de Ciências de Lisboa, Lisboa, Portugal)
  - Does plasticity evolve during the adaptation to a novel, stable environment?
- **S7-I-16** B. Doligez, E. Danchin, <u>T. Boulinier</u> (Université Claude et Marie Curie, Paris, France) Are conspecific based strategies of breeding habitat selection evolutionarily stable?
- **S7-I-17** J.S. Pedersen, F. Balloux, M. Reuter, M.J.B. Krieger, L. Keller (Université de Lausanne, Switzerland) Maintenance of altruistic behaviour in non-equilibrium populations: a study of unicolonial ants
- **S7-I-18** <u>S.R. Proulx</u> (University of Utah, Salt Lake City, Utah, USA) Spatial heterogeneity can resolve the paradox of the lek
- **S7-I-19** M. Escala, N. Xena, M.B. Raymundez and J. Mathez (IBE, U.C.V., Los Chaguaramos, Caracas, Venezuela) Myrmecochory, a strategy for the dissemination of herbaceous vegetation?

### Poster session I Symposium 12

- **S12-I-1** Agustí Galiana (Universitat de València, Spain) The ultimate great evolutionary transition
- **S12-I-2** <u>Ahtiainen</u>, J.J., Alatalo, R.V., Mappes, J., Parri, S. and Vertainen, L. (University of Jyväskylä, Finland) Does asymmetry on secondary sexual trait fluctuate with individual quality in the wolf spider *Hygrolycosa rubrofasciata*?
- **S12-I-3** <u>R. Cruz</u>, E. Rolán-Álvarez and C. García (Univ. Santiago de Compostela, Spain) Sexual selection on phenotypic traits in a hybrid zone of *Littorina saxatilis*
- **S12-I-4** J. Mappes, R.V. Alatalo, L. Lindström, A. Lyytinen, M. Riipi and L. Vertainen (University of Jyväskylä, Finland)

Tracking evolution of aposematic signalling in the novel world

- **S12-I-5** <u>Silja Parri</u>, Rauno V. Alatalo, Janne Kotiaho and Johanna Mappes (University of Jyväskylä, Finland) Offspring growth in a drumming wolf spider - effects of father size and sexual attractiveness
- S12-I-6 N.V. Vlasova (Central Siberian Botanical Garden, Russia) Seed morphology of some species of the Alsinoideae (Caryophyllaceae) and its significance for systematics
- S12-I-7 J. L Dudycha (Michigan State University, USA)
  - A reaction norm approach to the evolutionary ecology of senescence in Daphnia
- S12-I-8 J.J. Fanara, A. Fontdevila, and <u>E. Hasson</u> (Universidad de Buenos Aires, Argentina)Oviposition preference and life history traits in cactophilic *Drosophila koepferae* and *D. buzzatii* in association with their natural hosts
- **S12-I-9** Tom Van de Casteele and Eric Matthysen (University of Antwerp, Antwerp, Belgium) Post fledging movements and natal dispersal in the great tit *Parus major*

#### Poster session II Symposium 11

S11-II-1 Erwin Lansing, Jesper Dahlgaard and Volker Loeschcke (University of Aarhus, Denmark) Natural selection for reduced cost of heat-hardening in *Drosophila melanogaster* 

- S11-II-2 Niels Cadée (Université Pierre et Marie Curie, France)
- Genetic and environmental effects on morphology and fluctuating asymmetry in nestling barn swallows **S11-II-3** Laura Vertainen, Rauno V. Alatalo, Johanna Mappes and Silja Parri (University of Jyväskylä, Finland)

Genetic variation in isolated populations of the drumming wolf spider Hygrolycosa rubrofasciata

S11-II-4 E. Solé, J. Balanyà and L. Serra (Universitat de Barcelona, Spain)

Chromosomal inversions as a possible marker of a global climatic change **S11-II-5** Lucy Crooks (The University of Edinburgh, UK)

A trade-off in malaria infections: can it explain the parasite's life history?

**S11-II-6** Mark van Kleunen, Markus Fischer and Bernhard Schmid (Universität Zürich, Switzerland) Costs and limits of plasticity in the clonal plant *Ranunculus reptans* 

- S11-II-7 Mark van Kleunen, Markus Fischer and Bernhard Schmid (Universität Zürich, Switzerland) Clonal integration: coincidence or adaptation?
- S11-II-8 C.J. Breuker and P.M. Brakefield (Leiden University, The Netherlands) Window experiments and the effects of heat shock on wing eyespot asymmetry in *Bicyclus anynana*

S11-II-9 Marc van der Linde, Jan G. Sevenster, Paul M. Brakefield and Bas J. Zwaan (Leiden University, The Netherlands)

- Habitat-linked variation in life-history traits in Drosophila
- S11-II-10 P. López-García and P. Forterre (Universitè Paris-Sud, France) DNA topology and thermal stress in hyperthermophilic archaea
- S11-II-11 P. Michalak, <u>J. Sørensen</u>, J. Justesen and V. Loeschcke (University of Aarhus, Denmark) Expression of the heat-shock protein HSP70 in *Drosophila buzzatii* lines selected for thermal resistance

**S11-II-12** <u>Carla M. Sgrò</u> and Ary A. Hoffmann (University College London, U.K.) Effects of environmental stress on the expression of additive genetic variation

S11-II-13 Jesper Dahlgaard and Volker Loeschcke (University of Aarhus, Denmark.) Behavioural differentiation in oviposition activity in *Drosophila buzzatii* from mountain and lowland populations in Argentina

S11-II-14 M.Poirie, M.Hita, F.Frey, E.Huguet, F.Lemeunier, G.Periquet and Y.Carton (Université F. Rabelais, France) Drosophila resistance GENES against parasitoids: a gene-for-species concept

S11-II-15 <u>F.N. Zaki</u> (National Research Centre, Dokki, Cairo, Egypt) Effect of the entomopathogenic fungus *Beauveria bassiana* as a biological control agent on two thrips pests, *Heliothrips haemorrhoidalis* infecting roses and *Hamplothrips cotties* infesting carnation

S11-II-16 J. Vanoverbeke and L. De Meester (Laboratory of Aquatic Ecology, Leuven, Belgium) Intrapopulational genetic polymorphism in relation to temporally varying environments

S11-II-17 Christensen, Margit (University of Aarhus, Denmark)

Heat and cold protection by sugar and sugar analogous and by heat shock proteins

S11-II-18 A. B. Nielsen (University of Aarhus, Denmark) Estimates of genetic and phenotypic variance in *Drosophila buzzatii* under nutritional stress - a comparison of estimation methods

**S11-II-19** G. H. de Moed and <u>G. de Jong</u> (Utrecht University, The Netherlands)

Environmental dependence of larval growth rate and critical weight for pupariation

S11-II-20 Phillip T. Barnes and Kathryn E. Stellitano (Connecticut College, New London, USA) The effect of chromosomal inversions on flight morphology and physiology at different rearing temperatures in *Drosophila melanogaster* 

**S11-II-21** <u>V. Devenieve</u>, A. Paulauskas, and A. Sruoga (Institute of Ecology, Vilnius, Lithuania) Allozyme analysis of freshwater molluscs in Lithuania

S11-I-22 A.B. Korol, E. Rashkovetsky, K. Iliadi, T. Pavlicek, E. Nevo (University of Haifa, Israel) Incipient sympatric differentiation in *Drosophila*: a complex adaptative syndrome caused by strong microclimatic selection

S11-II-23 T.N. Kristensen (University of Aarhus, Denmark)

Inbreeding and environmental stress-effects on fitness parameters in Drosophila buzzatii

S11-II-24 P.Blier (Université du Québec à Rimouski, Canada) The evolutionary significance of Cytochome C Oxidase thermanl sensitivity in fish muscle mitochondria

#### Poster session II Symposium 18

University, The Netherlands)

| Diminishing returns from mutation supply rate in asexual populations  |
|---|
| S18-II-2 B. Haubold and B. Mehlig (Max-Planck-Institut für Chemische Ökologie, Germany)   |
| The rate of recombination in the human pathogen Neisseria meningitidis  |
| S18-II-3 Ladevèze V., Aulard S., Biémont C., Chaminade N., Périquet G. and  |
| Lemeunier F. (C.N.R.S., L.P.G.E., Gif/Yvette, France)   |
| Local transposition in Drosophila transgenic lines of hobo elements   |
| S18-II-4 B.Megías-Nogales, M.E. Gas, A.Pérez-Muñoz, R. Vázquez, M.Gandía,   |
| M.J.Martínez-Sebastián and R. de Frutos (Universidad de Valencia, Spain)  |
| Phylogenetic analysis of Drosophila class I and II transposable elements  |
| S18-II-5 J. Krajcovic (Comenius University, Slovak Republic)  |
| Reverse endosymbiosis? Losses of organelles in evolution and ontogeny   |
| S18-II-6T.F. Sharbel, L.W. Beukeboom and N.K. Michiels (Max Planck Institut, Germany)   |
| Is genetic leakage between apomictic flatworms a form of pseudosex?   |
| S18-II-7 A.M. Korayem, H.H. Salem (National research centre, Dokki, Cairo, Egypt)   |
| Effect of Saponin produced by genetically constructed microbial strains on root-knot nematodes  |
| S18-II-8 Douda Bensasson, De-Xing Zhang, and Godfrey M. Hewitt (University of East Anglia)  |
| Frequent assimilation of mitochondrial DNA by grasshopper nuclear genomes   |
| Poster session II   |
| Symposium 17  |
| Sjinposinin x.  |
| <b>S17-II-1</b> <u>M. Egas</u> , F. Vala and J.H.J. Breeuwer (University of Amsterdam, The Netherlands)<br>Cytoplasmic incompatibility in haplo-diploid species |

S18-II-1 Arjan de Visser, Cliff Zeyl, Phil Gerrish, Jeff Blanchard and Rich Lenski (Wageningen Agricultural

- S17-II-2 M. Puurtinen and V. Kaitala (University of Jyväskylä, Finland) Trade-off between mate search and foraging can stabilize simultaneous hermaphroditism in animals
- S17-II-3 P.C. Luttikhuizen and L.P. Pijnacker (Netherlands Institute for Sea Research, The Netherlands) Additional sperm siring haploid cells in mosaic haploid-diploid bivalve embryo's: possible connection with non-standard heterozygosities and mitochondrial inheritance?
- S17-II-4 James P. Randerson, Nicholas G. C. Smith and Laurence D. Hurst (University of Bath, Claverton Down, UK)

The evolutionary dynamics of male-killers and their hosts

- S17-II-5 K. Martens, I. Schön and G. Rossetti (Royal Belgian Institute of Natural Sciences, Brussels, Belgium) Ancient asexual scandals
- S17-II-6 Alf Ceplitis (Lund University, Sweden)

Population dynamics and sexual reproduction in the clonal plant Allium vineale

- S17-II-7 Marianne Elias and Doyle McKey (Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France) A novel type of cost of sex: plant architecture, human and natural selection, and sexuality in populations of a domesticated plant
- S17-II-8 Carolien G.F. de Kovel (Utrecht University, The Netherlands)

Consequences of genetic variation among offspring in Taraxacum, dandelion

- S17-II-9 Jari Valkama, Dave Currie, Erkki Korpimäki and Ville Pöyri (University of Turku, Finland)
- Sex roles, parental effort and offspring desertion in the Curlew
- S17-II-10 G. Schöfl and M. Taborsky (Konrad Lorenz-Institut für Vergleichende, Vienna, Austria) Mate guarding reduces sperm competition in the red firebug *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae)
- S17-II-11 M. Björklund and J. C. Senar (Uppsala University, Sweden)
  - Sex differences in survival selection in the serin, Serinus serinus
- S17-II-12 Robert Belshaw (Imperial College at Silwood Park, Ascot, U.K) Cryptic sex in the parasitoid wasp, Lysiphlebus (Braconidae: Aphidiinae)
- S17-II-13 Göran Arnqvist and <u>Tina Nilsson</u> (University of Umeå, Sweden) The evolution of polyandry: multiple mating and female fitness in insects

**S17-II-14** <u>Agustí Galiana</u> (Universitat de València, Spain) Secondary sexual traits in humans, women in particular

- **S17-II-15** J. Kurtz and K. P. Sauer (Universität Bonn, Germany) Does the immunocompetence handicap principle work in *Panorpa vulgaris* scorpionflies?
- S17-II-16 Christine Vassiliadis, Pierre Saumitou-Laprade, Philippe Vernet, Jacques Lepart (Université Lille 1, Villeneuve d'Ascq, France) Estimation of relative male reproductive success by paternity analysis in the androdioecious *Phillyrea* angustifolia L.
- **S17-II-17**<u>Anneli Hoikkala</u> (University of Oulu, Finland) Evolution of courtship interactions in *Drosophila* – complicated courtship or rape
- **S17-II-18** <u>R Torres</u>, F. Cooke, G. Robertson and S. Boyd (Instituto de Ecología, UNAM, México DF, México) Costs and benefits of early pairing in the Harlequin duck
- **S17-II-19** <u>E. Petit</u> (University of Lausanne, Switzerland)
- Do male noctule bats disperse randomly?
- S17-II-20 <u>F. Dufresne</u>, L. Bernatchez, and E Bourget (Université Laval, Québec, Canada,) Selection and genetic structure in the barnacle, *Semibalanus balanoides* as revealed by allozyme and microsatellite markers
- S17-II-21 Y. L. Dupont and M. Kato (Aarhus University, Denmark) Sex ratio variation in populations of six dioecious species of *Lindera* (Lauraceae) in Kyoto, Japan
- S17-II-22 M. H. Verduijn and P. van Dijk Netherlands (Institute of Ecology (NIOO-CTO), Heteren, The Netherlands)

Geographical parthenogenesis and mixed sexual - asexual dandelion populations

- S17-II-23 K. Kosuda ( Josai University, Sakado, Saitama, Japan) Could be the conflict between male and female the cause of melanotic tumor formation in *Drosophila melanogaster*?
- S17-II-24 M. Osorio-Beristain, D. Pérez and H. Drummond (Universidad Autónoma del Estado de Morelos, Cuernavaca, México)

Mating tactics and countertactics of males and females in the blue-footed booby **S17-II-25** <u>A. Kelly</u>, A. Dunn & M. Hatcher (University of Leeds, Leeds, LS2 9JT, UK) The effect of a microsporidian sex ratio distorter on the reproductive behaviour of *Gammarus duebeni* 

### Poster session II

### Symposium 6

- S6-II-1 <u>Christof Binder</u> (University of Basel, Switzerland) Optimal foraging of a clonal parasitic plant
- **S6-II-2** <u>H. Marak</u>, A. Biere, J.M.M. van Damme (Netherlands Institute of Ecology, Heteren, The Netherlands) Costs and benefits of iridoid glycosides in *Plantago lanceolata*
- **S6-II-3** <u>P. Villesen</u>, P. Gertsch, J. Frydenberg, U. G. Mueller and J. J. Boomsma (Univ. of Aarhus, Denmark) Mating system evolution in fungus-growing ants
- **S6-II-4** <u>D. Molbo</u>, E.A. Herre and L. Keller (Université de Lausanne, Switzerland) Breeding structure of fig associated wasps
- **S6-II-5** <u>Gerald Kerth</u>, Frieder Mayer and Barbara Kînig (Université Zurich, Switzerland) I DNA reveals evidence for benefits of group living in Bechstein's bats
- S6-II-6 <u>M. Egas</u>, M. van Baalen and M.W. Sabelis (University of Amsterdam, The Netherlands) Plant defences and herbivore deterrents: do plants advertise the presence of their bodyguards to herbivores?
- **S6-II-7** <u>S.P. Brown</u> (Department of Zoology, Cambridge, UK) Co-operation and conflict in host-manipulating parasites
- **S6-II-8** <u>E.A. Herniou</u>, R.A. Bray and D.T.J. Littlewood (The Natural History Museum, London, UK) Evolution of parasitism in deep sea fishes: evidence from *Steringophorus*
- S6-II-9 Coenraad L. Krijger and Jan G. Sevenster (Institute for Evolutionary and Ecological Sciences, Leiden, The Netherlands)
   The role of life history traits and temporal heterogeneity in the ecology and diversity of six neotropical Drosophila communities
- **S6-II-10** <u>B.R. Pittendrigh</u>, K.A. Pivnick, and T. Mitchell-Olds (Max-Planck-Institute for Chemical Ecology, Germany) Reproductive strategies in female diamondback moths, *Plutella xylostella*

S6-II-11 Katarina Olsson and Jon Ågren (Umeå University, Sweden)

Phenological variation in populations of Lythrum salicaria along a latitudinal transect

- S6-II-12 Wolfgang W. Weisser, Christian Braendle and Nicole Minoretti (Zoology Institute, Basel, Switzerland) Predator-induced morphological shift in the pea aphid
- S6-II-13 J.G. Sevenster, B. Werheim (Leiden University, Leiden, The Netherlands) Specialization does not mediate coexistence in a mycophagous insect community, competitor aggregation does
- S6-II-14 P. Neumann, H.R. Hepburn, S.E. Radloff (Rodhes University, Grahamstown, South Africa) The evolution of theolytoky in honeybees (Apis mellifera): the impact of the mode of worker reproduction on dominance hierarchies among laying workers and on cell construction

### Poster session II

Symposium 13

S13-II-1 C. Doutrelant and P. K. McGregor (University of Copenhagen, Denmark) Eavesdropping and mate choice in fish

S13-II-2 J. E. Frey, B. Frey, D. Frei, D. Forcioli and H. Müller-Schärer (Université de Fribourg, Switzerland) Variation in levels of chloroplast DNA polymorphism within individual Senecio vulgaris

### Poster session II Symposium 2

- S2-II-1 M. Bullejos and A. Sánchez (Universidad de Jaén, Spain) The SRY gene HMG-box in micro- and megabats
- S2-II-2 Abdelghani Ben Ali, Yves Van de Peer and Rupert De Wachter (University of Antwerp, Belgium) Evolutionary relationships between the eukaryotic crown taxa on the basis of large subunit ribosomal **RNA** sequences
- S2-II-3 Emmanuelle Renard, Jean-Luc Da Lage, Frédérique Chartois, Marie-Louise Cariou (CNRS Gif sur Yvette, France)
  - Evolution of the Amylase gene family in drosophilids: focus on Amyrel, a distant relative
- S2-II-4 David H. Ardell and Guy Sella (Department of Biological Sciences, Stanford University, Stanford CA 94305 USA)

On the Evolution of the Structures in the Standard Genetic Code as an Outcome of Code-Message Coevolution I

#### Poster session II Symposium 23

S23-II-1 K. Ikeo, Sacha Glardon, and W. J. Gehring (National Institute of Genetics, Mishima, Japan) The study of morphological evolution and molecular evolution from the phylogenetic analysis of the pax gene families

### Poster session II

Symposium 8

- S8-II-1 C. S. Tsigenopoulos, D. Naran and P. Berrebi (Université Montpellier II, France) Three different lineages of South African barbs (Barbus, Cyprinidae) revealed by mitochondrial DNA and karyological data
- S8-II-2 Greg J. Adcock, Lorenz Hauser, Peter Smith and Gary R. Carvalho (University of Hull, UK) Adding the time dimension to population genetics: the origins and recent history of New Zealand snapper, Pagrus auratus (Sparidae)
- S8-II-3 Petri Ahlroth, Rauno V. Alatalo, Anne Holopainen, Tomi Kumpulainen and Jukka Suhonen (University of Jyväskylä, Finland) Importance of propagule size and genetic variation for colonization success

- S8-II-4 L. Amsellem, J.-L. Noyer, and M. Hossaert-Mc Key (CIRAD-CA, Montpellier, France) Comparison of genetic diversity of the weed *Rubus alceifolius* Poir. (Rosaceae) in its introduced and native areas
- S8-II-5 Pedro Esteves, Nuno Ferrand, and Wessel van der Loo. (Vrije Universiteit Brussel, Belgium)
   Effect of population bottlenecks on the gene diversity at *IG* loci in wild rabbits (*Oryctolagus cuniculus* L.) of the islands of Porto Santo (Madeira) and Flores (Azores)
- S8-II-6 <u>F. Austerlitz</u>, S. Mariette, N. Machon, P.-H. Gouyon and B. Godelle (Université Paris-Sud, France) Effects of colonization processes on genetic diversity: differences between annual plants and tree species
- S8-II-7 <u>C. Juan</u>, J. Gómez-Zurita and E. Petitpierre (Universitat de les Illes Balears, Spain) Nuclear ribosomal ITS2 sequences are useful to resolve the basal relationships in the phylogeny of *Timarcha* (Coleoptera, Chrysomelidae)
- **S8-II-8** <u>Kaygorodova I.A.</u>, Sherbakov D.Yu., Martin P., Verheyen E. (Limnological Institute, Irkutsk, Russia) Molecular phylogenetic study of endemic *Lumbriculidae* (Oligochaeta) from Lake Baikal (Russia)
- S8-II-9 <u>C.C. Englbrecht</u>, U. Schliewen, K. Rassmann, J. Freyhof., A. Nolte and D. Tautz (Zoologisches Institut der Universität München, Germany) Phylogeography of the European sculpin *Cottus gobio*: evidence for a western and an eastern clade
- **S8-II-10** <u>Anna-Britt Nyberg</u> and Anna Westerbergh Mid Sweden (University, Härnösand, Sweden) Colonisation patterns of a polyploid plant on heavy metal soils in Scandinavia
- **S8-II-11** Jakob Müller, Stephanie Giesen and Alfred Seitz (University of Mainz, Germany) Dynamic genetic structures of invaded *Amphipod* and *Dreissena* populations
- S8-II-12 J. Gómez-Zurita, C. Juan and E. Petitpierre (Universitat de les Illes Balears, Palma de Mallorca, Spain) Mitochondrial phylogeny of the genus *Timarcha* (Coleoptera, Chrysomelidae) inferred from complete COII and partial 16S rDNA genes
- S8-II-13 E.K. Klein, C. Lavigne, P.-H. Gouyon and C. Larédo (Université Paris-Sud, France) Estimation of the dispersal function of maize pollen in order to assess the risks associated with deliberate release of transgenes
- **S8-II-14** <u>Tracey Parrish</u> and Peter van Dijk (Center for Terrestrial Ecology, Heteren, The Netherlands) Searching For Genetic Founder Effects in Tree Species on the Krakatau Islands in Indonesia
- S8-II-15 <u>T. Kontula</u> and R. (Väinölä University of Helsinki, Finland) Postglacial colonization of Fennoscandia by distinct phylogeographic lineages of the bullhead, *Cottus gobio*
- **S8-II-16** <u>F. Jordán</u> (Eötvös University, Budapest, Hungary) Keystone species in community organization
- S8-II-17 Paulo O.S., S. Ricardo, E.G. Crespo, R. Nichols, M.W. Bruford, J.A. Scolaro and J.Cei (Institute of Zoology, London, UK and Faculdade de Ciencias da Universidade de Lisboa, Portugal)
  - Genetic evaluation of the systematic of Liolaemus archeforus group from Argentina

S8-II-18 <u>E. Davis Parker</u> (Aarhus University, Arhus, Denmark) Testing hypotheses to explain geographic parthenogenesis: dessication tolerance in parthenogenetic and sexual *Pycnoscelus cockroaches* 

**S8-II-19** <u>C.C. Chinnappa</u> (University of Calgary, Calgary, Canada) Evolutionary significance of colonisation by *Stellaria longipes* (Caryophylidae)

S8-II-20 <u>LI. Montoya-Burgos</u>, C. Weber, J. Pawlowski (Museum of natural history of Geneva, Genève, Switzerland)
 Speciation events within the catfish genus Hypostomus (Loricariidae) relate the colonisation history and ancient patternes of neotropical river systems

- S8-II-21 M. L. Heddle, N. Davies, G.K. Roderick (University of Hawaii, Honolulu) Why are there only butterfly species in Hawaii? The biodiversity of Macrolepidoptera in Pacific Archipelagoes
- **S8-II-22** M.C. Varela, M.I. Reforço, R. Bráz, C. Meierose (Estaçao Forestal Nacional, Oeiras, Portugal) Flowering and fructifications studies in *Quercus ruber* and *Quercus ilex* in Portugal

### Poster session II Symposium 14

S14-II-1 Badge, R. M. and Armour, J.A.L. (University of Nottingham, UK) Fine mapping of meiotic recombination breakpoints: Hotspots or warm patches? S14-II-2 Claus Vogl (University of Oulu, Finland) Linkage mapping of loci controlling important traits in less studied species S14-II-3 Peter H, van Tienderen (Netherlands Institute of Ecology, Heteren, The Netherlands) Elasticities link demographic and evolutionary dynamics S14-II-4 Riihimäki, M.-A., Koelewijn, H. P. and Savolainen, O. (University of Oulu, Finland) Effect of sib competition on observed inbreeding depression in self incompatible species Arabis petraea (L.) Lam. S14-II-5 L. Ulizzi, P. Astolfi and L.A. Zonta (University "La Sapienza", Rome, Italy) Effects of environmental changes on natural selection active on human quantitative traits S14-II-6 Y. Naciri-Graven and J.Goudet (Université de Lausanne, Switzerland.) An extension of the Cheverud and Routman's model of physiological epistasis to more than 2 loci: Effects on the release of additive variance after bottlenecks S14-II-7 É. Ludvig, L. Vanicsek and G. Meszéna (Eötvös University, Budapest, Hungary) Heritability estimates of two metric traits by different methods in two Parus species S14-II-8 Carvajal, A. (Universidad de A Coruña, Spain) Dynamic systems and speciation events S14-II-9 S. Pérez, L. Santamaría, K. Schwenk (Centre for Limnology, Nieuwersluis, The Netherlands) The evolution of passive dispersal: A comparative study of seed morphology in aquatic plants S14-II-10 Hafid Laayouni, Mauro Santos and Antonio Fontdevila (Universitat Autònoma de Barcelona, Bellaterra, Spain) Physical map based on RAPDs in the cactophilic species Drosophila buzzatii Poster session II

Symposium 4

- **S4-II-1** <u>V. Zupunski</u>, D. Kordis, F. Gubensek (Jozef Stefan Institute, Slovenia) Positive Darwinian selection in *Vipera anmodytes* Kunitz-type inhibitor multigene family
- **S4-II-2** <u>M.H. Schierup</u>, X. Vekemans, D. Charlesworth (University of Edinburgh, UK) Balancing selection in a subdivided population
- S4-II-3 Wessel van der Loo (Vrije Universiteit Brussel, Belgium)
   The molecular clock runs at different rates among allelic lineages at the rabbit *IGKC1* locus: evidence from sequence comparisons and population studies
- **S4-II-4** <u>T. Daniel Andrews</u> and Simon Easteal (National Institute of Genetics, Mishima, Japan) Coordinated adaptive evolution may explain evolutionary rate accelerations observed for multiple genes of the mitochondrial electron transport chain in simian primates
- S4-II-5 X. Vekemans and G. May (Université Libre de Bruxelles, Belgium)
   A new method for detecting balancing selection from DNA sequences: application to the *b1* mating type gene of the fungus *Coprinus cinereus*
- S4-II-6 S. Doiron, P.U. Blier and L. Bernatche (Université Laval, Québec, Canada) A comparative analysis of complete sequence of mitochondrial genome between brook char (Salvelinus fontinalis) and arctic char (S. alpinus) (Pisces, Salmonidae)
- **S4-II-7** Dusan Kordis, Avner Bdolah and <u>Fran Gubensek</u> (Jozef Stefan Institute, Ljubljana, Slovenia) Did adaptive evolution operate in the *Echis coloratus* phospholipase A<sub>2</sub> genes?

#### Poster session II Symposium 19

S19-II-1 J. Costas (Univ. Santiago de Compostela, Spain)

A paleogenomic approach to the evolution of the ERV9 human endogenous retrovirus family

S19-II-2 H. Naveira, J. Costas and E. Valadé (Univ A Coruña, Spain) Evidence for two persistent lineages of the *blood* retrotransposon during the evolution of the *Drosophila melanogaster* species complex

S19-II-3 E. Lerat and P. Capy (CNRS, Gif Sur YVette Cedex, France) What the comparison of homologous domains tell us about the structural evolution of transposable elements?

S19-II-4 <u>E. Lerat</u>, C. Biémont and P. Capy (CNRS, Gif Sur YVette Cedex, France) Codons Usage: host genes *versus* transposable elements

- **S19-II-5** <u>T.F. Sharbel</u>, B. Haubold and T. Mitchell-Olds (Max Planck Institut für Chemische Ökologie, Germany) Patterns of relationship among *Arabidopsis* ecotypes
- **S19-II-6** <u>A. Domínguez</u>, T. Pérez, L. Alonso, F. Vázquez, J. Albornoz (Universidad de Oviedo, Spain) Rates of structural mutation for transposable elements and microsatellite loci in *D. melanogaster*

#### Poster session II Symposium 20

S20-II-1 Rosario Miralles, Andrés Moya and Santiago F. Elena (Universitat de València, Spain) Differences in the evolutionary outcome induced by dynamics of coinfection and superinfection in Vesicular Stomatitis Virus

S20-II-2 Jawhar Gharbi, Thomas Bourlet, Jean-Luc Bailly, Odette Germaine Gaudin,

Mahjoub Aouni and Bruno Pozzetto (Faculty of Medicine of Saint-Etienne, France and Faculty of Pharmacy of Monastir, Tunisia)

Phenotypic variations in the recognition of echovirus type 11 strains by a group-specific anti-vp1 monoclonal antibody

Poster session II Symposium 24

S24-II-1 Jerzy Dzik (Instytut Paleobiologii PAN, Warszawa, Poland) Relationships of the Ediacaran organisms

S24-II-2 R. Albalat, C. Cañestro and R. Gonzàlez-Duarte (Universitat de Barcelona, Spain) Amphioxus ADH class III: gene duplication and phylogenetic insights

Poster session II Symposium 25

### S25-II-1 E. Michel, J. A. Todd and I. Kingma (Univ. Amsterdam, The Netherlands) Life history variation in a species flock: Phylogenetic perspectives on linking early ontogenetic morphology with brood and embyro sizes in *Lavigeria* gastropods from Lake Tanganyika, Africa

- **S25-II-2** <u>W. Salzburger</u> and C. Sturmbauer (University of Innsbruck, Austria) Comparative phylogenetic analysis among major Tanganyikan Cichlid-Lineages
- **S25-II-3** Izeni Farias, Axel Meyer and Guillermo Ortí (Universidade do Amazonas, Manaus, Brazil)

Cichlid phylogeny: total evidence analysis and molecular rate heterogeneity among groups **S25-II-4** <u>LSchön</u> and K.Martens (Royal Belgian Institute of Natural Sciences, Brussels, Belgium)

Evolution and speciation in ancient lake ostracods – differences and resemblances **S25-II-5** <u>M.V. Klett</u>, A. Denk, L. Pouyaud, J.-F. Agnèse, S.O. Kullander and A. Meyer (University of Konstanz, Germany)

Molecular phylogeny of tilapiine cichlid fishes: the origin of complex parental care (?) behavior(s)

S25-II-6 Martin Taylor and Erik Verheyen (Royal Belgian Institute of Natural Sciences, Brussels, Belgium) Are demersal, sand-dwelling cichlid species from Lake Malawi as poor dispersers as the rock-dwelling mbuna?

S25-II-7 L. Kuusipalo (University of Joensuu, Finland)

Speciation over basic niche borders among endemic cichlids of Lake Malawi

### Poster session III Symposium 15

**S15-III-1** <u>S. Pakkasmaa</u>, N. Peuhkuri, A. Laurila, H. Hirvonen and E. Ranta (University of Helsinki, Finland) Egg size in freshwater salmonids - what is the significance of the male?

**S15-III-2** <u>Marie-France Ostrowski</u>, Philippe Jarne and Patrice David (Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier Cedex 5, France)

Genetical and environmental bases of a sexual polymorphism: aphally in snails

- **S15-III-3** <u>B. Bost</u>, C. Dillmann, G. Lardier and D. de Vienne (INRA/UPS/INA PG, Gif-sur-Yvette, France) Evolutionary patterns in metabolic pathways with constraints on enzyme availability
- S15-III-4 B.J. Zwaan and L.Partridge (University College London, United kingdom) Genetic basis of body size variation in *Drosophila melanogaster*: evidence for epistasis in chromosome substitution lines
- **S15-III-5** Patrick J.A. Goymer, Eleni Bantinaki, Sophie G. Kahn and Paul B. Rainey (University of Oxford, UK) The role of WspR, a signal transduction protein, in a change in niche specialisation in experimental evolutionary populations of *Pseudomonas Fluorescens*
- **S15-III-6** Jon Slate, Josephine Pemberton and Peter Visscher (University of Edinburgh, UK) Power to detect QTL in a free-living polygynous population
- S15-III-7 Sarah Robinson (University College London, UK)

Chromosomal contribution to adult body size in latitudinal clines of Drosophila melanogaster

- S15-III-8 Koen Verhoeven and Arjen Biere (Netherlands Institute of Ecology, Heteren, The Netherlands) Genetic basis and fitness consequences of differences in relative growth rate in *Hordeum spontaneum*: a QTL approach
- **S15-III-9** P. Oliveira, E. Coelho, I. Reforço, M.C. Varela, C. Meierrose (University of Evora, Portugal) Biometric survey of cork oak families representative of the whole species natural range
- S15-III-10 L.W. Beukeboom (University of Leiden, Leiden, The Netherlands)
- Sex determination in the haplodiploid Hymenoptera
- S15-III-11 Barbara Taborsky (KLIVV, Wien, Austria)
  - Life history trade-offs in broodcare of mouthbrooding cichlids
- **S15-III-12** J.-M. Guillon and C. Raquin (Université Paris-Sud, France and Muséum National d'Histoire Naturelle, Paris, France)

Strict maternal inheritance of chloroplasts in the horsetail Equisetum variegatum (Schleich)

- **S15-III-13** L. Råberg, E. Svensson, M. Stjernman, C. Koch and D. Hasselquist (Lund University, Sweden) Parental effort and immune responsiveness in the blue tit
- **S15-III-14** Constantino Macías Garcia and <u>Cesar Gonzalez Zuarth</u> (Instituto de Ecología, México, D.F., México) Does sensory exploitation prevent female choice in fish?
- S15-III-15 M. Le Thierru d'Ennequin, Z.M.Wang, K.M.Devos and O.Panaud (Université Paris-Sud, France) Genetic bases of foxtail millet domestication in the context of comparative mapping in cereals

### Poster session III

Symposium 3

- S3-III-1 Samuel, R.; Ehrendorfer, F.; Chase, M. W. and Greger, H. (University of Vienna, Austria) Plastid DNA sequences and secondary metabolites help to reconstruct the phylogeny of Aurantioideae (Rutaceae)
- S3-III-2 Rasmus Nielsen (Harvard University, USA)

Estimation of population parameters and recombination rates from single nucleotide polymorphisms (SNPs)

S3-III-3 F. Depaulis, N. H. Barton (University of Edinburgh, UK)

Gene genealogies in continuous populations with limited dispersal

S3-III-4 M. B. Raymundez, J. Mathez, Nereida Xena-Enrech and J.-Y. Dubuisson (Universidad Central de Venezuela, Caracas, Venezuela)

Preliminary results in a molecular phylogeny of the tribe *Valerianeae* Höeck (Valerianaceae Batsch) **S3-III-5** <u>B.S.W. Chang</u> and D.L. Campbell (Harvard University, USA)

Testing hypotheses of long-branch attraction, base compositional bias and codon bias effects on phylogenetic reconstruction, using rhodopsin sequences in vertebrates

**S3-III-6** J. Belliure, G. Sorci, A. P. Møller and J. Clobert (Université Pierre et Marie Curie, Paris Cedex 05, France)

Ecological and evolutionary consequences of dispersal in birds: Ecological plasticity and population differentiation

S3-III-7 <u>T. Wiehe</u>, M. Burset, J. Abril, S. Gebauer-Jung and R. Guigó (Max Planck Institute for Chemical Ecology, Germany)

Comparative genomics - at the crossroads of evolutionary biology and genome sequence analysis

- S3-III-8 Barral, J., Hasmy, A., Jimenez, J., Marcano, A. and Naveira, H. (Universidade da Coruña, España) DNA sequences: spectral density and nonlilear modelling analysis
- S3-III-9 <u>A.Sanchis</u>, A.Latorre, J.M. Michelena, D. Quicke, R. Belshaw, U. Gardenfors (Universitat de València, Spain)

Elongation factor-1 introns as molecular markers for recovering phylogenetic relationships among putative sibling species in european populations of genus *Pauesia* (Hymenoptera: Braconidae: Aphidiinae)

- S3-III-10 L. Alarcón, F. Rodríguez-Trelles, and A. Fontdevila (Universitat Autònoma de Barcelona, Spain) Molecular Evolution and Phylogeny of the *Drosophila buzzatii* Complex of Species: a Best-fit Maximum-likelihood Approach
- **S3-III-11**. J. Castresana (European Molecular Biology Laboratory, Heidelberg, Germany) Automatic selection of conserved blocks from multiple alignments for their use in phylogenetic analysis

### Poster session III Symposium 9

S9-III-1 J.S. Christie, P. Oliver, <u>J.A. Castro</u>, M.M. Ramon, A. Picornell and A. Moya (Universitat de les Illes Balears, Palma de Mallorca, Spain)

Study of some fitness components in two mtDNA haplotypes of Drosophila subobscura

- S9-III-2 S.Quérouil, E. Verheyen and M. Colyn (Université de Rennes I, Paimpont, France) Comparative phylogeography of four small mammal taxa with different ecological requirements in the Central African tropical forest
- **S9-III-3** <u>Izabela Lesna</u> and Maurice W. Sabelis (University of Amsterdam, The Netherlands) Diet-dependent female choice for males with "good genes" in a soil predatory mite
- S9-III-4 Erik Verheyen, Jean-Marie Timmermans, Karin Breugelmans, and Walter Verheyen (Royal Belgian Institute of Natural Sciences Brussels, Belgium)
   A molecular phylogeny of the African Muridae and patterns of nucleotide change in mitochondrial cytochrome b and two ribosomal RNA genes
- S9-III-5 Shaw, P.W., Pérez-Losada, M., Sanjuan, A. and Guerra, A. (University of Hull, UK) Isolation by distance, oceanographic barriers to gene flow and secondary contact between Atlantic and Mediterranean populations: new evidence from microsatellite DNA studies of the cuttlefish Sepia officinalis
- **S9-III-6** R.Corthay, P. Taberlet and <u>F. Felber</u> (Univ. Joseph Fourier, Grenoble Cedex 9, France) Genetic variation in a clonal species, blueberry (*Vaccinium myrtillus*), inferred from AFLP markers
- **S9-III-7** <u>Teija Aho</u>, Jorma Piironen, Craig R. Primmer and Esa Ranta (Uppsala University, Sweden) Genetic variation and founder effects in hatchery managed Saimaa salmon
- S9-III-8 Jaap C. de Roode, Margaret J. Mackinnon, Brian H. K. Chan and Andrew F. Read (University of Edinburgh, UK)
- Dynamics of mixed-clone chronic infections of the rodent malaria parasite *Plasmodium chabaudi* **S9-III-9** Anders Ödeen (Uppsala University, Sweden)
  - Phylogeography of the Western Palearctic Yellow wagtails (Motacilla flava L)

**S9-III-10** <u>A. R. Weeks</u>, J. A. J. Breeuwer and A. A. Hoffmann. (University of Amsterdam, The Neatherlands) Genetic variation in three thelytokous mite species

- **S9-III-11** J. A. J. Breeuwer, F. Vala and <u>A. R. Weeks (University of Amsterdam</u>, The Neatherlands) Molecular phylogeny of *Wolbachia* symbionts within four genera of the Tetranychidae
- S9-III-12Alexander Bolshoy and Eviatar Nevo (University of Haifa, ISRAEL

Ecological influence on distribution of DNA curvature in bacterial genomes

S9-III-13 T. F. Næsje, J. A. Vuorinen and O. T. Sandlund (University of Joensuu, Finland) Genetic differentiation of sympatric ecotypes of whitefish *Coregonus lavaretus* in lake Femund, Norway S9-III-14 M. Markmann and D. Tautz (Universität München, Germany) Outlook to future biomonitoring: development of a new method for Meiobenthology, based on rRNA signatures

S9-III-15 C. Cousyn, J. K. Colbourne and L. De Meester (Katholieke Universiteit Leuven, Belgium) Resting egg-banks of the cladoceran *Daphnia magna*: reconstruction of micro-evolution using allozymes, microsatellites and an ecologically relevant trait

S9-III-16 Jakob Damgaard (University of Copenhagen, Denmark) Phylogeny, historical biogeography and ecological phylogenetics of water striders (Heteroptera; Gerridae) belonging to the genera *Limnoporus* Stål, *Aquarius* Schellenberg and *Gerris* Fabricius based on molecular and morphological data

- S9-III-17 <u>F. Delmotte</u>, N. Leterme and J. C. Simon (INRA, Le Rheu Cedex, France) Population structure of aphid *Rhopalosiphum padi* (Linné, 1758) reveals gene flow between sexual and asexual populations
- **S9-III-18** M. Dres, I. Emelianov, J. Mallet (University College London.UK) Mate choice in host races of the Larch Budmoth Zeiraphera diniana
- **S9-III-19** I. M. Emelianov, M. Dres, J. Mallet (University College London.UK) Gene exchange between differentiated genomes
- **S9-III-20** Henrik Glenner (University of Copenhagen, Denmark) The evolution of parasitic barnacles (Rhizocephala)
- **S9-III-21** <u>M. Hannonen</u> and L. Sundström (University of Helsinki, Finland) Reproductive skew among multiple queens in the ant *Formica fusca*
- **S9-III-22** S. Bensch, S. Åkesson and T. Andersson (Lund University, Sweden) Morphological and molecular variation across a migratory divide in Scandinavian willow warblers
- S9-III-23 Cesaroni D., <u>Villani F.</u>, Sansotta A, Cherubini M. and Sbordoni V. (Istituto per l'Agroselvicoltura, Porano, Italia)
  Analysis and membralizing (Mill.) in Turkey using constinue and membralizing data

Analysing a hybrid zone of *Castanea sativa* (Mill.) in Turkey using genetic and morphologic data on seeds

- S9-III-24 Paulo O.S, J. Pinheiro, R. Nichols and M.W. Bruford (Zoological Society of London, UK and Universidade de Lisboa, Portugal)
  - Comparative Phylogeography of two Iberian Lizards, Lacerta lepida and Lacerta schreiberi
- S9-III-25 F. Van Rossum, L. Triest and V. Krizsik (Vrije Universiteit Brussel, Belgium) Genetic diversity and structure in declining populations of *Primula vulgaris* in relation to population size and habitat fragmentation
- S9-III-26 Angus Davison, supervised by Prof. Bryan Clarke (University of Nottingham, UK)

Area effects and geographic variation in the land snail Cepaea nemoralis

- S9-III-27 A. J. Helbig, M. Salomon and S. Bensch (University of Greifswald, Kloster, Germany) Mitochondrial and nuclear geneflow across a leaf-warbler hybrid zone (Aves: *Phylloscopus collybita*, *P. brehmii*)
- S9-III-28 T. Ertan, P. Berthold (Forschungsstelle fuer Ornithologie der Max-Planck-Gesellschaft, Germany) Phylogeny of the genus Phoenicurus and the effect of hybridization for the genetic structure of populations in East Turkey and Central Asia
- **S9-III-29** Palo, Jukka and Väinölä, Risto (University of Helsinki, Finland) Postglacial loss of genetic variation in ringed seals of the Baltic Sea and Lake Saimaa
- S9-III-30 S. E. Mitchell and W. Lampert (Max Planck Institute for Limnology, Plön, Germany) Population genetics and temperature reaction norms in a geographically widespread zooplankter, Daphnia magna
- **S9-III-31** Marcin Czarnoleski (Jagiellonian University, Krakow, Poland)

Allometries of zebra mussels' life history traits: testing optimality models

S9-III-32 C. Liautard and L. Keller (Université de Lausanne, Switzerland)

Restricted female dispersal within and between populations of the ant Formica exsecta.

S9-III-33 Anthony B. Wilson, Ingrid Ahnesjö, Amanda Vincent, and Axel Meyer

(University of Konstanz, Germany)

Detailed mtDNA phylogeny of seahorses and their relatives: Inferences on the evolution of male brooding structures

### S9-III-34 Henrik Stotz, Jürgen Kroymann, Mark Tobler, Heiko Vogel, Tom Mitchell-Olds.

(Max-Planck-Institute of Chemical Ecology, Jena, Germany)

Evolutionary genomics of insect resistance in Arabidopsis

- **S9-III-35** <u>Norbert Pongratz</u>, Martin Storhas, Salvador Carranza and Nico K. Michiels (Max-Planck-Institut fuer Verhaltensphysiologie, Germany) Intraspecific phylogeny and distribution of sexual and parthenogenetic planarians (*Schmidtea polychroa*)
- S9-III-36 <u>Harry M.</u>, Solignac M., Lachaise D. (Université Paris XII, Créteil, France) Molecular evidence for parallele evolution of adaptive syndromes in fig-breeding *Lissocephala* (Drosophilidae)
- **S9-III-37** <u>C. Poteaux</u>, S. Bidaux, L. Désiré and C. Baudoin (Université Paris-Nord, Villetaneuse, France) Evidence for a sexual monogamy in the mound-building mouse, *Mus spicilegus*
- S9-III-38 M.L. Palop, C. Palacios and F. González-Candelas (Universitat de València, Spain) Identification and application of polymorphic microsatellites loci in the genus *Limonium* (Plumbaginaceae)
- **S9-III-39** Jodie Painter, Ilpo Hanksi, Vesa Selonen & Ilkka Hanski University of Helsinki, Finland) Microsatellites reveal paternity in the flying squirrel *Pteromys volans*
- **S9-III-40** <u>Göran Spong</u> (Uppsala Univ., Sweden) Genetic Structure related to social behavior in *Panthera leo*
- **S9-III-41** Raquel Ortells, Terry W. Snell, Africa Gómez and Manuel Serra (Universitat de València, Spain) Genetic differentiation in resting egg banks of a rotifer species complex in Spain
- **S9-III-42** Keith Gardner, Alex Buerkle, Jeannette Whitton and Loren H. Rieseberg (Indiana University, USA) Inferring epistatic selection in natural hybrid zones
- S9-III-43 Peter O'Hanlon, David Briese and Rod Peakall (The Australian National University, Canberra, Australia)

Historical and contemporary colonisation of novel environments by hybrid Onopordum thistles

- S9-III-44 L.E.L. Raijmann and S.B.J. Menken (University of Amsterdam, The Netherlands) Temporal variation in the genetic structure of host-associated populations of the small ermine moth *Yponomeuta padellus* (Lepidoptera, Yponomeutidae)
- **S9-III-45** <u>F. Spirito</u> (La Sapienza University, Roma, Italy) Dominance theory of Haldane's rule and speciation
- S9-III-46 I. Till-Boutraud, M. Gaudeul, P. Taberlet (Université Joseph Fourier, Grenoble, France) Reproductive system and population structure of an endangered alpine plant (*Eryngium alpinum L*.): assessment of AFLP markers
- S9-III-47 I. Lesna and M.W. Sabelis (University of Amsterdam, The Netherlands) Maintenance of a genetic polymorphism by heterozygote advantage: studies on prey preference in soil predatory mites
- **S9-III-48** R. Johnson, R. H. Crozier (LA trobe University, Melbourne, Australia) Is silk weaving in ants a hygienic behaviour?
- **S9-III-49** <u>W. Goodall-Copestake</u>, N.J. Ouborg, J.M. van Groenendael (University of Nijmegen, Nijmegen, Netherlands)

Waterlilies, microsatellites and dispersal

- S9-III-50 <u>P. Oliveira</u>, C. Branco, I. Reforço, F. Rodrigues, M.C. Varela, C. Meierrose (University of Evora, Evora, Portugal)
  - Allozymes for the discrimination between two oak species and their hybrids
- S9-III-51 G. Procaccini, P. Famà, M. V. Ruggiero and F. Maltagliati (Stazione Zoologica 'A. Dohrn', Napoli, Italy)

Genetic variability in native and introduced meadows of the seagrass *Halophila stipulacea* from the Red Sea and Western Mediterranean

- S9-III-52 R. Eppe, <u>H. Persat</u>, P. Berrebi (Université Lyon I, Villeurbanne, France)
   High genetic differenciation among the south-western populations of the European sculpin, *Cottus gobio*, lineage (Pisces, Cottidae)
- S9-III-53 G. Echchgadda, L. Triest (Vrije Universiteit Brussel, Brussels)

The effects of habitat fragmentation on the genetic structure of Primula elatior populations

- S9-III-54 C. Rodríguez, R. Piccinali, E. Levy, <u>E. Hasson</u> (Universidad de Buenos Aires, Argentina) Contrasting population structures in *Drosophila buzzatii* using inversion polymorphism and allozyme loci as genetic markers
- **S9-III-55** <u>W.J. Etges</u>, L.L. Jackson (University of Arkansas, Fayetteville, USA) Epicuticular hydrocarbon variation among *Drosohila mojavensis* cluster species

**S9-III-56** M. M. Coelho, N. Mesquita, G. Carvalho, P. W. Shaw and E. Crespo (Faculdade de Ciências de Lisboa, Portugal)

Genetic Contribution for the Conservation of *Chondrostoma lusitanicum* based on cytochrome *b* and ND 5/6 analysis

S9-III-57 M. M. Coelho, M. J. Alves, H. Coelho and M. J. Collares-Pereira (Faculdade de Ciências de Lisboa, Portugal)

Genetic consequences of population reduction and subdivision of the Iberian fish *Anaecypris hispanica*, as determined by analysis of mitochondrial cyt *b* gene and control region

### Poster session III Symposium 10

- **S10-III-1** <u>Natalia Ruiz</u>, David Ward and David Saltz (Blaustein Institute- Sede Boquer, Isreael) Signal selection in a desert Lily
- **S10-III-2** J. A. J. Breeuwer, F. Vala and A. R. Weeks (University of Amsterdam, The Netherlands) Molecular phylogeny of *Wolbachia* symbionts within four genera of the Tetranychidae
- **S10-III-3** Pim van Putten; Arjen Biere (Netherlands Institute of Ecology, The Netherlands) Host race formation in the anther smut fungus *Microbotryum violaceum*
- S10-III-4 Niklas Wahlberg (University of Helsinki, Finland)

The evolution of host plant use in melitaeine butterflies: a phylogenetic analysis

- **S10-III-5** D. Martínez-Torres, R. C. H. J. Van Ham, A. Latorre and A. Moya (Universitat de València, Spain) Parallel evolution of aphids and their endosymbionts: a molecular approach to the phylogeny of the *Aphidoidea*
- S10-III-6 Pappers, S.M. and Ouborg, N.J. (University of Nijmegen, The Netherlands) Gene flow and host race formation in the waterlily leaf beetle Galerucella nymphaeae (Chrysomelidae: Coleoptera)
- **S10-III-7** <u>M.K. Sherstha</u>, A. Golan-Goldhirsh, d. Ward (Ben-Gurion University of Negev, Israel) Genetic diversity in isolated Negev desert populations of *Acacia raddiana*
- **S10-III-8** <u>K.D. McCoy</u>, T. Boulinier, S. Schjorring, Y. Michalakis (Université Paris VI, Paris, France) Investigating the local adaptation of ticks (*Ixodes uriae*) in a multi-host seabird colony
- S10-III-9 M.L. Thao, L. Baumann, P. Baumann (University of California, Davis CA, USA) Evolutionary relationships of psyllid endosymbionts based on 16S and 23S rDNA analysis

### Poster session III Symposium 26

- **S26-III-1** <u>A. Laurila</u>, K. Lahti, K. Enberg, S. Vilhunen and J. Piironen (Uppsala University, Sweden) Behavioural variation among migration forms and populations in the brown trout
- S26-III-2 G. D'Onofrio, E. Busico, M. Montresor, G. Procaccini and <u>D. Marino</u> (Stazione Zoologica 'A. Dohrn', Napoli, Italy)

Phylogeny of dinoflagellates by the rRNA 5.8 gene sequencies

- **S26-III-3** E. Gysels, V. Leentjes and F.A.M. Volckaert (Katholieke Universiteit Leuven, Belgium) Differential selection in marine versus estuarine populations of the sand goby, *Pomatoschistus minutus*
- S26-III-4 C. de Vargas, J. Pawlowski, R. Norris, S. Renaud and L. Zaninetti (Université de Genève, Switzerland)

Genome clues to fossil identity: molecular biodiversity and ecology in planktonic foraminifera

- **S26-III-5** <u>F. Santini</u>, L. Galleni and P. Cerrai (University of Toronto, and Royal Ontario Museum, Canada) Geophysiological modelling of the evolution of marine ecosystems
- **S26-III-6** <u>F. Santini</u>, R. Winterbottom and J. Tyler (University of Toronto, and Royal Ontario Museum, Canada)

Phylogeny and Biogeography of the Family Triacanthodidae (Tetraodontiformes, Pisces)

- S26-III-7 M.J. López-Piñón, R. Freire, A. Insua and J. Méndez (Universidade da Coruña, Spain) Sequence variation of 5S rDNA among several bivalve molluscan species
- S26-III-8 C. S. Oke, R. H. Crozier and R. D. Ward (La Trobe University Bundoora Victoria, Australia) Microsatellite analysis of stock structure in the commercially important teleost Orange Roughy (*Hoplostethus atlanticus*)

S26-III-9 L. Zane, L. Bargelloni, L. Maccatrozzo, S. Marcato, V. Varotto and T. Patarnello (Università degli Studi di Padova, Italy) Molecular zoogeography of Antarctic marine organisms: from species phylogenies to intra-specific patterns of genetic variation

- S26-III-10 S. Roques, Jean-Marie Sévigny and Louis Bernatchez (Université Laval, Québec, Canada) Evidence for introgressive hybridization at microsatellite loci between two marine fishes (Sebastes sp.) from the North Atlantic
- S26-III-11 S. Renaud, C. de Vargas, H. Hilbrechtand J. Pawlowski (Geological Institute, Zurich, Switzerland) Morphological, genetic and ecological differentiation of the planktonic foraminifer Globorotalia truncatulinoides in the South Atlantic
- S26-III-12 S. Launey and D. Hedgecock (University of California, Davis CA, USA) High genetic load explains segregation distortion and marker-associated heterosis in bivalve mollusks
- S26-III-13 M.Holmann, W.Piller, J.Fahrni and J.Pawlowski (Universitaet Graz, Austria) Molecular evolution of the soritidae, a group of large foraminifera
- S26-III-14 Jan Drent and Pieternella Luttikhuizen (Netherlands Institute for Sea Research, Den Burg, The Netherlands)

Population structuring in a free spawning marine bivalve Macoma balthica

S26-III-15 A. Magoulas, S. Marcato, R. Castilho, C. Carvalho, S. Caetano and T. Patarnello (Institute of Marine Biology of Crete, Iraklio, Greece) Strong population structuring in marine species with high dispersal capabilities: the case of European anchovy (Engraulis encrasicolus)

- S26-III-16 R. Hanel and C. Sturmbauer (University of Innsbruck, Austria) Mitochondrial Phylogeny Analysis of Eastern Atlantic and Mediterranean Seabream Species (Sparidae, Percoidei)
- S26-III-17 J. Turgeon and L. Bernatchez (Université Laval, Québec, Canada) North American ciscoes (Pisces: Salmonidae): a long history of introgressive hybridization and flawed taxonomy
- S26-III-18 K.T.C.A. Peijnenburg (University of Amsterdam, The Netherlands) Genetic variation in chaetognaths: first results on the neritic Sagitta setosa and the oceanic S. lyra
- S26-III-19 J.L. Olsen, W.T. Stam (University of Groningen, Aa Haren, The Netherlands) Genetic neighborhood size in the seaweed Ascophyllum nodosum (Fucales)
- S26-III-20 R.Sponer, P.V.Mladenov and M.S.Roy (Otago University, Dunedin, New Zealand) Phylogeography and cryptic species in a cosmopolitan echinoderm

#### Poster session III Symposium 5

- S5-III-1 S. Bovero, P. Michailova, N. Petrova, L. Ramella and G. Sella (University of Turin, Italy) Spontaneous chromosomal alterations in two populations of Chironomus riparius in the surroundings of Turin
- S5-III-2 Esther K. Davies, Andrew D. Peters and Peter D. Keightley (Edinburgh University, UK) Impact of new deleterious mutations on life history traits in C. elegans
- S5-III-3 L.W. Beukeboom, F.H.D. van Batenburg (Leiden University, The Netherlands) The effect of paternal leakage on the rate of Muller's Ratchet
- S5-III-4 Scott D. Pletcher, David Houle, and James W. Curtsinger (Max-Planck Institut, Germany) New estimates of the age-specific properties of spontaneous mutations that affect mortality rates in Drosophila melanogaster
- S5-III-5 M. C. Whitlock and D. Bourguet (Station de Recherches de Lutte Biologique, Guyancourt, France) Factors affecting the genetic load in Drosophila: Synergistic epistasis and correlations among fitness components

### Poster session III Symposium 16

S16-III-1 Helene Andersson (Lund University, Sweden)

- Female and hermaphrodite flowers on a chimeric gynomonoecious *Silene vulgaris* plant produce offspring with different genders a case of heteroplasmic sex-determination?
- **S16-III-2** <u>Markus Riegler</u> and Christian Stauffer (Universität für Bodenkultur, Vienna, Austria) Distribution of *Wolbachia* strains in populations of the cherry fruit fly *Rhagoletis cerasi*

#### Poster session III Symposium 22

**S22-III-1** <u>Toomas Tammaru</u> (Estonian Agricultural University, Estonia) Constraints on determination of adult size in a moth

- **S22-III-2** Sandro Cavicchi, Daniela Guerra, Maria Cristina Pezzoli and Flavio Garoia (Università di Bologna, Italy) Temperature-related divergence in experimental populations of *Drosophila melanogaster*. IV. Subunits of selection and developmental constraints in the wing
- S22-III-3 Johannes Streicher, Markus A. Donat, Wolfgang J. Weninger, Bernhard Strauss, and <u>Gerd B. Müller</u> (University of Vienna, Austria)
   3D-visualization of morphological structures and gene expression patterns in development
- **S22-III-4** Johannes Streicher, Bernhard Strauss, and <u>Gerd B. Müller</u> (University of Vienna, Austria)
- Homeotic duplication of the pelvic body segment in anuran tadpoles **S22-III-5** <u>T. Nyman</u>, A. Widmer and H. Roininen (Univ. of Joensuu, Finland)
- Evolution of gall morphology and host plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae)
- S22-III-6 M.T. El-Ibrashy, F.M. Soliman, H.S. Metwally (National Research Centre, Dokki, Cairo, Egypt) Induction of postimaginal moults in female actinedid mites (Acari) by juvenoid treatment of immatures: evidence for endocrine evolution by selection stress
- S22-III-7 D.J. Miller (Naturshistorisches Museum Basel, Switzerland) The role of predation in driving evolutionary trends: tests using neogene muricid gastropods from tropical America

### Poster session III Symposium 21

S21-III-1 Pal Johnsen, Gunnar Skov Simonsen, Ørjan Olsvik and Arnfinn Sundsfjord (University Hospital of Tromsø, Norway)

In vitro studies of competitive fitness between vancomycin resistant and sensitive *Enterococcus faecium* **S21-III-2** J. Javier Díaz-Mejía, Alejandro Carbajal-Saucedo, Francisco A. Ortiz-Navarro and

Carlos\_F. Amábile-Cuevas (Fundación LUSARA para la Investigación Científica, Mexico)

Enterococcus as an antibiotic resistance gene shuffler and mobilizer

S21-III-3 Mary Reynolds (Presented by <u>B.R.Levin</u>) (Emory University, Atlanta, USA)
 Experimental Evolution of 'Transcription-Impaired' and 'Transcription-Competent' Rifampin-Resistant
 *E. coli:* Functional Compensation? Enhanced Resistance? Or Reversion? What are the Outcomes of Secondary Adaptation?

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# ABSTRACTS

#### Senescence in Bacteria

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Senescence is a deterioration in state late in life that is manifested as a decline in reproductive value with age. Senescence can only evolve in organisms in which parent individuals produce offspring that differ in at least some aspects from the parents, as opposed to just splitting in two. For this reason it has been suggested that senescence should be confined to organisms with a distinction between soma and germ line (Williams, 1957) and that all prokaryotes should be free of aging (Rose, 1991:84). However, the critical requirement for the evolution of senescence - a distinction between a parent and an offspring individual - could be met in prokaryotes if cell division is asymmetrical. Such a mode of reproduction is found in stalked bacteria, which divide asymmetrically to produce motile swarmer progeny, which then differentiate into a stalked cell before initiating division. The aim of this project is to test whether the stalked bacterium Caulobacter crescentus is senescent. To approach this question, we developed a system to observe individual Caulobacter cells throughout their life. This system made it possible to record the life history of individual cells through more than 100 cell divisions. We extend these experiments to get reliable measurements of agespecific division and mortality rates. If the reproductive value of Caulobacter can be shown to decrease with age, this would be the first evidence for senescence in prokaryotes. This would clarify the requirements for the evolution of senescence and would establish a promising procaryotic model system to study the evolution of senescence. If, however, the reproductive value does not decrease with age, this would demonstrate potential immortality for bacteria, a feature that is traditionally inferred from the fact that cell division in most bacteria is symmetrical but that has never been shown directly.

# Adding the time dimension to population genetics: the origins and recent history of New Zealand snapper, *Pagrus auratus* (Sparidae)

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Population genetic studies often employ a single genetic marker type (e.g. allozymes) and apply it to samples that are static in time. While such studies have revealed much important information about the population biology of many species they can be affected by biases in the marker employed and in the time of collection of samples. Thus a preferred approach to understanding recent and more ancient population history would utilise temporal samples and several genetic markers. The assessment of the genetic impact of fisheries on the target species is an important example of the application of such a study where, in this case, the use of temporal information would allow more precise predictions of future trends and therefore better fishery management. We have extracted DNA from scales collected over the last fifty years for the sparid Pagrus auratus which lives off the New Zealand coast. Population samples from three regions, which define separately managed stocks, were examined for four time points to compare the affects of different levels of fishing on populations with different characteristics: Northeast with high abundance and high fishing pressure for more than a century, West-coast with high abundance but fishing only becoming significant in the 1970's and the East-coast with low abundance and negligible fishing. Migration, population structure and changes in diversity were calculated in temporal samples using 8 microsatellite markers. DNA sequences of a portion of the mitochondrial control region showed three distinct lineage groups in New Zealand populations. From the diversity within each lineage group and from comparisons with Australian sequences, it appears that each group represents separate migrations to New Zealand in the distant past with different subsequent dispersal and expansion. The SSCP method allowed detection of lineage with known sequence in scale population samples and therefore a temporal phylogeographic investigation of recent population history was possible.

### The global phylogeny of metazoans: inference from various types of genomic data

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Metazoan phylogeny has recently undergone a number of major revisions due to careful molecular analyses based essentially on the use of 18S ribosomal RNA sequences. Three salient points can be outlined. 1/ The "Articulata", grouping annelids and arthropods, has exploded, annelids, instead, becoming grouped with a set of other phyla displaying either a lophophore or a trocophore larvae (the Lophotrochozoans, Halanych et al, 1995). 2/ Brachiopods and other lophophorates, long thought to de deuterostomes, solidly branch within lophotrochozoans. 3/ Most strikingly, platyhelmimthes and nematodes, long thought to occupy basal positions in the metazoan tree as acoelomates and pseudocoelomates respectively, have moved much higher inthe tree, within protostomes, platyhelminths grouping with lophotrochozoans and nematodes grouping with arthropods, together forming the Ecdysozoa (Aguinaldo et al, 1997). The bilaterian tree thus simplified to three branches (a deuterostome branch as a sister group to protostomes comprising two branches) with cnidarians, ctenophores and sponges as outgroups, in an unspecified order of emergence.

Since this tree is based on a single molecule, we tried to test its validity using other types of genomic data, specially the number and type of Hox cluster genes. Analysis of amino acid signatures within and next to the homeodomain of central class genes had previously allowed to reveal the strong affinities of flatworms with lophotrochozoans (reviewed in Balavoine, 1998). In collaboration with the laboratories of M. Akam and S. Carroll, we extended this approach to a number of other key phyla including brachiopods, priapulids, annelids and molluscs (De Rosa, Grenier et al, Nature, 24 june 99). Central genes of brachiopods very clearly confirm their lophotrochozoan affinities while those of priapulids puts them towards ecdysozoans. In addition, we unexpectedly discovered two posterior (AbdB) genes in several of these phyla. Those of the priapulid, together with two AbdB genes discovered through complete genome sequencing in C. elegans, again showed very clear proximity to those of arthropods. Hox genes thus confirm the overall shape of the new metazoan tree and the rise of nematodes within ecdysozoa. This study also allows to infer that the last common ancestor to the Bilateria already had a quite elaborate Hox cluster made up of 8 to 10 genes, providing important implications for understanding early animal diversification.

### Punctuated gradualism in Plio-Pleistocene voles from Europe

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Among rodents, the family of the arvicolids has provided the most clear cases of phyletic gradualism among mammals (Chaline and Laurin, 1986; Agustí et al., 1993). The sudden origin of this holarctic family probably took place at the end of the Miocene (the oldest record of the family can be traced to *Microtodon*, from the latest Miocene or earliest Pliocene of Mongolia). They became the dominant rodent family during the middle Pliocene, 3 Ma ago, after the onset of the glacial-interglacial dynamics in the Northern Hemisphere. The members of this family bear very characteristic cheeck teeth, with hypsodont, prismatic molars, showing a pattern of re-entrant folds. The evolution of the several arvicolids lineages in Eurasia is characterized by some common trends, such as:

- a) Increasing hypsodonty.
- b) Increasing size.
- c) Development of extra-folds in the first lower molars.

These common trends can be interpreted in terms of heterochronic evolution in relation to the climate and environmental dynamics of the Northern Hemisphere during the Pliocene and the early Pleistocene.

#### Genetic variation and founder effects in hatchery managed Saimaa salmon

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Genetic variation is the basic resource of any successful commercial or rehabilitation culture programme. Rehabilitation aquaculture should maintain the genetic variation of the population to maximize the probability of success when the population is introduced into the wild. The landlocked Atlantic salmon (*Salmo salar m. sebago* Girard) population in lake Saimaa (southeastern Finland) is entirely dependent on stocking activities. The genetic variation of year classes (from 1986 onwards) of hatchery reared and wild-caught landlocked salmon was surveyed using microsatellite markers. Differences in allele frequencies and heterozygosities between hatchery brood stocks could be related to known number of founders of each year class. Despite of small population size, the genetic variation (number of alleles, heterozygosity) of landlocked Saimaa salmon has not reduced during the last ten years of hatchery rearing. However, genetic variation of Saimaa salmon is much lower compared to anadromous populations of Atlantic salmon in Finland. Relationship between individual genetic variation (heterozygosity and D-squared value) and reproductive parameters in landlocked salmon were also analysed. Our results show that carefully planned aquacultural practises can be successful in maintaining genetic variation of endangered species.

Does asymmetry on secondary sexual trait fluctuate with individual quality in the wolf spider *Hygrolycosa rubrofasciata*?

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Developmental stability in terms of fluctuating asymmetry (FA) has, sometimes indiscriminately, been associated with an individual's control over ontogeny during genetic and/or environmental stress. Moreover, those individuals that exhibit low or even zero asymmetry in traits allegedly relevant to developmental stability have been argued to have advantage in sexual selection over more asymmetric individuals. Since an increasing amount of rigorous studies have been published, these indexing capabilities of FA have become controversial. By using bilateral pedipalps as the target trait (n=804), and drumming activity and mobility as fitness-related covariates, we tested whether fluctuating asymmetry (FA) predicts male quality in the wolf spider Hygrolycosa rubrofasciata so that males with increased symmetry of secondary sexual trait would have higher performance in sexual selection. The between-sides variation due to fluctuating asymmetry was significantly greater than the variation due to measurement error allowing us to make valid conclusions. Our data exhibited an extremely leptokurtic distribution of signed fluctuating asymmetry, which may signal the presence of a significant genetic component originated from the pooled sample of 36 populations. We found no relationship between pedipalp asymmetry and either pedipalp lenght or drumming activity. The former result firmly establishes that bilateral pedipalps are not a sexually-selected trait in this species; the latter result illustrates the likely possibility that there is not always an inherited connection between Zahavian and secondary sexual trait. Despite these results, actively moving males were more likely to have symmetric pedipalps (Spearman's r=-0.087, p=0.016). This paper therefore provides correlational evidence that asymmetry in a trait that displays the population properties of fluctuating asymmetry has only a minor role in explaining the overall phenotypic variation in individual quality.

# Determining the contribution of adaptive molecular evolution from within and between species DNA variation in Drosophila

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Although the contribution of natural selection at the molecular level has been debated for over 30 years, the relevant data and appropriate statistical methods to address this issue have only begun to emerge. A method to identify the role of natural selection in molecular evolution by comparing within and between species DNA sequence variation will be presented. Computer simulations show that methods that compare both the frequency distributions of polymorphic mutations and the numbers of fixed differences between species are powerful for detecting even very weak selection. Examinination of DNA variation data from eight genes in *Drosophila simulans* suggest that "silent" sites evolve under a balance between weak selection and genetic drift. Simulated data also show that sequence comparisons are a powerful method to detect adaptive protein evolution, even when selection is weak or affects a small fraction of nucleotide sites. In the Drosophila data examined, positive selection appears to have been a predominant force in protein evolution.

# Molecular Evolution and Phylogeny of the Drosophila buzzatii Complex of Species: a Best-fit Maximum-likelihood Approach.

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The Drosophila buzzatii complex is one of several complexes that comprise the D. mulleri subgroup of the D. repleta group. The species of this complex have been ascribed into three clusters: stalkeri, martensis, and buzzatii. Previous attempts at reconstructing the phylogenetic relationships in the buzzatii complex include chromosomal inversions, and mitocondrial DNA markers. These studies failed to elucidate the phylogenetic relationships between clusters, and left the phylogenetic relationships within clusters partially unsolved. We have analyzed 2085 coding nucleotides from the xanthine dehydrogenase (Xdh) gene in the 10 available species in the D. buzzatii complex, and D. mulleri and D. hydei. We follow a statistical model-fitting approach within the maximum likelihood framework of phylogenetic inference. We first model the molecular evolution of the region relevant to phylogenetic inference using a tree topology that is approximately accurate. Then we use the most satisfactory description so attained in order to reconstruct the evolutionary relationships in the *buzzatii* species complex. We found that a minimally realistic description of the substitution process along the Xdh region should allow two transition and four transversion rate parameters, and different substitution rates for codon positions. Using this description we obtain a strongly supported fully resolved tree which is congruent with the already known relationships. Accordingly, the stalkeri cluster is the oldest lineage, and paraphyletic, with D. richardsoni derived before D. stalkeri. Next split the martensis and buzzatii clusters which are monophyletic sister clades. Within the martensis cluster, D. martensis is the earliest derived, followed by D. uniseta, and D. starmeri and D. venezolana. Within the buzzatii cluster D. buzzatii derived first, followed by D. koepferae, and D. borborema and D. serido. We have also analyzed published data from three additional mitochondrial gene regions (cytochrome oxidases I, II, and III). In our analysis, these relatively short DNA sequences fail to discriminate statistically among alternative phylogenies. When the data for these three gene regions are combined with the Xdh sequences, the phylogenetic signal emerging from Xdh becomes reinforced.
# Inherited dispersal avoidance in small and isolated populations of the waterstrider Aquarius najas

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Theoretically evolution of dispersal has been under intensive attention, but not much is known about genetic variation in dispersal between local populations. Aquarius najas is a wingless waterstrider in Finland and it is specialized to streams. Lack of wings sets limits to dispersal and the species is unable to survive on standing water, and thus any lakes within watershed represent dispersal barriers. We raised offspring from 10 populations of A. najas to adulthood in similar laboratory conditions, and released marked individuals in a natural stream to estimate their inherent dispersal tendency in similar conditions. The characteristics in the watershed of population origin affected strongly the inherent movement strategies. The total length of the natural living habitat increased the distances of movement, while the length of dispersal barriers (= summed distance of lake surface needed to connect all the river and brook sections) had an equally strong negative effect on dispersal rate. Thus, there is adaptive reduction in the instinct to disperse within populations that occupy only small and isolated fragments of suitable stream habitat. This result suggests that the costs of dispersal over the hostile surrounding habitats can be very high, in this case leading to genetic differences between populations within a relatively small geographical area. The result is highly relevant in attempts to conserve endangered animal populations in man-made fragmented habitats. If the species in question is not adapted to fragmentation, there might not be sufficient time for the evolution to reduce dispersal to the surrounding suboptimal habitats, thus increasing extinction risk within any small habitat fragments.

# Oreopithecus, bonobos, heterochrony, and the paradox of form

#### D. M. Alba, S. Moyà-Solà and M. Köhler

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Paleontology is an eminently morphological discipline, which has led to a blind confidence that morphology is enough to retrieve past adaptations and targets of selection. However, there has been no attempt to test whether our current confidence on shape is based on solid scientific foundations. In fact, as a result of our 'morphocentric' way of thinking, it has been disregarded the fact that morphology, behavior and life-history form an 'adaptive triad' and that, as a result of evolutionary constraints, these phenotypic aspects are intimately linked. Here, we contend that shape can be very misleading, since strikingly similar morphological patterns can evolve as a result of very different adaptive reasons (the 'paradox of form'). This is particularly true when selection acts upon behavioral and/or life-historical traits, but morphological changes are nonetheless dragged as non-adaptive by-products (spandrels). We exemplify this by comparing the bonobo (Pan paniscus) with Oreopithecus bambolii, an extinct insular great ape from the Late Miocene. Both taxa display a paedomorphic (probably neotenic) cranial morphology, so that the resultant overall pattern is strikingly similar (strong reduction of prognathism, microdontia, reduced sexual dimorphism...). A careful investigation shows that morphology was only directly selected in Oreopithecus as a result of the biomechanical demands of bipedal standing and locomotion, whereas in the bonobo the only likely target of selection seems to be the acquisition of a paedomorphic behavior in relation to changes in social structure. This would mean that the cranial paedomorphic characters of the bonobo, and some postcranial characters as well, should be considered non-adaptive by-products. Therefore, unlike the case of Oreopithecus, in the bonobo shape would have never been a major evolutionary concern, in spite of the fact that the resulting morphological pattern is paradoxically very similar in both cases.

# What is the nature of the history of life? Contingency vs. predictability in evolution

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The pervasive occurrence of homoplasy (convergence and parallelism) suggests that evolution is more predictable than suggested by a contingency-based view of the history of life. The thought experiment of 'rerunning life's tape' can be substituted by the investigation of 'natural experiments' like evolution on small islands isolated from the mainland, in order to evaluate to what extent evolution is repeatable and predictable. These are ideal 'natural laboratories' given their ecological simplicity and the recurrence of their ecological conditions (scarcity of resources and lack of terrestrial predators). We draw several examples from Mediterranean fossil islands to show that convergence is pervasive, for example in the locomotor apparatus. These examples show that evolution can be highly predictable at least under some ecological circumstances, but a major role for contingency could still be advocated for continental ecosystems, which seem to be much more unpredictable. Although some degree of unpredictability due to chance is inherent to evolution, evolutionary dynamics is essentially deterministic in both insular and continental ecosystems. Therefore, our greater inability to predict continental evolution could be due to current ignorance of the causal relationships operating on the mainland rather than hazardous factors. However, the alternative view that continental evolution shows a chaotic dynamics (which can be found even in simple deterministic physical systems), so that small perturbations could be dramatically amplified, cannot be discarded. As a hypothesis, we propose the existence of a threshold of complexity, not attained by insular ecosystems, which would cause evolution on the mainland to be chaotic and therefore inherently unpredictable, in spite of the underlying deterministic dynamics.

#### Amphioxus ADH class III: gene duplication and phylogenetic insights

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The comparative analysis of gene families in simple animals helps to understand the evolutionary strategies for the acquisition of new functions and to identify the ancestor forms of genes and proteins.

To that aim we have studied the medium chain dehydrogenase/reductase family (MDRs) in amphioxus, as it is the closest living representative to the vertebrates. It is known that this family is made of many different enzyme forms related through gene duplications. Among them, a well known MDR member is the alcohol dehydrogenase class III (ADH III), a ubiquitous enzyme with a housekeeping function.

The ADH-III complete coding region of the amphioxus (*Branchiostoma lanceolatum* and *Branchiostoma floridae*) has been characterised and the exon-intron gene structure has been established. Estimation of gene copy number has revealed that there is a single ADH-III gene in the amphioxus genome. However, intron sequences contain different tandem repeats, which show great variation in copy number among different individuals.

Alignment of the deduced protein sequences has shown 75% and 76% identity with the human and *Drosophila* enzyme, respectively. The evolutionary rate has been assessed and used to date the duplication event (around 500 million years ago) which gave rise to other vertebrates classes. The estimated split time suggests that the duplication occurred after the divergence of cephalochordates and vertebrates.

Finally, using the ADH-III as a molecular clock, the approximate divergence time between metazoan groups and the split of the major kingdoms has also been evaluated.

#### Senescence and dynamics of the mitochondrial genome in Podospora anserina

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*Podospora anserina* is a filamentous fungus with a limited lifespan. It expresses a degenerative syndrome called senescence, always associated with the accumulation of extrachromosomal circular molecules, called senDNAs. Several groups of senDNAs (a, b, g, etc.), which originate from separate regions of the mitochondrial chromosome, can be recovered from independently growing senescent cultures.

Since a long time, senescence in *Podospora anserina* was correlated with the presence of senDNAs. This correlation could be causal if senDNAs amplified to the detriment of the mitochondrial chromosome as in yeast petite mutant. This study shows clearly that it is not so simple. We show by quantitative studies of mt molecules that there is a decrease of the chromosomal mt regions corrresponding to amplified senDNAs. The correlation is then displaced and a causal relation between senescence and disapearance of some mt regions seems realistic. This was further supported by a large decrease of some mitochondrial transcrits in senescent culture.

A microevolutionary study in canaries (Genus *Serinus*) shows that the mtDNA molecular clock is different for different genera.

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Mitochondrial cytochrome b (mit cyt b) DNA from 20 out of 37 extant canaries (genus *Serinus*) has been sequenced from living specimens photographed around the world. Phylogenetic analysis has consistently resulted in the same groupings of birds, which have generally been related to geographical proximity. The fossil registry of chicken and pheasant and its divergence time have been used to calibrate the molecular clock; mit cyt *b* DNA dendrograms suggest that the *Serinus* birds lineage appeared in the Miocene (9 MYA), a time when the Mediterranean Sea was closing its western and eastern oceanic connections. Pleistocene glaciations (starting 2 MYA) may have only been important in the subspeciation and isolation of birds in the Northern and Southern hemispheres around the world, and not only in North America, where it has already been described. The European-isolated *Serinus citrinella* (Citril finch) is not a canary, but rather a true goldfinch. Only about 4% average nucleotide divergence is found among the different *Serinus* species; this suggests a remarkably rapid radiation when compared to other passerine (songbird) genera radiations. In addition, reproductive barriers are observed between closely related species but not between other more distant ones. Finally, a tentative classification for the genus *Serinus* species is put forward.

# Phylogeny and rapid Northern and Southern Hemisphere speciation of goldfinches during the Miocene and Pliocene Epochs.

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Mitochondrial cytochrome b (cyt b) from 25 out of 31 extant goldfinches, siskins, greenfinches and redpolls (genus *Carduelis*) has been sequenced from living samples taken around the world, specimens have also been photographed. Phylogenetic analysis consistently gave the same groups of birds, and this grouping was generally related to geographical proximity. It has been supposed that Pleistocene glaciations played a crucial role in the origin of extant diversity and distribution of Northern Hemisphere vertebrates. Molecular comparison of most extant songbird species belonging to the genus *Carduelis* does not support this assertion. The fossil record of chicken and pheasant divergence time has been used to calibrate the molecular clock; cyt b DNA dendrograms suggest that speciation in Carduelinae birds occurred during the Miocene and Pliocene Epochs (9-2 million years ago) in both the Northern and Southern Hemispheres. Only about 4% average amount of nucleotide substitution per lineage is found between the most distant *Carduelis* species; this suggests a remarkably rapid radiation when compared with the radiation of other passerine songbird genera.

European isolated *Serinus citrinella* (citril finch) is not a canary, but a true goldfinch. South American siskins have quickly radiated in the last 4 million years coinciding with the emergence of the Isthmus of Panama; probably, a North American siskin related to *C. notata* invaded a suitable and varied biotope (the South American island) for *Carduelis* birds. North American goldfinches may be renamed as siskins, because they have a distant genetic relationship with European goldfinches. Genus *Acanthis* could be dropped, and thus redpolls should be separated from twite and linnet, the latter (Europeans) probably being related to American goldfinches. Also, reproductive barriers are observed between closely related species and not between other more distant ones. Finally, a tentative classification for genus *Carduelis* species is suggested.

Comparative genetic structure between populations of Colombian and North-American *Drosophila pseudoobscura* using five microsatellite loci: gene flow, time of divergence, and effective numbers of the Colombian populations

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Since the report of a population of Drosophila pseudoobscura by Dobzhansky et al., (1963), in the high plateau of the Colombian Andes, in geographical isolation from the central range in North-America, many evolutionary biologists have shown interest on this population. To deeply analyze the comparative genetic structure of both populations, we studied 3 Colombian populations, and 4 U.S. populations, for 5 microsatellite loci (DPSX001, DPS2001, DPS3001, DPS3002 and DPS4001). Our major results were: (1) The 3 Colombian populations showed the same heterozygosity (H=0.67), being these values significantly lower than the H found in two of the U.S. populations, (Cheney, H=0.90; Goldendale, H=0.91), and similar significantly to those obtained in the other two U.S. populations (H = 0.71 - 0.76). This result could indicate that the Colombian populations have lost certain genic variability due to a founder effect, but the genetic depauperization is not as large as other authors have suggested. (2) The genetic heterogeneity between the Colombian populations was lesser than that found in the U.S. (GST=0.042 vs. GST=0.088). If we assume a neutral behaviour for these markers, the gene flow estimates for Colombia should be, Nm=5.6, and Nm = 2.59 in the U.S. (3) The unique marker which was not in H-W equilibrium in Colombia was DPSX001, and selection might be acting on this locus. (4) Asuming a mutation rate of  $6.5 \times 10^{-6}$ , the time of divergence in years between the North-American and Colombian populations, was for these 5 markers 1.27x105, and 3.14x105 for the DPS3002 marker alone. These results are in agreement with the divergence data obtained by Schaeffer and Miller (1991) of 1.55x105 to 5x105. (5) Using a step-wise mutation model these values would be of 1.09x105 to 1.56x105 flies.

Partial phylogenetic analysis of five Colombian species (*Cebus albifrons, Cebus apella, Saimiri sciureus, Lagothrix lagotricha and Alouatta seniculus*) and divergence time among species and genera using RFLP's on mtDNA.

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From mtDNA Restriction Fragment Length patterns analysed in five Colombian Primate species using three restriction endonucleases (Hinc II, Cfo I and Hinf I), partial phylogenies of these species were obtained. Several maximum parsimony methods with branch-swapping and implicit enumeration were employed. Some of the most outstanding results were the lost of important relationships between the two *Cebus* species and the no special relation between *Alouatta* and *Lagothrix*. In each analysis were determined the states of the hypothetical ancestral species in each clade nodes. The present phylogenetic results were compared with those obtained from a morphological point of view of Rosenberger (1981, 1984), Ford (1986), Kay (1990), Hill (1972), Hershkovitz (1972), with those, from an inmunological perspective, of Baba et al., (1980), and Sarich & Cronin (1980), to the caryotypic study of Dutrillaux et al., (1986) and the molecular ones referred by Schneider et al., (1993), Harada et al., (1995), Horovitz et al., (1998), Sampaio et al., (1991) and Schneider et al., (1994). Applying a mitochondrial sequence divergence of 2 % every million of years, we mesured the time of average divergence between the 3 haplotypes of C. *albifrons* in 812.500 years and in 633.500 years between the two haplotypes of *S. sciureus*. The divergence time values between C. *apella* and *S. sciureus* (10.136.000 years), between *C. albifrons* and *S. sciureus* (15.700.000 years) and between C. *albifrons* and A. *seniculus* (17.330.000 years) are noteworthy similars to the results of Schneider et al., (1993) and with some paleoprimatological data.

Comparison of genetic diversity of the weed *Rubus alceifolius* Poir. (Rosaceae) in its introduced and native areas.

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Many *Rubus* sp. native from South East Asia invade open areas in many tropical and sub-tropical countries. *Rubus alceifolius* was introduced into the Mascareignes (La Reunion, Madagascar, Mauritius), Mayotte and Queensland (Australia) since 1850, from unknown origins. Fifty years later, this bramble was already a serious weed in these islands, invading the native vegetation by mono specific patches.

To initiate a biological control of this weed, we intended to clarify the number of times and localities where it was initially introduced (genetic diversity of founders). To be able to choose a strain-specific pathogen, we performed a phylogeographic analysis, to determine the origin(s) of introduced individuals. We also compared genetic diversity of native and introduced areas.

We performed an AFLP study on 224 *R. alceifolius* individuals from 5 localities in both native and introduced areas. The two areas branch in 2 groups: the origin of introduced individuals is not localised. The native populations exhibit a high genetic diversity among individuals, contrasting with the absence of intra-locality variability in the introduced area, except in Madagascar where the level of polymorphism is the same as in the native range indicating a possible origin of colonisation. Moreover, each island show a unique clone, suggesting several independent colonisations.

These results yield on the origins and the biology of the introduced *R. alceifolius*. Introduced populations are likely to have switched towards a higher ploidy level and/or a higher rate of asexual reproduction. Moreover, observing a single clone per island could mean that competition took place in the early stages of colonisation, and that the most competitive genotype in each island exceeded the others because of its demographic and biological abilities.

Female and hermaphrodite flowers on a chimeric gynomonoecious *Silene vulgaris* plant produce offspring with different genders - a case of heteroplasmic sex-determination?

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In gynodioecious plant species individuals have either female or hermaphrodite flowers. However, individuals with both types of flowers i.e. "gynomonoecious" or "partially male steriles", are sometimes found. The standard explanation of gynomonoecious individuals is that their male sterilizing cytoplasm is incompletely restored by nuclear male fertility genes.

*Silene vulgaris*, the bladder campion, is usually referred to as being gynodioecious, though gynomonoecious individuals have frequently been observed. On gynomonoecious plants of *S. vulgaris* three types of flower stalks can be observed: stalks with only female flowers, stalks with only hermaphrodite flowers, and stalks with a mixture of both types of flowers.

In an attempt to determine if the segregation of flower types on gynomonoecious plants of *S. vulgaris* is associated with a difference in offspring gender, a series of crosses were performed. The results show that female and hermaphroditic flowers on non-chimeric stalks produce offspring of all three types, but the frequencies with which they do so differ.

Coordinated adaptive evolution may explain evolutionary rate accelerations observed for multiple genes of the mitochondrial electron transport chain in simian primates.

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We have demonstrated a coordinated evolutionary rate acceleration for the mitochondrial electron transport chain in simian primates. Prior studies have shown that the mitochondrial COII gene has a higher evolutionary rate along simian primate lineages, and that the nuclear-encoded cytochrome c protein has a greater amino acid replacement rate in humans. We have obtained the nucleotide sequences of several mitochondrial genes (cyt b, COI, and ND2) from a number of primate species, and combined these with published sequences to further investigate rate variation in primate mitochondrial genes. Both the cyt b and COI genes have a higher non-synonymous substitution rate in simian primates than in non-simian primates and in other mammals. A comparison of all mitochondrial protein-coding genes between apes and other mammals revealed three other genes (ATP8, ND1 and ND5) may also display the same pattern . This coordinated pattern of rate acceleration is best explained as resulting from an episode of adaptive evolution affecting multiple subunits of the electron transport chain. We have analysed inferred ancestral substitutions in the context of the 3D structure of the cytochrome c oxidase complex. This suggests that amino acid substitution in COII at D127F and E157Q may be candidates for the initiation of these adaptive changes.

# Modelling coevolutionary conflicts in the fig/ fig wasp mutualism

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Figs and fig wasps interact in a highly coevolved pollination mutualism. Fig flowers can only be pollinated by a species specific agaonid (Chalcidoidea) and represent the only egg laying site of these insects. When the new generation of wasps emerge, they become loaded with pollen of their natal fig that they will disperse. Thus, male fitness of the tree depends on its wasp production.

In monoecious fig trees, each female flower may "produce" either a seed or a pollinator offspring, that is, each female flower may contribute to female or male function of the tree. Trees are selected to produce both seeds and pollinators. However, wasps are selected to produce as many offspring as possible. What regulates seed and wasp production?

For long it was believed that there exist two different kind of flowers, one of them being unable to produce wasps. However, data do not support this assumption.

Here I will propose a coevolutionary simulation model between fig and fig wasps showing that a coevolutionarily stable strategy, regulated by the population density of the wasp, exists for this conflict. This may explain the stability of the monoecious fig/ fig wasp mutualism.

Randomization-based biophysical evidence suggests that strong selection on mRNA structure should act against too high and too low codon usage biases.

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Recent research shows that 1) unbiasing codon usage and 2) randomizing the positioning of confamilial synonymous codons (SCs) of genes, decreases average mRNA stability in silico by ~8% and ~3%, respectively (NAR 27: 1578). We have shown (JME 48, in press) that the trinucleotide motifs of the preferred (major) SCs are over-represented off-frame relative to those of the non-preferred SCs. These results indicate that the frequency and positioning of SCs are main currencies in controlling mRNA secondary structure and thus mRNA half-life and the gliding of the ribosome on the mRNA, two possibly opposed properties well known to be affected by mRNA structure. These structural requirements should lead to biases in codon usages and thus in tRNA pools, ultimately compelling the usages of highly expressed genes to exploit tRNA pool biases. Therefore, for most genes codon bias could be a modulator of mRNA structure non-mediated by codon-anticodon interactions. The hypothesis could explain why genes fixed for the major SCs are almost never found, as well as why tRNA pool biases and codon usages are quite similar across species. This challenges the assumptions of the rigid weak selection (Ns= 1.0) model of codon usage, but leaves room for semi-neutral patterns of divergence and polymorphism to arise when a gene shows nearly optimal SC usage and SC location structure. I will present ongoing work aimed at partitioning the contribution of 1) and 2) to native mRNA stability, at measuring GC content effects in 1), and at assessing whether and how the aminoacid sequence is sacrificed on the altar of mRNA structure. I will also discuss attempts at assessing the relative weights of the pressure to mirror tRNA pools biases and to satisfy frame-independent constraints on mRNA structure.

# Comparative phylogeography of 17 species of large African herbivores

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Genetic structure of sub-Saharan populations of 15 bovine species, elephant and zebra has been studied using mtDNA control region sequences from 1933 individuals. 15 of the species have largely similar requirements of relatively dry savanna and bush habitat. Only two opportunistic species the African buffalo and the elephant also inhabit moist and forested habitats. Levels of genetic variation are generally high, while the distribution patterns of the variation are diverse. For some species reproductive barriers have evolved between populations, while other well established morphological forms extensively hybridize and low levels of population differentiation are revealed by yet other species. Clades in haplotype trees are frequently correlated with different continental distributions, but are also recorded within limited regional distributions. Phylogenetic trees of haplotypes are interpreted in the light of present distributions and the paleontological record in an attempt to understand the species history. The present population structures have been formed by a complex, dynamic pattern of vicariant diversification, dispersal and local extinction. Traces of a major common vicariant event, possibly concordant with the FAD pulse 0.9-0.7 mya as suggested by paleontologists, can be found in most species histories.

#### Evolutionary Responses to Environmental Stress by the Pitcher-Plant Mosquito, Wyeomyia smithii.

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We performed truncation selection for increased fitness (r) under conditions of chronic stress from the combined effects of low nutrients and high temperature, representative of extremes likely to be encountered in nature by the pitcher-plant mosquito, *Wyeomyia smithii*. We performed selection on geographical parental populations and their hybrids to determine whether hybridization would facilitate or constrain adaptation under our selection protocol. The stressful environment decreased fitness (r) by 54% averaged across all populations, relative to near-optimal conditions. After 10 generations of selection under chronically stressful conditions, exactly one-half of the parental and one-half of the hybrid populations had gone extinct. Thus hybridization had no effect on the likelihood of population persistence. Fitness (r) of the surviving populations did not show any response to selection. Despite initial hybrid vigor under stressful conditions, the fitness (r) of surviving hybrid populations was either equal to, or worse than, the fitness (r) of surviving parental populations after 10 generations of selection. These results suggest that outcrossing populations to augment genetic variation and facilitate adaptation to a rapidly changing environment may not be useful over longer time scales, even in cases where hybridization does initially increase fitness.

Although we detected no direct response to selection for increased fitness (r) under lifetime chronic stress, selected populations showed a strong correlated response for survivorship through transient, acute heat and dessication shock. In evaluating how organisms might respond to future climate change, biologists must maintain a clear distinction between lifelong performance in chronically stressful environments and short-term survivorship through transient, acute stress.

Genetic variation in two species of pearl oyster of the genus *Pinctada* : impact of past and present ecological factors on restriction to gene flow

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Presence or absence of barriers to gene flow between natural populations are commonly attributed to specific biological properties and/or historical and ecological parameters. Few examples of genetic structuring in marine environment are found in the literature, particularly for bivalves, and when it is the case, it is not easy to determine which parameters explain most part of the observed pattern. We studied genetic variation within and among eighty populations of two closes species of pearl-oyster : *Pinctada margaritifera cumingi* from Cook Islands and French Polynesia, and *P. mazatlanica* from Mexican to Panama Pacific coasts.

On the basis of the variation in two mitochondrial genes, strong global structuring was observed between samples of *P. mazatlanica* from Mexico to Panama, whereas at the same geographic scale, none or little was underlined for *P. margaritifera* from Cook Islands to French Polynesia. Significant differences in levels of genetic variability were also observed between the two species.

Both species are sharing most of the biological traits known to have a great impact on dispersion pattern, especially a long pelagic larval stage and a strong substrate specificity for coral formations. This permit to focus on present and past biogeographical parameters which could both play a role in the functionment/dynamics of populations observed, and be responsible for differences underlined between the two species. We particularly emphasize on factors like habitat fragmentation, human perturbation, sea-level fluctuations and surface currents in the areas concerned.

## The Prospero effect or what we can learn from comparing patterns and processes in different Archipelagoes

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Because of their microcosmal nature and the impoverishment of their ecosystems, oceanic islands offer the experimental conditions required to understand how biodiversity is generated.

Even though it is sometimes argued that evolution rarely follows the same path twice, very similar patterns and evolutionary processes have been reported in different island groups. This suggests that, although independently evolved, there are some features held in common by oceanic islands that play an important role in the generation of their biota and the assembly of their communities. Such biological resemblances across independently arisen island chains are collectively referred to as the 'Prospero effect'.

To date, comparative studies of patterns of diversification on islands have been restricted to comparisons between different organisms in the same archipelago. While such studies have significatively increased our understanding about how different life strategies affect diversification, they are agnostic regarding the influence of the geographical and geological factors, preventing generalization and formulation of universal statements about the generation of diversity. Only through the comparison of patterns in different archipelagos could this goal be realized. Comparing species diversification across different archipelagos could help to distinguish local phenomena from general patterns. Thus the comparative method can identify the key factors in clade diversification.

### Sexual conflict and speciation rates in insects

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I review and analyse experimental studies addressing the direct effects of multiple mating on female fitness in insects. The results of these analyses clearly show that female insects gain directly from polyandry in terms of increased lifetime offspring production. Despite an overall negative effect of remating on female longevity in species without nuptial feeding, the positive effects of remating (increased egg production rate and fertility) more than outweighs this negative effect for moderate mating rates. However, the results also support the existence of an intermediate optimal female mating rate in general, beyond which a further elevated mating rate is deleterious for females. The existence of such optima implies that sexual conflicts over the mating rate should be very common and persuasive in insects, and that antagonistic coevolution between the sexes plays a key role in the evolution of mating systems and in the evolution of many reproductive traits. Recent theoretical and empirical studies have suggested that post-mating sexual conflict may facilitate speciation events. By contrasting pairs of related clades of insects differing in mating system, I show that the opportunity for sexual conflict is directly related to the rate of speciation. Groups where females mate multiply exhibit speciation rates more than four times as high as those in related groups where females mate only once.

### PLENARY LECTURE

## The first Europeans

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The major part of human history is, indeed, prehistory, and the scenary in which it is performed, during the first three or four million years, is Africa. Out of Africa came the ancestors of hominids that evolve in the last million and a half years in Eurasia. Yet, we have a reasonably complete fossil record of this eurasian evolution only for the last 100000 years. Not surprisingly paleontologists find it extremely difficult to asses how and when the present human type, our species, originated.

To some authors, the different Old World populations evolved locally during hundreds of thousands of years in an independent way, though with a partial genetic exchange, giving rise to the present main racial groups. To others, only one of all evolutionary lineages is the ancestor of present humankind, the remaining lineages being replaced by this one in a comparatively short time span (60000-30000 years b.p., depending of regions).

The lack of human fossils, mentioned above, finds a notorious exception in the beds of the Gran Dolina and the Sima de los Huesos, both caves located in the Sierra de Atapuerca (Burgos). In these and other close caves a research team of different Spanish specialists investigates the rich archeological and paleontological evidence of changes in climate, biodiversity and human activity during the last million years, and perhaps a bit more. In particular, la Sima de los Huesos represents the richest bed in human fossils ever found for the same period, and the oldest human fossils in Europe (ca. 800000 years old) have been found in the gran Dolina, after which the new species Homo antecessor has been erected.

We will discuss in this presentation the circumstances under which this exceptional accumulation of human fossils could occur, how is carried out the excavation work in these beds, what are the current and future research, and, above all, what is the contribution of this new evidence to the knowledge of human evolution.

# Effects of colonization processes on genetic diversity: differences between annual plants and tree species.

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Tree species are striking for their high within-population diversity and low among-population differentiation for nuclear genes. In contrast, annual plants show much more differentiation for nuclear genes but much less diversity than trees. The usual explanation of this difference is that pollen flow, and therefore gene flow, is much higher for trees. This explanation is problematic since it relies on equilibrium hypotheses. Since trees have very recently recolonised temperate areas, they have experienced many foundation events which usually reduce within-population diversity and increase differentiation. Only extremely high level of gene flow could counterbalance these successive founder effects. We develop a model to study the impact of life-cycle of forest trees, in particular of the length of their juvenile phase, on genetic diversity and differentiation during the glacial period and the following colonization period. We show that both a reasonably high level of pollen flow and the life-cycle characteristics of trees are needed to explain the observed structure of genetic diversity. We also show that gene flow and life-cycle also both have an impact on maternally inherited cytoplasmic genes, which are characterized both in trees and annual species by much less diversity and much more differentiation than nuclear genes.

### SINE's as phylogenetic markers in lizards.

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Scincid lizards (family Scincidae) are the largest family of lizards and are found on all continents (except Antarctica) and most of the diverse and isolated islands of the Pacific Ocean. Unlike Europe and North America, skinks are the dominant component of the herpetofauna of New Guinea and tropical Pacific archipelagos representing over one sixth of the global species diversity. Short interspersed repetitive elements (SINE's) have not been previously described from lizards. We isolated SINE's from an unusual group of scincid lizards from the South Pacific to identify new SINE families and investigate the phylogenetic relationships of this lizard radiation in order to examine aspects of novel physiological and morphological evolution.

#### Molecular Evolution of Self-Incompatibility loci in Arabis petraea

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In Brassica, self-incompatibility is controlled by haplotypes involving at least two related genes, S-glycoprotein (SLG) and S-related kinase (SRK). In a shared sequence domain (the "S-domain"), these loci exhibit extreme polymorphism similar to that of the MHC locus, with some regions being 'hypervariable'. This suggests that their role involves recognition functions though it is unknown which regions are involved in recognition, whether both loci have such functions, and whether the two loci interact in the self-incompatibility process. Our research is focused on the molecular evolution of these loci and other loci with similar S-domain sequences in natural populations of *Arabis petraea*. We have identified a number of S-domain loci, and are investigating patterns of nucleotide and amino acid diversity within this gene family across a number of populations. To date we have identified at least eight genes within this gene family. Segregation analysis shows that a number of these S-related loci in *Arabis* are unlinked to incompatibility phenotypes and exhibit moderate levels of diversity. We have identified one genomic sequence whose variants appear to be linked to incompatibility groups in three independent families. These sequences exhibit remarkably high levels of diversity but it remains to be determined whether this represents a single locus.

# Microsatellite mutation rates differ between repeat motifs - evidence from Drosophila melanogaster

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Microsatellites are one of the most popular genetic markers. While their evolutionary dynamics are not yet fully understood, the emerging picture is that several factors are influencing microsatellite mutation rates. Recent experiments demonstrated a significant effect of the repeat unit length on microsatellite mutation rates. Here, we studied the influence of the base composition of the microsatellite on its mutation rate. 42 microsatellite loci on the second chromosome with the three most abundant dinucleotide repeat motifs (TC/AG, AT/TA, GT/CA) were characterized in 6 different *Drosophila melanogaster* populations. Applying ANOVA to the variance in repeat number, we found a significant influence of repeat type on microsatellite variability. Calculating relative mutation rates, GT/CA appear to have the highest mutation rate and AT/TA the lowest. Similar differences in mutation rates were obtained by a alternative method which estimates microsatellite mutation rates from their genomic length distribution.

# Fine mapping of meiotic recombination breakpoints : Hotspots or warm patches?

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Despite the emerging wealth of information about the human genome, comparatively little is known about the processes of meiotic recombination underlying genome evolution. While much may be inferred from studies in model organisms, fundamental questions remain unresolved for human meiotic recombination. One such question is whether the regions frequently active in meiotic recombination are discrete and physically small. (less than a few kilobases : hotspots) or diffuse and large ( of the order of tens of kilobases : warm patches). We have set out to answer this question using a region of high germline recombination on human chromosome 16. The region 16p13.3 contains two highly informative minisatellite loci D16S309 (MS205) and D16S83 (EKM) separated by 90kb of subtelomeric DNA with an unusually high male recombination rate. Screening of the CEPH pedigrees using triplex PCR genotyping (MS205, EKM and a flanking minisatellite pMSP1.4) has identified six paternal recombination events within this region. These data imply a male genetic map length of 2.1cM for this 90kb cosmid contig, about twenty times the average recombination rate. High resolution segregation mapping using novel single nucleotide polymorphisms (SNPs) has localised the breakpoints of three of the six events to within the same three kilobase interval. This region thus shows a recombination rate of ~1% over 3kb, massively elevated relative to the genome-wide average of  $\sim 1\%$  per Mb. Analysis of haplotypes in three European populations at the SNPs defining this interval has revealed significant variation in linkage disequilibrium, strongly suggesting the presence of a recombination hotspot. Sequence analysis, with respect to general conformational properties and specific protein binding motifs has been ued to explain the activity of this region in meiotic recombination. Currently PCR analysis of molecular recombination events in sperm DNA is being used to directly measure the variation in recombination rate across this interval.

# Chromosomal inversions as a possible marker of a global climatic change

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The chromosomal inversion polymorphism of *Drosophila subobscura* has been extensively studied for the last 45 years. From the beginning it soon emerged that the distribution of the most frequent chromosomal arrangements followed a latitudinal cline, thus suggesting that the different arrangements were adapted to the different climatic conditions found along a N-S gradient. The fact that the same clines reproduced in the newly colonised areas of both North and South America reinforced the idea of the adaptive origin of the clines; less than five years were necessary for the new clines to be established. All these characteristics (arrangements adapted to different conditions and a quick response to environmental changes) makes the chromosomal polymorphism of *D. subobscura* a good candidate to monitor the adaptation of the species to a possible global climatic change. To test this hypothesis, seven Mediterranean populations sampled for the first time no less than 15 years ago have been resampled and the frequency of the chromosomal arrangements compared. The results show that the arrangements more common in the northern populations decrease in frequency whereas those arrangements typical of the southern part of the distribution range of the species become more frequent. This is what would be expected if the populations were adapting to warmer climatic conditions.

Sex-specific genetic markers suggest complete absence of male gene-flow across a hybrid zone of the common shrew (Sorex araneus)

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We analyse gene flow across a contact zone between two chromosomal races of the common shrew (Sorex araneus). Population structure is estimated with ten autosomal microsatellites, proteins and karyotypes. In addition, the relative contribution of males and females is estimated by mtDNA and a Y chromosome microsatellite. The Y chromosome microsatellite displays non-overlapping allele distributions for the two races, indicating complete absence of male gene flow. This result contrasts with the introgression observed for mtDNA and autosomal loci. The absence of male gene flow strongly suggests male hybrid sterility. Classical postzygotic isolation is generally acquired first by the heterogamic sex (males in mammals), whereas chromosomal incompatibilites are expected to act on both sexes. This suggests that the main barrier to gene exchange between the two races is not caused by their differences in karyotype. Furthermore, population structuring is much lower for autosomal microsatellites than for all other genetic markers. We show by simulation that this discrepancy stems mainly from the high mutation rate of microsatellite markers and their deviation from a single-step mutation model.

# **Overlapping of Mutagenic and Selective Activities of Antibiotics**

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An important part of the population biology of antibiotic resistant microorganisms is based on the interplay of bacterial mutation rates and the selective activity of antibiotics for the antibiotic resistant variants. Mutation and selection, the major drivers of the evolutionary process, are classically conceived in a pure darwinian manner as necessarily sequential steps. Experiments carried out in our laboratory do not alter this essential dogma, but suggests that both processes may be very closely related, and may overlap under precise environmental conditions. We used as a model the ability of the ß-lactam antibiotic ceftazidime to select bacterial variants with minor phenotypic differences in terms of ceftazidime minimal inhibitory concentration (MIC). The experiment is based on competitions between of the wild-type *E. coli* strain and a mono-mutated variant of TEM-1ß-lactamase. Intense selection of the variant occur at a precise narrow window of very-low antibiotic concentrations of ceftazidime, around the MIC of the wild strain.. At similar peri-MIC concentrations of ceftazidime, partially overlapping with the selective concentrations, the rate of mutation of *E. coli* (*mutS* variant) to an independent marker (rifampicin) is significantly increased. These observations suggest that during antibiotic therapy, the effect of antibiotics at precise inter-connected contiguous micro-compartments in the human body, where close antibiotic concentrations occur, a double mutagenic and selective effect may take place in a very small space-time complex.

# Dynamics of antigenic variation in RNA viral populations

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Virus antigenic variations are restricted by the structural constraints which are imposed by the recognition of the cellular receptor. In foot-and-mouth disease virus (FMDV), cell recognition is mediated by the G-H loop of capsid protein VP1 and its Arg-Gly-Asp (RGD) integrin-binding motif. In spite of being a target for neutralizing antibodies, the RGD motif is essential for virus infectivity and it is conserved in all antibody escape mutants of FMDV C-S8c1. However, serial propagation of FMDV in cell culture can render dispensable this attachment motif, and escape mutants with alterations at the RGD motif can be selected from C-S8c1 population at passage number 100 in BHK-21 cells. Analysis of the antigenic properties of a multiply passaged FMDV clone with an RGG sequence instead of the RGD motif confirmed that large antigenic variations can be prompted by replacements at capsid residues involved in receptor recognition. Although mutation Asp-143 to Gly at the RGD motif abolish FMDV interaction with its integrin receptor molecule, FMDV RGG replicates efficiently in cell culture and is genetically stable in a large proportion of serial infections. Interestingly, loss of integrin recognition by FMDV was accompanied by increased quasispecies complexity at the sequences around the RGG which greatly expand the repertoire of antigenic variants at the G-H loop of VP1.

In conclusion, the acquisition by FMDV of alternative mechanisms of cell recognition reduces former constraints at an important antigenic site involved in integrin-receptor recognition, and allows the virus to expand its spectrum of antigenic variants when the site ceases to be functional for receptor recognition.

## Recombination rate predicts inversion size in Diptera

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Most species of the Drosophila genus and other Diptera are polymorphic for paracentric inversions. A common observation is that successful inversions are of intermediate size. We test here the hypothesis that the selected property is the recombination length of inversions, not their physical length. If so, physical length of successful inversions should be negatively correlated with recombination rate across species. This prediction has been tested by a comprehensive statistical analysis of inversion size and recombination rate in 12 species of Dipterans for which appropriate data are available. We have found that (1) there is a wide variation in recombination map length among species; (2) physical length of successful inversions varies greatly among species and is inversely correlated with the species recombination map length; and (3) neither the among-species variation in inversion length nor the correlation are observed in unsuccessful inversions. The clear differences between successful and unsuccessful inversion so the most likely explanation for our results. Presumably the selective advantage of an inversion increases with its length, but so does its detrimental effect on fertility due to double crossovers. Our analysis provides the strongest and most extensive evidence in favor of the notion that the adaptive value of inversions stems from their effect on recombination.

Crossing the Gibraltar strait: Discordant phylogeographic patterns in seven Atlantic-Mediterranean fish species (Sparidae, Teleostei)

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From a zoogeographic point of view, the Mediterranean has been considered alternatively a biogeographic region by itself or just part of the larger North-East (NE) Atlantic region. In any case, exchanges between these two areas occur only through the Gibraltar strait. Such a connection has peculiar hydrological conditions and was also affected in the past by climatic changes, reducing or even abolishing any exchange. Recently, intraspecific genetic data have been reviewed for 16 marine species, both vertebrate and invertebrate ones (Borsa et al. 1997). Despite large difference in ecology and dispersal capacity, in most species moderate to strong genetic differentiation between the Atlantic and the Mediterranean side of the strait is observed, though few species present no differentiation. We report here on data on intraspecific genetic variation from seven species of Sparidae (D. dentex, L. mormyrus, S. cantharus, P. bogaraveo, P. pagrus). Sparids are coastal fishes, of great interest for fishing and aquaculture activities in the Mediterranean region. For each species, population samples (25-50 individuals each) were collected from three distant geographic areas: NE Atlantic (southern coast of Portugal), Western Mediterranean (Malaga) and Eastern Mediterranean (Ionian and/or Aegean Sea). All individuals were scored for sequence variation at a portion (200-350 bp) of the mitochondrial control region. Analysis of molecular variance as well as haplotype phylogenetic networks reveal remarkable differences among sparid taxa. Four species present a phylogenetic break between Atlantic and Mediterranean samples, while the remaining three show no differentiation at all, together with some indication for population bottlenecks in the past. These results seem to be unrelated to species ecology, and appear to indicate a major role for historical events in shaping the divergent evolution of sparid lineages.

# Gene flow among populations of Tropheus from the Zambian shore of Lake Tanganyika

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We examined microsatellite and mitochondrial DNA variation in the Tanganyikan species *Tropheus moorii* to determine gene flow among isolated populations. At least 30 individuals from five adjacent habitats were analysed. The selected rock habitats were situated along a continuous shoreline, separated by streches of mud shores and river estuaries. Our data give insight into the population structure of *Tropheus*, which is strictly confined to rock habitats and has a limited capacity for dispersal across open water. By comparing our results with data of other sympatric species, it is possible to demonstrate the contribution of ecological characteristics on the amount of genetic isolation over a given distance. We also show that knowledge of population-level phylogenies can provide valuable insights in combination with data on the geological history of the lake.

# The effect of chromosomal inversions on flight morphology and physiology at different rearing temperatures in Drosophila melanogaster.

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This study examined two questions: [1] Do differences in flight morphology and physiology exist between flies homozygous for the standard gene arrangement (ST) and those homozygous for various inversions (IN) on the third chromosome, and [2] are any such differences temperature dependent? Such a genotype-by-environment interaction in flight phenotype has been proposed as a possible mode of action of natural selection in generating latitudinal clines and seasonal variation in inversion frequencies in this species. It was hypothesized that ST flies would possess a combination of morphological and physiological characters that would lead to greater power output of the flight muscles at low temperature, while IN flies would show characters that would lead to greater power output at high temperature. Flight tests and morphological measurements on flies reared at 18;C, 23;C and 28;C showed that temperature caused a change in the overall mean of the characters examined, but that the hypothesized genotype-by-environment interaction did not occur. At all three temperatures, ST flies were significantly larger in wing size and body size, while IN flies had significantly greater wing-beat frequency. One trait, wing amplitude, did show a significant genotype-by-temperature interaction, but in the opposite direction of the hypothesis: IN flies had greater wing amplitude at low temperature (18;C), while ST flies had greater wing amplitude at high temperature (28;C). ST flies had significantly greater power output at 23;C and 28;C, because of their larger size. However, after adjustment for body size, either in a mass-specific manner or through analysis of covariance, there were no significant differences in general between ST and IN flies for power output.

#### DNA sequences: spectral density and nonlilear modelling analysis.

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Recently, numerous attemps have been made to provide some explanations regarding the structure, composition and informational content of DNA sequences. The expanding databases of genomic sequences and the development of methods used previously in other research areas allow a useful starting point to explore statistical properties of DNA chains. In this work, we analize DNA chains using two different approximations, a) the spectral density of the complete genomic DNA chains of some evolutionary categories and b)a nonlinear modelling technique. In both ways, differences are revealed between exonic and intronic regions. We computed the spectral densities of DNA chains decomposed into binary nucleotide sequences from different evolutionary categories ( phages, bacteria, viruses, yeasts, vertebrates and invertebrates, with sizes ranging from 16-300 Kb.). It is shown that, in contrast to other evolutionary categories, a three-periodicity does not exist in sampled DNA sequences from vertebrates. A systematic study of the composition of DNA chains reveals that this periodicity exists only in sequences consisting of approximately >25 % of coding regions. On the other hand, using a simple computational procedure, we examine DNA chains from different species in order to investigate their nonlinear deterministic structures. This procedure applies a nonlinear modelling technique based upon a quantitative comparison of the neighborhoods from similar DNA subsegments of size.Our results reveal that intronic regions exhibit a deterministic signature at sizes larger than a characteristic dimension. Caracteristic features of DNAs from different evolutionary categories and regions of specified functional properties are discussed. Trabajo parcialmente financiado por el proyecto XUGA 10304B97 (H. Naveira F.)

Multi-generation maximum likelihood analysis applied to mutation accumulation experiments Caenorhabditis elegans

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We develop a maximum likelihood (ML) approach to estimate genomic mutation rates (U) and average mutation effects (s) from mutation accumulation (MA) experiments in which mutations randomly accumulate in inbred lines, and in which phenotypic assays are carried out in several generations. We use simulations to compare the procedure's performance with the method of moments traditionally used to analyse MA data. Similar precision is obtained if mutation effects are small relative to the environmental standard deviation, but ML can be substantially more efficient if mutations with large effects have accumulated. Including data from intermediate generations may greatly improve the estimation precision. We analyse life history traits data from two MA experiments with the nematode *Caenorhabditis elegans*. ML estimates of mutation parameters have sampling variances of the order of 100-fold lower than the method of moments. Under a model with equal mutation effects, the two experiments provide similar estimates for  $U \sim 0.006$  per haploid, averaged over traits. Estimates of s are more divergent, and average at -0.38 and -0.15 in the two studies. We argue that a large class of deleterious mutations with small effects are not detected by the MA experimental approach.

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Isozyme variation in three endemic species of <u>Cistus</u> (Cistaceae) from Canary Islands: implications for species delimitation and conservation

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We examined the levels and distribution of isozymic variability for 13 loci in 11 accessions that constitute a representative sampling of the Canarian endemics *Cistus symphytifolius*, *C. chinamadensis* and *C. osbaeckiaefolius* with a view to suggest a sampling strategy for conservation purposes and to test the validity of their taxonomy. Although the absence of information regarding continental species of <u>Cistus</u> and the limited number of informative alleles detected prevent us from hypothesizing a possible sequence of colonization events, our isozymic data strongly suggest that *C. symphytifolius* was the first of these three species that colonized the Canaries. Isolation by distance emerges as the main factor to account for the differentiation of these species within and among islands on the grounds both of the results of Mantel tests and of the ecological uniformity in the pine forests where all Canarian *Cistus* populations occur. The low levels of variability detected cannot falsify current taxonomical circumscriptions. Our analyses demonstrate that population size is a poor predictor of levels of isozymic polymorphism in these species of *Cistus*. Therefore, the most sensible strategy to preserve their endangered variability has to focus on the levels of polymorphism detected. Sampling intensively in the more polymorphic populations of *C. symphytifolius* and *C. osbaeckiaefolius* would minimize effort and allow us to capture all of the detected variation.

## Evolutionary relationships of psyllid endosymbionts based on 16S and 23S rDNA analysis

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Psyllids (Homoptera: Psylloidea) are plant sap-sucking insects which have an obligatory sexual cycle and are oviparous. Like aphids psyllids are phloem feeders. Psyllids have bacteriomes consisting of bacteriocytes which contain the primary (P-) endosymbionts. These organisms have a Gram-negative cell wall and are found in host-derived vesicles. Previously it has been shown that the P-endosymbionts form a distinct lineage within the gamma-*Proteobacteria*. We have extended these studies by cloning and sequencing a 16S-23S rDNA fragment of the P-endosymbiont from 17 species of psyllids. The trees constructed on the basis of 16S rDNA and 23S rDNA are similar and, for the most part, in agreement with the previous classification of psyllids. The 16S and 23S rDNAs of the P-endosymbionts are unusual in having a G+C content of 35.5-37.2 moles % and 33.1-34.1 moles %, respectively. Comparisons with *Escherichia coli* 16S rRNA and 23S rRNA indicate conservation of the secondary structure of the P-endosymbiont rRNAs with major replacements of GCs by AUs. These results indicate that the association of psyllids with the P-endosymbionts are the result of a single infection followed by probable cospeciation of the host end the endosymbiont.

#### Genetic properties and adaptations of Buchnera to an endosymbiotic association with aphids

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Aphids are plant-sap suckers, consuming a diet rich in carbohydrates but deficient in amino acids and other nitrogenous compounds. Almost all aphids have within their bodies cells called bacteriocytes which contain Gram-negative bacteria assigned to the genus *Buchnera*. These organisms are essential for the aphid; treatment with antibiotics results in removal of the endosymbionts, loss of the ability to reproduce and premature death. There is evidence that one of the functions of *Buchnera* is the synthesis of essential amino acids for the aphid host. In this presentation we will review our work on the gene content of *Buchnera* which indicates that these organisms resemble other intracellular organisms in having many of the genes for DNA synthesis, DNA transcription, ribosomal proteins, amino acid tRNA synthases, ATP synthase, electron transport, protein secretion and glycolysis as well as cell wall synthesis. *Buchnera* differs from most intracellular organisms and some pathogens in having genes for the synthesis of amino acids. We will consider the genetics of biosynthesis of tryptophan and leucine. In both of these pathways overproduction of these amino acids may be mediated by plasmid-associated gene amplification of one or several genes which may lead to increased activity of the pathway. Congruent phylogenies are obtained from an analysis of plasmid-associated and chromosomal biosynthetic genes indicating that there is no plasmid exchange among *Buchnera* from different aphids.

#### Microevolution in an electronic microcosm

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The evolution of microbial populations in chemostats is still not fully understood. The classical interpretation of adaptation involves a process of successive substitution whereby a new dominant genotype, arises by mutation from the genotyp,e previously dominant and spreads more or less rapid1y through the population until it is nearly fixed. The population is thus nearly uniform most of the time. Some observations suggest that the process may be more complicated, but it remains formidably difficult to assemble the phylogeny of an evolving culture in sufficient detail to be sure. We report experiments with an electronic mierocosm inhabited by self-replicating algorithms whose phylogeny can be rendered completely transparent. The physiology of these algorithms is different in many respects from that of organic creatures, but their population biology has many features in common, including a very extensive, if not unbounded, range of variation. Experimental populations cultured with memory as a single limiting nutrient evolved smaller genomes convergently, although the sequence of genotypes underlying phenotypic change was highly contingent. With mutation rates of about 0.2 per genome per generation the most abundant genotypes rarely exceeded a frequency of about 0.4, and rare genotypes present in a few copies comprised a large part of the population. New dominant genotypes did not usually descend directly from previous dominants, but instead from one of the many rare or moderately abundant genotypes. A similar but less pronounced pattern was shown when mutation rates were reduced by an order of magnitude. Moreover, competition experiments showed that simple pairwise interactions could not explain the observed succession of genotypes, especially after the first hundred or so generations. We suggest that the conventional chemostat paradigm. May hold only as a special case at very low mutation rates, and that the dynamics and diversity of evolving populations, even in the simplest conditions, may be more complex than is usually recognised.

# Ecological and evolutionary consequences of dispersal in birds: Ecological plasticity and population differentiation

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Dispersal ability has been hypothesised to reduce intraspecific differentiation by homogenising populations. On the other hand, long-distance dispersers may have better opportunities to colonise novel habitats, which could result in population divergence. We investigated the evolutionary and ecological consequences of dispersal in birds. Using dispersal distances of 75 species of British birds, we tested whether dispersal was correlated with (i) population divergence, assessed as subspecies richness, and (ii) ecological plasticity, assessed as the number of habitats used for breeding. We found that the number of subspecies was negatively correlated with dispersal distances. This was the case also after correcting for potential confounding factors such as breeding distribution range, population size, body mass, migration, and similarity due to common ancestry. Dispersal was not a good predictor of ecological plasticity. The number of habitats occupied during breeding was not significantly correlated with dispersal distances, suggesting that long-distance dispersers do not have higher opportunities to colonise novel habitats. Overall, these results suggest that dispersal can have a homogenising effect on populations and that low dispersal ability might promote speciation.

# Cryptic sex in the parasitoid wasp, Lysiphlebus (Braconidae: Aphidiinae)

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Explaining the rarity of asexuals poses a problem for evolutionary biology given the likely advantages of an asexual mutant arising within a sexual species. Fundamental to this problem is the need to establish the evolutionary history of the asexual taxa concerned, and this is now possible with the development of molecular markers. We examined a genus of parasitoid wasp, *Lysiphlebus*, which appeared to contain both sexual (= arrhenotokous) and asexual (= thelytokous) species. By analysing mitochondrial and nuclear sequence data from specimens collected across Western Europe, we were able to show that the asexual females formed two distinct mitochondrial lineages (the older of which had diverged from the nearest sexual lineage approximately 500,000 years ago); however, the nuclear sequences showed no congruence with this pattern, with many nuclear recombination events having occurred between the sexual and the supposedly asexual mitochondrial lineages. From this result we infer that asexuality in *Lysiphlebus* (a) is under cytoplasmic control and (b) has a history of occasional sex with related sexual species. PCR screening did not reveal *Wolbachia* in these wasps, and the higher frequency of heterozygotes among asexual *Lysiphlebus* females compared to sexual females contrasts with the homozygosity-enforcing asexuality caused by *Wolbachia* in other parasitoid wasps. Examples of such rare or "cryptic" sex are emerging in a wide range of "asexual" taxa, with important implications for understanding their evolution.

Evolutionary relationship between the eukaryotic crow taxa on the basic of large subunit ribosomal RNA sequences

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Chlorarachniophytes, cryptophytes and haptophytes are unicellular algae, that contain plastids surrounded by four membranes. These extra membranes form important support for the hypothesis that these algae have acquired their plastids by the ingestion of another eukaryotic plastid-containing alga. Both chlorarachniophytes and cryptomonads contain a small nucleus-like structure called the nucleomorph, situated between the two inner and the two outer membranes surrounding the plastid, which is a remnant of the endosymbiont's nucleus. In haptophytes, such a structure is no longer present. In order to study the phylogenetic relationships between these algal groups and the remaining crown taxa, the large subunit ribosomal RNA (LSU rRNA) sequence from the chlorarachniophyte *strain CCMP621* (nuclear gene), the cryptophyte *Guillardia theta* (nuclear gene), the haptophytes *Prymnesium patelliferum* and *Phaeocystis antarctica* were determined. Additionally, we also determined the LSU rRNA sequence of the ciliates *Euplotes aediculatus* and *Spathidium amphoriforme*.

A variability map for the eukaryotic LSU rRNA, showing the distribution of variable and conserved sites in the molecule, was constructed by applying the substitution rate calibration (SRC) method that defines the variability or substitution rate of each nucleotide site as its substitution rate relative to the average rate of all sites of the molecule. Distance trees taking into account this among-site rate variation show a close relationship between ciliates and dinoflagellates-Apicomplexa, as expected, while the other three algal groups, viz. chlorarachniophytes, cryptophytes and haptophytes seem to form independent evolutionary lineages unrelated to the other algal groups represented by the LSU rRNA dataset.

#### Fossil embryos - a new source of information on animal origins

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Until a few years ago, the cornmon understanding was that embryos of marine metazoans were far too delicate to be preserved as fossils. This has changed dramatically with the recent discoveries of embryos of various kinds of animals in Cambrian and late Proterozoic rocks. The occurrences span a time period of ca. 570-520 Ma, which straddles one of the most dramatic reorganizations in the history of the biosphere, the 'Cambrian explosion'. This was the time when animals appear to have undergone their first major radiation. The fossil embryos have been preserved by impregnation or replacement of the organic tissues with calcium phosphate. Cleavage embryos as well as later developmental stages have been thus preserved. The latter include direct developers showing morphological features that may be compared with juvenile or adult forms; in at least one case we can confidently identify the fossil adults matching the embryos. The cleavage embryos are more difficult to identify; they seem to a represent a variety of cleavage patterns and gastrulation mechanisms. As it is impossible to follow the development of individual embryos in fossil material, it is necessary to study very large samples to ascertain which stages belong to the same organism. Such material is not always available, but the fact that new finds rapidly followed the first ones suggests that fossil embryos may be fairly cornmon but have previously been overlooked by palaeontologists. The cleavage pattern of the earliest known animal embryos resembles that of acoel flatworms, which is in agreement with the basal position of the Acoela within the bilaterian clade, according to recent analyses of molecular sequences. Most fossil embryos thus far discovered appear to have been large, direct-developing, lecithotrophic forms. This may, however, reflect a bias of fossil preservation or discovery.

# Frequent assimilation of mitochondrial DNA by grasshopper nuclear genomes

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Multiple copies of mitochondrial-like DNA were found in the brown mountain grasshopper, *Podisma pedestris* (Orthoptera: Acrididae), using the COI and ND5 regions. The same was discovered using the ND5 region in nine other grasshopper species from four separate subfamilies (Podisminae, Calliptaminae, Cyrtacanthacridinae and Gomphocerinae). The extra ND5-like sequences were shown to be nuclear in the desert locust, *Schistocerca gregaria* (Cyrtacanthacridinae) and probably so in *P. pedestris* and an *Italopodisma* sp. (Podisminae). Eighty-seven different ND5-like nuclear mitochondrial pseudogenes (Numts) were sequenced from twelve grasshopper individuals. Evidence of selective constraints on the differences between two Numts implies that they have separate mitochondrial origins. By comparing pseudogene sequences it was established that there have been at least twelve separate mtDNA integrations into *P. pedestris* nuclear genomes. This is the highest reported rate of horizontal transfer, between organellar and nuclear genomes which have been generated by separate integration events, appears to be a common phenomenon among grasshoppers.

# Morphological and molecular variation across a migratory divide in Scandinavian willow warblers

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A migratory divide is a narrow region in which two populations showing different migratory directions meet, and presumably also mate and hybridize. Ringing of willow warblers Phylloscopus trochilus in Europe has demonstrated a migratory divide latitudinally across central Scandinavia. In autumn, southern birds migrate south-west to tropical West Africa whereas northern birds migrate south-east to East and South Africa. The migratory divide is associated with concordant differences in size and plumage coloration. Based on morphology, we estimate the width of the transition zone between northern and southern willow warblers to be less than 350 km. The fact that several morphological clines occur together, suggest that the hybrid zone is a result of secondary contact between populations that have differentiated in allopatry. This interpretation is in accord with the knowledge of the recolonization pattern of the Scandinavian peninsula after the last glaciation; animals and plants appeared to have colonized either from the south or from the north around the northern bay of the Baltic Sea. If northern and southern willow warblers resided in allopatric populations during late Pleistocene glaciations, and the hybrid zone is a result of post-glacial range expansions, we would expect some degree of genetic differentiation accumulated during the period in isolation. In contrast, northern and southern willow warblers are near panmictic in the frequencies of alleles of mitochondrial DNA and at two microsatellite loci. The observed pattern, clear morphological and behavioral differentiation without genetic differentiation at neutral loci, suggests either (1) that the differences are maintained by strong selection on the expressed genes in combination with high levels of current gene flow, or (2), in the case of weak gene flow, that the divergence in morphology and behavior is very recent.

# Diversification on land and in the sea: different evolutionary regimes

#### Michael J. Benton

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The diversification of life through geological time indicates a rise from presumably one species to many millions today. The shape of that diversification has been debated, and three main kinds of models have emerged: (1) additive, or straight-line; (2) exponential; and, (3) logistic, or S-shaped.

The first, additive, pattern seems unlikely since it would imply a constantly declining probability of phylogenetic branching through time. The exponential pattern is biologically more likely, since it can be produced by a constant splitting rate. However, such curves imply that there is no upper limit to diversity. Logistic curves begin as exponentials, and then level off as some limiting diversity is approached.

Exponential and logistic curves imply very different understandings of ecology and evolution. An exponential curve implies that diversification is unconstrained so far, that taxa generally do not interact strongly competitively in a way that leads to wholesale extinction, and that new forms can continually evolve into new ecospace. A logistic curve implies that there is more biotic interaction (competition), in which new taxa evolve, but supplant pre-existing taxa, and that there is a fixed number of families (and species) on the earth, which cannot be exceeded. The reality of exponential and logistic curves in Nature has been debated in the past 40 years. Proponents of both viewpoints have presented strong evidence for the existence of exponential or logistic patterns in their data sets. Perhaps evolution follows either one or the other pattern, or perhaps different major segments of Life have evolved in different ways.

The diversification of marine families in the past 600 million years appears to have followed two or three logistic curves, with equilibrium levels that lasted up to 200 Myr. Continental organisms, however, clearly show an exponential pattern of diversification. It is not clear whether the empirical diversification patterns are real or artefacts of a poor fossil record, although the latter explanation seems unlikely.

The different patterns of diversification of marine and continental organisms could be real. Perhaps marine and continental organisms diversified in different ways, and there are still new sectors of ecospace to be conquered on land, but not in the sea. Or perhaps marine organisms have also diversified exponentially at the specific level, but the appearance of equilibrium patterns are artefacts of taxonomic structures.

#### Penetrating the penumbra of plasmid persistence: The role of cross-species gene transfer.

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Despite the near-ubiquity of bacterial plasmids, and the profound consequences of plasmid-mediated horizontal gene transfer for bacterial evolution, the evolutionary mechanisms responsible for the maintenance of plasmids are poorly understood. In this paper, we address the question of how plasmids — rarely essential to their hosts in all environments and prone to loss by segregation — manage to persist over evolutionary time. In the process, we also address a second and closely related question: whyare certain specific classes of genes typically borne on plasmids, insteadof on the chromosome, and why do plasmids typically code for these classes of genes, and not others? We present a general mathematical proof that if, as suggested by several empirical studies, plasmids are unable to bemaintained as purely parasitic genetic elements, they will not be able topersist by bearing beneficial genes either, in the absence ofcross-species or cross-strain plasmid transfer. We show that whencross-species transfer is possible, certain functional plasmids can bemaintained even when the costs of horizontal transmission preclude apurely parasitic existence.

# A molecular assessment of the diversification and community development of Neotropical fishes.

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Our general goal is to understand colonization and extinction as it relates to the assembly and maintenance of freshwater fish communities in lower Central America. Our research program utilizes mitochondrial DNA sequencing and restriction-site analysis to explore the history of Central American fishes. By defining genetic lineages within Central America and by characterizing genetic diversity within rivers and divergence between rivers, we are (i) describing geographic patterns of colonization, (ii) assessing the congruence of colonization patterns among species, (iii) comparing phenotypic divergence as reflected by taxonomy to genetic divergence, (iv) determining phylogenetic relationships among some enigmatic Central American endemics, (v) evaluating the role of founder events and population bottlenecks in constraining the genetic diversity of river populations, and (vi) establishing a rough 'evolutionary' time scale upon which we will chart patterns of genetic diversity, phenotypic divergence, and distributional shifts. Our results indicate that the freshwater communities inhabiting contemporary, isolated drainage basins of isthmian Central America are not closed, equilibrium systems but rather dynamic open systems subject to episodes of invasion and extinction.

### Selection and Random drift in the evolution of the vertebrate genome

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The discovery that the genomes of warm-blooded vertebrates are mosaics of isochores, long DNA segments that are homogeneous in base composition and belong to a small number of families covering a broad spectrum of GC levels, was followed by two observations. The first one was that gene density is strikingly non-uniform in the genome of all vertebrates, gene concentration increasing with increasing GC levels (even if the highest GC levels attained in the genomes of cold-blooded vertebrates are much lower than those of warm-blooded vertebrates). The second one is that the GC-richest and gene-richest isochores of mammals and birds are the result of two compositional transitions characterized by strong increases in GC levels that were then maintained. After a review of our current knowledge on the organization of the vertebrate genome, evidence will be presented in favor of the idea that the generation and maintenance of GC-rich isochores in the genomes of warm-blooded vertebrates were due to, and maintained by, natural selection.

# Sea of Cortez - Pacific Ocean disjunct populations and cryptic species of fishes

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Population disjunctions have been proposed to play an important role in speciation processes. In this study, we have examined the possible role of Pacific Ocean - Sea of Cortez disjunction as a contributing factor to cryptic speciation in several reef fish species representatives: *Leuresthes tenuis, Girella nigricans, Gillichthys mirabilis, Semicossyphus pulcher, Hermosilla azurea,* and *Halichoeres semicintus*. Mitochondrial D-loop and cytochrome b were sequenced and used to estimate phylogenetic disjunction and gene flow in these species. Three species: *Leuresthes tenuis, Girella nigricans, Gillichthys mirabilis* exhibited low gene flow levels (Nm<1.0) and had Sea of Cortez and Pacific Coast populations separated into two distinct monophyletic clades. In contrast, the three other species: *Semicossyphus pulcher, Hermosilla azurea,* and *Halichoeres semicintus* showed high levels of gene flow (Nm=6 to 37) and did not exhibit monophyletic populations.

No simple relationship was found between dispersal capability and gene flow levels. Thus, species with widely separated populations may represent incipient speciation events, while panmictic species may be explained by continuing levels of gene flow, or alternatively, may represent evidence for local extinctions followed by recent recolonization events.

# Sexy sperm in the red flour beetle

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Females of many species mate with more than one male during one fertile period, although mutliple mating frequently entails costs and no obvious benefit. A potential benefit is the increased probability that the sons of females mating with multiple males will inherit traits enhancing sperm competition success. To test this prediction we mated red flour beetle (Tribolium castaneum) females either repeatedly to the same male or to three different males. This procedure was carried out for three generations and 20 replicate lines, ten of which established with wild-type, and ten with Chicago black morph, a partially dominant phenotypic marker. The sperm competitiveness of the sons of females from multiple-male vs. single-male lines of contrasting morph was assessed by sequentially mating wild-type stock females to the two types of males. Wild-type second males achieved significantly higher paternity than black second males. Sons from mothers from multiple-male lines had significantly higher sperm competition success when mating as the female's second male. However, they had lower success compared to males from single-male lines when mating as the first mate. Both effects occurred only in the wild-type morph, were independent of the selection regime of the black competitor, and interacted significantly with the number of progeny laid by the female. These results show that manipulating female mating behaviour can influence the sonsë mating success, either through maternal effects or heritable traits.

# Differential sexual migration patterns in humans: comparison of mtDNA sequences and Y-chromosome 5TRs in Central Asia

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In order to study the intraspecific genetic diversity informative markers should be analysed. In the present work we have focus our reserach in tw non-recombiant regions of the human genome: the control region of the mitochondrial DNA (mtDNA) and several Y-chromosomal STRs. We present the genetic analysis performed in four Central Asian groups: Kazakh, Uighurs, lowland Kirghiz and highland Kirghiz. The complete sequence of the first mtDNA hypervariable region (positions 16,024-16,383) and eight Y-chromosome STRs were analyzed in the four samples.

Central Asian mtDNA sequences present features intermediate between European and eastern Asian sequences, in several genetic parameters. Several hypotheses could explain the intermediate position of central Asia between Europe and eastern Asia, but must plausible would involve extensive levels of admixture between Europeans and eastern Asians in Central Asia. The mtDNA sequence pool in all samples is very similar and the analysis of the molecular variance has revealed that the fraction of mitochondrial genetic variance due to altitude, language or ethnic group is not significant.

The analysis of Y-chromosome STRs in the same individuals showed a completely different pattern. Unlike mtDNA sequences, the analysis of the molecular variance showed a very high degree of differenciation among the samples tested. Furthermore, a dramatic reduction of the haplotype genetic diversity was observed at high altitudes compared to low altitude villages, which suggest a male founder effect in the settlement of high altitude lands.

The joint analysis of mtDNA and Y-chromosomes genetic material in the same Central Asian individuals seems to indicate the existence of high ration of female versus male migration, which could be explained by socio-cultural patterns of those populations.

# The effect of paternal leakage on the rate of Muller's Ratchet

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One argument for the, advantage of sexual reproduction is that sexually reproducing organisms can purge their genome of deleterious mutations through recombination, whereas asexual organisms will accumulate mutations over time and are doomed to extinction. Muller's Ratchet refers to the process in small populations that the least mutated class of individuals may fail to reproduce by chance (drift) resulting in an irreversible increase of the, mutation mean in the population.

Sperm-dependent parthenogenesis has been documented from 24 genera in 7 phyla (Beukeboom & Vrijenhoek, 1998, JEB 11:755) and refers to parthenogenetic organisms in which intrusion of a sperm into the, egg is necessary to initiate embryo development, but the sperin chromosomes are subsequently expelled. Sometimes the expulsion process is incomplete leading to retention of (fragmented) sperm chromosomes in the egg, a process known as `paternal leakage'. As an adaptive explanation for this reproductive mode, it has been suggested that paternal leakage may counteract the action of Muller's Ratchet in sperm-dependent parthenogens.

We constructed a simulation model to investigate the effect of paternal leakage on the rate, of Muller's Ratchet. The basic parameters are population size, number of loci, genomic mutation rate, fitness reduction per mutation and. fecundity. We test how (1) proportion paternal inheritance, (2) stability of paternally inherited ftagments, and (3) mutation accumulation on paternal fragments affect the rate of Muller's Ratchet and the mean population fitness.

#### Sex determination in the haplodiploid Hymenoptera

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Sex-determining mechanisms appear to be very diverse in invertebrates. Haplodiploidy is a widespread mode of reproduction in insects: males develop from unfertilised eggs and are haploid, whereas females develop from fertilised eggs and are diploid. There are no heteromorphic sex chromosomes. Several models have been proposed for the genetic mechanisms of sex determination in haplodiploid Hymenoptera (ants, bees and wasps), including one-locus, multi-locus, matemal effect and genomic imprinting sex determination. The one-locus multi-allele model (hernizygotes are male, diploid heterozygotes are female, but hornozygosity at the sex locus results in diploid males) is valid for some species, but its phylogenetic distribution remains unclear. In the chalcid *Nasonia vitripennis* sex determination cannot be explained by the one-locus multi-allele scheme. 1 used a mutant polyploid strain (females are triploid and males diploid) to test some predictions of the alternative models. Triploid females were knowm to produce both haploid and diploid eggs that develop into males when unfertilised. However, occasionally diploid parthenogenetic eggs were found to develop into fertile females. I will discuss how this observation fits with existing models and how application of genomic mapping may be informative.

#### Interspecific variation of esterase expression in Drosophila

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Esterases have been considered an important tool in studies of evolutionary process through gene amplification and functional divergence. In *Drosophila*, esterase genes include multigene families that have shown to vary in constitution and sequence across species. Comparison of species as to esterase expression revealed divergence in function in some cases while others showed conserved activity. We are studying esterase expression in *Drosophila* species belonging to the *D. buzzatii* cluster and to the saltans subgroup. In both cases they are close species. By now we are studying esterase expression in

polyacrilarnyde gels, using strains and hybrids. Hybrids of species *D. seriema* with *D. koepferae* (from the cluster *D. buzzatii*) hornozygous for alleles A and B respectively (locus E-11), exhibited suppression of the allele A when it comes from *D. seriema* males in crosses with *D. koepferae* females. In hybrids of the reciprocal crosses, however, both alleles are expressed normally. These results are interesting because they point to a mechanism similar to the imprinting, operating on allele A in *D. seriema* males. Absence of expression of A was not observed when *D. seriema* was intercrossed with *D. serido* that also has the allele B. In the saltans subgroup, one male-specific esterase we named E-12, present in 100% of males examined from the *D. saltans* strain S 1, exhibited expression in about 50% of hybrid females in crosses of that strain with *D. prosaltans* females. In both cases, the result suggest gene and/or regulatory divergence in the evolutionary process. These possibilities wil be examined in continuation of our work. (FAPESP)

#### Effects of inbreeding on pathogen resistance in Silene latifolia

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We investigated the impact of inbreeding in the dioecious plant species *Silene latifolia* on resistance to the anther smut fungus *Microbotryum violaceum*. This host-pathogen system is characterized by metapopulation dynamics with frequent extinction and recolonization and inbreeding in local host populations is probably a common phenomenon. The fungus produces its spores in the anthers of host plants, and is florally transmitted by insects that serve both as pollinators and vectors of the disease. After five generations of sib-mating, 65 inbred lines were obtained, originating from 8 host populations, with inbreeding coefficients ranging from 0 to 0.593.

Two components of resistance *sensu lato* were assessed. First, an inoculation experiment was performed to measure "biochemical" resistance. On average, resistance slightly increased upon inbreeding (p<0.05), but the most striking result was that inbreeding increased in some lines whereas it decreased in others (interaction inbreeding x line, p<0.001). Second, we measured effects of inbreeding on floral traits that are putatively related to "avoidance". For instance, smaller petal size is associated with higher field resistance, because of a lower visitation rate by spore-carrying insects. Significant inbreeding depression was found for petal size and nectar volume, but again, inbreeding effects strongly varied among lines.

We conclude that effects of inbreeding on the host-pathogen interaction are unpredictable at the local population level, because (1) Effects differ among lines, i.e. effects on the population level depend on genotype composition of the founder population, (2) The strength and direction of effects on biochemical resistance and avoidance are uncorrelated, and (3) In several lines, epistatic effects were found, making the effect of inbreeding dependent on the actual inbreeding level of the genotype.

## An identity-by-descent model of associative overdominance during a population bottleneck

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Correlations between marker heterozygosity and fitness have been observed in various species. Such correlations rely either on direct effects of the marker locus on fitness ("direct overdominance" hypothesis), or on indirect effects, if marker heterozygosity correlates with heterozygosity at selected genes ("associative overdominance" hypothesis). Models of associative overdominance (AO) have considered two possible sources of correlations among loci. First, the effect of linkage disequilibrium (correlations of allelic states) has been studied in finite populations at mutation-selection-drift equilibrium. Second, the effect of identity disequilibrium (correlations of homozygosity) has been investigated in infinite, partially inbred populations at equilibrium. Authors referring to the first approach usually emphasized the role of physical linkage. In this study, our aims are (i) to relax the restrictive assumption of population equilibrium, investigating AO during a bottleneck; (ii) to fill the gap between the two classical approaches, by showing that effects of finite population size can be expressed in terms of identity disequilibrium, and by re-evaluating the role of physical linkage in this context. Results were checked using computer simulations, which also allowed to include purging selection. AO (the difference between average fitness of heterozygotes vs. homozygotes at marker locus) is maximal just after the bottleneck, decreasing to equilibrium value within a few tens of generations. Purging causes only slight deviations between theoretical and simulation results. AO is sensitive to bottleneck size, to marker gene diversity and to deleterious genomic mutation parameters. Only strong physical linkage has large effects. We conclude (i) that AO following bottlenecks is much larger than in equilibrium finite populations, and (ii) that its main origin is random variation in individual inbreeding (IBD coefficients), rather than physical linkage.

#### Interaction between temperature stress and inbreeding in Drosophila

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The degree of stress caused by an environment can only be valued in relation to the organism or population experiencing this environment. Inbreeding, as is well documented, changes the architecture of populations and has recently been shown to significantly affect the susceptibility to high temperature stress in *Drosophila* (Bijlsma *et al.* 1999).

We have investigated the consequences of inbreeding for egg-to-adult survival (viability) in *D. melanogaster* in relation to the reactivity to growth temperature over the greater part of the physiological range of the species: from 12°C to 30°C. Compared to non-inbred lines, inbred lines showed on average not only a significantly decreased viability, but also the reaction norm for viability according to developmental temperature was clearly affected: inbred lines on average showed a much narrower temperature niche width. Moreover, inbred lines exhibited a significantly increased between-line variability both with respect to viability and the reactivity to temperature. The possible nature of the genes involved in this increase in temperature sensitivity will be discussed.

Bijlsma, R., J. Bundgaard and W.F. Van Putten (1999). Environmental dependence of inbreeding depression and purging in *Drosophila melanogaster*. J. Evol. Biol. (in press)

# Clonal diversity of wetland *Carex limosa* as a function of population size and isolation: a comparison between Irish and Swiss populations

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Wetlands, often dominated by sedges (*Carex sp.*), suffer world-wide from habitat fragmentation. The effects of fragmentation - isolation and decreased population size - may lead to a reduction of genetic diversity through inbreeding and random genetic drift. It has been suggested that clonality might buffer these effects through the ability to persist at the genet level.

*Carex limosa* has very strict habitat requirements. It is widespread and abundant in Ireland, but scarce and fragmented in Switzerland.

We collected *C. limosa* from 4 populations in Ireland and 8 in Switzerland and compared their clonal diversity. To assess their genetic diversity we used microsatellite markers.

The collected data shows that both clonal- and allelic diversity at the genet level of *C. limosa* positively correlate with population size and negatively with isolation. The role of clonality as a buffering agent is discussed, based on the results.

# Population structure of Laminaria digitata (Pheophyceae) in the Channel: Use of hypervariable markers

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*Laminaria digitata* (Class: Phaeophyceae, Order: Laminariales) is a brown macroalga, widely distributed along rocky coasts of the Channel and the Atlantic Ocean. It grows from wave exposed to sheltered environments, in infralittoral zone. Laminariales are characterised by a heteromorphic, haplodiploid life-cycle. The sporophyte is heavily harvested (60 000 T/year, mainly in the Channel) for its high alginate content. Because of such characteristics (life cycle, harvesting, as well as continuous populations), this species is particularly well suited to study different aspects of genetic diversity in marine environment.

Microsatellite markers, which are rare in this species, were characterised in order to study its reproductive systern, as well as the population structure in the Channel. Significant relatedness at one meter scale is present, flkely originating from the low dispersion ability of male gametes. Due to the high dispersion of spores, the effective population size is around 16000 individuals, *i. e.* one km long and allogamy is likely to be the main reproductive system. Population differentiation occurs according to the "isolation by distance" model, reflecting the long term currents in the Channel as well as other parameters such as the nature of the substratum.

This fine study of continuous populations of an alga displays prominently for the first time, two dispersal ways: male gametes on the one hand and, on the other hand, spores or fragmented thallus. Moreover, it points out population isolation by currents in an *a priori* homogenous environment.

# Optimal foraging of a clonal parasitic plant

## Christof Binder

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Foraging strategies have received much attention in the field of behavioural ecology, but only recently have clonally growing organisms and plants been considered.

Evolutionary theory predicts that parasites should evolve high host specificity and that foragers should evolve efficiency. Parasitic clonal plants in the genus *Cuscuta* comprise both highly host specific and unspecific species. *Cuscuta* also parasitizes many individual hosts at one time.

For a parasite such as *Cuscuta* to develop an optimal foraging strategy, differences in the quality of different resource patches have to be present. I will present data showing that for the species *Cuscuta campestris* Yunk., this basic assumption underlying most of the foraging theory was confirmed.

A dynamic programming model is being built to predict the optimal foraging behaviour of a *Cuscuta* individual in a mixed species environment and is now being tested in artificial plant communities where the host quality differs.

### Sex differences in survival selection in the serin, Serinus serinus

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The fact that natural selection is easily demonstrated in most natural populations suggests that these populations are displaced from their adaptive peaks to some extent. The reasons for this could, for example, be selection inconsistent with the genetic correlation between characters, or conflicting selection between the sexes resulting in phenotypes being compromises between all the conflicting selection pressures. We analysed the patterns of selection in a population of serins (*Serinus serinus*) outside Barcelona over a period of 15 years. There was strong univariate selection on wing and tail length in males, but not in females. A multivariate analysis showed that there was only a selection for increased wing length in males accompanied by strong disruptive selection on both tail and wing length and a selection against a positive correlation between the two characters. In females, the only consistent selection was stabilising selection on culmen length indicating selection on feeding efficiency. This was supported by the markedly more curved fitness surface for bill characters in females than in males. Thus, there are conflicting selection on the characters within a sex, but also conflicting selection on the same characters between sexes which may hamper the rate of access to the nearest adaptive peak. Thus, this kind of conflict may have considerable evolutionary effects.

# DNA polymorphic sequences in Drosophila

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A repository of polymorphic nucleotide sequences is a genetic resource of chief importance for workers studying DNA variation at the population level. However, Drosophilist community still lacks a specialized database on molecular polymorphism. As a first step for a project aiming to carry out several meta-analisis studies on DNA polymorphism, we are creating a specialized database of nuclear DNA polymorphism in Drosophila. By means of searching robots created ad hoc for this project, we have obtained from the crossed information of public databases such as FlyBase and GenBank those genes of any Drosophila species that are sequenced twice or more times in independent lines. Sequences that were unreliable were not included in the database. In a preliminary survey, we report here a series of tables and figures summarizing the extant polymorphic sequences and their distribution by genes, number of alleles, species, chromosome, genetic and cytological localization, accession number.

# The trade-off between egg size and number in the yellow dung fly in good and bad environments

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The trade-off between egg size and egg number (clutch size) is central to life history theory, but evidence for it is scant. In particular, evidence for a negative genetic correlation, which is expected if the trade-off is manifested in evolutionary terms, essentially does not exist. Negative phenotypic correlations have been reported in some organisms, but these show inconsistent variation among taxonomic groups and environments. The underlying economic principle predicts that the trade-off should be apparent if resources are limited but not necessarily if they are unlimited. I assessed the phenotypic (rp) and genetic correlation (rg) between egg size and number, as well as the heritabilities (h2) of both traits, in the yellow dung fly, Scathophaga stercoraria, in the laboratory at limited and unlimited food. At unlimited food, clutch size (h2=+0.41 & +0.74) and egg volume (h2=+0.38 & +0.37) were both heritable based on mother-daughter and half-sib/full-sib estimates, but the phenotypic (rp=+0.12 & +0.01) and genetic correlations (rg=-0.14 & +0.02) between them were nil. At limited food, in contrast, the heritabilities (clutch size: h2=-0.19 & +0.17; egg volume: h2=-0.14 & +0.28) were lower and partly non-significant, but at least the full-sib phenotypic (rp=-0.01 & -0.23) and genetic correlations (rg=+0.19 & -0.17) became negative, indicating a trade-off. I interpret this pattern as suggestive that at unlimited food h2 was maximized and there was no basis for the trade-off because environmental variance and maternal effects were minimized, whereas at limited food the treatment amplified variability in the physiological processes ultimately determining egg and clutch size and forced the trade-off upon the females. Non-significant half-sib (paternal) influences indicate that egg and clutch size are indeed maternal (as opposed to the offspring) traits featuring substantial variance components due to maternal effects. At both food treatments, clutch size was positively correlated with body size but egg volume was not. In a few cases, the genetic estimates changed drastically depending on whether body size variation was removed or not, underscoring the importance of body size for the underlying genetic correlation structure. SESSION No. 14, please

#### The evolutionary significance of Cytochome C Oxidase thermal sensitivity in fish muscle mitochondria.

#### P. Blier

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Environmental temperature variations have a strong effect on energy metabolism of ectotherms, which in tum, affects their physiology and ecology. Therefore, adaptations to cold habitats should proceed through adjustments of energy metabolism, partly by modifications of mitochondrial structure and function. In a previous study we have shown that the mitochondria of a temperate fish (brook charr) which possess mtDNA of a cold habitat species (arctic charr), have higher cytochrome c oxidase (CCO) activity than pure populations of brook charr. We have suggested that mtDNA of arctic charr could promote the synthesis of CCO with higher catalytic efficiency allowing higher aerobic capacity at lower temperature. In order to estimate how CCO thermal sensitivity affects the respiration of arctic charr muscle mitochondria, we determined the impact of CCO inhibition on mitochondrial respiration, *in vitro*, at four different temperatures (1, 6, 12 and 18°C). Our results suggest that the thermal sensitivity of mitochondrial respiration is unlikely to be dictated by CCO. The evolutionary significance of these results will be discussed.

Comparative mitochondrial DNA phylogeography and evolution in *Procavia* and *Heterohyrax* (Mammalia: Hyracoidea) from southern Africa

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Terrestrial vertebrates frequently show geographic partitioning of mtDNA polymorphisms and phylogeographic hypotheses predict that this is particularly evident in species with poor dispersal capabilities or where geographic barriers limit gene flow. Saxicolous small marnmals typically have disjunct distributions and the patchiness of their rocky habitat has strongly influenced the evolution of specialised morphological, reproductive and behavioral characters. Rock-dwelling hyrax, Procavia capensis and Heterohyrax brucei, are cormnon inhabitants of rocky habitats throughout the African continent. They exhibit extreme refuge-dependence; in East Africa, isolated granite outcrops represent spatially restricted islands with limited resources and genetic exchange between outcrops is rare. In southem Africa the refuge environment is varied; the Great Escarpment forms an extensive and connected network of rocks, while the Northem Cape, Northem Province and Zimbabwe are characterised by large rounded dome-like outcrops with scattered crevices, or isolated outcrops in a sea of grassland. We studied mtDNA variation (RFLPs and cytochrome b sequences) among 27 Procavia and 10 Heterohyrax populations. Both species were characterised by deep divisions within their intraspecific mtDNA gene trees and it seems likely that the distinct hyrax groups were already differentiated at the start of the Pleistocene and that they diverged further during the Quaternary. Heterohyrax, a specialist browser, is more restricted to suitable habitat. The phylogeographic break in Procavia is concordant with that of a co-distributed, but phylogenetically unrelated small marnmal, indicating shared vicariant histories.

# Adaptive dynamies in laboratory communities of bacteria and virulent bacteriophage

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Observations of laboratory communities of bacteria and their viral predators provide insight into the relationship between population dynamics and evolutionary change. The rate of evolutionary change in these communities is effected by interactions between. populations and the environment, with mutants arising sooner and invading faster in more productive environments. These evolutionary changes have dramatic effects on the population abundance and stability of the community members, as well as on the resulting community's response to changes in productivity. Moreover, subtle differences in the molecular bases of the interactions between bacteria and virus produce very different evolutionary trajectories and community structures. These experiments link the interactions of individuals through the dynamics of populations to the evolution of communities.

## Ecological influence on distribution of DNA curvature in bacterial genomes

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Computer analysis of completely sequenced prokaryotic genomes is the key to understanding the evolution of gene regulation and will provide invaluable direction for future experimental biological research programs in the subject. We analyzed the distribution of predicted intrinsic curvature along all complete bacterial genomes. Sequence-dependent DNA curvature is known to play an important role in transcription initiation of many genes. Our analysis supported this commonly accepted hypothesis. However, according to their curvature distribution, the genomes were divided into two groups. Curvature distribution in all bacteria of the first group indicated a substantial fraction of genes characterized by intrinsic DNA curvature located within or immediately upstream to adjacent untranslated regions. We did not find this peculiar DNA curvature distribution in bacteria of the second group. Remarkably, all bacteria of the first group are mesophilic, whereas bacteria of the second group are hypothesize that the DNA curvature plays a biological role in gene regulation in mesophilic as against hyperthermophilic prokaryotes, i.e. DNA curvature presumably has a functional adaptive significance determined by temperature selection. As more complete prokaryotic genomes are sequenced, further verification of this finding will pave the road for the future of Ecological Genomic Studies.

Polymorphic microsatellite markers for population analysis of a tephritid pest species, Ceratitis capitata.

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To asses the population genetic structure of the tephritid pest species Ceratitis capitata we have identified twenty-one simple sequence repeat sequences (microsatellites). Screening of partial, size-selected (<500 base pairs) library of the Mediterranean fruit fly yielded 30 positive clones. The most common dinucleotide repeat sequence was (TG)n [or (CA)n] that occurred in 28 of the 30 loci. The numbers of dinucleotide arrays range from at least 4 uninterrupted to a maximum of 20 uninterrupted arrays. The polymorphism of 10 of these 30 microsatellite loci was investigated in 122 flies from 6 natural populations collected in the species range: Kenya, Reunion, Madeira, Italy, Chios, and Peruí. Population genetic analyses indicated that the medfly populations can be divided into three main categories: ancestral (sub-Saharan populations), ancient (Mediterranean populations) and new (American populations), consistent with results obtained from allozyme studies and historically documented expansion of the medly. The consistency of the results obtained from microsatellite and enzyme markers and their evolutionary implications are discussed.

## Developmental expression of 412 retrotransposon in D. melanogaster and D. simulans

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Transposable elements, which are responsible for a large part of spontaneous mutations, participate to genetic variability. It is therefore very important to understand their dynamics and the mechanisms by which their copy number are regulated in natural populations. A study on 72 natural populations of *Drosophila simulans* revealed the existence of a latitudinal cline for 412 retrotransposon copy number. This copy number varied from 2 to up to 60 copies according to the population and a very important insertion site polymorphism along chromosomal arms was observed. Such variability was not observed in the sibling species *Drosophila melanogaster*. In order to understand the regulation of 412 copy number we investigated on 412 developmental expression in natural populations of *Drosophila simulans* and *Drosophila melanogaster*.

In *Drosophila melanogaster* populations we could distinct two categories of populations according to the absence or presence of 412 transcripts at the pupal stage. In this species no relation could be found between 412 transcript amount and copy number. In *Drosophila simulans* the developmental pattern of expression for 412 element varied greatly according to the population, with a strong expression in a few stages in populations with low 412 copy number, and a lower expression but in more stages in populations with high copy number.

These results show that 412 developmental expression depends on the population analyzed and that it is regulated by copy number and copy localization along chromosomal arms. Data suggest that 412 is regulated in part by host genes near which it is inserted and that total amount of 412 RNA along drosophila development decreases when copy number increases. Therefore it appears that no conclusion should be made on the developmental expression of a transposable element of a whole species from the study of only a few lines. These results will be completed by a study on male and female germ-line expression on different populations of *Drosophila melanogaster* and *Drosophila simulans*.

#### Negative cooperativity of heterodimers causes heterozygote advantage

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Ever since Simpson and Mayr set panselectionism in motion in the 1930s, the role of heterozygosity has been heavily debated. Wallace and Lewontin advocated for the balance position, arguing that heterozygotes are more vigorous than homozygotes. In contrast, Crow and Muller held the classical view assuming that heterozygotes are only a transient of purifying selection. Since Kimura's work on the neutral theory of evolution, it is controversial whether heterozygosity is based on neutral variants or is maintained by balancing selection. Apart from the haemoglobin polymorphism causing malaria resistance and sickle cell anemia, few studies have focussed on testing the alternative hypotheses based on mechanistic grounds. Many correlations between heterozygosity and fitness components have been observed, yet frequently polymorphic loci are used as neutral markers for studies in population biology. As a result of this conflict, the issue has reappeared recently in a number of reviews. Also, evidence has accumulated that balancing selection may operate at least at the phosphoglucose isomerase (PGI) locus in many species. Here, I present evidence for a molecular mechanism based on subunit interactions of the dimeric enzyme PGI of Daphnia magna that lend heterozygotes higher fitness. Since heterozygotes have both homodimeric and heterodimeric forms of a dimeric enzyme, it is only the heterodimers that can cause novel or superior function. I found that subunit interactions of heterodimers differed from those of homodimers. These interactions result in a dynamic shift in quaternary structure leading to negative cooperativity of the subunits. It is this negative cooperativity that causes higher efficiency of heterodimers and that explains overdominance not only in this system but perhaps also in many other multimeric and polymorphic enzyme loci

# Evolutionary patterns in metabolic pathways with constraints on enzyme availability

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As living cells have limited capacity to synthesize and to store proteins/enzymes, their metabolic activity may be constrained. A theoretical study was conducted to examine the consequences of such constraints upon the behavior of metabolic pathways under various evolutionary pressures. We considered linear pathways in which there was genetic variability for enzyme concentration. The metabolic efficiency of each genotype, measured by the flux through the pathway, was considered as the fitness of the genotype. The evolution of clonal populations of finite size was simulated, under selection for the flux, and adaptative landscapes were generated. Due to the constraint on the total quantity of enzyme, there is an optimal distribution of enzyme amounts along the pathway, that is to say a distribution which maximizes the flux. Upon evolution, the concentration of a particular enzyme in the population shifts towards its optimum value, with a variance depending on the population size and selection intensity. Interestingly, this distribution exhibits an asymmetrical shape as selection acts more strongly against concentrations that are above the optimum. This was confirmed analytically by studying the control of the flux through the pathway under constraint : for a given flux value, the absolute value of control coefficient is higher for the enzyme concentration above the optimum than for the concentration below the optimum. This asymmetrical response to selection for metabolic pathways allows testable predictions regarding variability of enzyme concentrations in natural populations. Further studies will include branched pathways, variability for the enzyme activities, and sexual populations.

# Compatibility between ants and their mutualistic fungi in two sympatric species of *Acromyrmex* leaf-cutting ants

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Interactions between organisms can give rise to co-evolutionary patterns that are different from habitat to habitat and from population to population. Studies on antagonistic interactions such as predation, competition and parasitism are theoretically well-founded, often experimental and have received much attention compared to studies on mutualistic interactions. The general hypothesis concerning mutualistic interactions is that, in contrast to antagonistic interactions, the most abundant phenotypes in the population should be favoured. After an initial period of strong mutual specialisation of the partners has taken place, interactions between mutualistic symbionts are therefore predicted to be less specific than for instance host-parasite interactions.

In order to test this prediction, lab experiments were conducted to reveal patterns of compatibility between leaf-cutting ants and strains of their symbiotic fungus. All possible combinations between ants and fungus of three colonies of each of two species of *Acromyrmex* were tested. In several cases incompatibility of ants and fungus strains lead to the death of the fungus in just a few days. Logistic regression with fungus mortality as the dependent variable revealed that differences between colonies are a more important factor contributing to fungus mortality than differences between congener species. The patterns of compatibility were used to assess differences between fungus strains originating from different colonies. The results found in this way matched differences in the genetic profiles of the fungi based on AFLP-fingerprinting techniques.

The fact that the same fungus strains are used by different species, seems to confirm the hypothesis that little specificity should be expected between partners in mutualistic interactions. However, the occasionally strong incompatibility between fungus and ants raises several intriguing questions.

# Are conspecific based strategies of breeding habitat selection evolutionarilly stable?

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Recent empirical work suggests that the use of local reproductive success of conspecifics to select a breeding habitat may be an optimal strategy and may thus affect dispersal. However, this may depend on both environmental predictability and species life history. We built a two-patch dernographic matrix model using game theory to address the question of the evolutionarily stability of breeding habitat selection strategies according to environmental predictability (leve; of temporal autocorrelation of patch quality) and species life cycle. We considered three non conspecific-based strategies: (1) random choice, (2) philopatry, (3) choice according to patch quality the previous year; and two conspecific-based strategies: choice according to previous year (4) presence, and (5) local reproductive success. Results suggest that the strategy of using local reproductive success is likely to be selected in migratory birds for intermediate and high leveis of temporal autocorrelation. When comparing the spatial distribution of individuais to the Ideal Free Distribution (IFD), we find that the use of this cue may lead to higher spatial aggregation of individuais than would be expected on the basis of environmental heterogeneity alone. We discuss the potential consequences of these results for understanding the dynamics of the spatial distribution of individuais and thus for conservation biology.

# Factors affecting the genetic load in *Drosophila*: Synergistic epistasis and correlations among fitness components

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Two factors which can affect genetic load were investigated in *Drosophila melanogaster*. A set of five chromosomal regions containing visible recessive mutations were put together in all combinations to create a full set of 32 homozygous lines fixed for different numbers of known mutations. Two measures of fitness were made for each line: productivity (a combined measure of fecundity and egg-to-adult survivorship) and competitive male mating success. Productivity, but not male mating success, showed a pattern of strong synergistic epistasis, such that the log fitness declined non-linearly with increasing numbers of mutations. Synergistic epistasis is known to reduce the mutation load. Furthermore, productivity and male mating success were highly and positively correlated across genotypes. Given that male mating success affects relative fitness without affecting the mean fitness of a population, this positive correlation would lead to lower frequencies and lower fixation rates of deleterious alleles without higher costs to the mean fitness of the population.

### Bicyclus butterflies and developmental aspects of stress

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The african butterfly, Bicyclus anynana, expresses phenotypic plasticity as an adaptive response to seasonal environments. The alternative wet and dry seasons reflect one favourable, and one stressful environment. This paper will discuss investigations of the mechanisms underlying this response both in terms of developmental time and developmental stability. We have performed selection experiments on egg-adult developmental time and obtained evidence that genetic variation at specific enzyme loci contribute to the response to selection. We have also applied window treatments of a heat stress to begin to explore how the timing of the stress influences the stability of eyespot development on the wings of the adult butterfly.
# Molecular phylogeny of Wolbachia symbionts within four genera of the Tetranychidae

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*Wolbachia* are a group of intracellular vertically transmitted bacteria, which can alter host reproduction in several ways. They are widespread in insects, have been found in isopods and nematodes, and have recently been reported in several mite species. Phylogenetic studies of *Wolbachia* strains have generally used sequences from three different genes: the 16S rRNA gene, the cell-cycle *ftsZ* gene and the surface protein *wsp* gene. The 16S rRNA gene evolves at a slower rate compared to the *ftsZ* gene, which evolves slower than the *wsp* gene. Presently, *Wolbachia* strains are classified into four distinct groups labeled A, B, C and D. Groups C and D include *Wolbachia* strains found only in nematodes where host and *Wolbachia* phylogeny are concordant. The effects of the bacterium in nematodes are unknown. Within groups A and B, *Wolbachia* have been shown to cause cytoplasmic incompatibility, parthenogenesis, feminization and recently male killing strains have been found. No relationship between host phenotype and *Wolbachia* phylogeny has been found in these groups.

In spider mites (Acari, Tetranychidae) *Wolbachia* infections have already been reported in some species from three genera, *Eutetranychus*, *Oligonychus* and *Tetranychus*. Here we report on *Wolbachia* infection in two thelytokous species of the genus *Bryobia* (Acari, Tetranychidae). We have also sequenced the *ftsZ* and *wsp* genes of *Wolbachia* strains found in infected species from each of the four genera of the Tetranychidae. All *Wolbachia* strains were from the B group. Sequence variation in the *wsp* gene is greater than the *ftsZ* gene and allows greater phylogenetic resolution within the B group of *Wolbachia*. *Wolbachia* strains found in the Tetranychidae do not cluster within the B group, indicating polyphyletic origins of the infection within this family. The phenotypic effects of *Wolbachia* within *Tetranychus urticae* and *Bryobia kissophila* will be discussed.

# Window experiments and the effects of heat shock on wing eyespot asymmetry in Bicyclus anynana

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Fluctuating asymmetry (FA) is used as a tool, for example in conservation studies, to study the effects of environmental and/or genetic stress. The goal of this project is to study the interactions between specific developmental mechanisms and the nature and timing of different stresses. This was done in two heat shock experiments, being replicates, using the tropical butterfly species *Bicyclus anynana* (Butler). Heat Shocks (39.5 °C) were applied at different stages of development (crawler, prepupal, 1, 14, 25, 48 and 62 hr stage) for different lengths of period (window experiments). The effects of the treatments were studied measuring FA of wing pattern elements, paying particular attention to the eyespots. FA, being a measure of developmental instability, should be higher in the stressed groups. The eyespots can be considered serial developmental homologues, each one being specified by the same basic developmental pathway. Results on the outcome of this experiment will be presented.

# What is the impact of transposable elements on host genome variability?

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The spread of a transposable element family through a wild population may be of astonishing rapidity. At least three families of transposable genetic elements have recently invaded *Drosophila melanogaster* worldwide, including the *P* element. The mechanism has been a process of effectively replicative transposition, and, for the *P* element, has occurred notwithstanding the sterility induced by unrestricted movement. This element's invasion into *Drosophila melanogaster* has been accompanied by the development of heterogeneity between *P* sequences, most of which now have internal deletions. Increasing evidence suggests that some deleted elements can repress P transposition, thereby protecting the host from the harmful effects of complete elements. Such repressing elements may rise to high frequencies in populations as a result of selection at the level of the host. We here investigate selective sweeps invoked by the spread of P sequences in *Drosophila melanogaster* populations, and which are associated with repression of P element transposition. Unexpectedly, sequences adjacent to high frequency P element sites do not show reduced levels of genetic diversity, and DNA variability is in linkage equilibrium with the presence or absence of a P element at the adjacent selected site. This might be explained by multiple insertions or through a selection for recombination analogous to that seen in "hitch-hiking".

# Retroposons and the creation of novel genes: The novel neuron-specific genes for BC1 and BC200 RNA were recruited from SINEs.

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A general tenet is that functional non-messenger RNAs are fossils or remnants from the RNA/RNP worlds and gradually are being replaced by protein molecules in modern cells. If this were the case, there would be no need to recruit or exapt novel RNAs for cellular tasks. However neuronal BC1 and BC200 RNAs are relatively recent acquisitions and restricted to rodents and primates, respectively. Both genes were generated by retroposition (reverse transcription of the founder RNA and integration of the cDNA copy into the genome) of tRNA-Ala and a monomeric Alu element, respectively. Although they are not homologues, BC1 and BC200 RNA are exceptional in their sub-cellular localization: both RNAs are transported into dendritic processes of neurons where they may regulate decentralized protein biosynthesis near synapses.

SINEs and other retrosequences (e.g. mRNA-derived) have not only contributed to the formation of novel genes but also are a source of numerous control elements that regulate expression of targeted genes.

# Evolution of a specialised ant-plant mutualism in the genus Leonardoxa (Caesalpinioideae).

## Carine Brouat and Doyle McKey

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In the genus *Leonardoxa*, evolution has produced species having different degree of myrmecophytic specialisation, from diffuse associations to specific symbioses between the plant and a specialised ant. In this last case, species are called myrmecophytes and develop hollow and swollen twigs in which symbiotic ants inhabit. Because it comprises both non-myrmecophytic and myrmecophytic species, the genus *Leonardoxa* provides a good opportunity to study the origin and evolution of ant-plant mutualisms.

In myrmecophytic *Leonardoxa*, many morphological characters appear related to the degree of specialization in the ant-plant interaction. Current ecological and morphological data suggest that the gradient in ant-plant relationships could be reflected by phylogeny. We present here the first phylogenetic relationships obtained on an ant-plant genus, based on the analysis of cpDNA non-coding sequences and AFLP markers. Our results reveal a more complex evolutionary history than expected, with possible introgressive events between myrmecophytic and non-myrmecophytic *Leonardoxa* taxa.

# Have lateral gene transfers up-rooted the universal tree of life?

## James R. Brown

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In the canonical view of the universal tree of living things, there are three major urkingdoms or domains of life, the Archaea (archaebacteria), Bacteria (eubacteria) and Eucarya (eukaryotes) with the latter two groups being more closely related. The flood of genomic sequence data now provides a more thorough examination of this hypothesis. The increasing frequency of protein phylogenies that are in conflict with the conventional universal tree suggests that lateral gene transfers have been a evolutionary major force in shaping genome architectures. In light of seemingly extensive intergenomic DNA exchanges among very disparate organisms, is the concept of the universal tree still a tenable hypothesis? The impact and possible accommodation of organelle endosymbiosis, genetic exchanges between Gram-positive bacteria and the Archaea, and other modes of lateral gene transfers into the universal tree hypothesis will be discussed.

(Invited talk: *Microorganisms, mobile elements and evolution* 18. Horizontal gene transfer: past and present role in evolution)

# Co-operation and conflict in host-manipulating parasites

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The existence of adaptive host manipulation by parasites has received increasing empirical support in recent years. An optimality model is developed of the extent of host manipulation, incorporating within-host group size, relatedness and a range of realistic cost / benefit functions. The model highlights the co-operative nature of host manipulation, and the potential for cheating this entails. When relatedness in parasite groups is minimal, manipulation is suppressed, but not eradicated - reflecting the importance of inter-host selection. A distinctive threshold phenomenon is predicted for a wide range of parameter values. Below the group size threshold, manipulation is zero. Above the threshold, the predicted behaviour depends critically on the biological details of the individual / group interaction. A range of test-cases are discussed, including macroparasite manipulation of intermediate hosts, concomitant immunity and quorum sensing bacteria.

## Bacteria-phage coevolution: the effect on host genetic diversity

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Theory suggests that host-parasite coevolution generally increases host genetic diversity as a result of selection increasing the ability of parasites to infect common (relative to rare) host genotypes. This is only likely to occur when the rate of host evolution is essentially static relative to that of the parasite. If host evolution is on a comparable time-scale to that of the parasite, host-parasite coevolution might be expected to decrease host genetic diversity (in asexual host species), as a result of common host genotypes having a higher probability of developing resistance against the parasite. We tested this hypothesis using the common plant-colonising bacteria, *Pseudomonas fluorescens*, and a naturally associated viral parasite (phage), in laboratory microcosms. In static culture conditions, *P. fluorescens* undergoes explosive genetic diversity. Moreover, the population structure differed hugely between replicates, suggesting this reduction in diversity was not simply the result of certain genotypes having an intrinsic advantage in the presence of phage. The interaction of phage and bacteria from different time points in the experiment revealed a number of steps of bacterial resistance followed by phage counter-resistance. Diversity increased and variation between cultures decreased after the most noticeable period of coevolution ended. Short-term competition experiments demonstrated that common genotypes had an advantage in the presence of the increased probability of beneficial mutations arising.

# Evolution of the neo-XY sex determination in grasshoppers of the genus Asiotmethis UV. (Orthoptera, Pamphagidae)

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Extreme karyotype conservatism has been demonstrated in the Pamphagidae grasshoppers (2n male=19 and 2n female=20 acrocentric chromosomes; sex determination is XOmale/XXfemale (Alicata et al., 1976; Camacho et al., 1981; Santos et al., 1983; Cabrero et al., 1985). However, comparative cytogenetic analysis of some Asiotmethis species from Kazakhstan, and Bulgaria does not support the view of uniform karyotypes in Pamphagidae. At least two types of chromosome sets have been observed: 1) standard karyotypes with acrocentric chromosomes only (*Asiotmethis muricatus* (Pall.) and 2) karyotypes with 2n%=16+neo-XY and 2n&=16+neo-XX (*A. limbatus* (Sharp.), *A. heptapotamicus* (Zub.), and *A. zacharjini* (B.-Bienko) as a result of mutual translocation of the large acrocentric autosome and originally acrocentric the X-chromosome.

Furthermore, results of the comparative karyotypical analysis of the presented Pamphagidae allow discussion of the origin of structural differences between the autosomal arm of the neo-X (X) chromosome and its homologue neo-Y. The initial stage of the heteromorphization of the neo-Y has been found in *A. zacharijni*. In this species the neo-Y chromosome and the X<sub>1</sub> arm of the neo-X chromosome appear isomorphic and they exhibit a typical distribution of chiasmata during meiotic prophase. The next stage of differentiation between the X<sub>1</sub> arm of the neo-X and neo-Y is demonstrated by *A. limbatus* and *A. heptapotamicus*. In this species the neo-Y has minute multiple heterochromatic blocks in proximal region (*A. limbatus*) or has a large double proximal C-block (*A. heptapotamicus*)

A progressive heterochromatinization of the neo-Y is a cytogenetic feature of the evolution of Pamphagidae grasshoppers with neo-XY%/neo-XY& sex determination.

# The SRY gene HMG-box in micro- and megabats

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In 1990, Sinclair *et al.* and Gubbay *et al.* identified an open-reading frame located on the human and mouse Y chromosome, called Sex Determining Region Y gene (*SRY/Sry*). The *SRY* gene contains a single exon, which encode a protein of the HMG family of nonhistone proteins. This protein is characterized by a DNA-binding domain of approximately 79 amino acids called HMG-domain. The sequence encoding the HMG-domain is designated as the HMG-box, which is similar across mammalian species. However flanking regions are poorly conserved and vary in both length and composition (Tucker and Lundriganm 1993; Whitfield *et al.*, 1993). Molecular genetic data suggest that *SRY* is the mammalian testis-determining gene. This gene is hypothesized to function as a transcription factor, triggering a cascade of gene interactions that induces the bipotential foetal gonads to develop into testes. However, how this gene works is unclear at the moment. Although the nucleotide sequence of the *SRY* HMG-box is currently available in a number of mammalian taxa, nothing is known concerning this gene in bats. We report partial sequences of *SRY* HMG-box from six microbats and four megabats species. Furthermore, we used the *SRY* HMG-box sequences from micro- and megabats to test the phylogenetic relationships between Microbats, Megabats and Primates.

# Factors affecting the stability of an insect-fungus mutualism

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Abstract. *Botanophila phrenione* flies act as "pollinating" parasites of the ascomycetous fungus, *Epichloe typhina*. Flies transfer fungal spermatia (gametes) among fungi as they visit their hosts for oviposition. Fly larvae consume the products of cross fertilization (ascospores). I tested if the cost to the fungus of engaging in the mutualism rises as fly visitation increases and if mechanisms operate to prevent excessive exploitation of the fungus. Fungi and flies were monitored over three years. I recorded the reproductive output of fungi, the amount of feeding by fly larvae on host reproductive tissues, and the mortality of fly eggs and larvae. In two of three years, fly eggs were randomly dispersed; eggs were clumped in the remaining year. *Epichloe* was insensitive to *Botanophila* egg load; fungi receiving one to several eggs did not differ in their reproductive output. Hence, the interaction appears quite stable. My data suggest the stability is due to three features: 1) high levels of egg/larval death due to unknown causes, perhaps disease, 2) high egg load leads to larval competition and 3) *Epichloe* appears to be spermatia limited.

#### Modularity and Mosaics in organisms: Consequence for disparity in Evolution

## A. D. Buscalioni

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The Cambrian explosion is a good example to explore the genesis of the metazoans body plans. A panoply of animal organisation is revealed in Cambrian fossils when compared with recent body plans. The body modules in many Cambrian fossils show at different levels of organisation (number of modules, number or combination of element) a wide range of variation. Cambrian fossils may be discussed as mosaic organisms in where the dissociation or duplication of a module or the elements that forms it occurs. Mosaics are viewed as a collection of uncorrelated traits that increased the phenotypic solutions of a morphospace, and thus the disparity (variation of body plans). Since mosaics are recognised as transitional organisms within lineage or body plans, they can be used to explore the evolution (homology, variation and canalisation) of body plans.

Are / were parasitoids really in vivo vectors for the horizontal transfer (HT) of Wolbachia amongst arthropods?

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Wolbachia are a group of intracellular parasitic a-proteobacteria found within a diverse range of arthropod hosts which frequently alter the host's reproductive physiology. Molecular phylogenies based upon several gene fragments show no congruency between the distribution of Wolbachia and the phylogeny of their arthropod hosts, but suggest that extensive horizontal transfer (HT) between phylogenetically distant hosts occurred over evolutionary time. Of the several possible vectors suggested for HT, insect parasitoids have been confirmed as vectors in vitro experimentally, with HT efficiencies dependent upon the parasitoid life history and as high as 1%. In contrast, several studies of Wolbachia within parasitoid giulds have found no evidence to support the predicted congruency between Wolbachia phylogenies found in parasitoids and their respective developmental hosts, calling into question the role of parasitoids as vectors for HT in vivo. However, the rate limiting step in establishing Wolbachia infections in new insects is shown to be principally due to the efficiency of subsequent vertical transmission, and also the ability to induce altered host reproductive physiology, which are both dependent upon host and Wolbachia isolate interactions. Thus parasitoid-mediated HT may occur relatively frequently in vivo but are rarely apparent as the infections fail to establish and spread. The data from ongoing field studies provide some, albeit equivocal, support for this hypothesis with two examples of localised temporal congruency of Wolbachia isolates found in insect hosts and their associated parasitoids, and one example of recombination between different Wolbachia strains.

#### On the average coefficient of dominance of spontaneous viability mutations

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Estimates of the average coefficient of dominance of mild deleterious mutations are essential for theoretical predictions in population and quantitative genetics. Classical estimates obtained from experiments conducted by T. Mukai and co-workers and O. Ohnishi in the 60's and 70's suggest average coefficients of about 0.4 for minor viability mutations in *Drosophila melanogaster*. These estimates have been generally accepted by population geneticists. However, both the analysis of the experiments and the results are controversial. We have re-analysed Ohnishi's data and obtained estimates of about 0.2, suggesting higher dominance than previously thought. We also run computer programmes to simulate experiments in which average coefficients of dominance are obtained from chromosomes extracted from natural populations or from mutation accumulation lines. In the analyses, we use different models of mutation, such as variable mutation rates, distribution and magnitude of effects and dominance. The results indicate that models with low mutation rates and average coefficients of dominance of the order of 0.2 are compatible with the empirical observations.

# Where do the Galapagos tortoises come from? A Phylogeny based on mtDNA data

## Caccone A.

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Although the Galápagos tortoises have become a symbol for efforts to conserve the unique fauna of the Galápagos islands, little is known about the tortoises' origins and evolutionary history. We present a phylogenetic reconstruction based on mtDNA sequence divergence among the subspecies of the Galápagos tortoise (*Geochelone nigra*) and other Geochelonids from mainland South America and Africa. The data clearly indicate that the closest relative to the Galápagos tortoise is the small-bodied Chaco tortoise, *G. chilensis*. Within the Archipelago, there are 11 extant subspecies or "races" of *G. nigra*. Previous morphological and allozyme studies did not permit discrimination between individuals of all subspecies. The mtDNA sequence data suggest that the subspecies on the two oldest islands (San Cristóbal and Española) are sister taxa, whereas the largest and youngest island (Isabela) has been colonized at least twice. These data are also consistent with the suggestion that four of the named subspecies on Isabela are not genetically distinct units. The identification of unique nucleotide substitutions distinguishing subspecies indicates that mtDNA can be used to identify the origin of captive animals heretofore of unknown origin. This finding is of great practical importance in the conservation efforts of these threatened giant reptiles.

## A transposable element mediated the generation of a Drosophila widespread chromosomal inversion

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The origin of chromosomal rearrangements, particularly that of the polymorphic inversions of the genus Drosophila, is a highly debated and still non-clarified issue. Here, we report the cloning and sequencing of the breakpoints of the cosmopolitan polymorphic inversion 2j of Drosophila buzzatii. We have found large insertions at both breakpoints of the inverted chromosome that are not present in the 2 standard (2st) arrangement. The presence of the insertions in 21 2j lines and their absence in four 2st lines has been confirmed by PCR amplification of the regions spanning the breakpoints. The insertions correspond to middle repetitive sequences that end in inverted repeats and are flanked by 7-bp target duplications. They presumably represent copies of a new class II transposable element, that has been named Galileo. The homologous sequences inserted in opposite orientation at both breakpoints and the exchange of the two pairs of target site duplications between the copies of the transposon indicate that the inversion arose by an ectopic recombination event. Thus, this is the first direct demonstration of the involvement of transposable elements in the origin of natural inversions in *Drosophila*. However, despite the transposon-mediated origin, the sequence diversity at the breakpoint regions in three 2st and five 2j chromosomes suggests that the inversion is monophyletic. Finally, although the transcriptional startpoint of the gene *Pp1a-96A* is located only 156 bp away from the proximal breakpoint, an expression assay has revealed that the breakage and inversion process did not affect neither this nor any other gene located close to the breakpoints.

## Genetic and environmental effects on morphology and fluctuating asymmetry in nestling barn swallows

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Developmental stability is an organism's ability to buffer its development against environmental and/or genetic stress. Random errors in the development of bilateral morphological traits are one measure of developmental stability, termed fluctuating asymmetry. Individual differences in stress resistance can be studied as heritability of fluctuating asymmetry. Heritabilities are generally high for morphological traits, and low for fluctuating asymmetry in those traits, while their magnitude can change with environmental conditions. A barn swallow *Hirundo rustica* nestling cross-fostering experiment with simultaneous brood size manipulation was conducted in two years with contrasting weather conditions. Heritability was estimated from both full-sib analysis and parent-offspring regression. Effects of year and brood size manipulation were stronger on morphology than on asymmetry. Significant heritabilities for morphological traits were found only in enlarged nests irrespective of year effects. Under some conditions, significant heritabilities were found for tarsus and tail asymmetry. Heritability of tail asymmetry was smaller, but heritability of tarsus asymmetry was of similar magnitude as heritabilities for morphological traits. The results are discussed with respect to the imperfect correlations between fluctuating asymmetry and developmental stability, and between nestling and adult traits.

Assessment of genetic variability in *Hydrobates pelagicus* (Aves ; Procellariiformes) along the French Atlantic coast.

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Hydrobates pelagicus is a sea bird distributed mainly (between 50% and 65% of the world population) in Great Britain and Ireland (Ratcliffe *et al.*, 1998). In France along the Atlantic coast its habitat is restricted to small islands resulting in a poor distribution of colonies. In the northern part of the Bay of Biscay, a population breeds in Brittany with important colonies in Banneg archipelago. In the southern part of the Bay of Biscay, there are two colonies at Biarritz, belonging to the Cantabric population (Atlantic coast of northern Spain). Ecological studies demonstrated that, despite contact between the Cantabric and Banneg colonies, no mating were observed (Hemery, in preparation).

In order to evaluate genes flux between distant colonies of *Hydrobates pelagicus* in Biarritz and in Banneg, we chose, as a first approach, to use a highly DNA based polymorphic marker. Cytochrome b DNA has been demonstrated as a useful tool to study closely populations (Avise, 1989). Here we report the first results of this study.

### X-Linked meiotic drive in *d. simulans*: where does the reduced fertility of *sex-ratio* males come from?

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The *sex-ratio* trait, known in several *Drosophila* species, results from X-linked meiotic drive that affects Y-bearing sperm and causes *sex-ratio* males to produce female-biased progeny. Driving X chromosomes are widespread in natural populations of *Drosophila simulans*, where their frequency varies from 2 to 60%. However, lab experiments have demonstrated that *sex-ratio* males suffer from reduced fertility. In order to understand the maintenance and the distribution of the observed polymorphism, the origins of this reduced fertility have been investigated.

Observations of spermiogenesis have shown that *sex-ratio* males present abnormal spermatid development and abnormal behavior of the Y chromosome during the second meiotic division. A relation between these two phenomena has been demonstrated through *in situ* hybridization. These abnormalities may explain some of the deleterious effects but they are not sufficient to explain the strong reduction of fertility observed in competition. Experiments performed when *sex-ratio* males are in competition with standard males revealed that *sex-ratio* males have a weaker mating ability than standard ones. Furthermore, in spermatic competition, sperm of *sex-ratio* males is strongly displaced by sperm of standard males, whereas sperm of standard males resists to displacement by sperm of *sex-ratio* males.

The evolutionary consequences of these properties will be discussed in regard to the geographic distribution of driving X chromosomes in natural populations.

## **Stress and Transposable Elements**

# P. Capy

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At the end of the 70's, transposable elements (TEs) were considered as "selfish". Few years later, in the 80's, it was suggested that such elements may have an important impact on the evolution of the genome structure. Indeed, their movements can be at the origin of many mutation types including translocations, inversions, insertions, deletions, imprecise excisions.

While most of these events have deleterious effects, some of them may generate slightly advantageous novelties that can be selected and then favor the adaptation of populations and species to their environment. More recently, it was also suggested that stresses may induce TEs mobility leading to a genome re-organization.

Several factors have already being analysed for their effects on TEs mobility. Among these factors, temperature was initially tested on elements belonging to the copia super-family. If the first results were encouraging, it was rapidly shown that it was necessary to test several populations since contradictory results were obtained.

The most demonstrative evidence is provided by the analysis the tnt1 retrotransposons of Nicotiana tabacum, for which biotic and abiotic wounding may induce the element transcription.

The mariner transposon also shows such a phenomenon. Its somatic activity (correlated to its germline activity) increase with the breeding temperature and after pesticide treatments. Some examples will be detailed and discussed.

# Genetic variation for host susceptibility and parasite infectivity in a Daphnia - parasite system

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Knowledge of coevolutionary interactions between parasites and their hosts contributes to the understanding of the spread of diseases, the evolution of virulence and the evolution of sex. Genetic variation for host susceptibility and parasite infectivity is an important assumption underlying theories of host and parasite evolution. We used the freshwater crustecean *Daphnia magna* and one of its microparasites, the bacterium *Pasteuria ramosa*, to study within population genetic variation for host susceptibility and parasite infectivity. We sought to answer the following questions: Do hosts differ in their susceptibility to parasite isolates ? Do parasite isolates differ in their ability to infect different hosts? Are there host - parasite isolate interactions? The analysis showed that there is considerable variation in both host susceptibility and parasite infectivity. Significant host - parasite isolate interactions indicated the potential for frequency dependent selection. In addition correspondence analysis revealed that different host clones are susceptible to the same set of parasite isolates and different parasite isolates may infect the same set of host clones. Thus some clones, although distinguishable with neutral genetic markers, shared resistance genes and different parasite isolates appeared to have virulence genes in common.

# The fate of generous and greedy strategies in the iterated Prisoner's Dilemma and the Chicken Game under noisy conditions

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The iterated Prisoner's Dilemma has become a standard for analyzing the success of cooperative strategies in repeated games. In order to broaden the perspective of these kind of games, we analyzed the success of two sets of strategies in both an iterated Prisoner's Dilemma and an iterated Chicken Game, under different levels of noise. In a Chicken Game mutual defection gives the lowest payoff while in a Prisoner's Dilemma cooperation against a defecting opponent gives lowest payoff. We introduce a new approach to describe strategy behavior, in which strategies are defined as generous or greedy depending on the frequency at which they play cooperate and defect, respectively, in the actual tournament. The results reveal a striking difference in the outcome between the two kinds of game, which suggests that analyses beyond the Prisoner's Dilemma paradigm are necessary to obtain a more general picture of the conditions favoring cooperative behavior among organisms.

## Male Biased Mutation Rates in Avian ATP Synthase a-subunit (ATP5A1) Sequences

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Whether the mutation rate differs between sexes has been a matter of discussion over years. Molecular analyses of mammals have indicated that males mutate more often than females, as manifested by faster rate of Y than X chromosome evolution. As suggested by Mc Vean & Hurst (Nature 386:388-392), however, these observations can as well be interpreted as specific reduction of the X chromosome mutation rate, which would be adaptive because of reducing the number of slightly deleterious recessive mutations getting exposed in hemizygote males. Recently, data from birds have provided strong evidence that vertebrate mutation rates indeed may be male-biased. In birds, females are the heterogametic sex, and analyses of the Z-linked CHD1Z gene have shown that it evolves faster than the W-linked (female-specific) CHD1W gene (Ellegren & Fridolfsson: Nature Genetics 17:182-184). We have now studied the second gene known to exist in one copy on the avian Z chromosome and one on the W chromosome; the ATP synthase a-subunit (ATP5A1). In a consistent manner for three pair of bird species from divergent linages, intron sequences of the Z-linked copy evolved faster than the W-linked copy. From these data we calculated an average male-to-female mutation rate ratio (a) of 3.0 in birds.

## Biogeography of the lizards Gallotia and Tarentola in Macaronesia

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Macaronesia comprises the archipelagos of Azores, Madeira, Selvages, Canary Islands and Cape Verde islands and is situated in the Atlantic ocean in the area 15°-39°N and 13°-31°W. The geographic situation, orography, climatic characteristics and the relatively rich endemic fauna of these archipelagos represents an ideal framework to investigate the ecology and evolution of biotas. For our study, we have chosen two reptile groups relatively abundant in Macaronesia: geckos of the genus Tarentola and the lacertids assigned to Gallotia. Tarentola comprises approximately 18 species of which 8 have mainland distributions in Africa and Southern Europe, 8 more are distributed among all the archipelagos of Macaronesia except the Azores and the remaining 2 are present in the Greater Antilles (Cuba and Jamaica). Gallotia is endemic to the Canary Islands and comprises 6 extant species and several subspecies that inhabit all seven islands of the archipelago. To study the biogeography of these two reptile groups we have used a molecular approach based on the partial sequencing of several fast and slow evolving mitochondrial genes (Cytochrome b, Cytochrome Oxidase I, 12S rRNA, 16S rRNA) and of a very slow evolving nuclear gene (c-mos). We analysed sequences from around 70 populations representing almost all the species of Tarentola plus several of its outgroups, and from 80 populations including all the species and subspecies of Gallotia and two close outgroups. The results show that the genus Gallotia is monophyletic and exhibits a westward colonisation pattern clearly influenced by the time of origin and geographic proximity of the islands. In contrast Tarentola shows a very different and unexpected pattern involving long distance inter-archipelago colonisation. The major biogeographic hypotheses generated, the taxonomy and internal phylogeny of each group and the characteristics and performance of the different molecules analysed will be discussed.

## Dynamic systems and speciation events

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The genetic change analysis raises a "microscopic" view over speciation process. Diffusion and other partial differential equations allow, under certain conditions, to describe the change in gene frequencies for all genes, alleles and interactions between them. However, the solutions or, even the behaviour of equations, are extremely difficult to obtain or study due to the great number of parameters implicated. Systems theory approach is integrative and deals more with interrelation sets (patterns) than with the analysis of parts (structures). System theory advantages are discussed in order to explain evolutionary processes. Interaction is defined as deviation from independence in the effect of the parts over the whole. It will be shown that it is possible to define the series: *individual, population, species* as a sequence of variable interaction sets  $\{I\}, \{I\}, \{I\}, with certain properties and an associated (connected with fitness) function <math>f(a, b, ...)$  in each case. An adequate abstract space where these interrelations could be represented it should be defined. A discussion about the properties of the distinct defined sets and the possible spaces it is done. The general condition for reproductive isolation:  $\P f [\{f(I)\}] / \P a = 0$ , a, because f is null; is obtained as a first step in the introduction of speciation as a result of a dynamic system. Trabajo parcialmente financiado por el proyecto XUGA 10304B97 (investigador principal H. Naveira F.)

# Evolutionary genetics of suppressors of "sex-ratio" meitoic drive in Drosophila mediopunctata

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"Sex-ratio" is a kind of X-Y meiotic drive known to occur in several Drosophila species: males carrying certain X chromosomes (called "SR") produce female-biased progenies due to the loss of Y-bearing sperm. We are using the sex-ratio trait of D. mediopunctata as an experimental model to study the evolution of sexual proportion. We have already obtained an experimental demonstration of Fisher's Principle and of the heritability of sexual proportion, and now we are studying the population genetics of the Y chromosome. We found a widespread Y-polymorphism in natural populations of D. mediopunctata: there are Y suppressor and Ynon-suppressor chromosomes; the former suppresses SR expression, and thus has a fitness advantage (~6%). This polymorphism is unexpected because theoretically it is very difficult to stabilise non-neutral Y-polymorphisms. We propose that non-neutral Y polymorphisms may be stabilised by an equilibrium between meiotic drive and Natural Selection, resulting from interactions in the population dynamics of X and Y alleles. Numerical simulations showed that this mechanism may stabilise non-neutral Y polymorphisms. It is also possible that the polymorphism is transient. We are currently testing the mechanism of Y-polymorphism stabilisation that we proposed. Field data spanning nine years shows that the frequency of Ysuppressor is not rising steadily (1988: 10%; 1996: 43%; 1997: 30%; chi-square test: P = 14%), so the polymorphism is not transient. The difference between 1988 and 1996 is almost significant (P =7%). Theoretical studies indicate that a substantial portion of the parameter space results in limit cycles, a possibility that is not excluded by the empirical observations of Ysuppressor frequencies. We are now isolating Y-linked molecular markers in D. mediopunctata. Our goal is to use the molecular clock to estimate the age of the Y-polymorphism, and thus verify its stability over a much broader time scale (e.g., million years).

A site-by-site analysis of vertebrate cytochrome b shows high substitution rate heterogeneity among lineages in accordance with a covarion model.

## Casane D., Lopez P., Le Guyader H., Philippe H.

It is well known that different amino acid residues of a protein have different functional constraints so that the substitution rate varies among sites. The gamma distribution has been widely used for modeling this rate variation. The effect of rate variation among sites on phylogenetic reconstruction and divergence time estimation has been discussed extensively. Current models always assume that the substitution rate, although it varies among sites, is the same among various evolutionary lineages at a given site. However, the covarion hypothesis states that at any particular point in the evolutionary history of a protein only a fraction of its amino acid positions are free to vary and that the memberships of the variable and invariable pools change over time.

The large sample of vertebrate cytochrome b available in GenBank allows us to test this hypothesis. We sampled fifteen large monophyletic lineages of mammalia, archosauria and "fishes". We found that although the shape of the gamma distribution is homogeneous among lineages ( $a \sim 0.3$ ), the rate of substitution at a site can varies greatly in different lineages. Using four rodentia lineages, a significant level of heterogeneity is already found (26%). Taking all the lineages together, 90% of the testable sites (variable enough to apply a statistical test) show heterogeneous substitution rate. We have shown that the percentage of heterogeneity depends on the number of lineages, but also on the phylogenetic distances between groups. We did not find evidence that the variation of amino acid substitution rate depends on variation of mutation rate. These observations are in accordance with the covarion model with a rapid rate of exchange of codon in the covarion class. We examined the consequences of such an evolutionary model on phylogenetic reconstruction.

# Endochondral ossification constrains minimum fledging time in birds

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Recent hypotheses on avian bone growth supported by empirical results suggest that species with relatively long wing bones would take longer to fledge than those with relatively short wing bones. Since fledging time is an expression of overall body growth, the question is why endochondral ossification limits overall growth rate. In general, the mathematical expression of growth for many soft tissues is an exponential function. That is the result of the whole expansion of the organ due to the division of all cells. In contrast, in mineralised tissues, cells included in the matrix do not divide. Growth can by reached only by peripheral apposition of new material but not by internal expansion as for soft tissues. Thus, mathematical expression of growth is a linear function or even a power function if we consider growth in every direction. But growth rates given by these functions never reach those from exponential function. Such a model is consistent with longitudinal growth of long bone and the endochondral ossification process: only chondrocytes in the limited area of proliferation of epiphyseal plates undergo mitosis, while hypertrophied chondrocytes and the osteoblasts that replace them remain unable to divide. In conclusion, the inability of wing long bones to grow as rapidly as the soft tissues would be a causal basis limiting the overall body growth that constrains a minimum fledging time of birds. A model predicting the scaling of avian fledging time as a function of the cell kinetics in longitudinal bone growth is suggested. Our results from a sample of 133 species of birds are consistent with these predictions.

## Study of some fitness components in two mtDNA haplotypes of Drosophila subobscura

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Previous studies on the distribution of mtDNA haplotypes in the Old World populations of *Drosophila subobscura* have shown the presence of two widespread and almost equally frequent haplotypes (I and II), as well as a set of less common haplotypes present at low frequency in the populations, with the exception of the Canary Islands, where an endemic haplotype is the most frequent. The same distribution pattern has been detected in the New World colonizing populations of *D. suboscura*. It is still an unresolved question which evolutionary processes account for this distribution. The difference between haplotype I and II is a synonymous change in the cutting site of *Hae*III in the NADH5 gene of the mitochondrial genome. We have studied some fitness components of these two haplotypes in order to detect some differences between them. The larva to adult viability and development time in non-competition conditions, the survival optimal density, the adult longevity, the egg to larva viability and emerging time or the differences in weight and the resistance to dryness are some of these fitness components. As a general rule, we have detected small differences between the two haplotypes, in some cases significant, and favouring the haplotype II. For example, the viability of haplotype I is  $63.23\pm2.40$  and that of haplotye II  $68.92\pm2.25$ . It is possible that the addition of these small differences could help to explain the dynamics of this species in nature with respect to the mtDNA.

## Automatic selection of conserved blocks from multiple alignments for their use in phylogenetic analysis

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The use of some multiple sequence alignments in phylogenetic analysis, particularly those that are not very well conserved, requires the elimination of poorly aligned positions and divergent regions, since they may not be homologous or may have been saturated by multiple substitutions. These regions are often manually deleted, without following objective criteria. I present here a computer program, called Gblocks, that applies a simple set of rules to perform this task. I also carry out several analyses on the resulting alignments, including computation of saturation curves and analysis of the amino acid composition, that show a clear improvement of the alignments for making trees. An apparent disadvantage of the elimination of these segments is the loss of relative support in the final tree. However, the alignment and amino acid composition may be biased in these regions and, in fact, it is better to construct a partially unresolved tree than a biased tree. There are other advantages in using a computerized method such as the one presented here: it reduces to a certain extent the necessity of manually editing multiple alignments, makes the automation of phylogenetic analysis of large data sets feasible, and facilitates the reproduction of the final alignment by other researchers.

Temperature-Related Divergence in Experimental Populations of *Drosophila melanogaster*. IV. Subunits of Selection and Developmental Constraints in the Wing

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From a laboratory stock of *Drosophila melanogaster* (Oregon), reared for more than 20 years at 18°C, two new populations were derived and maintained at 25°C and 28°C for 8 years. The chromosomal and cytoplasmic contribution to genetic divergence between the two most extreme populations was estimated at 18°C and 28°C. The surfaces of the five intervein regions of the wing were taken into account as representative of distinct subunits of development. Our analysis revealed that subunits of development can, in turn, be considered as subunits of selection with specific machanisms governing their norm of reaction. Genes located on chromosome 2 and 3 are principally involved in the divergence at 18°C, while the contribution of chromosome 3 is prevailing at 28°C. Genes located on chromosome 2 seem to be responsible for the norm of reaction. Cytoplasmic factors show a contribution as large as that of chromosomes. Chromosomal and nucleo x cytoplasm interactions are suggestive of gene pools and cytoplasms coadapted in constraining the development. The genetic constraints follow the anterior-posterior direction and are independent of the magnitude of the additive contribution of chromosomes to the size of various regions.

# Population dynamics and sexual reproduction in the clonal plant Allium vineale

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In *Allium vineale* (wild garlic) flowers are often partly or entirely replaced by bulbils, which act as asexual propagules. Flowers normally set seed, but the proportion of fertilised flowers varies over years, and, to a lesser extent, among populations. The rate of sexual reproduction thus depends not only on resource allocation to flower production but also on successful pollination and fertilisation.

In addition, there is large variation within and among natural populations of *A. vineale* for both bulbil and flower production. At the molecular level, RAPD markers have been used to study the genetic variation. Populations are typically composed of a few clones (multilocus genotypes), while most clones are restricted to single populations.

Five *A. vineale* populations from southern Sweden were studied over a period of four years. Flower and bulbil production was estimated for each clone and year, and showed significant variation among populations but not between years within population. Seed-set varied considerably between years.

Clonal frequencies remained relatively constant over years, with a small number of common clones dominating each population. There was some turnover of low-frequency clones, but this could be due to sampling effects. A few clones represented multilocus genotypes that may have been produced by recombination.

Thus, even if seed production is common, there seems to be little evidence of frequent recruitment of sexually produced offspring into *A. vineale* populations.

Testing hypotheses of long-branch attraction, base compositional bias and codon bias effects on phylogenetic reconstruction, using rhodopsin sequences in vertebrates

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Two spurious nodes were found in a phylogenetic analysis of a dataset of vertebrate rhodopsin sequences, in comparison with known vertebrate relationships. These spurious reconstructions were well-supported, and occurred independently of the method of phylogenetic analysis used (parsimony, distance, or likelihood). Use of this dataset of vertebrate rhodopsin sequences allowed us to exploit established vertebrate relationships, as well as the considerable amount known about the molecular evolution of this gene, in order to identify important factors contributing to the inconsistent behavior of these phylogenetic methods, as revealed by the substantial support of these spurious nodes. The spurious nodes were found not to be due to long branches or other topological effects, but rather are most likely due to convergences among taxa of base composition and codon bias. Several lines of reasoning support this conclusion. First, parsimony analyses that exclude either third positions or transitions (substitutions prone to compositional and codon biases) reduce bootstrap support for both spurious nodes. Second, support for the spurious nodes are partially corrected by the application of distance methods that take into account changes in base composition across the tree (LogDet). Third, simulation studies with parametric bootstrapping methods indicate that topological factors, such as long branches and short internodal distances, are not contributing to the inconsistent behavior of the parsimony analyses (known to be particularly susceptible to these effects), and thus cannot be construed as the reason for the high bootstrap support for the spurious nodes. Finally, the addition of taxa proximal to one of the spurious nodes and intermediate in base composition and codon bias resulted in decreased bootstrap support at that node. This study highlights the importance of identifying convergences in base composition and codon bias in molecular datasets, as these factors may lead to significant false phylogenetic signal. This study also demonstrates that a possible resolution of this problem is through better sampling. Note that here "better sampling" means not just addition of taxa to break up long branch lengths, but in particular, the inclusion of taxa which are intermediate in codon bias and base composition, in order to reduce problems associated with convergences in base composition and codon bias.

## Can we understand why inbreeding plants have less genetic variability than outcrossers?

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Data on DNA sequence variation within and between populations of the same species can give information about the frequency of recombination in the gene, which can help indicate the extent to which sexual reproduction and outcrossing occur, and about the action of natural selection on DNA and protein sequences, using deviations from the patterns expected under neutrality. When recombination or outcrossing are very infrequent, loci cannot be treated in isolation from each other, but selection at linked sites can significantly affect the level and structuring of neutral variability at a locus. For example, reduced neutral genetic variation in Drosophila genes from regions with low rates of meiotic crossing-over are probably caused by selection at linked loci, either "selective sweeps" as favourable mutations spread in populations, or selective elimination of deleterious alleles that constantly arise though mutation ("background selection").

Reduced genetic variation is also expected in inbreeding populations, so plants offer another case in which to estimate the magnitude of any such effects. I will describe how such data can be obtained, and mention some of the difficulties encountered, which are partly due to surprisingly high variability within many outcrossing plant populations, suggesting high neutral mutation rates and population sizes (though some have low diversity) and sometimes effects of balancing selection. Comparisons of closely related natural inbreeder/outbreeder populations from several plant taxa often show reduced neutral diversity in inbreeders. Low diversity is also found in non-recombining genes, such as genes on the Y-chromosome that do not recombine with their X homologues. In some cases, diversity is entirely absent, so it is impossible to obtain evidence on the cause of the effect, but when some diversity is present tests for selective sweeps can be applied to the pattern of variability. No clear evidence for such events has yet appeared in our studies.

# Evolution of self-fertilization under environment-dependent inbreeding depression

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Most of the models of the evolution of self-fertilization in plants are based on the balance between the 50% advantage of a gene causing selfing and its counterpart: inbreeding depression. Such models lead to the conclusion that only two stable equilibria exist *i e* complete selfing and complete outcrossing depending on the genetic load. Recent empirical studies show that independently of the genetic load, magnitude of inbreeding depression can be highly variable according to environmental conditions. Furthermore, recent inference on plant mating systems based on molecular markers indicate that mixed mating systems are frequent.

In our study, we examine the effect of such environmental variation in the expression of inbreeding depression. We suppose that different stages of ecological succession can modify inbreeding depression

We constructed a phenotypic model of ESS on the evolution of selfing rate where inbreeding depression varies in a temporal or spatial way. Analysis is done in the general framework of adaptive dynamics.

Our results demonstrate that if certain conditions are met, intermediate stable selfing rate can be maintained.

## Evolutionary significans of colonization by Stellaría longipes (Caryophyllaceae)

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*Stellaria longipes is* a polyploid herbaceous perennial and essentially a North American taxon. It grows in a variety of habitats and is widely distributed on the continent, but also extends into parts of Eurasia, and there by attaining a circumpolar distribution. We are attempting to understand the evolutionary strategies of this species. Two aspects are of particular importance in the success of this species. 1) High genetic variability is maintained due to polyploidy, facultative outbreeding and interspecific gene flow. 2) Development of phenotypic plasticity due to environmentally induced changes in the physiology and morphological expression of the genotypes. In order for the species to attain a wide geographical distribution, phenotypic plasticity must have been one of the forces. However, once the plants invade and colonize distinct habitats the result has been loss of phenotypic plasticity of certain traits. This genetic differentiation possibly leads to speciation.

# Heat and cold protection by sugar and sugar analogous and by heat shock proteins.

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Experiments with Drosophila melanogaster showed that an acclimation to either cold or heat increased the survival frequency after cold or heat stress, if the acclimation was of the same type as the stress. Furthermore a cold acclimation increased the survival frequency after heat stress. Two theories to explain the latter result are examined.

Sugar and sugar analogous have been shown to act as protectants to both cold and heat. They stabilize proteins against denaturation due to extreme temperatures; furthermore they seem to protect the cells from dehydration by changing intracellular solute concentration and by their hydrophilic nature, whereby they bind water. Therefore it might be that a cold acclimation increases the accumulation of sugar and sugar analogous and thereby increases the resistance to heat stress.

It has been shown that an organism that has been exposed to a prolonged cold treatment, expresses heat shock proteins (HSP) during re-heatening. This induction of HSP gene expression might increase the resistance to heat stress.

To examine whether one of these theories can explain the increased survival frequency of cold acclimated flies when exposed to heatstress as compared to non acclimated flies, I have examined cold acclimated flies for sugar and sugar analogues by the high performance liquid chromatography (HPLC) technique and for the increased expression of HSPs by the Western blotting technique.

Interspecific divergence in a group of Accessory gland protein genes (*Acps*) among species of the *Drosophila* melanogaster group.

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In Drosophila, seminal fluids produced by the male's accessory glands are transferred to the female during copulation. Fourteen accessory gland protein genes (Acps) have been so far identified and sequenced in *Drosophila melanogaster*. Some of these gene products have been found to trigger or to be associated with specific physiological effects in the female after mating, including receptivity to further mating, egg-laying rate, sperm utilization and storage. Interspecific sequence divergence has been previously analyzed for three Acp genes (Acp26, Acp29, and Acp70) and a common pattern of high divergence between closely related species has been found. Moreover, two such products have been suggested to have evolved under positive selection. In this study, we have collected and analyzed sequences from six Acp genes in species of the *melanogaster* group, and compared their rate of evolution to other genes sequenced in members of this group. We use intraspecific and interspecific sequence diverged for up to 6 Myr.

# Bet-hedging and the population dynamical consequences of seed germination in fluctuating environments

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Temporal variation in life history parameters significantly affects population dynamics and life history evolution. For annual plants in variable desert environments, delayed seed germination is predicted to evolve as a bet-hedging strategy that reduces temporal variance in fitness while also decreasing arithmetic mean fitness. More xeric populations are predicted to experience stronger selection for delayed germination. In a four-year demographic study, I assessed seed germination fractions and the fitness consequences for germinated and non-germinated individuals in four populations of Plantago insularis located along a precipitation gradient. In two years with greater than average precipitation, populations grew (8>1), whereas, in two drier years, populations declined, with 8 was as low as 0.03. All populations exhibited delayed germination of some viable seeds. Using elasticity analysis, I demonstrate that delayed germination resulted in a reduction in both the temporal variance and the arithmetic mean for population growth at all populations. In wet years, non-germinated seeds slowed growth and elasticities for germinating more were large and positive. In dry years, non-germinated seeds slowed population decline and elasticities for germinating more were large and negative. Comparing fitness surfaces for alternative germination strategies, I found that delayed germination maximized the geometric mean growth rate over the four-year study in the three more xeric populations. As predicted by models of adaptation to temporal variability, delayed germination functioned as an adaptive bet-hedging strategy in these desert annual populations. Furthermore, delayed germination was most critical for the growth rate of the population experiencing the most temporal variance in reproductive success.

# The forest fires of Kalimantan: an analysis of the impact of disturbance on the community structure of tropical forest butterflies

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Although the forest fires of Kalimantan (Indonesian Borneo) have received enormous media attention there has been little else than speculation about the actual impact. The present study is one of the first to address the issue with quantitative data both before and after the fires in areas of Kalimantan.

The severe level of disturbance caused by the forest fires (in East Kalimantan) led to a significant decrease in species richness and radical restructuring of the whole butterfly community. This general pattern was observed over all plots, both burned and unburned. The radical restructuring of the butterfly community was typified by the hyperabundance of formerly rare 'pioneer' species such as *Jamides celeno*, which initially significantly expanded their ranges after the fires and became the most dominant species in the butterfly community. A year after the fires, the community is still experiencing radical changes as new species (re)colonize the area and formerly abundant pioneers begin to disappear. A comparative study of the butterfly community at a site (in Central Kalimantan) unaffected by the fires shows that under moderate levels of disturbance high levels of biodiversity can be maintained. In undisturbed areas the community shifts at a regular spatial scale while disturbance causes a radical, but local shift in the community that tends to decrease as the forest regenerates. Overall though diversity remains high and is even significantly enhanced at the local (plot) level compared to undisturbed plots.

# Genetic Contribution for the Conservation of *Chondrostoma lusitanicum* based on cytochrome *b* and ND 5/6 analysis

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*Chondrostoma lusitanicum* is a Portuguese endemic cyprinid with a very restricted distribution area and very reduced numbers at some basins which justifies its threatened species status. We examined genetic population structure using samples from overall geographical range, using the sequence of the cytochrome *b* gene and restriction fragment length polymorphism analysis of the segment coding for the NADH dehydrogenase subunits 5 and 6. There was reduced within-population genetic variability but considerable among-population differentiation, particularly marked between both Arade and Mira basins and the other populations. These results are in accordance with previous allozyme studies for *Chondrostoma lusitanicum* and with allozyme and mitochondrial DNA differentiation of others coexisting cyprinid species of the genus *Leuciscus*. The levels of genetic variability and differentiation achieved for the mitochondrial DNA loci through sequence and RFLP analysis were correlated with high significance. Strong geographic genetic structuring, with the possible definition of two or three geographic groups was observed. The high values of nucleotide divergence and pairwise sequence divergence of the Mira and Arade group, when compared with all other samples, support a distinct taxonomic status probably at the species level. Results are also discussed in relation to conservation of this highly fragmented species, in terms of Evolutionary Significant Units and Management Units.

Genetic consequences of population reduction and subdivision of the Iberian fish *Anaecypris hispanica*, as determined by analysis of mitochondrial cyt b gene and control region.

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Anaecypris hispanica is a small cyprinid that is restricted to the Guadiana basin in south Iberian Peninsula. In the 1970s this endemic was relatively abundant. Since then, its abundance and geographic range have progressively contracted, being presently confined to a few disjunct sites. Consequently, *A. hispanica* is recognized as the most threatened Iberian non-migratory fish, being classified as "Endangered" in the Portuguese and Spanish Red Data Books, and in IUCN Red List. In the present study, in the frame of a LIFE–Nature project, we used mitochondrial (mt) DNA to investigate the effect of habitat fragmentation and population decline on population structure and genetic variation of *A. hispanica*. Specimens were collected from all nine tributaries where the species can still be found in Portugal, and a portion of the pelvic fins was cut before releasing the fish. The mt cytochrome (cyt) *b* gene and the control region were amplified by PCR and sequenced for up to 5 specimens from each locality. For tributaries where enough individuals were caught, cyt *b* sequences from 15 additional specimens were examined by RFLPs using 13 restriction enzymes. Levels of within and inter- sample genetic variation, and the phylogenetic relationships among local populations were tentatively determined, and analyzed in light of conservation issues.

# Modeling long-term evolution in multi-dimensional multiple-peak interacting fitness and coexistence space:

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1. Fitness has multiple peaks in multi-dimensional space, with local stabilising selection. A fraction of the fitness peaks are occupied by existing species, in equilibrium between stabilising selection and the variance of new mutations.

2. There is a limited co-existence of species under any ecological conditions.

3. Longer periods of stable selection select for a larger number of specialized positive interactions, amplifying a self-reinforcing stronger stabilising selection. Variable selection selects for generalised interactions between genes, leading to generalised fitness peaks and weaker stabilising selection. The genetical stability of different characters represents the long-term history of stability of their fitness peaks.

4. Species will occupy new peaks if a fraction of the population extends into the domain of attraction of the stabilizing selection of a new peak, caused by weakening or changes in direction of the stabilising selection. The species will split to two new species, if they can coexist, or one will eliminate the other if they cannot. Rapid . speciation with large phenotypic changes occurs in special evolutionary opportunities of mass extinctions or opening of new habitats, with large changes or relaxing of the stabilising selection, and with a large number of available fitness peaks. Rapid immigration and establishment of pre-adapted species from other areas inhibit speciation in newly available areas.

5. Long-term large evolutionary changes are expected to occur along extended series of adaptive peaks with higher transition probabilities between them. Evolutionary stagnations occur in lineages at the ends of series of adaptive peaks. Unconnected series of adaptive peaks remain unoccupied.

6. The first few species that start the new speciation at a new opportunity quickly occupy and block the ecological and evolutionary opportunities for speciation by other species that arrive later, leading to typical adaptive radiations of many new species from few founder species.

#### New data on genome size variation of Centro-European Cyprinidae (Pisces, Osteichthyes)

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Distinct kinds of polyploidy appear to be a common feature of some lower euteleosteans, and one of the most peculiar group possessing such complex polyploid relationships is the family Cyprinidae. To date, nuclear DNA content is known for 161 species (only around 8% of the described cyprinids) and the reported range varies from 1.8 to 19.3 pg. In the present study, some new data were obtained by using flow cytometry methodology (FCM), for species collected at Danube (R. Dyje and Becva) and Elbe (R. Libechovka) catchments, as follows: *Aspius aspius, Abramis sapa, A. ballerus, Blicca bjoerkna, Chondrostoma nasus, Gobio albipinatus, G. kessleri* and *Rhodeus sericeus*. The already known genome sizes of other nine taxa, the majority by using less reliable methodologies and smaller samples, were also scored under the same standardised procedure, to confirm previous determinations and / or to assess for intraspecific variations in nuclear DNA content: *Alburnus alburnus, Abramis brama, Carassius auratus gibelio, Gobio gobio, Leuciscus idus, Pseudorasbora parva, Rutlius rutilus, , Scardinius erythrophthalmus* and *Tinca tinca*. All these cyprinids belong to the so-called "diploid" group as they have karyotypes with 2n= 48-52, but *Carassius auratus gibelio*, which has a "polyploid" karyotype (2n= 150). The results now obtained were also compared with the published data regarding the Old-World species, and finally discussed, in order to help understanding both the chromosomal evolution and the diploid-polyploid relationships within the family.

# Molecular, morphological and paleontological perspectives on the radiation of the Gastropoda.

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There are distinct advantages to combining independent data sets in order to elucidate the evolutionary history of a group. Areas of agreement among independent data types give us confidence that some aspects of the actual evolutionary history of the group have been discovered. Areas of disagreement, on the other hand, are indicative of inadequate data, lost or conflicting historical signal, or failure of analytical methods. We have combined molecular, morphological, and paleontological data in order to clarify aspects of the evolutionary radiation of the Gastropoda. We focus in particular on evolution and diversification within the Caenogastropoda and the Heterobranchia, documenting areas of agreement and disagreement among data sets. Areas of disagreement are used to investigate data quality or shortcomings of analytical approaches. For example, congruence of molecular characters with morphological characters and calibrations from the fossil record can improve molecular analytical methods and resulting phylogenies. Incongruence of morphology with molecular data and fossil appearances may indicate errors due to the rapid accumulation of morphological distinctness. Congruence of morphology and molecular data may suggest that certain portions of the fossil record of a group are currently missing or unrecognized.

# Environmental variation determines the mode and tempo of natural and sexual selection in a fluctuating population of feral sheep

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Natural and sexual selection result from non-random variation in lifetime breeding success (LBS). Selection pressures are not necessarily constant, however, as the mode and intensity of selection may vary with fluctuating environmental conditions such as population density. It is difficult to test this idea in free-living vertebrate populations due to practical limits to assessing LBS in males. We have measured the reproductive success of 699 Soay rams born on St Kilda, Scotland, since 1985 using molecular genetic paternity analysis. Variation in LBS, hence the opportunity for selection, varied systematically with demographic changes in this fluctuating population of feral sheep. The opportunity for selection was greatest in cohorts born in years of high population density due to density-dependent reduced juvenile breeding success and over-winter survival. These cohorts underwent strong natural selection on body size (measured as hindlimb length) in their first winter due to differential survival. In contrast, in cohorts born in years of low population there was no significant natural selection on hindlimb in the first year of life. Instead, large body size was associated with increased fecundity over the entire lifetime in these cohorts. Natural and sexual selection thus act with similar intensity in the same direction at different life-history stages in Soay rams, depending on the population density in the year of birth.

# The Cambrian explosion: artefact or reality?

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About 545 Myr ago, there is a geologically abrupt appearance of skeletons, paralleled by a diversification of trace fossils. As Bruce Runnegar asked many years ago: is this an explosion of animals or only fossils? Whilst no palaeontologist would argue that the known fossil record is an unblemished history, recently a considerable divergence in opinion has emerged between those who view the fossil record as broadly indicating an origination of the Metazoa about 600 Myr ago, as against those who look to molecular data that have indicated the origin to extend back even as far as the Archaean. The latter view is based on considerations of the molecular clock, combined with strongly uniformitarian assumptions that look to either planktotrophic larvae or the meiofauna as a guide to the early metazoans. Difficulties, however, abound. Proponents of the molecular clock, wittingly or otherwise, adhere to a neutral view of molecular evolution, and disregard any neo-Darwinian framework of selection and population bottlenecks. Similarly, notions of ancestral larvae and a meiofauna suffer severe internal contradictions. The alternative, that the Cambrian explosion is a real event, is also not free of difficulties. What is the status of the Ediacaran assemblages and if such taxa as Kimberella, Parvancorina and Spriggina are reliably identified as complex protostomes why did they fail to make plausible traces in co-existing sediments? In addition, molecular data that indicates a complex array of homeotic genes in even primitive metazoans begs the question as to what triggered the Cambrian radiation and why it was apparently substantially later than the first metazoans. A simple explanation is that the Cambrian explosion was triggered by an environmental change, of which a substantial rise in atmospheric oxygen remains the most popular.

# A paleogenomic approach to the evolution of the ERV9 human endogenous retrovirus family

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The paleogenomic approach has been successfully used to infer the evolution of L1 and Alu families of human interspersed DNA sequences. The major conclusion of this approach has been that most Alu and L1 elements are produced by only one or a few source genes ("master elements") at any time during their evolution. Accumulation of substitutions in the master elements, or replacement of these masters by others from their own progenies, give rise to distinct subfamilies of pseudogene copies defined by shared differences from the consensus of the family. In this work, this paleogenomic approach has been applied to study the evolution of the ERV9 family, one of the human endogenous retrovirus families mobilized during primate evolution. By searching the GeneBank database with the first 676 bp of the ERV9 LTR, we identified 156 different element insertions. These elements were grouped into 14 subfamilies by ~125 characteristic nucleotide changes. The age of each subfamily was roughly estimated by the average sequence divergence of its members from the subfamily consensus sequence (the best possible reconstruction of the master gene). Determination of the sequential order of diagnostic substitutions led to the identification of four lineages with different evolutionary success. ERV9 evolution has been driven by a major lineage all over primate evolution. Two minor lineages arose from this major one. The oldest of them underwent its most significant expansions about 30 MYA. The youngest one retained its capacity of transposition over an extended period of time. A fourth lineage arose by recombination between this minor lineage and the major one. Both this recombinant and the major lineage have been giving rise to new subfamilies at least until a relatively recent period (15-10 MYA), suggesting the possibility that the ERV9 family may still be active in humans. This research was supported by grant XUGA 10304B97 to Horacio Naveira

Resting egg-banks of the cladoceran *Daphnia magna*: reconstruction of micro-evolution using allozymes, microsatellites and an ecologically relevant trait.

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We studied micro-evolutionary changes in a resting egg bank of a *Daphnia magna* population in a small pond which has been used for fish culturing in the past. We monitored changes in microsatellite allele frequencies in the eggs isolated from different depths (3 loci) and studied allozyme frequencies of populations that hatched from the sediments. To determine evolutionary responses to changed selection pressure that may have occurred in the *Daphnia magna* population in response to changes in fish predation pressure, an ecologically relevant trait, phototactic behaviour, was determined in subpopulations that were hatched from different sediment depths. Our results indicate that there is a strong relationship between the average change in phototactic behaviour in response to fish kariomone and the stocking densities of fish at the beginning of the growing season in the studied subpopulations, indicating evolution on a very short time-scale.

# Population structure of *fucus* sp in the skagerrak-kattegat (baltic sea) as determined by microsatellites

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A well-developed marine to brackish salinity gradient exists in the Skagerrak-Kattegat (S-K) region of the geologically young (ca. 7000 year old) Baltic Sea ecosystem. In this area, the endemic *Fucus serratus* (dioecious) occurs widely, whereas the introduced (ca. 1900) *Fucus evanescens* (monoecious) is less abundant and patchily distributed. Additionally, putative F. serratus x *F. evanescens* hybrids frequently are observed. Microsatellite analysis was used to examine the genetic population structure of the two fucoids. Individuals of *F. serratus* were collected from seven areas in the S-K plus Roscoff (F) and Bergen (N); *F. evanescens* was collected from three areas in the S-K plus Maine (USA). Six microsatellite loci in *F. serratus* displayed polymorphism, but loci examined in *F. evanescens* were monomorphic. Population structure of the endemic and introduced species will be discussed.

# Differentiation among populations and species possessing a common phenotypic polymorphism: evidence for balancing selection?

## A. J. Crawford

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When two independent sets of molecular markers from the same individuals and populations show contrasting patterns of geographic variation, natural selection is often inferred to be acting on one of them. Datasets may give significantly different estimates of population structure because, while migration and genetic drift tend to act on whole genomes, natural selection may act upon specific gene regions within chromosomes. This reasoning is applied here to a study of the evolution of a dorsal color pattern polymorphism shared among populations of two closely related species of Neotropical leaf litter frogs, *Eleutherodactylus bransfordii* and *E. stejnegerianus*. The relative frequencies of dorsolateral and middorsal striped morphs are very similar between populations. To investigate the possible role of balancing selection on the maintenance of these uniform frequencies across populations I test the neutral hypothesis that independent measures of population differentiation ( $F_{.}$ ) from arbitrary molecular markers and morph frequencies are not significantly different. Data from mtDNA sequences show a dramatically different pattern of geographic variation relative to color morph frequencies, and the null hypothesis is rejected. Thus, this study provides indirect evidence for the pervasive and persistent action of natural selection in maintaining a dorsal color pattern polymorphism across populations, species, and over long stretches of evolutionary time. Data on DNA sequence variation at a nuclear marker are currently being collected and will be incorporated into the above analysis of population structure.

## A trade-off in malaria infections: can it explain the parasite's life history?

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Malaria parasites exist as two forms within the red blood cells of their hosts; gametocytes and asexuals. Only gametocytes can be transmitted. Natural selection amongst parasites is expected to promote increased production of factors which are beneficial to transmission. Yet, during most malaria infections, the majority of parasites are asexuals, with only low levels of gametocytes. This characteristic of the parasite's life-history has yet to be explained.

Asexual numbers increase by continuous cycles of replication. Gametocytes cannot replicate; they are produced only when the products of an asexual cycle are diverted from further replication and differentiate instead. Hence, firstly, the number of gametocytes that can be produced from any cycle is constrained by the number of asexuals beginning the cycle. Secondly, each cycle, there is a trade-off between the number of gametocytes that are produced, and the number of asexuals at the end of the cycle. Therefore, current gametocyte production has a transmission cost by decreasing the maximum number of gametocytes that can be produced at any future time. I present a model for optimising fixed relative investment into gametocytes when selection is acting entirely on

between-host transmission. The trade-off becomes one between the fraction of asexual progeny which become gametocytes, and the total number of asexuals generated. A single value of investment maximises the total number of gametocytes produced (a measure of R0). The value decreases as either the infection length or the number of progeny per asexual increases. This suggests that low levels of gametocytes may be an adaptation of the malaria parasite resulting from their high multiplication rate and long infectious period. This work has a corollary for the virulence of malaria, which is associated with asexual multiplication. An important application could be designing intervention strategies that manipulate transmission and virulence.

# Sexual conflict in an insect

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Evolutionary theory predicts that variation in potential rates of reproduction often leads to a conflict of interests between the sexes over reproduction. Varied behavioural, physiological and morphological adaptations to sperm competition that have arisen in males of many insect species may prove costly to females. Such traits are predicted to select for the evolution of counter-adaptations in females that function to ameliorate male-imposed costs and regain control of reproduction. I present results from an investigation into several components of the mating interaction in the bruchid beetle, *Callosobruchus maculatus*. Aspects of mating behaviour and morphology in both sexes are interpreted within the functional framework of sexual conflict theory.

## Sexual selection on phenotypic traits in a hybrid zone of Littorina saxatilis

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The marine snail Littorina saxatilis (Olivi) can be found on exposed rocky shores of Galicia (NO Spain): two morphs (ecotypes), which differ in many morphologically and inherited characters, are associated to different habitats. The distribution of these two morphs overlap in a narrow midshore zone where hybrids with mixed shell characters are produced. Previous studies have shown that natural selection is promoting the present morph distribution on the vertical environmental gradient. We have assessed a quantitative study to estimate the contribution of sexual selection with respect to the morphological variability across the environmental gradient. We sampled individuals from two different localities and seasons and used the Lande and Arnold method of multiple regression of phenotypic traits on a fitness component to find the most important morphological differences between mated and non-mated individuals. We estimated separately male and female sexual selection using common and sex-specific phenotypic traits and we also tried to consider the environmental effects on the fitness.

The comparison between the results obtained using individuals living in allopatry and in sympatry suggest a minor role of sexual selection for explaining the present morph distribution across the environmental gradient.

# Allometries of zebra mussels' life history traits: testing optimality models.

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Many studies of fish and reptiles reveal that life history traits of indeterminate growers are allometrically interconnected. These allometries were described as interspecific correlations between certain life history traits such as mortality rate, asymptotic size, Bertalanffy's growth constant or proportion of asymptotic size attained at maturity. Optimal resource allocation theory predicts that such allometries arise if organisms which live in a seasonal environment optimise their energy allocation throughout the entire life, i.e., if they divide energy between growth and reproduction to maximise their lifetime reproductive success. The theory not only explains such allometries on an interspecific level but it also predicts their presence between populations of the same species. In this study I searched for the correlations between life history traits in several European populations of zebra mussels Dreissena polymorpha. Most allometries are qualitatively similar to those found for different species of fishes and reptiles and to the relationships predicted by the model. Some of them, however, show the opposite trends, contradicting theoretical predictions. There was also found a positive correlation between mortality rate in zebra mussel populations and production rate of clams before maturity. The optimality models did not take into account this relationship, which may explain some inconsistencies between theoretically predicted allometries and those found in nature. This study confirms that, in general, optimal resource allocation models effectively explain inter- and intraspecific allometries between life history traits present in nature; however, some simplifying assumptions of these models may affect the pattern of the expected allometries.

## The origin and evolution of metabolic pathways: a common origin of nif and bch genes

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Very little is known about the origin and evolution of nitrogen fixation and the molecular mechanisms responsible for the construction of *nif* genes and driving the assembly of *nif* metabolic pathway. A detailed analysis of *nif gene products revealed that nifDK* and *nifEN*, encoding the a and b subunits of nitrogenase, and the two subunits of the NifEN enzymatic complex, involved in FeMo-Co biosynthesis, belong to a paralogous gene family, in that they are the descendants of a common ancestral gene by gene duplication followed by evolutionary divergence. This analysis also permitted to trace their possible evolutionary history; according to the proposed model the four genes are the result of two successive duplication events, very likely predating the appearance of the Last Universal Common Ancestor (LUCA). The first paralogous duplication event involved an ancestral gene (encoding a slow enzyme with a low substrate specificity able to catalyze several reactions) leading to a bicistronic operon which, in turn, underwent a paralogous operon duplication event originating the ancestors of the present-day *nifDK* and *nifEN* operons. Moreover the products of these genes exhibited a significant degree of sequence similarity to two subunits of protochlorophyllide reductase (BchIB and BchIN), suggesting that their encoding genes might have arisen from duplication of *nif* genes.

# Behavioural differentiation in oviposition activity in *Drosophila buzzatii* from mountain and lowland populations in Argentina

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During a collection trip to Argentina, March 1997, a remarkable difference was observed in the activity pattern of several cactophilic Drosophila species inhabiting two geographically separated populations of cacti. Flies of a population located 2460m above sea level displayed increased activity during early and mid afternoon, whereas flies of a population located 586m above sea level exhibited increased activity during late afternoon. To test for a genetic component of differences in activity, females of the cactophilic Drosophila species, D. buzzatii, were brought back to the laboratory to found separate mass populations. In the laboratory, crosses between the two populations were carried out and oviposition activity during 24h was estimated with 2h intervals for both parental populations and their reciprocal crosses. Oviposition activity was highly variable over the day, in both populations and in both reciprocal crosses, with a peak in oviposition activity between 4 and 6 p.m. and another, but smaller peak, between 0 and 2 a.m.. Activity levels close to maximal activity were attained between 2 and 4 p.m. in the mountain population, where average activity significantly exceeded that of the lowland population. Activity in the lowland population exceeded that of the mountain population by almost a factor 3 between 8 and 10 p.m., prior to the beginning of the dark period. This difference, however, was only at the border of significance. Differences in activity between the mountain and the lowland population were not significant during the rest of the day. Activity of reciprocal crosses was intermediary between the two parental populations but was not significantly different from each other. This result suggests that nuclear genetic factors rather than cytoplasmic factors contribute to differences in oviposition activity between the two populations. Oviposition activity from 2 until 10 p.m. was regressed on the proportion of the genome derived from the mountain population. This variable significantly predicted oviposition activity between 2 and 4 p.m. and between 8 and 10 p.m.. Oviposition activity between 4 and 8 p.m. was independent on the proportion of the genome derived from the mountain population. Temperatures in the field differed greatly between the two populations both over the year and on the days of the collection trip with a late evening temperature exceeding 36oC in the lowland while it was only 18oC in the mountains. It is known that adults of this species normally display increased oviposition activity during late afternoon, perhaps as a mean of behavioural avoidance against extreme temperatures. The present results, therefore, are discussed in the light of thermal adaptation and local natural selection.

#### Population structure of the hoki Macruronus magellanicus in past and present populations.

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The Southern Atlantic hoki *Macruronus magellanicus* represents the most abundant fish in Patagonian waters. The possible presence of in-shore stocks and the fact that it will soon be one of the main catches in the area, make the population genetic study important for its conservation and management. This project addresses the study of spatial structure and temporal genetic variation of this species, before large scale exploitation begins. A total of 400 fish taken from 12 sampling sites across the Patagonian platform were studied with RFLP of the 5 kb mtDNA region ND5/6, and with 6 microsatellite loci. These markers revealed no structuring of the populations. However, the presence of a widely distributed haplotype and positive *Fis* values in different populations and microsatellite markers may point to a low Ne, high mortality of juveniles, selection and /or schooling behaviour. Ancient DNA was extracted from otoliths collected in 1976, 1988 and 1992. These samples were studied with 3 microsatellite loci, and display the same pattern. No evident decline/increase in diversity was so far detected in a temporal analysis in the 22 years period.

Phylogeny, historical biogeography and ecological phylogenetics of water striders (Heteroptera; Gerridae) belonging to the genera *Limnoporus* Stål, *Aquarius* Schellenberg and *Gerris* Fabricius based on molecular and morphological data.

# Jakob Damgaard

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Water striders are familiar inhabitants of different types of aquatic habitats all over the world. The are conspicuously adapted for life on the surface film of water, especially with respect to locomotion, feeding, and reproductive behaviour, and their two-dimensional habitats make water striders ideal subjects for ecological and behavioral studies. Recent interests in Gerridae has been focused on the three principal, Holarctic genera *Limnoporus, Aquarius* and *Gerris*, and the systematics, faunistics and ecology of these genera is now relatively well understood. The introduction of sequence data from the mitochondrial gene *cytochrome oxidase subunit I* (COI) and the nuclear gene *elongation factor 1-a* has provided a new basis for tests of prior hypothesis about the phylogeny, adaptive evolution and historical biogeography of these three genera.

# Fitness components and advantageous alleles in partially self-fertilizing populations

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The expected fixation probability of an advantageous allele was examined in an partially selffertilizing hermaphroditic plant species using the diffusion approximation. The selective advantage of the advantageous allele was assumed to be either increased viability, increased fecundity, or an increase in male fitness. The mode of selection, as well as the selfing rate, the population size, and the dominance of the advantageous allele, effect the fixation probability of the advantageous allele.

Evolutionary consequences of different selection modes operating on advantageous alleles in partially self-fertilizing species is discussed.

## Anti-darwinian "intelligent" evolution driven by the MHC system

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The adaptation of living systems to fluctuations of environmental conditions requires a careful optimisation of the equilibrium between mutagenesis and selection, plasticity and specialisation. The evolution of anti-darwinian self-determined processes of mutagenesis and selection could be useful to counteract the negative aspects of random mutagenesis and natural selection. At cellular level the response to stressing conditions leads to a synchronisation between metabolic rhythms and recombinogenic activities. These processes are mediated by proteins which are processed and secreted or presented on the cell surface by the MHC proteins. The MHC mediated immunisation against endogenous regulative protein might be involved in a positive selection of the maternal immune system for the embryos with incompatible MHC alleles. If these alleles are linked in cis or in trans with different variants of genes involved in the regulation of metabolic activities, a physiological adaptation may be transformed, in only one generation, into adaptive changes of the genetic population structure. This scenario is confirmed by many experimental data, produced in our labs too, about differences in gene expression during the processes of cellular activation, numerous association between MHC alleles and metabolic or immune pathologies, mimicrism between endogenous antigenic peptides and viral epitopes, convergent evolution of the region binding to antigenic peptides of different MHC genes, fractal distribution of MHC polymorphisms in different population, and non-mendelian segregation of MHC aplotypes.

# Cold stress tolerance in Drosophila: a major adaptive difference between tropical and temperate species

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Tolerance to cold temperatures, around 0°C, is poorly documented in Drosophila, in spite of the fact that such temperatures are more likely to be encountered than extreme cold in temperate countries. When set at 0°C, *D. melanogaster* enter a narcosis state, called chill coma. Brought back at ambient temperature, around 20°C, adults will progressively wake up and recover a normal activity. We investigated the recovery process in *D. melanogaster* and found that, for young adults treated 16 hrs at 0°C, recovery time was about 20 min. We then compared numerous temperate and tropical species, all grown at the same temperature (21°C) and found a major difference. Temperate species were, basically chill coma resistant, with an average recovery time of about 1 min. Tropical species were very sensitive, with average recovery close to one hour. The physiological and genetical bases of this adaptive difference is not known but might involve the nervous system.

J. R. David, P. Gibert, E. Pla, G. Pétavy, D. Karan and B. Moreteau - Cold stress tolerance in *Drosophila*: Analysis of chill coma recovery in *D. melanogaster*. Journal of thermal Biology, 23 (1998) 291-299.

# Impact of new deleterious mutations on life history traits in C. elegans

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The fitness effects of new deleterious mutations are important for a number of issues in evolutionary biology, including the evolution of sex and conservation of small populations. We have generated a number of lines of the nematode worm *C. elegans*, homozygous for a known number of induced mutations. The effects of these mutations have been measured, using a number of different fitness assays, including productivity, longevity and intrinsic growth rate. None of the fitness assays reveal the effects of more than 5% of the mutations induced, despite the fact that they are known to be deleterious in natural conditions. The extent to which different life history traits are affected by the same mutations, and interactions between the traits, will be discussed.

# Island sex: speciation and sexual selection on oceanic islands

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Organisms that colonize remote islands face challenges but also opportunities. The challenges include a small population size that might make finding a mate more difficult and lead to problems associated with inbreeding. It could also be significant that the genetic consequences of colonization are likely to be particularly severe for sex-linked genes and cytoplasmic elements due to their smaller effective population size. Countering these negative forces, isolated islands are expected to harbor fewer parasites, competitors and predators.

Given these characteristics, certain models of evolution make predictions concerning the nature of mating systems and the degree of sexual dimorphism on islands. For example, it has been proposed that colonization can alter the operational sex ratio and affect the degree of choosiness that individuals exhibit with respect to their mates. In addition, if individuals select mates for good genes for disease resistance, sexual selection should be relaxed on islands that have low parasite loads. Together these theories predict that recent colonists will exhibit a reduction in secondary sexual characters, lower levels of sexual dimorphism, and simplified courtship behaviors compared with ancestral populations.

Here we review data on the sexual dimorphism exhibited by island taxa. The data suggest that colonization often leads to major changes in sex-limited traits. The reason for these changes, however, are not fully resolved, partly due to inadequate information concerning the relationships of island species and the genetic basis of sex-limited characters. We propose that the phylogenetic study of insular species and their parasites, together with information on their mating systems and degree of sexual dimorphism, could provide important information with respect to speciation and the forces that drive sexual selection.

# Making mistakes in predicting the effects of global warming on species ranges.

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Predictions of global warmingbs effect on species ranges usually assume that they are affected only by abiotic factors but in nature species also disperse and experience interactions with other species. Using a simple insect assemblage in a laboratory ecosystem we show that including these two biological factors can greatly change how species ranges react to climate change. We conclude that ignoring these two factors will lead to mistakes in predicting the effects of global warming.

## Area effects and geographic variation in the land snail Cepaea nemoralis

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The study of land snails has been fundamental to understanding the origins and maintenance of biodiversity. The discovery that the frequencies of *Cepaea* shell colour and banding morphs are affected by selection for crypsis by thrushes has lead inevitably to other work, including the discovery of 'area effects', patterns of gene frequencies in which particular shell-colour or banding morphs predominate over areas much larger than the Mendelian population. The areas are separated from each other by steep morph ratio clines and their existence has raised questions about their origins and maintenance.

Studies of allozymes have helped to estimate the relative contributions of selection, gene flow and history in bringing about differences between neighbouring populations. We have now developed microsatellite primers for *C. nemoralis*, to help in studying the relationships of snails within and between populations. We are using the microsatellites in an attempt to reconstruct the recolonisation of Britain by *C. nemoralis* after the last glaciation. Microsatellite and mitochondrial phylogenies are compared with maps of the gene frequencies at loci coding for shell colour and banding. The aim is to distinguish between ultimate (historical) and proximate (environmental and demographic) factors in determining 'area effects' and other patterns of gene frequencies.

# Bayesian inference of population history and identification of marker loci that have responded to selection

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I present a Bayesian method (using Markov chain Monte Carlo computations) for inferring the parameters of a simple neutral model of the divergence of a pair of populations, and the application of this method to the problem of identifying marker loci that have been strongly influenced by selection during divergence.

The data from each marker locus is used separately, to make Bayesian inferences about the parameters T1 = t/N1, T2 = t/N2 ("branch lengths"), which should be sensitive to selection during divergence. So, for each marker locus, I compute the Bayesian "confidence region" (at some chosen probability level, such as 95%) for the joint posterior distribution of T1 and T2. If the data from any locus generates a confidence region that does not overlap with the others, then this locus is declared an "outlier", and selection is suspected.

However, these Bayesian confidence regions depend on the choice of prior. So, I am currently investigating the performance (in the frequentist sense) of these confidence regions, by performing large numbers of coalescent simulations of a chosen model where all the parameters are known), in order to determine what proportion of times the Bayesian confidence region with declared probability level p, actually contains the true value of the parameter of interest. The results of this frequentist "power analysis" of a Bayesian "interval estimator" will be presented. Ideally, this type of analysis should be performed for a wide range of parameter values.

Comparative genome mapping between Arabidopsis thaliana and Arabis petraea including the phytochrome gene family.

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*Arabis petraea* is a close relative of *Arabidopsis thaliana*. In this study, marker loci developed in *A. thaliana* are mapped in *A. petraea*, and chromosomal locations are compared between the two species. We used Cleaved Amplified Polymorphic Sequences (CAPS) and Simple Sequence Length Polymorphisms (SSLP). CAPS markers can identify homologous genes in different species. The sequences of the primers were either based on the published primers (http://genome-www.stanford.edu/Arabidopsis/aboutcaps.html), or new primers were designed based on conservative parts of the gene. Not all CAPS loci were polymorphic for restriction sites in our mapping population. Therefore, also SSLPs were included (http://genome.bio.upenn.edu/SSLP\_info/SSLP.html). Some rearrangements of chromosomal areas are found, but many loci that are linked in *A. thaliana* are also linked in *A. petraea*. Loci on chromosome I in *A. thaliana* are found in two linkage groups in *A. petraea*, which is consistent with *A. petraea* having eight chromosomes, and *A. thaliana* five.

Earlier comparative genome studies between *A. thaliana* and other Brassicacea showed triplications suggesting a hexaploid ancestor of the *Brassica* species (Kowalski et al, 1994; Lagercrantz et al, 1996). The copy number of the five phytochrome genes found in *A. thaliana* was assessed in order to detect di(tri)plications of chromosomal areas. Furthermore, sequence comparison of a unique part of the phytochrome genes between the species is in progress.

## Unpredictable selection in a structured population and differentiation in evolved reaction norms.

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Unpredictability during development of the optimum phenotype under future selection leads to a compromise reaction norm with a slope that is shallower than the slope of the optimum reaction norm. Unpredictability of selection can lead to an evolved curved reaction norm when genetic variation for curvature is available even if the optimum reaction norm is linear. This requires asymmetry in the frequency distribution of the habitats of selection; at small population size, stochasticity in the number of individuals per selection habitat is sufficient to generate such asymmetry.

Unpredictability of selection in structured populations leads to local genetic differentiation of reaction norms. The mean habitat of a subpopulation is defined as the subpopulation's focal habitat. The evolved mean reaction norm of each subpopulation is anchored at the optimum genotypic value in its focal habitat. Linear reaction norms are parallel if the conditional distribution of adults around the focal habitats is the same for each subpopulation.

Adult migration but absence of zygote dispersal represents the ultimate structured population, each habitat playing the role of focal habitat. Absence of zygote dispersal requires that the flow of individuals through the habitats is used instead of the habitats' frequencies. Adult migration in absence of zygote dispersal leads to an evolved pattern of locally differentiated reaction norms with optimum genotypic value anchored in the focal habitat and, for linear reaction norms, parallel slopes

# Environmental dependence of larval growth rate and critical weight for pupariation.

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Fitness components as age and size at maturity show both genetic variation and phenotypic plasticity in *Drosophila melanogaster*. As part of a study into the thermal adaptation of larval development time and adult body size, we looked at two lines from each of two populations, France and Tanzania. Larval growth rate was faster at higher temperature and on good quality food; at each temperature / food combination, the lines from the France population grew faster than the lines from the Tanzania population. Oxygen costs of growth were equivalent in all cases. The larval weight at which 50 % of larvae pupate if further deprived of food was taken as the critical weight for pupariation. Food level led to lower larval survival even at high larval weight. The critical weight did not depend upon food supply. In the two Tanzania lines, the critical weight was low and did not depend upon temperature; in the France lines, critical weight is much higher than in the Tanzania lines, and markedly decreased with temperature. In these lines, fast larval growth correlates with high critical weight.

## Consequences of genetic variation among offspring in Taraxacum, dandelion

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One of the most obvious consequences of sexual reproduction is the production of genetically variable offspring by one mother. A number of ideas have been launched about the short-term consequences of this strategy, but few empirical data are available. This study used *Taraxacum*, dandelion, a species that consists of sexual and apomictic types. Progeny from sexual and apomictic mothers were compared under four conditions in the greenhouse. Sexual families had a more even biomass production across treatments than apomictic families. In a parallel experiment mixtures of apomictic genotypes were compared with monocultures of these genotypes. No differences were found between mixtures and monocultures. In the simplified greenhouse environment, genetic variation did not confer any advantage, even though different genotypes had their optima in different treatments. Ecological differentiation between the reproductive modes was more important than genetic differentiation among genotypes of the same reproductive type.

# The hka test into the new millenium

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The HKA test (Hudson et al, 1987), proposed to determine significant departures from neutral expectations in the levels of intra- and interspecific DNA variation, has been widely applied without modifications during the last decade. The test itself is nevertheless very conservative, its sensitivity and robustness has not been examined, and the statistic originally proposed is not always adequate to detect deviations from neutral evolution of sequence data (because it does not differentiate between categories of mutations, it can hardly detect the effect of forces modifying the frequency distribution of polymorphic changes).

We propose a series of modifications of the HKA test, aimed not only to increase the power of the test, but also to detect departure from neutrality of the frequency distribution of polymorphic mutations, taking advantage of what is known about the forces driving evolution of DNA sequences.

Different estimators of q are proposed for improve the power of the test, and a new statistic is suggested to detect deviations not only in the proportion of intra- and interspecific polymorphism for two chromosomal regions, but too for detect departure from neutral expectations in the frequency spectrum of mutations.

These modifications have been analyzed and compared with the original HKA test by computer simulation under different evolutionary scenarios, and finally applied to real molecular data. The interpretations obtained with all considered possibilities are analyzed, and an optimal expression for the HKA test is suggested.

# Local adaptation of Daphnia populations: some emerging patterns

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Several recent studies have investigated local genetic differentiation in quantitative traits related to predator stress in natural *Daphnia* populations. A survey of these studies and some results from new experiments indicate that (1) even neighbouring populations can be genetically strongly differentiated for quantitative traits; (2) the target of local adaptation to predator stress can be the average value of the trait over environments as well as the amplitude of the predator-induced phenotypic response; (3) striking local genetic differentiation is not limited to predation pressure, but may also occur in response to other stress factors; (4) local adaptation can occur in a short time-span (probably much less than 10 years, as revealed from populations derived from resting egg banks). The emerging pattern is that many *Daphnia* populations are highly locally adapted and genetically specialised to local habitat conditions, even though the genotypes can often be considered generalists with respect to variation in environmental conditions within habitats.

## Physics, morphogenesis and evolution

## Miquel De Renzi

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The current evolutionary paradigm ordinarily concerns with genes and natural selection, and its consequence is adaptation. This point of view is part of the Aristotelian functionalism. However, physical and chemical forces would explain the shape of organic structures according to D'Arcy Wentworth Thompson. Functional explanations would come later, but such a promising way of biological thinking was given up by the followers of the Modern Synthesis. Genes and their expression would be the only causal explanation for every aspect of organisms. Moreover, developmental biology was not included in the Synthesis. However, morphological structures are generated during development. Processes such as differentiation involve directly gene expression, but the understanding of the shape of organs and other structures needs the knowledge of physical forces and how they work on living matter. Genes produce the raw materials. New materials interplay, according to their physical and chemical properties, and local form is the result of a dynamical balance of forces. In order to be achieved, gene expression in itself requires forces and local form within the cell. Self-organization would be the reason for both the epigenetic processes and gene expression. Phenotypes (morphology) are whole stable steady states that result of balance of forces; they are emergent as referred to local steady states. Phenotypes are physically subjected to an effective environment. Environmental forces modify the initial situation and a new balance is reached (adaptation can be improved through the life cycle by use). On the other hand, their physical and chemical stability would take place within a more or less narrow rank of conditions. There are separate regions for stability. Restricted variation is allowed in each region and species are often in morphological stasis. Transitions between regions would be discontinuous; this would be the main domain for macroevolution.

## Dynamics of mixed-clone chronic infections of the rodent malaria parasite Plasmodium chabaudi

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Mixed-clone infections of malaria parasites are common in both humans and animals. One of the questions to be asked in such situations is how these mixed infections determine host fitness. Another is how they affect the fitness and persistence of the different strains within the host.

In evolutionary biology, the general view is that the more virulent clones within the host will determine the outcome of the infection, and outcompete the less virulent clones. However, there is no experimental evidence for this.

Using the rodent malaria parasite *P. chabaudi*, an experimental test for this hypothesis is made using a four-clone mixed infection in mice. The four clones used vary in their levels of virulence, from being highly virulent to avirulent. Using PCR amplification of the MSP-1 gene, presence and absence of the four strains can be monitored throughout the course of the infection.

Besides the implications for understanding mixed-clone infections in terms of evolutionary biology, problems arising when using PCR markers in mixed-genotype infections will be discussed. Special emphasis will be given to repeatability of band patterns. Implications for controlled experiments and, more importantly, field studies of the chronicity of malaria infections will also be addressed.

#### Microsatellite variability of honeybee populations from the Canary Islands.

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*Apis mellifera* populations from the Canary Islands have been surveyed for variation at 8 microsatellite loci and compared to continental populations from Murcia (Southeastern Iberia) and Tetuán (Morocco). The information provided with these nuclear markers has been used to investigate the genetic structure of these populations and to evaluate the levels of genetic differentiation within the islands and between them and the continental populations. Different levels of genetic variation have been found. The island populations show a low level of genetic variation in terms of average number of alleles (< $5.8\pm3.1$ ) and expected heterozygosity (He < $0.489\pm0.237$ ) as it is expected for isolated island populations. The African population displays the highest genetic variation (He =  $0.738\pm0.068$ , number of alleles =  $6.6\pm1.1$ ). The allele distribution at these microsatellite loci fits the infinite allele model of evolution better than the stepwise model. *F* statistics suggest that no clear isolation by distance mechanisms have caused significant differentiation among the Canarian and the African populations and that the islands populations display a closer relationship with Iberia. Phylogenetic analyses support this result which can be explained by honeybee introductions from the Iberian Peninsula from the XVI century onwards. The gene introgression from foreign queens and drones is evident in the sample from Tenerife and drives this population to cluster in a separated position in a neighbor-joining cladogram.
## Genome clues to fossil identity: molecular biodiversity and ecology in planktonic foraminifera

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The pelagic foraminifera have a worldwide distribution. The continuous rain of their tests -calcareous shells- onto the seabed built, during the last 160 Myr, hundreds of meters of sediment that constitutes one of the best conserved and complete fossil record. According to morphological analyses of fossil and modern specimens, the planktonic foraminiferal species occupy huge distribution ranges, are not and have never been numerous -only 50 today-, and evolve through gradualistic or anagenetic patterns due to parapatric mode of speciation.

We have tested the species concept in planktonic foraminifera by sequencing or by assessing RFLP of the SSU rDNA and ITS genes for hundreds individuals from different species representing the 3 main families, collected at 35 locations along a 50°S-50°N transect in the Atlantic ocean, in the Caribbean, Sargasso, Mediterranean seas, and California boarderlands.

The phylogenetic and phylogeographic analyses reveal that all morpho-species can be splitted into several genetic species, whose distribution across the Ocean is patchy and alternating. The different genotypes clearly fall into different hydrographic provinces and also present phenotypical differences which had either been overlooked or attributed to ecophenotypy by paleontologists. For example, the 3 cryptic species we detected in *Orbulina universa*, a 15.4 Myr old spinose species, are found -independently from the geographic distances- in different water-masses having specific levels of chlorophyll concentration. Ocean productivity apparently also played a role in the very recent speciation events we genetically detect in *Globorotalia truncatulinoides*, a 2.8 Myr old non-spinose species that adapted to the subpolar nutrient rich water masses only 300 000 years ago. Molecular clock-based and morpho-ecological arguments suggest that foraminifera are high-dispersal organisms in which reproductive mechanisms and behavior, rather than just geographic barriers, play key roles in species formation and maintenance.

# Diminishing returns from mutation supply rate in asexual populations

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Mutator genotypes with increased mutation rates may be especially important in microbial evolution if genetic adaptation is generally limited by the mutation supply of mutations. We tested this by manipulating mutation rate, population size and initial adaptedness of of the bacterium *Escherichia coli* that evolved in the laboratory. The rate of adaptation was proportional to the mutation supply rate only in particular circumstances of small or initially well-adapted populations. These experiments also demonstrate a "speed limit" on adaptive evolution in asexual populations, one that is independent of the mutation supply rate.

# Symbiotic bacteria in Western Flower Thrips (Frankliniella occidentalis).

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Symbiosis between insects and microorganisms is a wide spread phenomenon, and can be parasitic or mutualistic. Mutualistic interactions have been described in many insect systems, ranging from very tight associations like bacterial mycetomes in Homoptera to facultative symbionts in gut lumen. Symbionts can play a role in host plant adaptation by supplying essential nutrients or detoxifying toxins. We investigate if a correlation exists between genotypes of gut microbes and the use of food plants by the insect host. Western Flower Thrips is used as model system. This is an important pest insect, which has recently expanded its geographic distribution. We study the role of bacteria in thrips adaptation to its food source.

We have isolated bacteria from the thrips hindgut and midgut and cultured them on artificial medium. Analysis of 16s rDNA sequences and biochemical tests showed that these bacterial strains are all closely related Enterobacteriaceae (*Erwinia* spec TAC). By means of RAPD markers it was confirmed that these bacteria were constantly associated with the thrips culture in our lab during a long period of time. The same RAPD markers were used to compare symbiotic bacteria in thrips populations from different countries and various host plants. Genetic variation found in thrips bacteria was very low.

The role of symbionts was studied using bacteria-free thrips. It was shown that the effect of the symbionts on thrips fitness depends on the food source of the thrips. Transmission of bacteria to larval thrips takes place via the food source. Strong correlation exists between bacteria in the mothers and in the offspring.

Present studies include the comparison beteen *Erwinia* bacteria found in thrips and strains found in the guts of other phytophagous insects.

#### The Amplification and Evolution of Mammalian SINEs.

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SINEs are short, mobile elements that make up a significant portion of all mammalian genomes. They have spread throughout their respective genomes through a RNA-mediated insertion process. They typically range in copy number from 10<sup>4</sup> to 10<sup>6</sup> copies per genome. Each specific family of SINEs is specific for a single mammalian Order, and sometimes to a single species. Some mammalian Orders have only a single SINE family, while others have up to three different SINE families in a single genome. Each SINE appears to have originated independently from a different RNA polymerase III transcribed gene, such as tRNAs and 7SL RNA. The amplification of SINEs throughout the mammalian genome has had a major impact on the evolution of those genomes. In humans, approximately 0.1% of all human diseases are caused by insertion of an Alu element, the primate SINE. Earlier in primate evolution the insertion rate was two orders of magnitude higher and therefore SINE insertion made up a major portion of the genetic damage occurring in the genome. In addition to damaging the human genome, however, these insertions also have had tremendous potential for altering gene expression and creating alternative gene products from those genes. Furthermore, the distribution of SINEs throughout the genome creates tremendous potential for unequal recombination events between SINE elements. In humans, these recombination events currently contribute to approximately 0.2-0.3% of all human disease. These recombinations have caused numerous examples of exon duplication, exon deletion, and chromosomal translocations. Taken together, these various mechanisms have allowed SINEs to play a major role in the evolutionary re-shaping of mammalian genomes.

Population structure of aphid *Rhopalosiphum padi* (Linné, 1758) reveals gene flow between sexual and asexual populations

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Reproductive strategies of aphids show a seldom diversity, ranging from cyclical parthenogenesis (sexual clones) to strict asexuality. The cereal aphid, *Rhopalosiphum padi*, presents the attractive peculiarity that sexual and asexuals clones coexist in natural populations. This originality contributes to make *R. padi* a very good biological model to test theories of the evolution of sex.

Here, we use this aphid in order to evaluate the influence of reproductive mode on the repartition of genetic variation in natural populations. Previous studies of population genetics of *R. padi* have been limited by low polymorphism detected by allozyme, mitochondrial DNA and RAPD analyses. Thus, we began a comparative study of genetic diversity and spatial structuration of 8 sexuals and 7 asexuals French populations of *R. padi* using 8 microsatellites markers. We found that asexuals clones of *R. padi* have little allelic polymorphism and a high heterozygosity at most loci. This high rate of heterozygosity in asexuals clone indicates that intraclonal allelic divergence has occured at most loci and suggests long term persistance of asexual clones. In contrast, sexual populations of *R. padi* show high allelic polymorphism but little geographic differentiation. Cyclical parthenogenetic clones reproduce by parthenogenesis on cereals and by sexual reproduction on *Prunus padus*. The latter has a fragmented distribution in France that might force sexual clones to have large scale dispersion to complete their life cycle. Therefore, host alternance imposed to sexual clones could explain their relative genetic homogeneity at a large geographic scale.

#### Gene Genealogies in Continuous Populations with Limited Dispersal

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Coalescent theory is a simple and economical way of modeling the history of a sample of gene copies through gene genealogies. It usually assumes a neutral model with panmictic demes, possibly linked to one another *via* migration. However, natural populations may not fit this model and may often be closer to a continuous populations with limited dispersal. It is thus important to adapt theory to this kind of system. Previous attempts to do so were based on the Wright-Malécot theory of identity by descent. However, as shown by Felsenstein, some difficulties underlie this approach: it leads to increasing population structuring in clusters increasing in size and more and more distant from one another. Finally, this theory predicts an effective population size for the ancestral population that increases linearly, backward in time, eventually extending beyond the range of the species. Some solutions to these problems are suggested and tested.

cpDNA and mtDNA diversity in beets (*Beta vulgaris* ssp (L.), Chenopodiaceae) and association between the two organelle genomes.

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Beta vulgaris ssp is a crop-wild complex of large interest. We sampled 528 ind. from 100 pop. in southern France and Spain along the Mediterranean coastlines but also in inland areas. Cytoplasmic genetic diversity was investigated both with PCR-RFLP markers to assess cpDNA polymorphism and RFLPs for mtDNA polymorphism. Over the whole study, 14 chlorotypes and 21 mitotypes were observed. High diversity values for both French and Spanish groups were estimated with H values of 0.58 and 0.70 (cpDNA) and 0.59 and 0.62 (mtDNA) respectively. The overall Fst estimate value equalled 0.48, which suggests a strong genetic cytoplasmic differentiation. When considering the linkages between the two organelle genomes, 27 combinations were found, with 1.29 cpDNA types per mtDNA type and 1.86 mtDNA types per cpDNA type. Linkage disequilibrium appeared to be very strong, with a value of 0.96. Only 4 out of 21 mitotypes were associated to more than one chlorotype. This number was even reduced to one when 3 (out of 8) cpDNA loci, exhibiting polymorphisms based on small indels (1 or 2 bp), were excluded of the analysis. In that case, the number of chlorotypes decreased to 7, with 1.05 cpDNA types per mtDNA type. D' then reached 0.99. Nevertheless, the indications provided by all the cpDNA loci have to be taken into account as the rare combinations found were not geographically randomly distributed. In conclusion, (i) PCR-RFLP markers based on universal primers appeared to be valuable tools to investigate within-specific chloroplastic variation, in beets; (ii) it is often assumed that the structure and the evolution of the plant mitochondrial genome may lead to recurrent apparition of the same mitochondrial variants in different populations. From the present study (D' = 0.99), this seems to be unlikely in Beta vulgaris. The genetic combinations observed here suggest that mitochondrial variants are mostly distributed via migration among populations.

# An adaptive dynamics model for the coevolution between the globeflower *Trollius europaeus* and its pollinator flies (*Chiastocheta* spp.)

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The globeflower *Trollius europaeus* (Ranunculaceae) is unique in its genus in that its flower has a totally closed globe shape. It is exclusively pollinated by several species of *Chiastocheta* flies which larvae are seed predators of the host plant. Molecular data suggest that speciation of *Chiastocheta* spp. took place recently within the host plant. We constructed an adaptive dynamic model based on three variable ovipositing behavioral traits of the female flies: flower stage at oviposition, clutch size and the level of avoidance of already parasitized flowers. Simulations of the evolution of these three traits where done separately for flies ovipositing in a population of closed flowers and in a population of open flowers. The model shows that because of competition between larvae for seeds, two divergent strategies differing for flower stage at ovipositing strategy, whatever the flower shape. Moreover, we assumed that when the flower is closed, the early-ovipositing strategy is advantaged in terms of eggs survival. This leads to a higher competition between larvae of this strategy: the clutch size is selected to decrease. As a result, early-ovipositing flies visit more flowers (higher pollination efficiency) and lay less eggs per flower (lower predation costs) than late-ovipositing flies, being more beneficial to *T. europaeus*. The predictions of our model fit well the field data, and support the hypothesis of coevolution between flower shape in *Trollius europaeus* and ovipositing strategies in *Chiastocheta* flies.

### Allozyme analysis of freshwater mollum in Lithuania

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One of the mechanisms of adaptation is biochemical and physiological responses to environmental changes. The introduction of different substances and agents into environmental by man has change equilibrium of nature.

What are correlates between genetic variation and environmental variation in such situation?

Freshwater molluscs *Limnaea stagnalis* and *Planorbarius Corneus* are widespread in the aquatic ecosystems of Lithuania. They are perfect bioindicators. in pollutants bioaccumulation due to they sedimentary way of life, ability to concentrate chemicals up to very high concentration. These molluscs can be use as bioindicators of environmental variability.

Molluscs, for genetic variability studies, were collected from non-industrial (Sakiai district, Simnas and Kroku water meadow) and industrial regions (Elektrenai, Siauliai and Kedainiai) of Lithuania in 1997-1998.

Using polyacrilamide gel electrophoresis were, identified six isoenzymes systems (EST-esterase, MDH-malate dehydrogenase, LDH-lactate dehydrogenase, G-6PDH-glucose- 6 phosphate dehydrogenase, ME-malic enzyme, 6-PGDH-6phosphogluconate dehydrogenase) three of them (G-6PDR MDH and EST) were polymorphic.

These sampled populations has been investigated and, described by frequency of gene and of genotype, the proportion of polymorphic loci (P), the total gene diversity (Ho) and, expected mean heterozygosity(He), the mean number of alleles at all loci (A).

The analysis among populations showed genetic differences between industrial and non-industrial regions.

Enterococcus as an antibiotic resistance gene shuffler and mobilizer.

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The evolution of antibiotic resistance has been an extraordinarily fast process. The speed at which resistance to a given drug arises among clinically-important bacteria depends on several factors: the previous availability of resistance genes within the bacterial "gene pool", and its ability to being mobilized between different bacterial taxa. It appears that some bacterial species are more capable than others to perform gene rearrangements and mobilization. On Enterococcus two particularly interesting phenomena has been observed: (1) the organization of the vancomycin-resistance operon, showing different codon-usage for several of the included genes; and (2) the possible emergence of bifunctional (acetyltransferase (6')/phosphotransferase (2")) aminoglycoside-modifying enzymes (AAC/APH). The bifunctional enzyme is 479 amino acids long; the amino acid sequence analysis showed a putative acetyltransferase domain at the N-terminal region that can be aligned to the sequences of other known AAC enzymes; sequence homology were observed in the order AAC6'>AAC3'>AAC2', all of them from gram-negative bacteria. The C-terminal region of the AAC/APH enzyme showed slight homology to other APH enzymes, mainly to gram-negative APH3'. Both known AAC/APH enzymes, one from Staphylococcus and other from *Enterococcus*, share high amino acid sequence-homology, but codon usage suggests that the enzyme originated in *Enterococcus*, and was then transferred to *Staphylococcus*, where it has been diverging, especially at the AAC domain. Although the enzyme seems to have appeared in enterococci, around 90% of aminoglycoside-resistant staphylococci produce the bifunctional enzyme, alone or in combination with other modifying enzymes. We propose that *Enterococcus* is therefore acting as a gene rearranger for the bacterial community.

# Evolutionary Branching in Sexual Populations: A New Model for Sympatric Speciation

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Understanding speciation is a fundamental problem in evolutionary biology. While it is generally accepted that many species have originated through allopatric divergence in geographically isolated populations of the same ancestral species, the possibility of sympatric speciation has often been dismissed.

Recent results in the theory of adaptive dynamics, however, suggest that once density and frequency dependence, naturally arising from the ecological feedback between a population and its environment, are properly incorporated into models of evolutionary change, convergence to disruptive selection becomes a common and robust phenomenon. The resulting process of evolutionary branching, where a population with a unimodal distribution for a metric character undergoes directional selection to a state at which selection turns disruptive, has been suggested as a paradigm for sympatric speciation in clonal species.

In this paper we extend the results of clonal adaptive dynamics to sexual populations. We use explicit multilocus genetics to describe sexual reproduction in an individual-based model, and we consider the evolution of assortative mating, depending either on the character under disruptive selection or on a selectively neutral marker trait. In both cases we show that, for generic models of resource competition, evolution of assortative mating often leads to reproductive isolation between ecologically diverging subpopulations. Our results conform well with mounting empirical evidence for the sympatric origin of many species and we thus suggest to reopen the case for sympatric speciation.

#### Bacterial "ménage à trois"

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It appears that conjugative plasmids are the most important and widespread causative agents of horizontal gene transfer in bacteria. Often plasmids carry virulence factors or genes conferring resistance to metal ions or antibiotics. Because bacteria have to share their habitats with different bacterial species or strains, such as the human gut or soils, we wonder whether this could influence the spread of plasmids. In general, it has been shown that conjugative plasmids transfer themselves more efficiently to bacteria of the same strain than to different bacteria. However, in a survey of nine natural isolates of *Escherichia coli* and three different species of enterobacteria (*E.coli, Salmonella enterica* and *Erwinia chrysantemi*), and using the plasmid R1, we found that the rate of conjugation from one given strain, "X", to cells of another strain, "Y". This means that some bacterial strains/species can be helping the spread of plasmids among other bacterial strains/species. Eventually, in a bacterial human infection, this ecological phenomenon may disrupt the efficiency of treatment with antibiotics if the plasmid carries antibiotic-resistance genes, or even to help the appearance of disease if the plasmid carries virulence factors. In this phenomenon, plasmids and bacteria have different interests, hence giving the possibility to conflicts. The evolutionary meaning of this conflict will be discussed.

# Variable investments and the origin of cooperation and mutualism

## Michael Doebeli, Tim Killingback, and Nancy Knowlton

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Interspecific mutualisms are widespread, but how they evolve is not clear. The Prisoner's Dilemma is the main theoretical tool to study cooperation, but this model ignores ecological differences between partners and assumes that amounts exchanged cannot themselves evolve. However, cooperation is rarely all or nothing, and its evolution probably involves the gradual extension of initially modest degrees of assistance. Therefore, we consider a framework for cooperation based on the concept of investment: an act which is costly, but which benefits other individuals, where the cost and benefit depend on the level of investment made. To study the evolution of cooperation and mutualism we consider the *Continuous Prisoner's Dilemma* in spatially structured models and in iterated games. In 2-species models for mutualism the payoff obtained from interspecific interactions determines the outcome of competition within each species separately. Our results show that if investments are considered in a spatially structured context or in iterated interactions, selfish individuals who make arbitrarily low investments can be invaded by higher investing mutants. This results in the mean level of investment evolving to significant levels where it is maintained indefinitely. Our approach provides a natural solution to the fundamental problem of how cooperation and mutualism gradually increase from a non-cooperative state. Symposium no. 6: Origin, evolution and stability of coevolved mutualisms

A comparative analysis of complete sequence of mitochondrial genome between brook char (*Salvelinus fontinalis*) and arctic char (*S. alpinus*) (Pisces, Salmonidae)

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Wild brook char populations completely introgressed for the mitochondrial genome (mtDNA) of arctic char are found in seven lakes in eastern Quebec, Canada. The respiratory enzymes of these populations are thus encoded by their own nuclear DNA and by arctic char mtDNA. A recent study has demonstrated a nonequivalent catalytic efficiency at only low temperature between introgressed and nonintrogressed *S. fontinalis* for cytochrome *c* oxidase (complex IV). These results suggested that there may be differences in function of this enzyme complex encoded by mtDNA in *S. alpinus*. In this study, we compared the complete sequence of mtDNA for these two species in order to test this hypothesis. This analysis revealed no amino acid differences for CO1 and CO2 and Cyt b. In contrast, amino acid differences were found in all, but one subunit of the NADH dehydrogenase complex (complex I). These results suggest that coding genes of complex I instead complex IV may be considered as potential sites for adaptation to specific thermal regime in these fishes.

### Rates of structural mutation for transposable elements and microsatellite loci in D. melanogaster.

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Eukaryotic genomes maintain vast quantities of repetitive DNA. Knowledge of the rate and nature of changes these sequences are involved in are of main significance to understand the possible role, if any, of the different kinds of this apparently superfluous DNA. We report a study of spontaneous changes affecting two kinds of repetitive sequences, transposable elements (TE) and microsatellite repeats, in mutation accumulation lines. Mutations for TEs (P, hobo, foldback, gypsy, 412, copia, blood, 297, 1731, mdg1, Neb, jockey) were revealed by Southern blotting. Clustering of alterations for different TE families in the same lines indicated that they were not independent. Mean rate of mutation was 1.2\*10-5 per element per generation. Most alterations could be interpreted as structural changes, mainly deletions, that have small or null effect over fitness. This applied to the

different families of elements. Congruently, in a study that to the date is limited to element 297, many genomic copies were shown to be defective. The existence of these probably dead copies of TEs can help to understand their persistence in populations.

Rate of mutation for microsatellite repeats, based in the study of 19 loci, was 3.8\*10-6. The only mutation occurred in the lines was a DNA lose of, presumably, six repeats.

# Towards a Meaning-Based Theory of the Evolution of Language

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The emergence of language constitutes the most intriguing puzzle in the evolution of the human species. The crux of the puzzle is the apparent paradox of the *functional* nature of language. Modern discussions of the evolution of linguistic knowledge are based on the common-sense presupposition that linguistic knowledge can be adequately described and explained in functional terms - as a tool for the communication of *meanings*. Ironically, the majority of scholars who spend their time trying to figure out the intricacies of natural language grammars, professional syntacticians, *reject* this presupposition as totally inadequate. Noam Chomsky's Generative Grammar, by far the most influential linguistic theory of the second half of the century, famously asserts that the universal, innate basis of linguistic knowledge is in its essence *structural* and *formal*, and *autonomous from meaning*. If this is true, then a functional characterization of language, and a Neo-Darwinian theory of the evolution of language, are *impossible in principle*.

In this paper, I will claim that a wide range of empirical discoveries, made in the last decade in the domain of *linguistic meaning*, leads the way to a synthetic, functionally-oriented characterization of linguistic knowledge - which can provide the theoretical foundation for a theory of the evolution of language. Research in the domain of *linguistic meaning* has centered on the careful study of the meanings of words and constructions, and has revealed the dramatic extent to which linguistic meaning actually determines linguistic structure. The results of this line of research help discredit the Chomskian presupposition of the autonomy of syntactic structures, and allow for a new conception of the nature of grammar: Not an autonomously-formal generative system, but a *functional mapping-system* between the constitutive, innately-given domain of linguistic meaning and the parallel domain of linguistic sound; a system developed by evolution to allow for the encoding of *a specific, constrained set of meanings* by means of sound concatenation. This view of the functional basis of linguistic knowledge allows for a major reframing of the evolutionary question: It can now be constructed as the question of the increase, over evolutionary time, of the internal complexity of the domain of linguistic meaning, and the increase in the intricacy of the mapping between linguistic meaning and linguistic sound. In other words, the evolution of language may be thought of as the process of the gradual expansion of the *expressive envelope* of language, and the gradual development of the encoding-decoding system for this expressive envelope.

## Conflict and co-operation in animal-microbial symbiosis

#### A. E. Douglas

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Many animals bear symbiotic micro-organisms from which they derive nutrients. Both the animal and microbial cells co-operate in nutrient exchange, in the sense that each releases specific nutrients that would otherwise enhance their own growth and proliferation rates. However, the amount and identity of nutrients translocated from the micro-organisms to the animal do not invariably maximise animal fitness, and this discrepancy may reflect conflict between the selective interests of the animal and microbial partners or limitations to the nutritional versatility of the micro-organisms. These processes will be illustrated by examples among algal-invertebrate symbioses and insect-microbial associations.

# Eavesdropping and mate choice in fish

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Males usually obtain and defend a territory through conspicuous signalling and aggressive interactions. During these signalling interactions, males advertise and estimate their respective quality and / or motivation. This information can be intercepted and used by other observing individuals, such individuals have been called eavesdroppers (McGregor & Dabelsteen 1996). Until now, very few studies have investigated if this eavesdropping behaviour is common and what kind of information can be obtained. Yet eavesdropping could constitute an easy and safety way to acquire some information and thus could be common. Although the cues used in mate choice are now well identified, the processes by which females assess their mate is not well understood. Observing the outcome of male-male interactions could allow females to directly estimate the relative quality of these males and could constitute a process by which mates are evaluated.

This poster will present the results of an experiment with fighting fish (*Betta splendens*) designed to discover (1) if females are interested in monitoring fighting interactions between two males and (2) if this eavesdropping behaviour can provide information used in mate choice.

# Population sruturing in a free spawning marine bivalve macoma balthica

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The sea is often regarded as a continuous environment where there are no distinct geographical barriers hampering gene flow. Under these circumstances population structuring seems unlikely. However, many cases of population differentiation in marine species have been observed. This suggests the occurrence of diversifying mechanisms in sympatry.

As part of a study on population structuring and local adaptations in *Macoma balthica* (an intertidal and shallow subtidal living, free spawning bivalve with a pelagic larval phase) we investigated two possibilities which would hinder gene flow. First, asynchrony of spawning which would leave the population in a number of interbreeding entities, and second, the scale of fertilization. During the reproductive phase in spring, animals were collected at four locations 5 to 10 km apart in the Wadden Sea and North Sea. Fractions of gravid males and females and the likelyhood of spawning were determined as well as effects of sperm age and concentration on fertilization. Results show that within a site spawning takes place over a period exceeding one month. Overall, spawning is earlier in the Wadden Sea than in the North Sea. Fertilization success is highly dependent on the sperm concentration and age, making fertilization a small scale process (meters). Fertilizations between the monitored sites are therefore unlikely. Furthermore differences in timing of gamete release can have an influence on dispersal and survival of the larvae, leading to large variance in individual reproductive succes. This amounts to the conclusion that there is no random mating in the studied population of *Macoma balthica* in the Wadden Sea and North Sea.

## Mate choice in host races of the Larch Budmoth Zeiraphera diniana

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Sympatric larch and pine forms *Zeiraphera diniana* (Lepidoptera:tortricidae) may be examples of hosts races. The two forms display a number of phenotypic and genetic differences but will hybridize in the lab with no F1 sex ratio distorsion. Here we report on the results of field tests of long range cross attraction, and labortory tests of short range mate choice which suggest that the two forms also hybridize in the wild. From preliminary data we estimate that the level of hybridization is approximately two percent per generation-further studies using molecular markers are expected to provide an indirect measure of gene flow between twe two forms.

## PLENARY LECTURE

## Morphological evolution and transitionism

### Denis Duboule

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The evolution of morphologies largely relies upon variations in developmental mechanisms. Changes in the regulation of those genes involved in these processes often induces modifications that are either reminiscent of evolutionary transitions, or that exist in other species. In this lecture, I would like to discuss one such mechanism involved in the establishment of positions along various body axes and which has a very long evolutionary history. First, I would like to discuss the potential use of orthologous genetic systems which, however, are implemented in a different way in diptera and vertebrates. Secondly, I would like to illustrate how a particular developmental mechanism could be recruited within the same species and transposed to another emergent structure, where its function is similar but differently achieved.

Finally, I shall discuss the impact that the most recent knowledge of our genome will have over evolutionary theories. The fact that we share our genes with most other metazoans has crucial impact on how we ought to think evolution at the mechanistic level. In the *transitionist* view, these novel arguments are taken into account and micro- and macro evolution are only the two extremes of one of the same process, evolving from one to the other along with the complexification of functions. In this scheme, evolution is neither inherently gradualist nor saltationist but tends to shift from one to the other, implying an increasing importance of the variation over that of selection.

## A reaction norm approach to the evolutionary ecology of senescence in Daphnia

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Although food and temperature are well known to modify rates of senescence, little is known about genetic variation or ecological relevance of the plasticity of senescence. I examine the genetic variation and phenotypic plasticity of senescence within and between two species complexes of *Daphnia*, a common freshwater crustacean. I quantified senescence in four environments (two temperatures and two food levels), seeking to understand the plasticity of mortality and fecundity schedules with respect to the ecological conditions of the species' natural habitats. To quantify senescence, I estimated the age-specific contribution to two common fitness measures, *r* and R. In general, senescence patterns were highly plastic, but the degree of plasticity varied across species. Population growth rate (*r*) was most responsive to food, but in contrast, senescence was most responsive to temperature. Temperature also strongly influenced the degree to which genetic differentiation within species complexes was phenotypically expressed, with little different habitats, genetic variation of senescence was strong and robust across environments. Species of *the D. mendotae-dentifera* complex, which both live in stratified lakes, had more similar senescence patterns. Most of the genetic variation in senescence occurred within species complexes, rather than between complexes, indicating that evolutionary divergence of senescence in *Daphnia* is recent and dynamic.

Selection and genetic structure in the barnacle, *Semibalanus balanoides* as revealed by allozyme and microsatellite markers.

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The presence of genetic clines in marine environments provide an ideal system to understand how diversity is maintained in spite of typical homogenising factors such as long larval dispersal and lack of physical barriers. A recent study of Semibalanus balanoides populations from the Gulf of St.Lawrence (Canada) revealed a genetic discontinuity of allelic frequencies at two enzymatic loci (Mpi and Gpi) in the vicinity of the Miramichi estuary in the southern part of the Gulf. Holm and Bourget (1994) proposed that selection imposed by thermal gradients was most likely responsible for such genetic patterns in absence of physical barriers to gene flow. In order to further elucidate the respective roles of selection and gene flow on the genetic structure of S. balanoides from that region, we screened eight populations at six microsatellite loci and at the two allozymic loci previously found to be polymorphic (Mpi and Gpi). .Three alleles were detected for both Mpi and Gpi. By contrast, the number of alleles per microsatellite locus ranged from 6 to 49. Some high Fst values were detected with allozyme markers (up to 0.19) whereas much lower estimates were found with microsatellite markers (0.002-0.039), although a higher number of them were significant. UPGMA clustering revealed that the populations formed two groups, two south of the Miramichi and the other six north of the river. By contrast, there was no clear grouping of populations south and north of the Miramichi with microsatellite markers. As microsatellite markers are expected to be neutral, the lack of genetic subdivision around the Miramichi strongly suggests that selection is operating on the allozymes. Our results are congruent with those of a recent study which showed that Mpi genotypes experienced differential mortality associated with high temperature.

# Sex ratio variation in populations of six dioecious species of Lindera (Lauraceae) in Kyoto, Japan.

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Variation in population sex ratio, i.e. the relative number of male and female individuals, has been reported for many dioecious plant species. However, few studies have considered differences in sex ratio among different species within a clade. In this study we investigated sex ratio variation in natural populations of six species of *Lindera* (Lauraceae) found in deciduous forests of Kyoto, Japan. It was hypothesized that variation in population sex ratio among a set of closely related species are connected to ecological and morphological traits. Interspecific differences in sex ratios of the *Lindera* species were examined in relation to patterns of population structure, flower dimorphism and fruit set. It was found that population sex ratios were predominantly equal or biased in favor of males. Generally, flowering female individuals tended to be larger in girth, had smaller flowers and bore the cost of fruiting, in contrast to conspecific males. Intersexual differences in floral investment were not found to influence sex ratio. Differences between species in fruit allocation may, however, affect population structure and sex ratio. Results of this study suggest that population sex ratios are not merely products of phylogeny, but may potentially be influenced by several ecological factors.

## Genetic drift in populations of Ultraselfish Gene Complexes

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We use stochastic population models to study the evolution of Ultraselfish Gene Complexes (USGC's). USGC's are chromosomal regions characterized by meiotic drive: a heterozygotes bearing the USGC passes it to more than 50% of offspring. USGC-bearing homozygotes are esterile. Although USGC's promote themselves at the expense of others genesw in the same genome, USGC's have been successful in evolution: they have beeb observed in animal, plant and fungal species and may lie, undetected, in many others. While the molecular drive mechanisms differ, USGC's exhibit similar genetic features, suggesting that the population genetic mechanisms that allow such gene complexes to evolve may be shared.

We present Markov models and Monte Carlo simulations of genetic drift in populations of USGC's. Genetic drift, the stochastis behavior of allele frequencies in a small populations, is a fundamental force in the process of evolution, yet the role of genetic drift in the evolution of USGC's is not well understood. Our analysis shows how USGC's evolve different characteristics in species typified by small and large populations, respectively. We apply our results to two well studied USGC's: the t-haplotype in *Mus musculus* and Segregation Distorter in *Drosophila melanogaster*.

## Chloroplast genetic diversity in a tropical rainforest tree species, Vouacapoua americana (AUBL.)

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Along with the other molecular markers, the chloroplastic genome has been efficiently used to describe the genetic diversity in plant species. Because of its maternal inheritance in angiosperm species and low mutation rate, it is specially well adapted to infer patterns of seed dispersion and historical events, such as recent colonizations. We studied the variation of chloroplastic DNA using PCR-RLFP in 95 individus among 13 populations of *Vouacapoua americana* (Caesalpiniaceae) from French Guiana with 5 pairs of chloroplastic primers. Population diversity, total gene diversity and differentiation among populations were estimated following Nei's method as Hs=0.10, Ht=0.86 and Gst=0.88 respectively. This is consistent with the limited gene flow associated with seed dispersion in the species studied. The strong genetic structure observed at the regional level can be interpreted as resulting from regressions and transgressions of French Guiana's forest that took place in the late Pleistocene and Holocene. The actual distribution of *V. americana* is discussed in the light of recent colonizations from several forest refuges.

#### Sequence variation in Pinus sylvestris

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Scots pine (*Pinus sylvestris*), as many other pine species, has a large current population size. The observed levels of inbreeding depression suggest that Scots pines may have high mutation rates. Many Scots pine marker genes are highly variable. These observations suggest that the levels of nucleotide variation may be high. In Scots pine the mutation rates per year may be lower than in many other taxa, resulting in lower per year rates of evolution. Scots pine is highly heterozygous, but sequence amplification and analysis can be performed in haploid megagametophytes to avoid problems caused by heterozygosity. We examine the patterns of nucleotide polymorphism in three Scots pine populations, two from Finland (latitudes 67°N and 60°N) and one from Kharkov, Ukraine (50°N). In this study we use genes that encode several important enzymes or structural proteins, e.g., phenylalanine ammonia-lyase is a key enzyme in the phenylpropanoid pathway in the lignin biosynthesis for the development of secondary xylem in wood formation.

## **Relationships of the Ediacaran organisms**

#### Jerzy Dzik

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The Vendian and Cambrian fossils of soft-bodied organisms are of very different taphonomic origin. The Ediacaran and Namibian preservation style provides information on the relative pressure of internal animal body fluids, rigidity of its tissues, flexibility and elasticity of membranes. Instead, the dominant Cambrian style of preservation of soft tissues shows mainly the content of organic matter in particular parts of the body. The differences between the Ediacaran frond-like Rangea and its Burgess Shale relative Thaumaptilon are thus partially of preservational nature. The available evidence enables restoration of their common body plan, similar to that of the Cambrian ctenophore Maotianoascus. Probably the Precambrian 'sea-pens' were sedentary ancestors of the ctenophores. Fossils of unrelated Ernietta from Namibia represent sand-filled organic skeletons, preserved as sinking within hydrated mud layers. Their deformation pattern suggests that the wall material was probably a collagenous fabric resembling the basement membrane of a hydraulic skeleton units. These were series of parallel muscular chambers (possibly coelomic). Such chambers formed the dorsal quilt of the Ediacaran Dickinsonia, which is the end member of the morphocline formed by a large unnamed animal from the Vendian of the White Sea, Praecambridium, Marywadea, and Spriggina. They all had serially arranged dense organs probably representing gonads, and metameric intestinal caeca below the quilt. In Dickinsonia, the medial chamber of the quilt is symmetrical, while in the remaining forms it is arched to the left exposing anteriorly the intestinal caeca. These Vendian organisms have nothing to do with the annelids or arthropods but some homologies with the Nemertini and some deuterostomian phyla can be postulated. The dorsal coelomic cavity may be a plesiomorphic feature within the clade of metazoans lacking ability to secrete cuticle. The rhynchocoel, notochord, and myomeres could have been derived from it.

# Comparative evidence for positive associations between parasitism and plant life-histories, and possibly the degree of plant outcrossing

#### Dieter Ebert and Christophe Thébaud

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Plants have evolved a remarkable diversity of breeding systems, ranging from complete selfing to obligate outcrossing even within clades of closely related taxa. This diversity has puzzled evolutionary biologists, because the costs of outcrossing are high when compared with selfing. It has been suggested that outcrossing is advantagous when plants experience changing environments. Therefore, it was predicted that longer living plants and plants with more recorded pathogens preferably outcross. We tested these hypotheses with a comparative analysis using data from 1402 angiosperm species. The degree of outcrossing was possitively associated with plant height and life form. Further, we found a positive association between the number of recorded fungal pathogens (corrected for sampling bias) and the plant height as well as plant life form (annual, perennial ect.). A highly significant association between the degree of outcrossing and the number of fungal pathogens was found, however this association become non-significant when we corrected for sampling bias in the number of fungal pathogens. We believe however, that this is an artefact, as larger and woodier plants are more often outcrossing, but are also more often studied (larger sampling effort).

# Morphospace and Disparity Approaches to Constraint

#### Gunther Jensen Eble

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Morphospace studies are rich in pattern and process. Techniques for the quantitative description of morphologies have been increasingly applied, the same being true of metrics for relevant parameters, like disparity (the spread or spacing of forms in morphospace). Morphospace and disparity profiles in a number of groups have consistently suggested large-scale inhomogeneities, expressed as apparently nonrandom distributions of morphologies within clades and through time. This in turn has usually been interpreted in terms of constraint, but with little agreement on how to distinguish developmental from selective constraints in a macroevolutionary context. Here I discuss a range of approaches to the inference and interpretation of constraints on morphospace occupation and on the generation of disparity. They involve use of ancillary taxonomic, environmental, functional and developmental data, the employment of new conceptual frameworks to study morphospace and disparity, and the test of explicit hypotheses of evolutionary process. Atelostomate echinoids are used as a case study. Morphospace and disparity are quantified by means of landmark-based morphometric analyses. Contrasts between morphological disparity and taxonomic diversity can suggest the existence of constraint, and when tied with environmental and functional information can lead to the identification of selective constraints. Conversely, developmental data can directly suggest to what extent developmental constraints are involved. The notions of developmental disparity and developmental morphospaces (defined by incorporation of developmental data) are here illustrated as a means of approaching issues such as clade shape in ontogenetic time, general changes in rate and timing, testing of developmental "laws", and links between phylogenetic and ontogenetic trends. In the absence of developmental data, different kinds of constraints can still be distinguished by partitioning morphospaces and disparity into the contributions of different character complexes, and accordingly by testing for the possibility that different sets of characters, with different functional or developmental implications defined a priori, might contribute differentially to an overall pattern. Examples from atelostomate echinoids are given to illustrate all of these approaches.

### The effects of habitat fragmentation on the genetic structure of Primula elatior populations

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Many formally continuous areas of natural habitat have been subdivided into relatively small patches, as a result of human activities. The level and distribution of genetic diversity was investigated in a obligate outcrossing, perennial herb, Primula elatior. The destruction of forests during the last centuries resulted in fragmented and isolated populations of this species in Flanders in Belgium. The goal of the study was to analyse the impact of the reduction of population size level of genetic diversity maintained by these remaining populations.

Enzyme-electrophoresis was performed on leaf tissue of 524 individuals from 7 populations in Flnaders. Five enzyme loci were analyzed. The genetic variability measures obtained are the following: percent age of loci polymorphic 20-40, mean number of alleles per locus 1.3-1.4 expected heterozygosity within populations 0.059-0.124. deviations from Hardy-Weinberg equilibrium were estimated by fixation indices (F=0.221-0.291). All populations were closely related to each other among population diversity was low. Populations consisting of hundreds of individuals maintained similar levels of genetic variability and showed no lower levels of heterozygosity.

Most likely *Primula elatior* suffer from genetic crosion at most extreme and lower population sizes, which was suggested by the data obtained from the smallest examined population.

# Local adaptation and the effect of environmental stress on interpopulation hybrids of the intertidal copepod *Tigriopus californicus*

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Hybridization between genetically divergent populations can cause a decline in fitness due to a breakup in either coadapted gene complexes or local adaptation. Prior studies of the intertidal copepod *T. californicus* repeatedly showed that hybridization disrupts coadapted gene complexes (intrinsic coadaptation). The present study looks at whether this species also exhibits local adaptation (extrinsic adaptation) and whether this is disrupted by hybridization. Populations up to 1800 km apart were assayed for fitness in three treatments: Normal (15EC, 35 ppt), Low Salinity (15EC, 18 ppt) and High Temperature (25EC, 35ppt). Significant gene x environment interactions were found, indicating local adaptation. Surprisingly, salinity adaptation changed substantially over time: populations collected in 1996 and 1997 showed decreased fitness under low salinity conditions, while populations collected in 1999 showed increased fitness under low salinity. This change may be related to the 1997/1998 El Niño. Nearly all populations and inter-population hybrids showed reduced fitness under high temperature. However, the smallest fitness reductions were found in first and second generation hybrids, suggesting that hybridity may be advantageous under environmental stress.

# Plant defences and herbivore deterrents: do plants advertise the presence of their bodyguards to herbivores?

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There is a wealth of literature showing that secondary plant metabolites have a deterrent effect on arthropod herbivores. The usual hypothesis to explain this deterrent effect is that these metabolites are toxic to the herbivore, or associated to low plant quality. We argue that there is room for the existence of both constitutive and induced chemicals that deter herbivores from predator-defended plants. Investigations into the function of herbivore deterrents should therefore not only consider association with the plant's inferior food quality or its high investment in direct defence, but also consider the plant's indirect defences - advertising the presence of bodyguards to herbivores.

# Cytoplasmic incompatibility in haplo-diploid species.

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The vertically transmitted endosymbiont bacteria of the *Wolbachia*-group cause cytopasmic incompatibility (CI) in their hosts: uninfected females mating with infected males produce a reduced amount of progeny. This feature is beneficial to the bacteria in a mixed population of infected and uninfected hosts. Sperm from infected males aborts uninfected embryos, thereby increasing the proportion of infected individuals in the population.

Several models have investigated the population dynamics of this interaction for diploid species. The major prediction of these models is that a reduced fecundity due to the infection, and/or failure to transmit the symbiont to all offspring provides the symbiont with the problem of overcoming an invasion threshold: only a sizeable fraction of infected females allows the infection to spread through the population. *Wolbachia* infections are also known from haplo-diploid species. It was suggested that this different mode of sexual reproduction does not alter the model predictions. However, by extending the models to haplo-diploid species, we show that the predictions differ on two accounts. First, the feature that sperm from infected males cannot abort uninfected male offspring (since males are produced from unfertilised eggs), increases the threshold to invasion. The second deviation arises when it is considered that infected females may produce a different offspring sex ratio (haplodiploidy potentially enables females to control offspring sex ratio by determining the fertilisation of eggs). If *Wolbachia* alters this sex ratio to produce relatively more daughters, the threshold to invasion will decrease and eventually vanish. Data from a strain of the two-spotted spider mite (*Tetranychus urticae*) will be presented, illustrating the existence of infection-related sex ratio differences in nature. We will dicscuss the implications of the evolutionary conflict that arises between *Wolbachia* and the infected female over offspring sex ratio.

#### Arthropod R2 elements and the origin, evolution and integration mechanism of non-LTR retrotransposons

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Non-long terminal repeat (non-LTR) retrotransposons (also call L1-like elements) are an abundant, diverse class of eukaryotic mobile elements. Based on studies with the sequence-specific R2 of arthropods, these elements insert by a simple mechanism in which an encoded endonuclease cleaves the chromosomal target site and an encoded reverse transcriptase utilizes this cleavage to prime polymerization of a new DNA copy of the element directly onto the chromosome. This non-LTR machinery is also likely to supply the enzymology for the integration of SINEs and processed pseudogenes. The non-LTR integration mechanism is highly similar to that used by group II introns of mitochondrial and bacteria, while differing entirely from that used by LTR-retrotransposons and retroviruses. We have also shown that R2 elements have been inserting into the 28S rRNA genes of arthropods since the origin of this phylum. Using the rates of sequence change derived from these studies of the vertical inheritance of R2, we found little evidence for horizontal transmission in other lineages of non-LTR elements. Finally, using their highly conserved reverse transcriptase (RT) domain we have attempted to reconstruct the phylogeny of the entire class of non-LTR elements. All elements can be divided into a limited number of distinct clades that date back to the Precambrian era. The first non-LTR elements were sequence-specific and encode a restriction-like endonuclease downstream of their RT domain. Evolving from this group were elements that acquired a non-specific endonuclease domain upstream of their RT domain. These studies represent one of the most comprehensive effort to date to trace the chronology of a major class of transposable elements.

Induction of postimaginal moults in female actinedid mites (Acari) by juvenoid treatment of immatures: evidence for endocrine evolution by selection stress

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In Arachnida, very little is known about endocrine regulation of postembryonic development and reporduction. But from an evolutionary comparative perspective, ectodermal glands that exist within the prosoma might secrete, by analogy with insects, endogenous juvenile and moulting hormone-like substances and the acarines are not exceptions. In this overview an account is given of a morphogenetic study on *Tetranychus urticae* Koch, the most surprising finding of which was the induction, only in females, of postimaginal moults as a consequence of juvenoid treatment of immatures; the highest proportion of which (ca. 20%) was encountered with active deutonymphs. These adults were short-lived and proved to be wholly infertile. Apart from the self-evident significance of the study from the applied perspective, discussion is to restricted1y be made to basically provide an evidence for the endocrine evolution by selection stress. A hypothesized model is advanced in which all three preimaginal developmental stages may rather assume various endocrinological events parallel to those occurring all along the metarnophic stadium of an insect. It may be hoped that such a study will he1p stimulate work along this line of evolutionary endocrinological research to include a wide range of animals pertaining to the Class Arachnida as a whole.

## Clonal interference and the evolution of RNA viruses

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In asexual populations, beneficial mutations that occur in different lineages compete with one another. This phenomenon is known as *clonal interference* because one beneficial mutation may interfere with, or even prevent, the fixation of another. Such competition insures that those beneficial mutations that do achieve fixation are of large effect. Besides, clonal interference also increases the time between fixations such that its net effect is to slow the adaptation of asexual populations. Here, we have demonstrated that clonal interference, never before considered in the study of viral evolution, is particularly important in experimental populations of the RNA virus Vesicular Stomatitis Virus (VSV). We specifically confirmed two predictions of the model: (i) the larger the effective population size, the greater the fitness effect fixed in the evolving population and, (ii) the rate of adaptation is an increasing, but decelerating function of effective population size. In addition, as a consequence of the clonal interference model, we were able of estimating the beneficial mutations produced (but not necessarily fixed) to be about 30%, with a quasi-exponential distribution. These results constitutes the first estimate of the beneficial mutation rate for an RNA virus as well as the first characterization of the distribution of beneficial effects. We discuss the evolutionary and epidemiological implications of our findings.

# A novel type of cost of sex: plant architecture, human and natural selection, and sexuality in populations of a domesticated plant

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Vegetatively propagated domesticated plants are believed to have lost, at least partially, their capacity for sexual reproduction. In traditional farming systems, however, farmers of vegetatively propagated crops (potato *Solanum tuberosum*, ensete *Ensete ventricosum*., cassava *Manihot esculenta*), sometimes incorporate seedlings (the product of unmanaged sexual reproduction) into the harvest and in material used for propagation. This practice should maintain sexuality. The case of cassava is particularly interesting, because sexuality is directly linked to plant architecture, which is also implicated in vegetative propagation, performed with stem cuttings.

We studied cassava cultivation by Makushi Amerindians in Guyana (South America). In a village of 30 households, more than 70 different varieties are grown. We confirmed that in all varieties architecture conforms to a simple model of a succession of modules with terminal sexuality ("Leeuwenberg model"). Branching occurs only when the apical meristem differentiates into an inflorescence. However, there is great variation among varieties in the extent of branching, from completely unbranched to highly branched. Fertility among varieties was positively correlated with the extent of branching, and unbranched varieties were totally sterile. On the other hand, diameter of branches decreases with level of branching. We showed that the Makushi used only cuttings above a threshold diameter, and that they tended to compensate for small diameters of cuttings with greater lengths. As a result, the less a plant is branched, the more useful stem cuttings it produces. Little-branched varieties are more easily multiplied, and have a lower probability of being accidentally lost than much-branched varieties. This novel type of cost of sex has not previously been recognised.

Aside from vegetative propagation, the Makushi often use volunteer cassava originating from sexually produced seedlings they find in their farms, and incorporate them into their pool of varieties. Such volunteer plants are expected to come from highly fertile varieties, i.e. much-branched varieties, and to be on average much-branched and highly fertile. This practice insures a constant input of genotypes leading to much-branched plants.

In traditional farming systems, cassava sexuality and extent of branching are thus submitted to a disruptive selection, which favours both genotypes producing highly fertile phenotypes as well as those leading to sterile phenotypes. Since most of the morphological characters that vary among cassava varieties are direct or indirect consequences of the extent of branching, we suggest that much of the phenotypic diversity observed among cassava varieties, which was previously thought to be neutral, originates as the direct or pleiotropic consequence of this disruptive selection.

# Colonisation and diversification of the species Brachyderes rugatus (Coleoptera) on the Canary Islands: evidence from mtDNA COII gene sequences.

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Volcanic island archipelagos are increasingly being used as model systems for studying evolution, particularly the Hawaiian and Canary Islands. The attractiveness of these archipelagos stems from their isolation, range of environmental diversity, and known geological history providing a chronological template for studying evolution. But while many studies have sought to reconstruct evolutionary histories above the species level, little attention has been paid to population level processes. This study addresses issues of colonisation and subsequent diversification within islands for recent colonists by looking at genetic diversity within a species of weevil, Brachyderes rugatus, occurring on the Canary Islands. The genus is represented by four subspecies on the Canary Islands, one on each of the islands of Gran Canaria, Tenerife, La Palma, and El Hierro. Eighty individual Canarian Brachyderes, sampled from across the distributions of each subspecies, have been sequenced for 570 base pairs of the mtDNA cytochrome oxidase II gene (COII). Maximum likelihood and distance based phylogenetic analyses have shown that islands do not share haplotypes; Tenerife is composed of a single monophyletic clade of mitotypes, El Hierro is composed of a single monophyletic clade occurring within a larger clade comprising all the La Palma mitotypes, and the mitotypes of these three islands form a monophyletic group distinct from Gran Canaria. New methods for estimating divergence times without the assumption of rate constancy have been used to reconstruct the direction and approximate timing of colonisations among the islands. Colonisation has occurred from older to progressionally younger islands, and these colonisations are estimated to have occurred less than 2.6 Ma, although the timing of the initial colonisation of the archipelago is not discernable.

New methods for the estimation of diversification rates that use branching times as the variable analysed have been applied to each island fauna. Hypothesized effects of different levels of recent volcanism among islands were not apparent. All islands exhibit a gradually decreasing rate of genetic diversification which is marked by periodic sudden changes in rate.

Recent origin for a speciose fauna: a molecular phylogeographic analysis of the genus Calathus (Coleoptera: Carabidae) on the Canary Islands and Madeira.

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Continuing research into the molecular phylogeography of Coleoptera on the Canary Islands is providing independant reconstructions of colonisation and speciation across phylogenetically and ecologically diverse groups of beetle. In this study we present results for the Carabid genus Calathus, and demonstrate the reciprocal illumination provided by phylogeny, geology and ecology for understanding evolution on the Canary Islands. The genus Calathus Bonelli comprises 24 species on the Canary Islands and 5 on Madeira. Sequences of 927 bp and 687 bp of the mitochondrial cytochrome oxidase I and II genes respectively have been obtained for 21 of the Canary Island species and 4 of the Madeiran species. Phylogenetic analysis of these sequences delineates three genetically divergent and unequivocally monophyletic groupings on the Canary Islands and two on Madeira. The major monophyletic group on the Canary Islands comprises all the species of Gran Canaria, La Gomera and El Hierro, and two Tenerifean species. A second clade comprises the remaining Tenerifean species, and the third contains the species of the eastern islands. Phylogenetic analysis has clearly shown that nearly all island faunas of Calathus are recent in origin. This provides a marked contrast with diversification patterns observed for other Coleoptera on the Canary Islands. Some degree of concordance with these contrasting diversification patterns is obtained when taking account of the ecologies of the different groups studied to date, and the geological histories of individual islands.

#### Gene exchange between differentiated genomes

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Many organisms find mates using long-distance sex signals, for instance sex pheromones. Can differentiated host preference lead to reproductive barrier between sympatric host races of such organisms? If this barrier is incomplete, what is the rate of hybridisation, and why host races retain their genetic distinctiveness despite continuing gene flow between them? We addressed these questions in the studies of the larch budmoth Zeiraphera diniana using linkage mapping of differentiated molecular markers in combination with field mate choice and host choice experiments. Larch budmoth consists of two broadly sympatric host races feeding on Larch and Pine and genetically differentiated in many characters including pheromone communication system. There is no pre- or post-mating isolation in the lab. In a field host choice experiment we found significant differentiation in host-landing preference. Only 16% of the larch race and 12% of the pine race preferred to land on host other than their own. In a long-range mate choice field experiment with both larch and pine race females positioned on Larch and Pine trees we measured I female attractiveness, · race-specificity of pheromone communication, excess of heterozygosity at differentiated loci. I and significantly reduced when females were forced to call from the host other then their own. Significant, among males attracted by pine race females but not among larch-attracted males was indicative of hybridisation. Hybrid males are known to have pheromone response similar to partially dominant pine race pheromone response and are expected to be attracted by pine race females. Back-cross linkage map of the entire larch budmoth genome (28 linkage groups / 28 chromosomes) was constructed using 258 AFLP, allozyme and morphological markers. Chromosomal locations of 12 differentiated markers tended to cluster with each other, with 5 out of 12 markers located on only 2 linkage groups.

Our work has shown that the race-specific host preference is a necessary component of pre-mating reproductive barrier between sympatric host races of the larch budmoth. Residual gene exchange not accounted for by differentiated host preference or pheromones is about 2%. Genetic differentiation at several life-history traits exists despite continuing gene exchange between host races. This implies selection against recombination in genomic locations of these traits and lack of such selection in the rest of the genome. Non-random genomic distribution of differentiated markers can be an evidence of such selection.

Population dynamics at a small scale: evolution of the genetic structure of a population of the red haplo-diploid alga, *Gracilaria gracilis* 

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The genetic structure of populations provides insight into the patterns of dispersal and the demographic processes that govern the genetic composition of populations in space as well as in time. *Gracilaria gracilis* is an interesting model for the study of genetic structure because it has a unique combination of life-cycle features: coexistence of independent haploid (male and female) and diploid individuals in populations, three different dispersal vectors (haploid spores, diploid spores and male gametes) and zygote amplification (cystocarp). The impact of these features on within-population genetic structure has not been extensively studied. One *G. gracilis* population was chosen for the study of small-scale genetic structure over a four-year period. Once a year, all individuals were mapped, measured, sampled and genotyped using 10 microsatellite loci. Using the multilocus genotypes, the mating system, the relatedness and spatial structure of the population was analysed and compared among years. The results will be used to describe in detail population dynamics in terms of effective population size, dispersal and demography.

#### Phylogeography of the European sculpin Cottus gobio: evidence for a western and an eastern clade

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European sculpins, Cottus gobio, show a great deal of genetic variation among drainages in southern Germany as determined by allozyme analysis. This may suggest that the divergence among the different sculpin populations could be preglacial, however it could also merely reflect the differences in population sizes. To clarify in detail the genetic and phylogeographic structure of this freshwater species, we sequenced 523 bp of the mitochondrial D-loop from 411 individuals from 57 populations. Most sample sites were located in Germany and Poland including the Upper- Danube, Upper- and Lower Rhine, Main, Elbe, Oder and Vistula rivers. Additional population samples were taken from the Weser in Germany, from France, Italy, Finland and the Lower-Danube in former Yugoslavia and Romania. The D-loop sequences revealed 46 different haplotypes. Network analysis of the whole dataset showed six distinct phylogenetic groups. Groups I and II were found in Central and East European drainages while groups III to VI were found in Central and West European river systems. Phylogenetic analyses (neighbor-joining, maximum parsimony, and maximum likelihood) including the most frequent haplotypes support a division of C. gobio into two major clades, one consisting of group I and II, the other of groups III to VI. The network analysis revealed additional substructure among the group I sequences. The populations of the Main, Upper-Danube and Elbe rivers don't share identical haplotypes and group by drainages. The results for this group are in accord with the allozyme data and we suggest that this pattern may be preglacial. Using this as an calibration for the molecular clock, the origin of the two major West and East European clades would date back to the Pliocene.

# Phylogeny of the genus Phoenicurus and the effect of hybridization for the genetic structure of populations in East Turkey and Central Asia

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The former opinion, that hybrids are a rare and unimportant side-effect in nature has changed during the past decades and several studies have shown, that not all hybrids have a lesser fitness compared to their parent species, especially when habitats are changing through climatic effects or human activity. One group where we have a high degree of hybridizing species and therefore the opportunity to investigate this phenomenon, is the genus Phoenicurus. Today there are described 10 to 11 species throughout Europe and Asia with a concentration in the Caucasus and the Himalayas, where up to 6 live sympatrically. In this study we concentrated on several hybridizing populations in East Turkey and Central Asia. Using a combination of classical methods (comparing morphology, behaviour etc.) on the one hand and breeding experiments (hybridization and backcrossing) and biochemical tools on the other (Cyt-b-sequencing and microsatellite-analysis), it was possible to show the impact of hybridization (and cross-specific geneflow) for population- and genetic structure.

## Myrmecochory, a strategy for the dissemination of herbaceous vegetation ?

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From studies on myrmecochory (dissemination by ants) conducted in regions of southern Europe, this dissemination strategy is largely associated to the herbaceous stratum (Sernander, 1903; Bresinsky, 1963). Also, the same tendency has been observed in neotropical venezuelan communities studied by the authors (Escala y Xena, 1991, 1993; Xena et al., 1995). In order to reinforce these statements, a study was started in herbaceous plant communities in southern France (F), and results were compared with those obtained in venezuelan Neotropic (V). Observations so far seem to corroborate that there is a relationship between myrmecochory in the studied regions and herbaceous vegetation. Forty two (42) neotropical herbaceous species and twenty (20) southern french species has been found to feature characteristics which are associated to the myrmecochory syndrome. The morphoanatomical features present in diaspores studies in both regions are the same, namely: 1. Externally differentiated eleosome of the seed, 2. Fat storage by epidermal cells of the seminal membrane, 3. Eleosome formed from flower remains and fruit parts. These characteristics could result from a similar response to selective pressures, which leads to efficient dissemination, regardless of the plant taxonomic group and geographic location. Of the total number of ant species found to transport diaspores in both regions, the majority are omnivorous species (V: Anochetus emarginatus, Camponotus rufipes, C. lindigi, Ectatomma ruidum, Odontomachus chelifer, O. bauri, Pheidole sp, Solenopsis geminata, Tapinoma sp; F: Cataglyphis cursor, Pheidole pallidula), and other are exclusively granivorous species (F: Messor structor, M. barbarus, M. capitatus). Studied herb features strategies that are strongly related to autochory, anemochory and myrmecochory, and may be considered an overall response for herbaceous plant dissemination, while avoiding predation and fire damage.

# Evolution on an fmdv clone debilitates by muller's ratchet

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The evolution of an FMDV clone very debilitates by the effect of Muller's ratchet was studied in different conditions of propagation. This clone contained as the main debilitating change an elongation of an internal poly A tract next to the second initiating AUG. a) The viral clone, and several subclones derived from it were passages in massive infections to investigate whether they could recover fitness and which was the molecular basis of the fitness recovery. b) The viral clone, and several subclones derived from it were subjected to further plaque transfers trying to draw them to extinction. The determination of complete or partial genome sequences of the viruses at different stages of the viral evolution allowed to draw the following conclusions: a) The viral clones can follow different molecular pathways for fitness recovery when subjected to massive transfers. Only in two out of eight viral clones fitness recovery was associated with true reversion of the length of the internal polyadenylate tract. An identical deletion of 69 nucleotides encompassing the elongated internal poly A tract was observed in 50% of the clones. b) Only one out of thirteen viral clones was driven to extinction (<10 pfu in the plaque) by repeated bottleneck passages in the conditions of our plaque assays. The rest of the viral clones were not driven to extinction provided enough time for viral replication was allowed. Subtle changes in the genome sequence were associated with the escape to extinction by these viral clones subjected to repeated bottleneck events.

#### Epicuticular hydrocarbon variation among *drosophila mojavensis* cluster species

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Components of the mate recognition systems in *Drosophila* species usually involve epicuticular hydrocarbons (EHCs) as cues during courtship. Extensive geographical variation in EHC profiles within *D. mojavensis* has been documented that is correlated with patterns of premating isolation between populations. EHC variation has not been extensively analyzed in the sibling species, *D. arizonae* and *D. navojoa*. Because *D. mojavensis* and *D. arizonae* can readily hybridize, but hybrids with *D. navojoa* are difficult to produce, EHC differences may serve as species recognition systems. EHC expression is influenced by rearing substrates in *D. mojavensis*, so two populations of each species were cultured on fermenting *Opuntia* and pitaya agria, *Stenocereus gummosus*, tissues. We assessed EHC variation in aged adult flies from this completely balanced design (3 species X 2 populations X 2 cacti X 3 replicates).

EHCs of these species include 2-methylalkanes, alkanes, alkenes, 2-methylalkenes and multimethylene interrupted alkadienes. *D. navojoa* have less 2-methyloctacosane (6-8%) than do *D. arizonae* (8-14%); however, 2-methyltricosane is greater in *D. navojoa* (18-24%) than in *D. arizonae* (10-13%). The C<sub>2</sub> and C<sub>3</sub> alkenes are 7- and 9-isomers; whereas, the C<sub>3</sub>, C<sub>4</sub> and C<sub>3</sub> alkenes are 8-, 10- and 12-isomers. This suggests that there are separate biosynthetic pathways for the two groups of alkenes. The three tritricontadiene isomers are more abundant in *D. arizonae* (12-16%) than in *D. navojoa* (8-14%) and preliminary data indicates some isomer differences. The three pentatricontadiene isomers (C<sub>3</sub>) are also more abundant in *D. arizonae* (30-38%) than in *D. navojoa* (26-33%). Variation due to rearing substrates will be discussed.

# Is Junk DNA Neutral?

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Less than 10% of the mammalian genome codes for either proteins or RNA sequences, much of the rest is thought to be non-coding, and is often referred to as "junk" DNA. However, this "junk" DNA is not without structure; there is for example large scale variation in base composition. This variation appears to reflect a fundamental level of organisation in the genome since the density of genes, repetitive DNA elements and recombination varies with G+C content. However, the reasons for the variation in base composition is unknown. Some have suggested it is due to variation in the pattern of mutation, whilst others have suggested selection or biased gene conversion as the cause. Here I test whether mutation biases are responsible for large scale variation in base composition by using two population genetic tests on variation segregating at synonymous and intron sites in mammalian MHC genes. The data suggest that mutation biases are not responsible for base composition bias. The data are however consitent with the action of selection or biased gene conversion. I argue the biased gene conversion is unlikly to affect G+C content in mammals, and that selection is therefore acting upon the base composition of large sections of the mammalian genome.

Predicting Correlated Responses in Natural Populations: Changes in JHE activity, Fecundity and Calling Rate in the Bermuda population of the sand cricket.

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Quantitative genetic methods have been used to examine selection responses in domesticated organisms but there are few cases of their application to predict changes in natural populations: there are, to our knowledge, no cases in which correlated responses to selection have been predicted. In the present talk we use quantitative genetic parameters estimated from a series of pedigree analyses and selection experiments to predict juvenile hormone esterase (JHE) activity, fecundity and call rate in the Bermuda population of the wing dimorphic cricket, *Gryllus firmus*. JHE activity, fecundity and call rate are genetically correlated with wing form in this cricket and hence changes in the proportion macroptery (volant morph) are predicted to bring about correlated responses. The Bermuda population has a higher proportion of macropterous individuals (95%) compared to the stock (35%, originally from Florida) from which the heritabilities and correlations were estimated. The quantitative genetic analysis predicts 1) an increase in the population mean JHE activity but a decrease in mean activity within each wing morph, 2) a decrease in both the mean population fecundity and a decrease within each wing morph, 3) a decrease in both the mean population call rate and a decrease within each wing morph. All three predictions are supported.

## Cichlid phylogeny: total evidence analysis and molecular rate heterogeneity among groups

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We present phylogenetic analyses of DNA sequences of mitochondrial and nuclear loci from a large taxonomic sample of cichlids (about 46 taxa). This study combines 16S rRNA and nuclear data (*Tmo-M27*, *Tmo-4C4*) to maximize the number of phylogenetically informative sites and test current phylogenetic hypotheses among the major groups in the family. Finally, we also incorporate morphological data (from Kullander, 1998) in a total evidence analysis. Partition-homogeneity tests for each combined data set showed non-significant heterogeneity levels among molecular and morphological data. In agreement with results based on molecular data alone, total evidence confirms the placement of *Heterochromis* as the sister-taxon to all other African cichlids. Among a large number of South American genera, *Retroculus* is placed as the most basal lineage of the Neotropical assemblage, followed by *Cichla, Astronotus*, geophagines (including crenicichlines) + chaetobranchines, and cichlasomines + heroines lineages. Relative rate tests applied to mitochondrial DNA suggest significantly higher levels of genetic variation in Neotropical than in African taxa, and both mitochondrial and nuclear sequences shown that rate heterogeneity among Neotropical lineages is confined to the geophagine group.

## Genetic variation in a clonal species, blueberry (Vaccinium myrtillus), inferred from AFLP markers

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Genetic variation of blueberry (*Vaccinium myrtillus*) was inferred from AFLP markers in the Alps at two different altitudes in order (i) to estimate the sizes of the clones, (ii) to determine if they differed genetically with altitude, (iii) and to assess the pattern of genetic variation within and between plots. Samples were collected in both sites on a grid with progressive scales of sampling, and in a square with a regular grid. Three AFLP combinations of primers revealed 92 fragments, from which 55 were polymorphic. Most clones were detected once, and may be considered of small size. Nevertheless, evidence of clones up to 22 m was found. The two plots shared no genotype. Genetic diversity of the lower population was higher than that of the higher population, indicating a loss of diversity with altitude. The results are discussed in the perspective of adaptive potential in case of global warming.

# The adaptive dynamics of dispersal and cooperation

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How does individual mobility affect the evolution of social behavior? Classical models suggest that cooperativeness is favored under conditions of low dispersal (through kin selection and/or reciprocity). This prediction, however, is obtained under restrictive assumptions imposed on very simplistic models. We have used stochastic spatial models to address two questions: (i) the coevolution of steady or cyclic polymorphism of dispersal and sociality, which would involve varying (on the evolutionary timescale) degrees of spatial population structure; (ii) the evolution of dispersal and sociality from independent into conditional traits that respond to one another.

Low dispersal can favor the evolution of cooperativeness through the development of spatial pattems . In tum, selPorganized spatio heterogeneity creates selective forces that may cause the evolution of higher dispersal rates, thereby destabilizing cooperation. The end result may involve coevolutionary cycles of a philopatric, social phenotype alternating with a high1y dispersing, non-social one. Also, the two types can coexist steadily, thereby offering an explanation for dispersal polymorphism as a by-product of dispersal and sociality coevolution. Rather than being fixed, social behavior and dispersal may evolve as strategies that allow for an individual to respond to signals. In particular, the social strategy of a neighbor may act as a signal interpreted by the focal individual-and vice-versa. Thus sociality and dispersal may coevolve into a conditional response of one trait to the other: The decision of dispersing then evolves to respond to the cooperativeness of neighbors; likewise, the decision of cooperating evolves to respond to the tendency of interacting conspecifics to remain philopatric.

# Fitness and adaptive dynamics in non-equilibrium populations

#### R. Ferrière

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In current evolutionary theory, a very general measure of fitness is provided by the invasion exponent of a phenotype, that is, the long-term growth rate at low density in a resident community of established phenotypes. When applying this definition, it is usually assumed that the community dynamics of resident phenotypes is characterized by a unique attractor. However, multiple attractors (and more generally, multiple invariant states) might be the rule, rather than the exception, in most nonlinear ecological models. Here we show that multiple resident invariant states may have different invasibility properties. This generates short-term fluctuations in a rare phenotype's invasion exponent, with two significant effects. First, rare 'invading' phenotypes with small but positive invasion exponent may none the less face an initial phase of decline in the early stage of the invasion process. Should such a rare phenotype survive the initial invading stage it would still have to cope recurrently with periods of extreme rarity and high risk of extinction occuring along sustained burst-and-crash dynamics. Second, 'noninvading' phenotypes with small but negative invasion exponent may still have a positive growth of an 'Invading' phenotype, and the probability of fixation of a 'noninvading' phenotype can be estimated from the long-term invasion exponent and the variance of the distribution of short-term invasion exponents. I will discuss the consequences of such peculiar patterns of invasion on the evolution of correlated life-history traits.

# ProSeq v. 2.3: A new sequence editor and analyzer

# **D**.Filatov

# ICAPB, University of Edinburgh, UK

Processor of Sequences (ProSeq) is a new Windows 95 program for convenient sequence alignment editing and various molecular - evolutionary analyses. It accepts sequence alignments in the following file formats: NEXUS, NBRF/PIR, MEGA, ClustalX. The program has user-friendly multiwindow interface and can handle many alignments at the same time. Sequence editor features include translating and splicing sequences, finding polymorphic / ambiguous sites and many other useful utilities. An analysis module includes calculation of DNA diversity, divergence and linkage disequilibria measures with sliding windows options, for all sites or silent sites, estimation of the recombination rate, permutation-based detection of population subdivision and various tests of neutrality. Several useful tools based on coalescence with recombination are included in the program: calculation of critical values of tests of neutrality, simulation of sequence data sets, and a tool for coalescent simulations with recombination.

## Genetic variation in clone characters of Ranunculus reptans

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A genet (clone) of a clonal plant consists of a number of ramets. A genet may be characterized by the demographic schedule of the ramets, the demographic schedule of the genet, and the organisation of the ramets within the genet. So far, demographic studies on clonal plants concentrated on the ramet rather than the genet level. Moreover, it is not clear whether organisation characters represent constraints or evolve themselves as easily as demographic characters. Important selection pressures for life-history evolution are density and competition which are both inevitable consequences of exponential growth. In the response to competition plasticity may be important and the question arises whether plasticity is an evolving trait itself. We studied variation among genotypes in reproductive allocation (a demographic trait) and spatial spread (an organisation character) and their response to competition using vegetatively propagated offspring of 104 genotypes of R. reptans. We assessed reproductive allocation as the proportion of flowering rosettes per plant and the tendency for spatial spread as distance between the most distant rosettes of each plant divided by the total number of rosettes per plant. For both measures we found significant variation among genotypes and significant genotype-by-competition interactions, suggesting genetic variation in means and plastic response. To test whether this represents additive genetic variation we are performing an artificial selection experiment. We selected 20 genotypes with the highest and 20 with the lowest character expressions for each of the four traits (proportion of flowering rosettes and plasticity therein, tendency for spatial spread and plasticity therein). Crosses within these groups of 20 genotypes yielded four 'high' and four 'low' offspring lines. The proportion of flowering rosettes was significantly higher in genotypes of the corresponding high line than in those of the low line (+25%) indicating heritable variation for this clone character. Differences between high and low lines of the three other traits were smaller and not significant. Thus, we can report heritable variation for the clone level only for the demographic character (reproductive allocation) but not for the organisation character (spatial spread), and not for plasticity in these characters.

# Population differentiation and bottlenecks

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Some of the most discussed models of evolutionary change are Wright's shifting balance theory and Mayr's theory of allopatric speciation through founder effects. Behind these models there is an assumption that organisms consist of well-coordinated gene complexes, which constrains the evolution in certain directions. At of low population sizes these complexes could be broken. Theory predicts that by the stochastic effects of inbreeding and low population size, genetic drift becomes an important factor and since during the following population flush the selection is weak, novel genotypes can survive and create new and favorable gene combinations in the following generations.

If founder effect speciation is to occur in nature, populations will have to go through bottlenecks. Hence, the detection of historic bottlenecks is an important way of investigate the plausibility of Wright's and Mayr's scenarios.

Species living on patchily distributed ephemeral resources and having a high fecundity could be especially prone to go through population bottlenecks and possible founder events. To discern the possibility of this, this study focus on population differentiation and detection of possible bottlenecks in natural populations of the blowfly, *Lucilia illustris*. This is done by using microsatellite loci. Preliminary results indicate that subpopulations, even geographically close, show differentiation and signs of inbreeding. This supports the view of this type of lifestyle being subject of frequent bottlenecks.

# Variation in levels of chloroplast DNA polymorphism within individual Senecio vulgaris.

### J. E. Frey, B. Frey, D. Frei, <u>D. Forcioli</u> and H. Müller-Schärer

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Single plant cells may host several hundred chloroplasts, each containing up to nine hundred copies of DNA. This confers a huge potential for accumulating and maintaining mutations, and consequently, the chloroplast genome of individual plants should be expected to be highly polymorphic. However, so far there is a striking lack of evidence for cpDNA polymorphism and the chloroplast genome is still generally believed to be monomorphic within individual plants.

We found that the chloroplast genome of Senecio vulgaris is polymorphic for a point mutation that confers resistance to triazine herbicides. The level of cpDNA polymorphism can vary within and among different leaves of a single plant, and the polymorphic state seems to be stably transmitted to the progeny.

Within-plant polymorphism of chloroplast DNA allows for environmentally imposed selective changes in chloroplast gene frequency within the life-span of an individual plant. Chloroplast DNA polymorphism therefore provides an additional level of selection that gives plants a powerful mechanism by which they can adapt rapidly to specific environments. This mechanism may in part be responsible for the very rapid evolution of triazine resistance in *S. vulgaris*.

High within population polymorphism for a selected insecticide resistance gene in the Western Flower Thrips, *Frankliniella occidentalis* 

# D. Forcioli and J.E. Frey

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The arrhenotokous Thrips *Frankliniella occidentalis* is a major pest for greenhouse productions as it can damage plants either directly by feeding on them or through its very efficient virus vector capabilities. Although introduced relatively recently in Europe, numerous instances of pesticide resistance have been already reported and resistance to pyrethroid insecticides is known to be widespread in this species. Although still lacking wild populations, at least in Northern Europe, gene flow can occur among greenhouses populations through "pest tourism", as it has been shown that the insects can travel on plants shipped from grower to grower. In this context we amplified and sequenced a 760bp DNA fragment from the genomic sequence of the *para*-like voltage dependent Sodium channel gene in 60 diploid females collected from a single "open" population of *F.occidentalis*. This gene, the target of pyrethroid insecticides, is known to harbour pyrethroid resistance conferring point mutations (*kdr* and *superkdr*) in different insect species. At least nine different haplotypes were thus identified within this single population, that differed from the canonical *kdr* and *superkdr*, to tolerance to high levels of a pyrethroid compound in this population. As the observed variability was higher than what could be expected for a selected gene in a haplodiploid species, the potential impact of "pest tourism" on the spreading of resistance genes could be high in *Frankliniella occidentalis*.

#### Biogeography and the tempo of speciation in strombinid gastropods

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Land barriers and distances are still considered the most obvious trigger for speciation in the sea, but increasing biogeographic and genetic evidence show population discontinuities suggesting that mechanisms like currents and gradients can lead to isolation and species origination in contiguous marine populations. Unfortunately, most of these studies lack historical perspective on the amount of speciation related to each of these factors, resting on the fundamental assumption that the species involved are indeed the closest relatives to one another. The well documented formation of the Isthmus of Panama during the late Neogene, and the existence of large molluscan fossil collections, allow an evaluation of species level evolution and of the speciation events that occurred within a single ocean or across the developing land barrier. Cladistic phylogenies based on 49 shell characters were constructed for 42 fossil and recent species of the tropical American gastropod genus Strombina ranging from Trinidad to Panama through Florida to Columbia in the Caribbean sea, and from Mexico to Ecuador in the Eastern Pacific. Results show that the two main clades [S.(Strombina) and S.(Lirastrombina /Spiralta)] were dominant in one of the two oceans from the start and did not mix since the Middle Miocene. Only one out of five new subgenera originated across the isthmus and only eight out of 41 speciation events are transisthmian events. The evaluation of geographic distributions for each ancestral/descendent pair show that 90% of all speciation events occurred in a single ocean over distances smaller than 1000 Km regardless of mode of larval development. Overall results show that speciation tends to occur over very short distances and barriers need to be sought in changing paleoceanographic conditions.

Producing a helper component to mediate vector transmission: is this associated with a selective cost during cauliflower mosaic virus infection cycle?

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Some of the viruses transmitted by vectors in a non-circulative manner may interact with their vectors directly via the coat protein (cucumo- and alphamoviruses), whereas others encode for a non-structural protein that binds to both the virus particle and the vector (poty-, caulimo-, waika- and probably closteroviruses). This non-structural protein is named helper-component (HC). In poty- and caulimoviruses, naturally occurring strains that are self- (producing a functional HC) and non self-transmissible (producing no HC or a non-functional one) by vectors have been described <sup>(1)</sup>. Two HCs were described in the cauliflower mosaic virus (CaMV). They are encoded by the virus genes II and III <sup>(2 & 3)</sup>. Gene III is required for CaMV infectivity and can not be deleted. Gene II, however, seems to be dispensable for the virus cycle *in planta*. Indeed, the naturally occurring isolate CM4-184 exhibits a 421-pb deletion in the central region of gene II <sup>(4)</sup>. This isolate does not produce the corresponding HC and hence, though perfectly infectious in the host plant, it is never self-transmitted by aphids (the natural CaMV vector). Transmission of CM4-184 by aphids is however possible if the plant is co-infected with another isolate harboring a functional gene II. Previous reports described a number of other strains which are non self-transmissible by vectors, due to point mutations or partial deletions in gene II <sup>(5 & 6)</sup>, indicating that the appearance of "non self-transmissibility" may be a rather frequent phenomenon in CaMV populations. A question then arises: is coding for a helper component associated to a selective cost?

To address this question, we engineered three different GII defective clones of CaMV and evaluated their infectivity and pathogenicity for the host plant. The gene II defective clones were altered as follows: "Chri-S" has a 421-pb deletion identical to that exhibited by the isolate CM4-184 mentioned above; "S-Top" has a point mutation which introduces an early stop-codon in gene II coding sequence; "S-Tart" has a point mutation that changes the gene II start-codon from ATG to AAG. The genome of these clones was otherwise strictly identical to that of the wild type clone, Cabb-S.

Co-infections of plants were made with wild type Cabb-S and the mutant clones (Chri-S, S-Top or S-Tart). We measured the fitness of each mutant, relative to that of Cabb-S and tested whether this relative fitness was frequency dependent. The poster presents and discusses the characterization of various biological features of each mutant, both when infecting singly a host plant and when in competition with the wild type Cabb-S virus.

(1) Pirone & Blanc, 1996. Ann. Rev. Phytopathol. 34:227-247. (2) Blanc *et al.*, 1993. Virology 192:643-650. (3) Leh *et al.*, 1998. 7th International Congress of Plant Pathology. Edinburgh, Scotland, 9-16 August 1998. Abstract 1.13.2S. (4) Howarth *et al.*, 1981. Virology 112:678-685. (5) Woolston *et al.*, 1983. Gene 23:15-23. (6) Al-Kaff & Covey 1994. J Gen. Virol. 75:3137-3145.

Do life-history traits have higher mutational variances than morphological traits? A comparison of homozygous and heterozygous mutational effects in *Drosophila melanogaster* 

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Comparing mutational variances (V) of different types of traits can give insight into the factors maintaining quantitative-genetic variation in populations. Houle *et al.* (1996, Genetics 143:1467) reported that life-history traits have six-fold higher mutational coefficients of variation (CV divided by the trait mean) than morphological traits, paralleling the observed higher standing genetic CVs of life-history traits. If correct, this conclusion would support the mutation-selection balance hypothesis for the maintenance of variation. The data on which the conclusion was based, however, consisted mostly of CV estimates obtained from homozygous mutation-accumulation lines; such estimates are of questionable relevance for outbreeding populations, in which mutations will seldom occur in homozygous condition. By reanalyzing previously published data, and by using a new set of mutation-accumulation lines, we are investigating whether the reported large difference in mutational CVs between a life-history trait (pre-adult viability) and two morphological traits (numbers of sternopleural and abdominal bristles) largely disappears when mutations are studied in heterozygous condition. Such a result might be expected due to the greater recessiveness of viability mutations than of bristle number mutations.

#### Estimation of the age of the most recent common ancestor of a sample of DNA sequences

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The age of the most recent common ancestor (MRCA) of a sample of DNA sequences from a population is an interesting quantity, especially for human population study. To date, several methods have been proposed for estimating the age of MRCA from the number of segregating sites and from haplotype frequencies. Single Nucleotide Polymorphism (SNPs) are rapidly becoming a major form of data with the progress of Human Genome Project. I will present in this talk a method for estimating the age of MRCA from the SNPs frequencies.

#### The use of L1 DNA for phylogenetic analyis and population studies in primates.

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L1 (LINE-1) elements constitute a large family of mammalian retrotransposons which have been replicating and evolving in mammals for more than 100 million years and now comprise 20% or more of the DNA of some mammals. Therefore, L1 activity undoubtedly has had a major effect on the structure and function of modern genomes. However, the impact of L1 activity in present day populations remains unclear. Here, we investigated the dynamics of an active L1 family, the Ta family, in recent human history. We demonstrated that a very recent and heretofore undescribed subset of Ta, the Ta-1 subfamily, is responsible for most of the recent L1 insertions in the human genome. The Ta-1 subfamily began amplifying rapidly about 2 million years (My) ago and is probably still expanding. About 70% of the Ta-1 elements have been inserted in the genome during the last 1 My of human evolution and more than 50% of the Ta-1 insertions are polymorphic.

## Genome Organization and Social Evolution in Hymenoptera

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The evolution and maintenance of variation in recombination rate among taxa has puzzled theoretical biologists and remains one of the major problems in evolutionary biology. We used comparative genomics to study evolutionary trends in genome organization in relation to life history and ecology in Hymenoptera. To compare recombination frequencies of different species we calculated relative recombinational genome sizes of solitary-parasitic (*Nasonia* spp. *Trichogramma brassicae, Bracon hebetor*) and social hymenopteran species (*Apis mellifera* and *Bombus terrestris*) from linkage maps. *A. mellifera* had the highest relative recombination frequency followed by *T. brassicae, B. hebetor, B. terrestris* and the smallest map of *Nasonia* spp.. We could rule out structural explanations for variation in recombinational size of genomes within the Hymenoptera. How can these differences, notably between *A. mellifera* and *B. terrestris*, be explained? Currently, the most promising hypothesis is that more genotypic diversity results in more complex and stable division of labour. Multiple, variable QTL have been demonstrated for foraging and defensive behavior in *A. mellifera*.

Based on this first study, we predict that highly eusocial hymenopteran species with large colonies and a highly developed system of division of labor (e.g. leaf cutter ants, *Atta* spp.), should have higher recombination frequencies than their closely related but socially less developed relatives.

# Secondary sexual traits in humans, women in particular

#### Agustí Galiana

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Surprisingly little progress has been made since Darwin on the study of human secondary sexual traits. I argue that a number of "extravagant" secondary sexual traits that are not directly related to fitness benefits, nor to the action of sex hormones, has evolved in women. The stricking fact that females are the "sexy" sex in the human species has been seldom acknowledged. This is the reverse situation to the one usually found in animals (for instance birds and insects).

Evolution of extravagant traits in one sex is often associated with a lack of resource investment on reproduction by that sex and with mate choice by the other sex, either by previous perceptual biases ("sensory exploitation" hypothesis) or, more likely, by an indirect genetic benefit ("good genes" hypothesis). Hence, in humans we should admit that ancestral women have had a negligible reproductive investment and ancestral men have had a strong mate choice.

Several pro and con evidences are discussed, and an evolutionary scenario is suggested. Hunter-gatherer societies allow a strong mate choice by leading males, who usually are the individuals with the best access to resources, while women value male status over male attractiveness in mate choice.

I suggest three of those extravagant secondary sexual traits: large breasts (which don't improve breast-feeding), wide hips (which don't improve child-bearing), and a pronounced juvenile peak in attractiveness. The two first ones could be taken as handicap traits as they hinder running, that was so essential to the primaeval human way of life. The third one could be associated to the human slow reproduction and early menopause.

## The ultimate great evolutionary transition

### Agustí Galiana

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J.M. Smith and E. Szathmáry suggested in 1995 the existence of several great evolutionary transitions in the evolution of life. I suggest a further pending transition involving cultural evolution in human societies, namely the origin of an integrated scientific knowledge.

The new group of replicating elements is formed by the different scientific bodies of knowledge. The new form of inheritance is the scientific education. I imagine interdisciplinary knowledge having a fitness benefit —in cultural transmission— over partial knowledges, as societies guided by partial scientific knowledge would be prone to collapse. Also, there is a division of labor among the sciences.

Smith and Szathmáry cited as the last transition that of human societies by means of language. In the last paragraph of their book they comment on the possible new transition in societies where "science and reason" substitute for "magic and ritual". I think the transition is in fact to be experienced by the sciences, not the societies, although societies would change accordingly. An important novelty of this ultimate transition is that a conscious cultural evolution is required. An effort in the scientific education of scientists (in areas outside their expertice) would be essential.

The use of the concept of evolutionary transitions could estimulate the necessary changes in the scientists and in society. I argue that an evolutionary-ecologic phylosophy is already unifying diverse scientific disciplines. I suggest that finding ways both to obtain a sustainable resource flow and to control the population maintaining a high living standard are required for such a new kind of society.

# **JMS LECTURE**

#### Non stationary models of nucleotide substitution and the evolution of base composition.

#### Nicolas Galtier

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Base compositions (A-, C-, G- and T-percent) are highly variable among genes and genomes. Heterogeneous base compositions have been observed in most taxonomic groups sampled, for organellar or nuclear genomes, in coding and non-coding regions. Base composition has some functional implications: depending on the organism, it relates to codon usage, gene density, resistance to high temperature.

Observing unequal base compositions between genomes or between homologous genes implies that distinct lineages have undergone distinct evolutionary processes. This raises several interesting questions. First, one may wonder about the robustness of DNA sequence analysis methods - and especially phylogenetic inference methods - when the base composition varies between compared sequences. Secondly, the history of diverging base compositions deserves attention: what were the ancestral states, which lineages experienced severe compositional changes? Finally, the mechanisms of compositional divergence are unknown in most cases: what are the evolutionary forces that underly the observed changes in base composition? Is natural selection acting to shape genomic base compositions, or is the variation between genomes mainly due to variable mutation processes? This problematics instanciates the dual goal of molecular evolution, namely (i) recovering the history of species and populations through that of their genomes, and (ii) understanding better the structure and function of genomes thanks to the evolutionary perspective.

The above questions are addressed thanks to a non-homogeneous, non-stationary model of DNA sequence evolution, allowing diverging GC-content in time and between lineages (Galtier & Gouy 1995, 1998). Maximum-likelihood analyses based on this model allow to (i) correctly estimate phylogenies in case of variable GC-content between sequences, and (ii) estimate ancestral base compositions. The latter possibility is applied to ribosomal RNA sequences from species sampled in all three domains of life (Galtier et al. 1999), yielding evidence that the last universal common ancestor was not a thermophilic organism.

Galtier, N., and Gouy, M. 1995. Inferring phylogenies from sequences of unequal base compositions. Proc. Natl. Acad. Sci. USA. 92: 11317-11321.

Galtier, N., and Gouy, M. 1998. Inferring pattern and process : maximum likelihood implementation of a non-homogeneous model of DNA sequence evolution for phylogenetic analysis. Mol. Biol. Evol. 15: 871-879 Galtier, N., Tourasse, N.J., and Gouy, M. 1999. A non-hyperthermophilic ancestor to extant life forms. Science 283: 220-221.

# Nuclear and mitochondrial markers result in controversial phylogenies in *Buthus occitanus* subspecies (Scorpiones: Buthidae)

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Buthus occitanus (Amoreux, 1789) (Scorpiones: Buthidae) occurs in Europe (Southern France and Spain) and in North Africa where several subspecies were described. Populations from both sides of the Strait of Gibraltar were analysed using allozyme electrophoresis (15 loci scored) and DNA sequencing of a 460 bp fragment of the mitochondrial 16S rRNA gene. The samples were collected from three sites in Spain and France (ssp. occitanus), eleven sites in Morocco (ssp. occitanus, ssp. mardochei and ssp. paris) and one site in Tunisia (ssp. tunetanus). Also, B. atlantis from five sites along the Atlantic coast of Morocco were included. This taxon was previously considered to be a subspecies of B. occitanus. A sample of Androctonus mauretanicus (Pocock, 1902) from Morocco and a sample of Androctonus crassicauda (Olivier, 1807) from Turkey were included as outgroups in the allozyme analysis; and a sequence of A. crassicauda was used as the outgroup in DNA analysis.

Phylogenetic analysis based on allozyme allele frequency data results in tree topologies that divide the populations into two clades, i.e. an European population clade and a Moroccan population clade. Within these clades low levels of variability are observed for allozymes. Conversely, phylogenies constructed with mtDNA sequence data split the Moroccan populations into several distinct lineages that largely coincide with described subspecies. The divergence among these lineages is about the same as between populations separated by the Strait of Gibraltar (approximately 12% sequence divergence).

Nuclear and mitochondrial markers reveal a complex phylogeographic structure for *Austropotamobius pallipes* (Decapoda: Astacidae) in the Alpine region

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In the Alpine region, five genetically distinct groups of the *Austropotamobius pallipes* (Lereboullet 1858) species complex were detected in a joint analysis of nuclear (allozyme) and mitochondrial markers (sequence and RFLP analysis). The geographic distribution of these evolutionary lineages coincided largely with several taxa (*A. p. pallipes, A. berndhauseri, A. (p.) italicus*) defined on the basis of morphological characters. A low level of genetic variability was found within these lineages. The strongest differentiation was found between three lineages that have already been described in previous allozyme studies. A Northern group consisted of populations from North of the Alps in the Rhine and Rhône drainages and encompassed all presumed *A. berndhauseri* -samples. All presumed *A. berndhauseri, A. (p.) italicus* -samples clustered within a Southern group. This group included samples from South of the Alps (Pô drainage) and also from the Central Alps (Upper Rhine and Rhône drainages). The third lineage consists of only one population from near Vicenza (Italy). Furthermore, the populations from the Upper Rhône drainage form a sub-clade within the Southern group considering mtDNA-variation, but no differentiation was found based on allozymes. In contrast, allozymes revealed considerable genetic differentiation between the presumed *italicus* -samples and the remaining Southern group, whereas at the mtDNA no differentiation was detected. In some cases, the combination of the two marker classes allowed to assess the natural or artificial origin of populations.

## Genetic structure and variability of plant virus populations

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The high potential for genetic variation of RNA viruses has been well documented. This potential is due to high error rates of RNA-dependent RNA-polymerases, but also to frequent genetic exchange by recombination and reassortment. High genetic variability has also been reported for animal RNA viruses such as influenza A, foot and mouth disease or hepatitis C viruses. On the other hand, work from plant RNA viruses belonging to the genera Tymovirus and Tobamovirus show high genetic stability rather variability. Indeed, when available sequence data from plant viruses belonging to various families or genera are analysed, low genetic variability seems to be the rule. In addition, data show that plant RNA viruses are not more variable than plant viruses with DNA genomes. We have been interested in understanding the genetic stability of RNA plant viruses, and have approached this issue by focussing on viruses from the genus Tobamovirus, to which the well-characterised tobacco mosaic virus (TMV) belongs. Mutation rates for TMV have been estimated form the number of mutants in the movement protein (MP) gene. For this, RNA transcripts from a biologically active cDNA clone were multiplied in transgenic plants that express the MP and complement the movement function. This system has allowed the estimation of mutation rates in the absence of selection, and the obtained values are not lower than those reported for animal RNA viruses. Thus, the observed low variation of TMV populations must be due to other factors. Negative selection to maintain the function of encoded proteins seems to be one such main factor and the ratios of nucleotide diversities at non-synonymous and at synonymous position for TMV-encoded proteins are similar to those of moderately conserved eukaryotic proteins. Analysis of tobamoviral populations infecting wild host plants indicates that positive selection may also be important in restricting variation. An additional important factor may be the interaction between different virus populations, and one such interaction has been analysed leading to the mutational meltdown of one of the two interacting populations.

# Hox-like gene duplications at the Cambrian explosion? (if it did exist)

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The conservation and divergence in developmental control genes and their functions between divergent taxa is fascinating, and have captured the imagination of developmental and evolutionary biologists. Genes of the Hox cluster are restricted to the animal kingdom and play a central role in axial patterning in divergent animal phyla. Hovewer, despite its evolutionary and developmental significance, the origin of the Hox cluster is still obscure. We recently described a novel Hox-like gene cluster (ParaHox cluster) in the genome of the cephalochordate amphioxus, the closest living relative of vertebrates. We argue that the ParaHox gene cluster is an ancient paralogue of the Hox and ParaHox gene clusters shows the phenomenon of collinearity along the antero-posterior body axis, with Hox genes predominantly patterning ectodermal derivatives, and ParaHox genes patterning endodermal derivatives.

Whether one, three, or even none explosions, most bilaterian animal phyla appeared and diversified during the Cambrian (or sligthly before). Our data suggest that the duplication of the primordial ProtoHox cluster predated or was coincident with the origin of major billaterian phyla. An interesting suggestion of the hypothesis is that ProtoHox cluster duplication, followed by functional recruitment to different tissues, may have facilitated an increase in body complexity during the Cambrian explossion. The presence of ParaHox and ProtoHox clusters in Protostomian phyla and ancient billaterian animals respectively, central to this hypothesis, will be discussed

#### The evolutionary history of trout (Salmo trutta) in the north-western Iberian glacial refuge.

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The quaternary glaciations have produced range changes on brown trout (*Salmo trutta*) populations. Allele frequency variation at 25 protein-coding loci was compared among collections from the glacial refuge in north-western Iberian Peninsula. After correcting allele frequencies to dismiss the influence of exogenous hatchery fish presently released in the region, 21 loci remained polymorphic. The high divergence observed among native gene pools ( $F_{=}=0.645$ ), coupled with the geographical patterns for some genetic variants (*GPI-B2\*135, aMAN\*90, sMDH-B1,2\*75, MPI\*105* and *PEPLT\*70*), suggested the existence of distinct evolutionary histories among populations of the north-western Iberian glacial refuge. A (i) Tajo River Group, a (ii) Duero River group, a (iii) Sil River group and a (iv) Cantabrian Sea-flowing rivers group groups were defined. Their origins are related to interglacial isolation of the rivers populations, the existence of large populations of migratory anadromous fish during glacial peaks, and, in the case of the Tajo River, to recent evolution of the river network. The future of these genes pools is seriously compromised by present man-directed activities on habitat and fish populations.

# Evolution of salmonid species. The role of chromosome rearrangements.

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Salmonids are tetraploid-derived taxa supposed to be still in the process of rediploidization; therefore the comparison of chromosomal locations of genes and sequences in salmonid species is of special interest in order to understand the mechanisms involved in chromosome evolution of this family. Rearrangements based on centric fusions followed by pericentric inversions have been suggested as a general mechanism of chromosome evolution in salmonids. This study compares chromosome organizations of two closely related salmonid species, Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.), compiling evidences of rearrangement mechanisms occurred during the evolutive history of each species. Studies of: inheritance of Robertsonian-like chromosome variants, chromosome polymorphism present in wild populations of both species, chromosomal location of gene families and repeated sequences in both species, and hybrid karyotype analyses, were combined to identify, as far as possible, the mechanisms of chromosome evolution of the *Salmo* genus.

# Inferring epistatic selection in natural hybrid zones

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Natural hybrid zones provide a unique window on the evolutionary process. They can be used to study the quantitative genetics and fitness effects of individual loci in a range of organisms, including those that are long-live or difficult to propagate. Furthermore, they provide the most appropriate scenario for studying the genetic architecture of species barriers. The narrowness of hybrid zones and their effectiveness as barriers to gene flow could result from underdominance (heterozygous disadvantage at individual loci) or from the break-up of coadapted gene complexes yet there are surprisingly few data that allow these alternative explanations to be tested. Reports of epistatic interactions affecting hybrid sterility or inviability in controlled crosses support the coadaptation hypothesis but comparable data have not yet available from hybrid zones. We examined the contributions of epistatic selection to linkage disequilibria and genetic isolation in three independent hybrid zones between two wild sunflower species, Helianthus annuus and H. petiolaris, using 88 markers of known genomic location. The majority of observed linkage disequilibrium in these hybrid zones was explicable by the genotypic (generational) structure of the hybrid zone (i.e. it is largely the result of dispersal), However, we were able to infer that a significant amount of linkage disequilibrium in these hybrid zones does appear to result from epistatic selection, and it is the most likely explanation for variation in cline width for individual loci. Interestingly, these inferred epistatic interactions were largely between chromsomal blocks of loci with large effects on pollen viability, the major isolating barrier between these species.
## Detection of reduction in population size using data from microsatelllites

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Populations which suffer reductions in size can face many problems, such as inbreeding depression, decreased resistance to epidemics and reduced evolutionary potential. However, detecting such reductions is not always easy without historical demographic data, because events such as subsequent population growth (e.g. the northern elephant seal) can obscure small past population sizes. Moreover, some populations might have always existed at small size. We present a new method for using data from microsatellite DNA markers to detect past reductions in population size. This method exploits the fact that during a population reduction, the number of alleles decreases faster than the range in allele size at microsatellite loci. We demonstrate the validity of this method for loci which evolve under either a strict one-step mutation model or a two-phase model, when realistic estimates of mutation parameters are employed. We also show that this method appears to be consistent with data from a large number of natural populations for which demographic data is available.

## About the BIONJ algorithm: principle, topological accuracy and shape effect

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BIONJ is an improved version of NJ. It follows the same agglomerative scheme, which consists in iteratively picking a pair of taxa, creating a new node that represents the cluster of these taxa, and reducing the distance matrix by replacing both taxa by this node. Moreover, BIONJ uses a simple, first-order model of the variances and covariances of evolutionary distance estimates. This model is well adapted when these estimates are obtained from aligned sequences. At each step it permits the selection, from the class of admissible reductions, of the reduction which minimizes the variance of the new distance matrix. In this way, we obtain better estimates to choose the pair of taxa to be agglomerated during the next steps. Computer simulations show that when the substitution rates are low or when they are constant among lineages, BIONJ is only slightly better than NJ. When the substitution rates are higher and varying among lineages, BIONJ has a clearly better topological accuracy. In the latter case, for the model trees and the conditions of evolution tested, the topological error reduction is on the average around 20%. With highly varying-rate trees and with high substitution rates (maximum pairwise divergence

1.0 substitutions per site), the error reduction may even rise above 50 %, while the probability of finding the correct tree may be augmented by as much as 15% (Mol. Biol. Evol. 14(7), 685-695, 1997).

Recently, we have compared FITCH (PHYLIP package) and BIONJ. Basically, both algorithms have similar topological accuracy. However, BIONJ is much faster and deal easily with hundreds (and even few thousands) of taxa. Moreover, BIONJ is slightly more accurate when the true tree is "bushy" (or well balanced), while FITCH performs a little better when the true tree is "sparse" (or chain-like). We explain this fact on the basis of the a priori tree shape distribution involved by both algorithms, and indicate the practical implications (unpublished results).

Extensive nucleotide variability within the Major Histocompatibility Complex: Association with polymorphic frozen blocks and recombination.

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The recent availability of the genomic sequence spanning the major histocompatibility complex (MHC) has allowed a detailed study of its organisation, gene content and level of polymorphism. Previous analyses of polymorphism in the MHC has focused on the coding regions of the human leukocyte antigen (HLA) Class I and II genes. Particularly, the peptide binding residues, which are under balancing selection. Non-coding polymorphism has been considered a by-product of exonic diversity. However, with the advent of genomic sequencing, the extent of non-coding polymorphism within the MHC has just begun to be appreciated (Guillaudeux et al., 1998; Horton et al., 1998). In this study, we compared different human haplotypes within three regions of the MHC to show the following: 1) unusually high levels of non-coding polymorphism, up to 80 times greater than elsewhere in the genome; 2) non-coding polymorphism greater than 1% at nucleotide sites distant to the Class I genes; 3) polymorphism greater than 1% maintained over regions containing highly linked loci; 4) distinct troughs and peaks in the level of polymorphism; and 5) polymorphism peaks do not always correspond to the HLA loci. The data supports the hypothesis that within the MHC there exists stretches of sequences (polymorphism, flanked by regions of low polymorphism. Polymorphism may act to repress recombination within the block with potential recombination sites most likely occurring outside the block in the regions of low polymorphism.

#### **References:**

Dawkins, R.L., Leelayuwat, C., Gaudieri, S., Tay, G.K., Cattley, S., Martinez, P., Kulski, J.K., in press. Genomics of the Major Histocompatibility Complex: Haplotypes, duplications, retroviruses and disease. Immunol. Rev. Guillaudeux, T., Janer, M., Wong, G.K., Spies, T., Geraghty, D.E., 1998. The complete genomic sequence of 424,015bp at the centromeric end of the HLA class I region: Gene content and polymorphism. Proc. Natl. Acad. Sci. USA 95, 9494-9499.

Horton, R., Niblett, D., Milne, S., Palmer, S., Tubby, B., Trowsdale, J., Beck, S., 1998. Large-scale sequence comparisons reveal unusually high levels of variation in the HLA-DQB1 locus in the Class II region of the human MHC. J. Mol. Biol. 282, 71-97.

Marshall, B., Leelayuwat, C., Degli-Esposti, M.A., Pinelli, M., Abraham, L.J., Dawkins, R.L., 1993. New major histocompatibility complex genes. Hum. Immunol. 38, 24-9.

# Asymmetric competition for partners explains the evolutionary stability and diversification of mutualistic associations

#### R. Ferrière, J. Bronstein, M. Gauduchon, S. Rinaldi and R. Law

Widespread mutualisms pose two difficult problems to the evolutionary biologist:

(i) Selection is expected to favor individuals that get what they require from other species while investing as little as possible into them; then the coevolution of the two species is expected to lead to the continued reduction of cooperativeness, which may result in the collapse of the interaction and species extinction.

(ii) Entire species with no history of providing benefits may be able to reap commodities produced for mutualist species. If these commodities are removed entirely by non-mutualists, the mutualist that requires them may abandon the relationship. Thus, when such an invasive species enters the interaction, new selective pressures are induced on the mutualistic pair that may have the same effect as before, leading to the breakdown of mutualism. We found a simple solution to this double evolutionary puzzle. There is a necessary and sufficient ecological mechanism that may ensure the evolutionary stability of mutualistic associations<sup>3</sup>/<sub>4</sub>it is asymmetric competition for access to partners.

Competition for access to partners is basic in sexual selection theory, but to date its impact on the evolution of sociality and cooperation has remained unexplored. We have carried out the detailed mathematical analysis of a simple model that incorporates mutualism as a continuous strategy. Being more cooperative implies a larger density-independent cost and a direct, density-dependent benefit which results from a better ability to collect the rewards offered by the partner species (to which the same assumptions apply).

Investigating the adaptive dynamics of this model yields the following insights.

1. If competition is symmetric (no competitive advantage for being more mutualist), the association may be stable on the ecological timescale, but the coevolutionary process unavoidably leads to extinction of both species through a joint 'evolutionary suicide'.

2. The degree of competitive asymmetry and the shape of the density-independent cost function both determine the evolutionary dynamics of the system. A generic prediction is the diversification of the association, each species becoming polymorphic. This means that various evolutionarily stable degrees of cheating are represented by different groups of individuals in each species.

3. The specific rates of evolution (determined by the mutation rate and the magnitude of mutation effects) may or may not influence the evolutionary pattern, depending on conditions on the competitive asymmetry.

4. The coevolutionary process may cause one species to 'miss' a branching event (i.e., the divergence of two strategies after a certain phenotype had been established in the population).

5. The phenotypic diversity in each species may vary over evolutionary time, due to repeated events of branching and extinction.

6. The invasion of a new species may dramatically alter the coevolutionary dynamics of the system.

Our ongoing work is aimed at identifying conditions under which the observed patterns of branching may trigger speciation through assortative partnership and specialization.

### Dynamics of speciation on holey adaptative landscapes

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A holey adaptative landscape is and adaptative landscape where relatively infrequent well-fit combinations of genes form a contiguous set that expands throughout the genotype space. I present simple models describing the dynamics of speciation on holey adaptative landscapes driven by mutation and random genetic drift. Unlike most previous models that concentrate only on some stages of sepciation, the models studied here describe the complete process of speciation from initiation until completion. The evolutionary factors included are selection (reproductive isolation), random genetic drift, mutation, recombination, and migration. In these models, pre and post-mating reproductive isolation is a consequence of cumulative genetic change. I study possibilities for speciation according to allopatric, parapatric, peripatric and vicariance scenarios.

## Population genetics in wood mice (Apodemus sylvaticus)

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To date, genetic structure of populations has typically been examined by comparing allele frequencies of individuals of different subpopulations which had been trapped at the same time. However, data about the temporal dynamics of the genetic structure are required for information about the stability of populations and dispersal events.

In this study, the temporal and spatial dynamics of a wild living population of wood mice (*Apodemus syvaticus*) were examined monthly over a period of 2.5 years. The spatial distribution of more than 350 animals living in an 1.4 ha area of a forest was estimated using the capture-mark-recapture method. DNA was extracted from small samples of ear tissue. Genetic structure of the population and relatedness of individuals were estimated based on allele frequencies at five previously cloned microsatellite loci. By comparing allele frequencies of animals living within the same area at different times of the year seasonal change in dispersal and immigration events were revealed. While gene flow was high during the summer months, the population was more stable during winter, indicating lower dispersal behavior in times of harsh climate. Reproductive success of males and females could be evaluated as well as the spatial distribution and recruitment of offspring.

A promiscuous mating system was revealed, with a high degree of multiple mating by females within an estrous period that resulted in large numbers of half sibships among the offspring. Frequently female offspring overtook the territory of their mothers, as shown by sex related kin clusters.

Phenotypic variations in the recognition of echovirus type 11 strains by a group-specific anti-VP1 monoclonal antibody

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Mab 5-D8/1 is a monoclonal antibody (Mab) which was shown to be directed towards a conserved epitope of the capsid protein VP1 among the genus enterovirus. The use of this Mab for the routine detection of enteroviruses in clinical specimens led to the observation that several strains of echovirus type 11 (EV-11) could not be detected on spontaneously detached cells from 26 hour-cultures using a two-step inmunofluorescence (IF) assay. Conversely, these strains were detected positive whit the same Mab when tested on adherent or trypsinizated cells. IF tests at different times of the viral cycle brought evidence that the detection of a variant strain of EV-11 decreased rapidly with time, becoming undetectable 26 hours post infection, since the reference strain remained positive up to 46 hours post infection. The infective titres of the variant strains were shown to be high in comparasion to those of well-recognised strains. Sequencing the Mab binding epitope confirmed that the variant strains exhibited no antigenic shift. These results suggest that the poor recognition of some strains of EV-11 by Mab 5-D8/1 is due to a rapid decrease of the expression of the binding epitope on the surface of the cell, maybe in relation with the high lytic power of these strains. On a practical point of view, our data indicate that the negative result when Mab 5-D8/1 is used for enterovirus typing must be interpreted cautiously with highly replicative strains.

## Relationship between larva; ecology and species extinction in gastropods

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Larval ecology of gastropods, that can be deduced from protoconch morphologies, has been used to analyze some general macroevolutive topics (dispersal ability, longevity, speciation and extinction rates, etc.). The aim, of this study is to make more concrete the role played by larval ecology in species extinction events caused by environmental crises.

Pairs of sibling species that only differ on its larval ecology, from the Pliocene to Recent of the atlanto-mediterranean region, are used. In each of these pairs, one of the species shows planctotrophic larvae (multispiral protoconch) while the other species shows non-planctotrophic larvae (paucispiral protoconch), but coincide on its adult morphological. and ecological characters. There is a good knowledge on the palcoecology, stratigraphy and paleobiogeography of these pairs of sibling species.

The response of each kind of larva to environmental changes is not homogeneous. In some cases the planctotrophic species becomes extinct and the non-planctotrophic resists, whilst in other cases the contrary is observed. There is a close relation between the species of each pair that becomes extinct and the kind of environmental crises. Some environmental modifications favor species with planctotrophic development; other changes benefit species with non-planctotrophic development. Also, geographical spread reached by each species at the moment when environmental crises begin play a preeminent role.

### Evolution of a spider community in the Hawaiian Islands

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Islands, because of their microcosmal features, provide model systems for understanding the mechanisms underlying species formation. Similarly, because islands often differ in age and isolation, they can provide insights into community and ecosystem development. For Hawaii, the extreme isolation, topographical diversity, and ecological extremes have provided fertile ground for some of the most spectacular species radiations. In addition, the chronological arrangement of the main Hawaiian Islands, from Kauai (>5myrs) to Hawaii (still forming), allows visualization of "snapshots" of the different stages in the processes of terrestrial species formation and community and ecosystem development. Together, these features provide an extraordinary opportunity for understanding causal mechanisms underlying the generation of species and their assemblages, including the initial divergence of populations and community evolution. The current study uses the Hawaiian Islands and a radiation of spiders in the genus Tetragnatha, to examine the question: Is community organization a consequence of historical contingency and chance ecological events, or is it governed by local processes? I use phylogenetic analysis to investigate convergence of ecological equivalents within the spider radiation. Results to date indicate that similar sets of "ecomorphs" have evolved independently on each island. The youngest island contains few endemic species - most taxa are shared with East Maui. East Maui, however, has more than two times as many endemic species as any other mountain. All the older mountains have a single representative of each ecomorph. Together, the results suggest that ecomorphs appear, either by dispersal or evolution in situ, under condition of reduced competition. It may therefore be the lack of competition that allows adaptive radiation to be initiated, but competition may play a role in dictating the "final" composition of species.

## Quantitative trait loci for Drosophila melanogaster courtship song

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Courtship plays a major role in the sexual isolation of species, yet the genetics underlying courtship behavior are poorly understood. Drosophila melanogaster courtship song improves the mating success of males and probably contributes to sexual isolation. The most important parameter of courtship song for species discrimination is the interpulse interval (IPI), the amount of time between each pulse. Conventional crosses imply that strain differences have a polygenic additive genetic architecture. The difference in mean IPI between species has also been demonstrated to be determined by additive genes distributed evenly throughout the genome. Although genes affecting D. melanogaster courtship song have been identified through conventional mutational analyses, few of these influence the length of IPI. Because mean IPI is a quantitative trait and because mutations in genes that affect mean IPI do not necessarily reflect the natural variation underlying the trait, a quantitative trait loci (QTL) approach has been taken to elucidate the genetic architecture of mean IPI. Mean IPI was measured in 92 recombinant inbred (RI) strains of D. melanogaster. Although the original strains used to construct the RI lines do not significantly differ in mean IPI, the range of mean IPI for the RI lines reflects the amount of variation previously found within the species. These lines were scored for 76 molecular markers and composite interval mapping was used to determine the approximate locations of putative QTLs. Three QTLS were identified: one on the second chromosome and two on the third. In all, these account for about 30% of the variation between strains. Only one candidate song gene is located within one of the intervals for a mean IPI OTL, implying that mutational analyses have not be successful in identifying genes relevant to speciation.

## The evolution of parasitic barnacles (Rhizocephala)

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Rhizocephala is a group of specialized parasitic crustaceans that as adults have lost all morphological resemblance to their barnacle relatives. Conventional barnacles, Acrothoracica (the borrowing barnacles) and Thoracica (the acon and goose barnacles), are all filter-feeding organisms that use their thoracic appendages as particle catching organs. Rhizocephalans have lost all traces of thoracic and mouth appendages and use a root system embedded into their host as the sole trophic organ.

However, recent morphological evidence shows that although different in adult appearance, most organs of the rhizocephalan can be directly homologized to corresponding organs in the thoracican barnacle.

The aim of the present study is therefor, by the use of morphological and molecular techniques, to construct a rough internal phylogeny of the rhizocephalans and to establish their relation to other barnacles. Ultimately this will clarify the otherwise obscurer evolutionary transition that led the rhizocephalans from an ancestral filter-feeding organism to an internal parasite.

#### Clinal morphologic and genetic variation in Drosophila melanogaster

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Variation of adaptive traits in populations along geographical transects provide a good model system to understand how natural populations adapt to their environment. We describe clinal variation in body size of Drosophila melanogaster populations from Papua New Guinea, Australia and Tasmania, measured in wing size. Our data confirm previous studies on the clinality of wing size variation. With body size being a fitness related trait, it is important to understand the nature of selection acting.

In order to determine if morphological differences between the populations are due to natural selection, we will correlate morphological and genetic differences between the populations by using microsatellite markers. We will further use these markers to map quantitative trait loci (QTL) and to determine which populations are part of the same cline with respect to polymorphisms at the underlying set of QTLs.

#### The Ecology and Evolution of a Selfish Gene: An Estimate of Gene Horizontal Transfer Rate

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Gene transfer between species is known, however, the frequency with which this occurs is unknown. A model system using a selfish gene in yeast has been employed to estimate a rate of gene horizontal transfer. Homing Endonuclease Genes (HEGs) are optional, non-essential genes that are found in all Kingdoms of life. HEGs manage to over-represent themselves in the next generation due to their non-Mendelian inheritance which they achieve by gene conversion. Their inheritance bias (up to 95%) means they are predicted to quickly sweep through a population and reach fixation. Once at fixation the selective pressure for functionality is greatly reduced since they encounter no empty alleles to infect; it is, therefore, not easy to see how such HEGs are able to maintain their function over long time periods. One hypothesis argues that HEGs escape degeneration through mobility - that they are horizontally transferred to HEG-less species. I tested this hypothesis using a specific HEG, called w, found in the mitochondrial LSU gene of yeast. 20 closely related taxa were surveyed for w and established phylogenetic methods were employed to test the hypothesis of w horizontal transfer. These tests demonstrated that w had indeed been horizontally transferred between species. However, these tests could not describe how frequently horizontal transfer occurs, therefore, new tests were developed to estimate the rate of horizontal transfer. The results indicate that this selfish gene is functionally maintained due to the fact that it repeatedly invades species to re-establish its presence once lost, the cycle is estimated to turn once every 5.7MY. These results show that w is horizontal transferred once event every 1-10MY, and perhaps more frequently than this. It is apparent that the evolutionary history of w is highly dynamic, and further, this is the first estimate of gene horizontal transfer rate and the methods used here will be widely applicable to other systems.

# Comparative analysis of the *Deinococcus* genome indicates infrequent horizontal transfer between the three dornains of life

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Members of the deep branching bacterial lineage *Deinococcaceae* (e.g. *Thennus* and *Deinococcus*) are classified as Bacteria. However, *Thermus thennophilus* does not have a typical bacterial F-ATPase, but a complete AV/ATPase flke those in Archaea and Eukaryotes. The A/V-ATPase genes are not the only evidence of non-bacterial type genes in the *Deinococcaceae*. *T. flavus* has a malate dehydrogenase that in phylogenetic analyses groups with eukaryotic homologues. Genetic screening of a *Meiothermus ruber* genomic library with random1y primed probes made from *Thermoplasma acidophilus* genomic DNA identified a number of clones which hybridized to the archaeal probes. One of these encoded a prolyl-tRNA synthetase, which is more closely related to archael and eukaryotic proly1 tRNA synthetases than to the majority of bacterial prolyl tRNA synthetases. The most plausible explanation for the presence of non-bacterial genes in members of the *Deinococcaceae is* horizontal gene transfer from the archaeal lineage to this bacterial lineage.

We used a bioinformatics approach to search for other candidate genes in the *Deinococcus radiodurans* genome that might have been horizontally transferred from the archaeal domain. Putative open reading frames (ORFs) from the *Deinococcus* genome were searched against representative genomes from each of the three domains of life. Those ORFs that showed highest matches against archaeal and eukaryotic genes were collected and ranked. Among the top ranked hits were the A/V-ATPase catalytic and non-catalytic subunits, and the prolyl-tRNA synthetase. These analyses show relatively few instances of horizontal gene transfer from the Archaea into the *Deinococcaeae*.

#### Intragenic Variation of Synonymous Substitutions and its Evolutionary Implication

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It has been observed that synonymous substitution rates vary among genes in various organisms, although the cause of the variation is unresolved. At the intragenic level, however, the variation of synonymous substitutions is somewhat controversial. By developing a rigorous statistical test and applying the test to 418 homologous gene pairs between mouse and rat, we found that more than 90 % of gene pairs showed a statistical significance in intragenic variation of synonymous substitution rates. Moreover, by examining all conceivable possibilities for the cause of the variation, we successfully found that intragenic variation of synonymous substitutions in mammalian genes is caused mainly by a nonrandom mutation due to the methylation of CpG dinucleotides rather than by functional constraints. This can also explain an observed correlation between synonymous and nonsynonymous substitutions. Thus, it seems that nonrandom mutation is more important than selective constraints to understand the intragenic variation of synonymous substitutions rates.

## A Method for Detecting Positive Selection at Single Amino Acid Sites

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A method was developed for detecting the selective force at single amino acid sites, given a multiple alignment of protein coding sequences. The phylogenetic tree was reconstructed using the number of synonymous substitutions. Then, the neutrality was tested for each codon site using the numbers of synonymous and nonsynonymous changes throughout the phylogenetic tree. Computer simulation showed that this method estimated accurately the numbers of synonymous and nonsynonymous substitutions per site, as long as the substitution number on each branch was relatively small. The false positive rate for detecting the selective force was generally low. On the other hand, the true positive rate for detecting the selective force depended upon the parameter values. Within the range of parameter values used in the simulation, the true positive rate increased as the strength of the selective force and the total branch length, namely the total number of synonymous substitutions per site, in the phylogenetic tree increased. In particular, most of the positively selected codon sites, with the relative rate of nonsynonymous substitution to synonymous substitution being 5.0, were correctly detected when the total branch length in the phylogenetic tree was 2.5 or more. When this method was applied to the human leukocyte antigen (HLA) gene, which included antigen recognition sites (ARSs), positive selection was detected mainly on ARSs. This finding confirmed the effectiveness of the present method with actual data. Moreover, two amino acid sites were newly identified as positively selected in non-ARSs. Three-dimensional structure of the HLA molecule indicated that these sites might be involved in antigen recognition. Positively selected amino acid sites were also identified in the envelope protein of human immunodeficiency virus and the influenza virus hemagglutinin protein. This method may be helpful for predicting functions of amino acid sites in proteins, especially in the present situation that sequence data is accumulating at an enormous speed.

### Sex, parthenogenesis and the genetic structure of rotifer populations

### Africa Gómez\* and Gary R. Carvalho

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Cyclical parthenogenetic rotifers offer a unique opportunity to study the relationships between reproductive mode and population structure. Here, we used seven polymorphic microsatellite loci developed for the rotifer *Brachionus plicatilis* to analyse (1) the changes in the genetic structure of rotifer populations along the parthenogenetic phase, (2) the genetic structure of the resting egg bank, (3) the structure of the population after its initiation from resting eggs. This set of microsatellite markers are a powerful tool for clone identification, revealing a surprisingly high clonal diversity. Rotifer populations become more structured along the parthenogenetic phase: the last sample in the parthenogenetic cycle shows linkage disequilibrium and lowest clonal diversity, indicating clonal selection. The resting egg bank is in genetic equilibrium, and contains a high genotypic diversity. Thus, sexual reproduction is responsible for the production of clonal diversity, and clonal selection plays a role in the structuring of populations of this rotifer species.

### Chloroplast microsatellite markers reveal evolutive history of Aleppo pine in Spain.

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Nine pairs of chloroplast microsatellite primers and 144 samples from six Spanish populations have been used in order to study the evolutionary history of *Pinus halepensis* in Spain. Only one of the cpSSRs has resulted in monomorphic product and the other have been used to design 28 haplotypes.

To establish a representation of relationships among the haplotypes, we have used a tridimensional figure. In general, the variants for each cpSSR vary only in one or two mutations from other variant verifying the single step-wise mutation model for microsatellites.

Detected chloroplast haplotypes, relationships among them and the level of haplotype diversity show that migration of Aleppo pine to Spain from Greece took place a long time ago and during last glaciation refugia remained in Spain. Probably, actual range of distribution of this species in Spain was reached by those individuals which the most frequent haplotypes detected belong to.

# Mitochondrial phylogeny of the genus *Timarcha* (Coleoptera, Chrysomelidae) inferred from complete COII and partial 16S rDNA genes

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Flightless leaf-beetles of the genus *Timarcha* comprise about one hundred species mainly distributed in Southern Europe and North Africa. We have analysed complete mitochondrial cytochrome oxidase II (685 pb) and partial 16S rDNA (510 pb) sequences in order to infer the phylogenetic relationships in a sample of 54 individuals of 27 European plus 4 North African taxa of the three recognised Palaearctic subgenera. Both markers are studied separately and, after assessing the compatibility of these phylogenetic reconstructions, combined in a "total evidence" approach. The obtained phylogeny show conflicts with prevalent systematics for the genus based on morphology, biogeography and karyology, and no clear monophyletic groupings for each subgenus is either obtained. An attempt for molecular clock calibration in Timarcha COII is done using an assumed species vicariance due to the final opening of Gibraltar Strait dated around 5.3 MYA. The evolutionary rate obtained considering all substitution types is considerably lower than the standard rates assumed for insect mitochondrial DNA evolution, and alternatively a more conservative transversions-based rate is estimated. This rate is 1.1 x 10-9 substitutions/site/year, similar to the corresponding estimation for the divergence of Drosophila melanogaster and D. obscura groups. The mitochondrial phylogenetic reconstruction is also used to study the evolution of trophic selection in the genus Timarcha. There is apparently a widening of trophic spectrum in the evolution of the genus from a Rubiaceae regime to mixed diets with other botanical families. Furthermore, trophic selection seems to be related to selective adaptation rather than phylogenetic relatedness.

## Isozyme diversity in Phoenix canariensis and P. dactylifera populations from the Canary Islands.

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Isozymes variation was used to characterise genetically two *Phoenix* species present in the Canary Islands, the endemic *Phoenix canariensis* and *P. dactylifera*, a cosmopolitan species introduced in recent times. The fact that both species hybridize in natural conditions, stands in the way of streamlining a sensible conservation strategy for the endemic *P. canariensis*. Analysis of 17 isozymes loci identified two exclusive alleles (MDH-1D, PGM-2D) in *P. dactylifera* and one (IDH-1C) in *P. canariensis*. The extent of differentiation between the two species was assessed through Nei's genetic distance and Wright's F-statistics. Mean genetic identity between both species was (I=0.705). Both cluster analysis and principal components analysis of allele frequencies clearly separated both species and situated hybrids in an intermediate position between them. Our results show that isozyme electrophoresis is a suitable technique to identify *Phoenix canariensis* and *P. dactylifera* from the Canary Islands.

#### Does sensory exploitation prevent female choice in fish?

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The sensory exploitation hypothesis posits that males use pre-existing responsiveness of females to sensory stimuli, so as to gain access to mates. It may be that 1) males tune into sensory biases arising from the way the senses and neural systems of females are built, or 2) males imitate signals to which females have been selected to respond (for instance mimicking female responsiveness to clues signifying food). Sensory exploitation can generate a conflict of interests between sexes because non-discriminating females would be deprived of the opportunity to exert effective mate choice, and natural selection should penalise females that relinquish control over matings. Under (1), females would be permanently exposed to sensory exploitation. However, if the attractive male traits are exploiting adaptive responsiveness, such conflict may result in a) females ceasing to respond to those clues altogether, or, if such option were too costly, b) female discrimination between the model (i.e. food items) and the mimic (i. e. the male trait). We sought evidence of the above using fish of the family Goodeidae. Males of many species have a coloured outer strip in the caudal fin, and we hypothesised that the movement and colour of the fin edge simulates an edible worm. We tested the prediction that fin edges of males should evoke female feeding responses. Then we compared feeding responses to fin edges of conspecific and of heterospecific males, so as to assess whether females have evolved discrimination against conspecific male sensory exploitation. Our methods exposed females of three species of Goodeid to computer-edited video animations of manipulated and non-manipulated caudal fins of males. We discuss our data in relation to the theory of sexual selection by sensory exploitation.

Ryan a través de su hipótesis de explotación sensorial, ha propuesto que los machos utilizan prefererencias preexistentes en las hembras para conseguir apareamientos.

Genetic variation along a South-North cline in *Pinus pinaster* Ait.: a comparison of molecular and quantitative traits.

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The variation among seven native populations of *Pinus pinaster* Ait. situated along a cline from Morocco (Latitude  $30^{\circ} 22'$  N) to North Spain (Latitude  $42^{\circ} 51'$  N) is investigated by means of seven polymorphic isozyme loci and three quantitative traits. All the isozyme loci included in this work fit the hypothesis of neutrality as shown by Ewems-Watterson test. Estimates of population differentiation (F) for three quantitative traits (survival, total height and stem form) and the overall isozyme F\* are made. A stepping-stone model of genetic variation is shown by means of F\* estimates for adjacent populations along the cline. Strong correlation between Nei's genetic distances and geographic distances between pairs of populations (r=0.68) indicates a clear geographic structuration for the isozyme markers.

Linear models are used to test the significance of the deviation of quantitative traits F and allozyme F\* for adjacent populations. While the main effect of the different loci analysed is not significant, the main effect of F versus F\* is highly significant for all the quantitative traits studied. Stem form is the most divergent parameter followed by height growth and survival. The combined analysis of morphological and molecular patterns of population subdivision allow the detection of specific adaptive processes to local conditions.

Molecular and morphometric differentiation in *Limonium dufourii* (Plumbaginaceae), an endangered Mediterranean plant.

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One recurrent theme in conservation biology relates to the relevance of genetic variability as inferred from molecular markers for the assessment of population viability and the design and control of effective conservation measures. One common criticism to these studies lays on the lack of correlation between molecular and adaptively significant genetic variation. We have studied genetic variability in extant populations of L. dufourii, an endangered plant endemic to the East Mediterranean coast of Spain, using RAPDs and AFLPs as molecular markers. With both markers, we have established the existence of two distinct groups of molecular variants in the populations of one geographical location (Marjal del Moro, Valencia). We have analyzed the morphometric and molecular variation on L. dufourii individuals from one of these populations, in order to evaluate whether variation at both levels was correlated or not. Ten traits were evaluated on 72 individuals and their molecular phenotype was ascertained from the RAPD pattern obtained with primer OPA-8. Principal component analysis of those traits resulted in 3 significant dimensions explaining 63% of the total variation. No significant clustering of individuals was observed from this analysis. However, when the molecular phenotypic group was taken into account, a discriminant function was obtained that allowed the correct classification of the molecular group to which one individual belonged from its morphometric data in 80% of the cases. We conclude that in this case there is a significant correlation between morphometric (and, therefore, presumably adaptive) variation and molecular genetic variability, thus providing justification for the use of molecular markers in the design and control of conservation strategies for this species.

### Waterfifies, Microsatellites and Dispersal

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The Yellow water lily, *Nuphar lutea*, is a common aquatic macrophyte widely distributed throughout many of Europe's niver systems. In study 1ng the phylogeography of this species, rnierosatellites were chosen as tools to address within and between population components. 11 polymorphic markers were developed and have proven applicable for research from local scales up to, those of entire river systems. Here results are presented from initial studies using these markers in reproductive and dispersal analysis, with particular reference toward levels of elonality and uni-directional geneflow.

#### Evolutionary transitions in parental care in cichlid fish

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Fish in the family Cichlidae provide many forms of parental care for their offspring, ranging from substrate guarding to mouthbrooding, provided by either males, females or both. I use a composite phylogeny to test the evolutionary pathways that have led to this unusual variation. Mouthbrooding has evolved from ancestral substrate guarding 10-14 times with few if any reversals, and uniparental female care evolved from biparental care 21-30 times with few if any reversals. These transitions are the most numerous reported for any family of vertebrates and provide the first quantitative support for models of parental care evolution in fishes.

# Evolutionary relationships between the primary lineages of life: effect of more realistic models of molecular evolution.

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Identification of the primary lineages of life and of their evolutionary relationships is essential for understanding early cellular evolution, particularly the transition between prokaryotes and eukaryotes. Most molecular phylogenetic analyses of small subunit (SSU) and large subunit (LSU) ribosomal RNA sequences (Woese 1987; Gouy & Li, 1989; Woese et al., 1990; De Rijk et al., 1995) as well as analyses of isoleucyl-tRNA synthetase (Brown & Doolittle, 1995) and of the largest subunit of RNA polymerase (Puhler et al., 1989) supported the existence of three monophyletic domains, Archaea, Bacteria, and Eukarya. In contrast, analyses of elongation factors 1a/Tu and 2/G (Rivera & Lake, 1992; Baldauf et al., 1996; Hashimoto & Hasegawa, 1996) and of the second largest subunit of RNA polymerase (Iwabe et al., 1991) suggested that Archaea are paraphyletic and that Eukaryota are specifically related to a subset of Archaea, Crenarchaeota (previously eocytes) as advocated by Lake (Lake, 1988). We have re-analyzed this question using the large numbers of sequences now publicly available and recently developed methods of phylogenetic analysis (Jin & Nei, 1990; Yang, 1995; Tourasse & Gouy, 1997). These methods differ mainly from previous ones in being based on more realistic models of molecular evolution which account for the extensive variation among sequence sites of the rate of substitution. We report that this approach gives considerable support to the crenarchaeote - eukaryote relationship, both from rRNA and protein sequence data.

The role of WspR, a signal transduction protein, in a change in niche specialisation in experimental evolutionary populations of *Pseudomonas Fluorescens*.

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The bacterium *Pseudomonas fluorescens* rapidly diversifies in a heterogeneous environment producing a range of niche specialists. One of the dominant niche specialists colonises the air-broth interface, forming a mat, and is identified by its wrinkly colony morphology on plates. Mutagenesis of this morph identified two principle loci involved in the evolutionary transition from ancestral (SM) to wrinkly spreader (WS) niche specialist. One of these, the *wss* operon, encodes enzymes sufficient for the biosynthesis of a cellulose-like polymer and is the phenotypic target of selection. The second locus, termed *wsp*, encodes enzymes involved in a novel chemosensory pathway and is involved in the regulation of *wss*. The product of the final gene in the *wsp* operon, WspR, is a putative transcription factor and is required for activation of the *wss* operon. In the evolved morph, WspR is constitutively expressed and results in over expression of *wss* and generation of the WS phenotype. In order to understand the role of this protein in adaptive evolution we have generated a range of allelic variants of WspR and show that these can radically affect niche specialisation.

### Estimating the effective population size of a single ideal population

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The effective population size (N) measures the magnitude of genetic drift and inbreeding in a population. Thus, N is a central parameter in our understanding of evolutionary processes. The concept of the effective population size is based upon the Wright-Fisher ideal population, which is subdivided into an infinite number of subpopulations of constant size. The effective size of a given population is defined as the subpopulation size of the ideal population which is evolutionarily equivalent to the studied population.

I developed an individual based Monte Carlo simulation model. The model describes a single ideal population, which is equivalent to one subpopulation of a Wright-Fisher ideal population. I analysed the influence of several factors on the estimation process of Napplying this model: (i) The number of studied individuals should be as few as possible, (ii) The number of investigated loci should be limited, (iii) The observed degree of polymorphism may influence estimates of N, (iv) The molecular marker chosen may result in biased estimators of autozygosity and allozygosity used in different definitions of N, (v) We will neither observe identical nor an infinite number of populations. In particular, we wish to know the effective size of one unique natural population.

I found, that N estimated as a change in the average inbreeding coefficient gave good approximations only if the probability of autozygosity (identical by descent) is close to the probability of homozygosity (identical in state). In this case we found that 10 loci and 25 individuals gave sufficient approximations of N. Estimating N based upon the rate of loss of heterozygosity requires many more loci and individuals even if the observed heterozygosity is close to the allozygosity. How many they need depends on the underlying stochastic process. In the case of estimating average inbreeding coefficient and rate of loss of heterozygosity I derived a method which allows us to extrapolate N calculated on the basis of a small sample (number of individuals and loci) to the whole population.

## Parasitic gnathiid isopods: the key to the evolution of fish cleaning behaviour

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Fish cleaning behaviour, where cleaner fish remove parasites and other materials from client fish is used extensively as an example of mutualism. However, although cleaners obviously benefit from cleaning there is controversy on why clients seek cleaners and how the association evolved. Indeed it has been suggested that the Hawaiian cleaner fish parasitizes clients' responses to tactile stimuli to obtain food, mostly mucus. I examined whether cleaning associations involving the Indo-Pacific cleaner fish Labroides dimidiatus were mutualistic. Individual cleaners cleaned 2500 clients day<sup>-1</sup> from over 130 species. Most clients were cleaned daily, with some seeking cleaners more than a 150 times day<sup>-1</sup>. In contrast to studies in Hawaii, parasites, rather than tactile stimuli, were the proximate cause of cleaning as parasitized fish sought cleaners while those without parasites did not. Gnathiid isopod juveniles, which are blood feeders, were one of the most common parasites of coral reef fish on the Great Barrier Reef. Each cleaner ate almost 1200 gnathiids day-1. By placing fish in cages on coral reefs I showed that gnathiids infest fish at a rapid rate. Reared gnathiids remained on fish for only 30-60 min; thus fish are attacked by many gnathiids each day. Interestingly, gnathiid abundances on wild fish decreased between dawn and sunset. I demonstrated, in a field experiment, that this daily decrease is due to cleaner fish. These findings demonstrate that gnathiid removal is a selective pressure in cleaning behaviour and that the cleaner fish-client association is mutually beneficial. Conflicts, such as cheating by cleaners (eating scales) or clients (eating cleaners) do, however, occur. How the stability of this multispecies mutualism is therefore maintained is being examined by investigating the role of quality of reward, competition, partner choice, and partner control in cleaning interactions.

#### Did adaptive evolution operate in the Echis coloratus phospholipase A genes?

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Snake group II PLA multigene families represent a striking example of extreme conservation of non-coding regions, while the mature protein-coding exons are highly diversified. In order to get better insight into the sequence variability and the molecular evolution of the PLA genes in Viperidae snake species we have PCR amplified, cloned and analysed the complete *E. coloratus* PLA genes. The structural organization of both genes is the same as in other Viperinae PLA multigene families, consisting of five exons and four introns. Comparison of *E. coloratus* PLA genes with other Viperidae PLA genes has shown that the nucleotide sequence of all introns and flanking regions are highly conserved. 41 amino acid replacements are present in *E. coloratus* PLAs, all located in mature protein coding region. The relative role of natural selection and genetic drift in the evolution of the *E. coloratus* PLA genes has been studied by comparing divergence estimates both between genes and between species. For the Viperinae PLA genes the Ka/Ks ratio was higher than one in all comparisons between genes at intra- (except in *E. coloratus*) and inter-specific (Viperidae) level. In the case of *E. coloratus* PLA genes, the rate of synonymous substitutions (0.3628) exceeds that of non-synonymous substitutions (0.1983), indicating that these PLA genes are subject to purifying selection, rather than they evolved by positive Darwinian selection.

## Sex determination in the gametophytes of horsetails (genus Equisetum)

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Horsetails are homosporous, i.e. they produce sexually indetermined spores. Indeed, in the genus Equisetum, sexual differentiation occurs after dissemination and germination of the spore and is under influence of environmental conditions encountered by the gametophyte. In vitro, significantly different sex ratios are obtained when gametophytes are grown on media containing sucrose at various concentrations. In our experimental conditions, male outnumber female gametophytes in the presence of sucrose (30-40g/l), whereas in the absence of sucrose most gametophytes differentiate as female. Interestingly, this result is reproducible within and across species representative of the two subgenera Equisetum and Hippochaete. Our observations suggest that environmental sex determination is a distinctive feature of the entire genus Equisetum. The evolutionary significance of this finding will be discussed in relation with the life history of these plants.

## Strict maternal inheritance of chloroplasts in the horsetail Equisetum variegatum (Schleich.)

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Reliable data concerning the transmission of chloroplasts in the Pteridophyta are needed to study the evolution of this trait in connection with the evolution of life cycle and sexual reproduction in land plants. This work is the first to examine organelle transmission in the division Sphenophyta, represented by the extant genus Equisetum. By following the fate of polymorphic cpDNA through three intraspecific reciprocal crosses we found no trace of paternal transmission in Equisetum variegatum. The seemingly strict maternal transmission of cpDNA in this species suggests that uniparental chloroplast inheritance preceded the evolution of heterospory in the seed plant lineage.

## The Phylogeny of Prokaryotes: Does Horizontal Gene Transfer Preclude Its Determination?

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Two contrasting views of prokaryotic phylogeny are emerging from the analyses of molecular sequence data. The predominant view is that extensive and indiscriminate horizontal gene transfers have taken place among species due to which the evolutionary relationships among prokaryotes cannot be understood, except for the distinction between Archaebacteria and Eubacteria. An alternate view of prokaryotic phylogeny is being developed in our work based on the presence of conserved inserts or deletions in various proteins that are restricted to specific taxa (referred to as signature sequences) (Microbiol. Mol. Biol. Rev. 62, 1435-1491, 1998; Mol. Microbiol. 32, 893-906, 1999). The existence of such signatures provide evidence against random widespread horizontal gene transfers among species. These signatures were likely introduced in proteins at specific stages in evolution and they provide molecular markers for identifying different groups of prokaryotes and in understanding the evolutionary relationships among them. Based on signature sequences identified in different proteins it is possible to infer that the various eubacterial phyla evolved from a common ancestor in the following order: Low G+C gram-positive High G+C gram-positive Deinococcus-Thermus Green nonsulfur bacteria Cyanobacteria Spirochetes Chlamydia-Cytophaga-Aquifex-Flavobacteria-Green sulfur bacteria Proteobacteria (and) and Proteobacteria (and). Archaebacteria are indicated to be specifically related to the gram-positive bacteria both by their cell structures (both surrounded by a single membrane i.e., monoderms, in contrast to the diderm nature of all true gram-negative bacteria) as well as signature sequences and phylogenies based on numerous proteins. Thus, although horizontal gene transfer is observed in many cases, it is not so prevalent to preclude the determination of prokaryotic taxonomy.

## Genetic variation and population structure in desert bighorn sheep

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Bighorn sheep populations experienced a drastic reduction in both distribution and abundance until the advent of modern wildlife management, where improving viability of extant populations and translocating animals into historical habitat range have been the most important management policies. The fact that subspecies relationships among bighorn are ambiguous, together with the importance of selecting appropriate source stock and the expense of translocation projects, makes an understanding of subspecies relationships and genetic variation—within and between populations—important for the management and conservation of this species. In this study, two different molecular genetic surveys were used to understand the levels and patterns of genetic variation in 279 bighorn sheep from 13 study sites in Arizona, California, New Mexico and Alberta, Canada. First, ten microsatellite (MS) loci were used to characterize the neutral genetic variation and determine interpopulation differentiation and relationships between closely related taxa. Second, one major histocompatibility complex (MHC) locus was used to study adaptive genetic variation in the same desert BHS. All populations contained a substantial amount of genetic variation. Genetic differences between populations were large and roughly proportional to geographic distance. The significance of this to desert subspecies relationships and management is discussed.

#### Reproductive skew among multiple queens in the ant Formica fusca

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Ant colonies in many species contain multiple queens. When several queens share the resources of one colony they usually experience a reduction in their personal reproduction. Recent models of reproductive skew predict how reproduction should be shared among cobreeding individuals. According to the models the relatedness of the cobreeding individuals should have an effect to the reproductive skew. The Optimal skew model predicts positive correlation between skew and relatedness, whereas the Incomplete control model predicts skew to be insensitive to or correlate negatively with the relatedness among queens. We studied reproductive sharing among queens in *Formica fusca* to test the predictions of skew models. We found that queens contributed unequally ( $s = 0.25 \pm 0.29$ ) and were higly related within the nests ( $r = 0.59 \pm 0.08$ ). The degree of skew correlated negatively with the relatedness among field on effect on its reproductive share. We will discuss the role of worker behaviour on the reproductive shares of queens, as well as the applicability of skew models to ants with multiple queens.

# Gene flow in a river system and its consequences for population fitness: a case study of the river bullhead Cottus gobio

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We studied gene flow in the bullhead *Cottus gobio* using 6 microsatellite loci and 17 allozyme loci. Samples were taken at 32 sites from the River Derwent catchment (northern England) where the bullhead is very abundant. Gene flow was very low even within a short geographical distance and appeared to be mainly uni-directional, down stream. Upstream samples were more isolated and displayed lower levels of variability than samples from lower sites. Survival and growth of offspring from 9 locations along the river course were compared under laboratory conditions to analyse the fitness consequences of this limited gene flow.

Patterns of sequence variation in the chromosomal region surrounding a polymorphic locus affecting flowering time in *Arabidopsis thaliana* 

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*FRIGIDA* (*FRI*) affects the flowering-time response to cold treatment in *Arabidopsis thaliana*. *FRI* is naturally polymorphic, possibly as a result of strong selection for adaptation to different local environments. In order to investigate the pattern of sequence variation in the chromosomal region surrounding *FRI*, interspersed 0.5 kb fragments were sequenced in a collection of ecotypes whose flowering-time phenotype had previously been determined in greenhouse experiments. In agreement with theoretical predictions, extensive linkage disequilibrium is found throughout the region, between different markers as well as between markers and phenotypic values. However, the decay of linkage disequilibrium with physical distance as a result of recombination is clearly visible on a scale of 10 kb. The results support the notion that linkage disequilibrium mapping could be a useful tool in highly selfing species.

# Mitochondrial Phylogeny Analysis of Eastern Atlantic and Mediterranean Seabream Species (Sparidae, Percoidei)

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Seabreams are among the most valuable fishes for small-scale and semi-industrial fisheries throughout the Mediterranean and are of increasing interest to aquaculture. Nevertheless, the phylogenetic relationships between Sparidae species are not at all clear. The current phylogenetic hypothesis is based solely on morphology and suggests that more complex trophic morphologies evolved only once from a less specialized ancestral condition. A 486-bp segment of the mitochondrial 16S rDNA of all 24 seabream species described for the North-Eastern Atlantic and the Mediterranean was amplified and sequenced to elucidate their generic and subfamily level relationships. Several distinct mitochondrial lineages were found that do not agree with present species assignment and traditional phylogeny. Our results indicate that not only the genus *Sparus* must be seperated from *Pagrus*, but together with *Pagellus bogaraveo*, *Pagellus acarne* and the more distantly related *Lithognathus mormyrus* it forms a sister group to the genus *Diplodus*, whereas *Pagrus* together with the remaining two *Pagellus species* and the *Dentex* species form a monophyletic clade. Hence, the species complex *Sparus/Pagrus*, as well as the current genus *Pagellus*, collapse in two distinct clades which evolved independently. This demonstrates multiple independent origins of similar trophic specializations within the Sparidae and disproves the current classification in 3 to 4 subfamilies based on trophic morphologies.

## Genetic structure of fennel pondweed populations

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The cosmopolitan plant fennel pondweed, *Potamogeton pectinatus*, is a clonal submerged aquatic macrophyte. In established vegetations it mainly reproduces asexually through subterraneous tubers. At the same time, abundant seed production may occur but seedlings are only occasionally found.

Bewick's swans feed on the tubers and therefore could well affect the genetic structure of *P. pectinatus* populations. Sexual reproducing genets may be favored since they can escape grazing and the seedlings have a higher chance to establish in the grazed patches. Swan grazing would thus lead to higher genetic variation.

The population genetic structure might also be related to the latitude at which the population occurs. In the Northern Hemisphere organisms that reproduce asexually are often thought to have the tendency to occur further to the north than the sexually reproducing organisms. This might also be the case for *P. pectinatus*. Shorter growing seasons in the north would favor asexual reproduction with as a result low genetic variation within populations.

In this study we looked at the genetic structure of populations in The Netherlands and Northern Russia with different grazing pressures. Random Amplified Polymorphic DNA (RAPD) markers were used to analyse genetic diversity.

The genetic basis of host control of life history traits in the yellow fever mosquito *Aedes aegypti* infected with *Vavraia culicis* microsporidia

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The phenotypic characters of hosts infected by parasites may be viewed as extended phenotypes influenced by both host and parasite genes. Conflicting selection pressures acting on the two genotypes will lead to a coevolutionary conflict of interests for the control of host traits. The ecology and life histories of both host and parasite influence the outcome of this conflict. Using the yellow fever mosquito *Aedes aegypti* and its natural microsporidian parasite *Vavraia culicis*, we investigated the genetic basis of host control of life history traits. We compared groups of infected and uninfected half-sibs, performing a quantitative genetic analysis of traits of importance to both host and parasite life history. The traits studied were larval development time, parasite-induced mortality, adult wing length, fecundity of infected females, parasite load and vertical transmission rate of the parasite. We estimated host fitness from female fecundity and wing length, and parasite fitness from spore densities in individual hosts.

## Modeling genetic architecture: A multilinear model of gene interaction with applications in quantitative genetics

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Genes do not exert their effects in isolation from the genetic system in which they are parts. The effect of any gene must be understood as conditional on a genetic background.

In this paper we present a new model of gene interaction based on describing the effect of a gene as a function of a changing genetic background. By assuming that the effect of any genetic change in any genetic background can be described as a linear transformation of its effect in a reference genotype and that the effect of a genotype is independent of history, we show that the effect of a genotype can be described as a multilinear form in the effects of the individual genetic changes that separates that genotype from the reference. Although this formulation allows gene interactions of any order, it contains some strong symmetries that makes it ideally suited to study the evolution of genetic architecture. Here we apply the model to interpret the standard elements of a quantitative genetic analysis. We use this to clarify the effect of epistasis on the additive genetic variance, to derive scaling relationships between epistatic variance components of different orders and to derive a simple formula for the response to selection under multilinear epistasis. We propose new ways of estimating epistasis based on resemblance between relatives, response to selection, line-cross analysis and QTL analysis.

#### Detecting selective sweeps in cattle populations

#### S.Hanslik

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During the last decades cattle breeds such as the Holstein Friesian have been strongly selected for milk production. In North American Holstein populations milk production increased within 20 years from 4,5 to 6,8 tons/cow. Thus, Holstein cattle provide a good model to study directional evolution. Directional selection is expected to reduce variability at selected loci and their flanking genomic region. Neutral markers such as microsatellites can be used to screen for patterns of reduced variability, which may be indicative of a selective sweep.

We used a data set of 131 microsatellite loci, which have been typed in an US Holstein population. 13 loci with low values of heterozygosity were selected from this data set. These 13 "candidate" loci and a set of flanking loci were further analyzed in additional Holstein populations from the US, Canada and Europe. Three loci showed reduced heterozygosities for the "candidate" loci as well as their flanking loci in American and Canadian Holstein populations only. As European Holsteins did not show this effect, this pattern suggests a selective sweep in the US Holstein populations. Hence, we propose that our method may represent a new approach for detecting quantitative trait loci.

#### Population genetics of mouse LINE-1.

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Recently, analysis of LINE-1 subfamilies has been applied to the construction of phylogenies. We have examined the arrangement of LINE-1 lineages and subfamilies in the house mouse *Mus musculus domesticus* and in *M. spretus* to see how well the evolution of LINE-1 matches the phylogeny of species that carry it. We have identified 6 LINE-1 lineages, at least 3 of which retained activity while passing through the *musculus/spretus* speciation. One of these, the A2 lineage, splits between *spretus* and *musculus* versions at the estimated speciation time about 1 Mya. Another, the L1Md4 or TF lineage, splits at least 0.5 Myr after the speciation, implying a horizontal transfer. Horizontal transfer of individual

LINE-1s and of unique sequences between these two species has also been observed, so horizontal transfer of an active LINE-1 locus is not unreasonable. The profile of insert production along each lineage is quite different. *M. domesticus* TF has its members clustered at 0.1 Mya or less. The *spretus* version, the Ms475 lineage, was relatively continuously productive over the last 0.5 Myr, although there was a particularly intense period of production within the last 15 Kya. The *M. musculus (domesticus)* A2 lineage was continuously active over the first 0.5 Myr after the split from *M. spretus*, but then was quiescent prior to a radiative burst of transposition about 0.2 Mya. The *spretus* version was quiescent for a short early period before a radiative burst about 0.8 Mya, and has apparently since been inactive. A third lineage, the L1MdZ lineage, mainly amplified prior to the *musculus/spretus* speciation, with only a small subfamily descending through it. We notice significantly different frequencies of truncation in the different lineages. As a first step towards determining the population distribution of these different subfamilies, we have surveyed a panel of 33 inbred strains for the presence of several inserts from the terminal transposition bursts of the *domesticus* TF family, the *domesticus* A2 lineage, and the *spretus* Ms475 lineage. Supported by NIH grant GM51847.

Spatial autocorrelation of quantitative characters and genetic markers within a natural population of *Centaurea jacea* (Asteraceae).

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The pattern of spatial variation of genetic characters is essentially dependent upon the extent of gene dispersal and selection pressures. The relative importance of each of these forces is of great concern in evolutionary biology. A comparison of the spatial pattern between putatively neutral characters (molecular markers) and potentially selected quantitative characters (morphological or life-history traits) could assess the importance of natural selection relative to gene dispersal in natural populations. Such comparisons have been realised in experimental studies with subdivided populations.

Here we develop an approach to carry out similar comparisons within a continuous population in the framework of spatial autocorrelation analysis (Moran's *I* statistic). We show that, for natural maternal families, the ratio of Moran's *I* over the intraclass correlation coefficient has the same expectation for any neutral character when environmental effects are independent of location. This approach is used to compare the microgeographical genetic structure of quantitative traits and allozyme markers in a small population of knapweeds (*Centaurea jacea* L.). Our results show that, on average, the observed pattern of spatial structure for quantitative traits is very similar to that for allozyme markers. We conclude that the same evolutionary process - isolation by distance – is the principal cause of the observed microgeographical structure for both allozyme markers and quantitative traits.

A pseudo-control region in the mitochondrial genome of *Buteo buteo* and its application for phylogenetic analyses

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The phylogenetic relationships within the palearctic buzzards (genus Buteo) are still unclear, especially concerning the various taxa of the B. b. buteo - B. b. vulpinus complex. First, extreme intraspecific morphological variability sometimes prevents an unambiguous diagnosis of specimens. Second, buzzards display a broad spectrum of migratory behaviour, spanning from sedentary populations (B. b. menetriesi) to long distance migrators (B. b. vulpinus). The lack of clear-cut geographic separation harbours a potential for hybridization and introgression. In a molecular approach to elucidate the unsolved phylogeny of B. buteo we planned to use the mitochondrial control region (CR) as a phylogenetic marker. Surprisingly, at the proposed location of the CR (between the ND6 and 12S rRNA genes) another non-coding sequence was found in B. b. buteo. It comprises a 336 bp non-repetitive section and a cluster of 27 repeat units of 48 bp. This section is supposed to be a derivative of a duplicated CR and therefore was designated pseudo-control region (YCR). The location of the genuine CR has still to be determined. For our phylogenetic analysis we isolated and sequenced the variable section of the YCR from various populations of the buteo-vulpinus complex including taxa of uncertain taxonomic status (e.g., B. b. insularum, B. b. menetriesi). In addition, B. b. japonicus and several closely related species were analysed (B. oreophilus, B. rufinus, B. hemilasius, B. lagopus). B. hemilasius, B. lagopus, and B. b. japonicus, are clearly separated (sequence divergences 3.4% - 5.8%), whereas the haplotypes from the remaining taxa (including also B. rufinus and B. oreophilus) cannot be correlated with any taxonomic or geographic grouping. It can be concluded that they represent ancient polymorphisms, which have persisted during the radiation of these taxa. The results suggest that the buteo-vulpinus complex, B. rufinus, and B. oreophilus form a superspecies, where the various taxa are not yet differentiated at the genetic level.

#### Successive waves of horizontal P element transmission in drosophilids

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The first interspecific *P* element transfer from a member of the *Drosophila willistoni* group into *D. melanogaster* was reported in 1990. Since then, several other cases of horizontal *P* element transmission have been detected that involve the M- and O-type subfamilies. These two distinct *P* element types were first discovered in *D. bifasciata* and subsequently found in other species. Both types (M, O) occur in two pairs of sibling species from different genera: *D. bifasciata / D. imaii* and *Scaptomyza pallida / S. elmoi*. Within these species pairs sequence divergence of M-type elements measures 8.5%, whereas the O-type elements are almost identical. The different degree of divergence suggests that two independent intergeneric transfers must have occurred between the *D. bifasciata* and the *S. pallida* lineages. The first was that of the M-type, which by now seems to be transpositionally inactivated. The O-type has been transmitted more recently, a finding that is confirmed by our investigations concerning copy number, transcriptional activity, and splicing patterns.

The patchy distribution of both *P* element types raised the question from where they may have originated. In the course of large-scale PCR screenings, both types were detected in several species groups of the genus *Drosophila* (*obscura, willistoni, saltans* groups, *montium* subgroup). Moreover, they were found in a number of species of the genera *Scaptomyza* and *Lordiphosa*. Several of the *Lordiphosa* species contain both types, and again the M-type seems to be the more ancient invader. Sequence comparisons suggest that both *P* element types have undergone phases of vertical transmission followed by successive horizontal spreads. In the most recent wave of horizontal transfer the O-type has invaded *D. bifasciata / D. imaii* as well as *Lordiphosa* and *Scaptomyza*. The North American species *D. athabasca* appears as the most plausible source, whereas the cosmopolitan species *S. pallida* could have served as a transmitter to the whole Eurasian region.

The work was supported by the FWF (project P11819-GEN).

Molecular evidence for parallele evolution of adaptive syndromes in fig-breeding *Lissocephala* (Drosophilidae)

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Afrotropical *Lissocephala* (Drososphilidae) breed strictly in figs of *Ficus* (Moracea) and have accordingly evolved specific features including modified female and eggshell morphologies, ovipositing, larval foraging and mating behaviors. These various traits may exist as two or three alternative states. Each species displays a specific suite of traits so closely coordinated that alternative states of the overall suites can be seen as « adaptive syndromes ». Three clear-cut adaptive syndromes can be recognized while two taxonomic lineages (*juncta* and *sanu* species groups) are traditionally accepted on the basis of male terminalia. A crucial evolutionary question results from the consideration that ecological clusters and taxonomic groups have conflicting compositions : the three syndromes are found in the *juncta* group while two of them occur in the *sanu* group. To resolve this conflict, we present molecular data which provide a robust phylogeny: mitochondrial DNA (12S+16S ribososmal DNA and Cytochrome b) sequence data are in agreement with one another regardless of the algorithm used. All molecular data consistently support male terminalia dichotomy. such a level of consistency unambiguously indicates that parallel evolution of adaptive syndromes occurred. Thus, homoplasy may affect morphological and behavioral traits concomitantly when these are involved in a network of functional relationships

## Power and pitfalls of molecular phylogenetics

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Although molecular phylogenetics has become an important tool in evolutionary biology, the existing methods used in phylogenetic inference are still immature, and there are a lot of pitfalls in this field. I my talk, I will present several examples which we have encountered in analyzing mitochondrial DNA data in the study of vertebrate evolution.

# Contrasting population structures in *Drosophila buzzatii* using inversion polymorphism and allozyme loci as genetic markers

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D. buzzatii is a cactophilic subcosmopolitan species originated in the Argentinian arid regions. Natural populations are polymorphic for several inversion arrangements of its second chromosome. Inversion frequencies are extensively differentiated among populations located in different phytogeographic regions and vary clinally along latitudinal and altitudinal gradients. Although these evidences are suggestive of selective differentiation, alternative mechanisms such as genetic drift, gene flow and historical factors can also account for the population structure observed. The objective of the present study was to test the role of selective vs historical events, using the comparative approach between population genetic structures determined with different genetic markers: the inversion polymorphism and seven allozyme loci. The electrophoretic loci assayed: Esterase 1 and 2 (Est-1 and Est-2), Peptidases 1 and 2 (Pep-1 and Pep-2), Leucyl aminopeptidase (Lap), Aldehyde oxidase (Aldox) and Xantin dehidrogenase (Xdh) show different degrees of association with the segments involved in the inversions. The analysis of population structure by means of Wright's F-statistics showed that differentiation of inversion frequencies was on average an order of magnitude higher than for allozymes. However, among population differentiation varied greatly among electrophoretic loci. Allele frequencies did not significantly differ for Lap and Pep-2, differentiation was low to moderate for Pep-1, Est-1 and Aldox, and high for Est-2 and Xdh. These contrasting patterns of variation suggest that selective differentiation is the most likely explanation for the inversion polymorphism, and for *Est-2* and Xdh, while for Est-1 and Aldox differentiation might be the result of hitchhiking with the inversions. Finally, the lack of differentiation for Pep-2 could be interpreted as result of balancing selection.

Oviposition preference and life history traits in cactophilic Drosophila koepferae and D. buzzatii in association with their natural hosts

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Drosophila koepferae and D. buzzatii are two closely related cactophilic species inhabiting the arid lands of southern South America. Previous studies have shown that D. buzzatii breeds primarily on the necrotic cladodes of several Opuntia cacti and D. koepferae on the rotting stems of columnar cacti of the genera Trichocereus and Cereus. In this work, we analyze the patterns of host plant utilization in a locality where both Drosophila species are sympatric. Field studies showed an absence of differential attraction of adult flies to the rots of two major host cacti: O. sulphurea and T. terschekii (cardón). However, the proportion of D. buzzatii flies emerged from the rotting cladodes of O. sulphurea was significantly higher than in cardón. In laboratory experiments, egg to adult viability in single species cultures varied when both Drosophila species were reared in media prepared with O. sulphurea or cardón. In addition, between-species comparisons of flies emerged from single species cultures showed differences in oviposition preferae. In addition, analysis of flies emerged in mixed species cultures showed differences and suggest that these traits are the result of adaptation to specific patterns of spatial and temporal predictability of their respective preferred host plants: columnar are less dense and less ephemeral resources, whereas the opuntias are more abundant, and fast rotting cacti.

## Death and dishonesty - a sexual selection model

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The origin of extreme structural ornaments and bright coloration in sexually dimorphic or dichromatic species of animals, and that of elaborated courtship displays, have for long been an area of investigation by evolutionary ecologists. Using an individual based simulation model we analyse the differences between the runaway and good genes sexual selection models within the framework of correlations between an individual's quality, sexual signalling, and viability. We examine how the processes produce differences in the relational patterns between these three parameters, and predict how the differences can be discerned in the field. Intentional or unintentional dishonesty with respect to the male sexual signalling will cause a variation in viability of individuals of the same genetic quality within a population. Hence our model predicts that both systems of sexual selection will evolve a negative correlation between signal and viability in the males with the strongest signal. A pure runaway system will not result in a correlation between mortality and signal in the sub-extreme males, while the good genes model will produce a positive correlation. Our predictions have been confirmed by field data from studies of Collared flycatchers (*Ficedula albicollis*).

### The rate of recombination in the human pathogen Neisseria meningitidis

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We have analyzed two published multilocus data sets for *Neisseria meningitidis*, one consisting of 107 isolates characterized by multilocus sequence typing at six loci and the other consisting of 688 isolates characterized by multilocus enzyme electrophoresis at 15 loci. It is argued on theoretical as well as empirical grounds that all isolates should be included in the analysis rather than genotypes only. On the basis of this procedure the number of recombination events per mutation estimated from the sequence and the allozyme data sets was 0.024 and 3.314, respectively. This leads to the conclusion that recombination in *N. meningitidis* is rare.

#### Molecular evolution of Arabidopsis, Arabis and related genera (Brassicaceae)

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The aims of this study are (1) to infer the phylogeny of *Arabidopsis* and its relatives and (2) to date this phylogeny. For this purpose we have analyzed sequence variation for chalcone synthase (*Chs*) and alcohol dehydrogenase (*Adh*) in 24 species in the genera *Arabidopsis*, *Arabis* and related taxa from tribe Arabideae. Additional sequence information for several taxa was obtained from data bases and was used to study the phylogeny of those taxa. Although we detected recombination at *Chs*, a robust phylogeny could be inferred. A relative rate test showed no divergence from the molecular clock at *Chs*, while at *Adh* 5% of comparisons diverged from uniform expectation. Using a permutation test we detected significant differences between the rate of synonymous substitution at *Chs* and *Adh*. Using the rate of synonymous substitution at *Chs* in conjunction with biogeography and historic pollen information, we conclude that the *Brassicaceae* are about 30 million years old, indicating a relatively recent origin for this plant family. Further, the age of allelic polymorphisms within *Arabidopsis thaliana* is estimated to be approximately 600,000 years.

## Spontaneous introgression of (trans)genes from crops to wild species

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Many plant species are known to hybridize spontaneously and sometimes to exchange genes by introgression. With the commercialisation of transgenic crops, the transgenes may spread to related weedy and wild species by spontaneous introgression, and possibly change their ecological functioning and interactions with other species in the ecosystem. This scenario is interesting from an evolutionary point of view, but has also caused intense public debate and concern.

In an ongoing project, we study the spontaneous hybridization and introgression between oilseed rape (*Brassica napus*) and a related weedy species, *B. rapa*. Hybrid (F) seeds can be found in weed populations and also in field trials. F1 plants survive and reproduce, and may under some circumstances have a fitness higher than the parental species. Backcross seeds can be produced spontaneously in field trials, and even though backcross plants in general have a relatively low fitness, some of them do survive and set many flowers and seed. These results therefore suggest that spontaneous introgression from oilseed rape to *B. rapa* will take place. However, the frequency and dynamics of such an introgression is very dependent on the ecological conditions, and may under some conditions be severely reduced. For example, lack of seed dormancy of F hybrids may hinder their survival in conventional fields with crop rotation. In contrast to this, we have found clear evidence of intensive introgression in an organically grown field with reduced weed management.

## Biogeography and Evolution of the Genus Scotorythra (Geometridae: Ennominae) in Hawaii

## M. L. Heddle and R.G. Gillespie

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The sequential formation of the islands of Hawaii, and the extreme isolation of the archipelago provides a unique opportunity to study processes of speciation in a variety of taxa. Despite the apparent mobility of the larger flying insects, initial observations indicate that some genera containing around 40 endemic species have been derived from a single colonization. In order to study this phenomena in more detail I have resolved the taxonomy of *Scotorythra*, an endemic genus of macrolepidoptera. In order to understand some of the processes that may have led to the radiation observed in this genus, I have recorded the distributions for all 43 extant species, and gathered host plant information. Species found in multiple habitats on all islands were observed to be polyphagous, while single island endemics appear to be host plant specialists, feeding on only one species. Future work will include the development of an evolutionary hypothesis for this group, leading to further understanding of the processes of specialization.

# Why are There Only Two Butterfly Species in Hawaii? The biodiversity of Macrolepidoptera in Pacific Archipelagoes.

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Relative to birds in the Pacific, butterflies are poor colonizers of oceanic islands and demonstrate low levels of endemism. It has been hypothesized that this is due to lower flight speeds, shorter life spans and a dependency on specific host plants. However, some other groups of macrolepidoptera (i.e., moths) are constrained by these same characteristics yet demonstrate extremely high levels of endemism, and have successfully colonized islands throughout the Pacific multiple times. In order to re-evaluate the comparison of birds and butterflies, we examined the distribution of ten superfamilies of macrolepidoptera across the Pacific, including the Papilionoidea (butterflies). The fauna for each island was divided into three distribution classes: (i) endemic - found only within a given archipelago, (ii) Pacific - found only on Pacific islands, and (iii) continental - found on continental regions in addition to Pacific islands. The influence of archipelago area, isolation, and maximum elevation on species richness was examined through stepwise multiple linear regression for each superfamily and each distribution class. It is unlikely that all species have an equal probability of colonizing oceanic islands, for example, a diurnal habit may reduce colonization success due to the predator pressure of birds, or a certain flight habit may be particularly amenable to long distance dispersal. Some of these characteristics may be shared among species in the same superfamily. For example, butterflies seem underrepresented in Pacific archipelagos, such as Hawaii, compared to moths. Two random models, rarefaction and hypergeometric draw, were used to test this hypothesis and the distribution of macrolepidoptera families in general. Rarefaction generates the expected number of families if species are drawn randomly from a source, while hypergeometric draw generates the expected number of species within a family.

# Combining Stochastic Context Free Grammars with Molecular Evolution in Predicting RNA Secondary Structure

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Many computerized methods for RNA secondary structure prediction have been developed. Few of these methods, however, employ an evolutionary model, thus relevant information is often left out from the structure determination. This article introduces a method which incorporates evolutionary history into RNA secondary structure prediction. The method reported here is based on stochastic context-free grammars (SCFGs) to give a prior probability distribution of structures. The phylogenetic tree relating the sequences can be found by maximum likelihood (ML) estimation from the model introduced here. The tree is shown to reveal information about the structure, due to mutation patterns. The inclusion of a prior distribution of RNA structures assures good structure predictions even for a small number of related sequences. Prediction is done using maximum a posteriori (MAP) estimation in a Bayesian approach. For small sequence sets, the method performs very well compared to current automated methods.

# Mitochondrial and nuclear geneflow across a leaf-warbler hybrid zone (Aves: *Phylloscopus collybita*, *P. brehmii*)

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Common Chiffchaff *Phylloscopus collybita* and Iberian Chiffchaff *P. brehmii* meet in a narrow zone of sympatry and hybridization in SW France and N Spain. The taxa are almost indistinguishable morpho-logically, but differ clearly in vocalizations (song, calls). We mapped the extent of the contact zone and studied the mating pattern (n = 260 breeding pairs). Mating was assortative with *brehmii* females prefering *brehmii* males, but *collybita* females did not display any preferenes. This resulted in mixed matings being highly asymmetric with collybita *female x brehmii* male being much more common than vice versa. Mixed matings accounted for 23.7 % of all pairs and at least some of these did produce viable offspring. However, the estimated percentage of F1-hybrids in the adult breeding population was significantly lower than expected, indicating strong selection against hybrids. Mitochondrial haplotypes significantly segregated with phenotype (n = 100; 5 % "mismatched" birds), leading to a geneflow estimate of 0.065 females per generation. Microsatellite markers also revealed significant differentiation between the taxa (n = 105 individuals, four loci), but the geneflow estimate was about 60 times higher (3.8 migrants per generation) than for mitochondrial markers. Hetero-zygosity at microsatellite loci was significantly lower in *brehmii* than in *collybita*, corresponding to a much smaller world population of the former. The results suggest that assortative mating, selection against hybrids and unisexual hybrid sterility are the most important mechanisms restricting geneflow in this hybrid zone.

#### Evolution of parasitism in deep sea fishes ñ evidence from Steringophorus

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We sampled nine species of *Steringophorus*, a fellodistomid digenean parasite, from their marine teleost definitive hosts at various depths including the abyss. In spite of the presumed monophyly of the Fellodistomidae, *Steringophorus* host fishes inhabit markedly different depth ranges (10-5,000m). We have developed a molecular phylogeny of the group based on two partial genes (coding for mitochondrial ND1 and nuclear 28S rRNA) on which we have mapped host depth range in an attempt to detect whether there is a relationship between phylogeny and depth. We compare our results with a similar study on a lepocreadiid genus which demonstrated that intrageneric colonisation events between shallow and deep-water are rare relative to specific radiation, and that lineages retain strong ties to their host-families.

## Heritabilities of characters with reciprocal fitness effects in fig-wasp mutualisms

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An essential prerequisite for coevolution between mutualists to occur is the existence of heritable variation in characteristics of each member of the mutualism that affect fitness of the other. Further, it is widely recognized that in order to maintain the stability of the mutualism, the disruptive potential of conflicts of interest between the two partners must be constrainted. Although many of the conflicts of interest in the mutualistic interaction between figs and their pollinating wasps have been broadly identified, relatively little attention has been paid to the consequences of variation among individual mutualists, and showing how this variation influences the resolution of the conflicts. For example, both within- and among- species, differences in body size of fig pollinating wasps are associated with differences in seed output in the host fig. Similarly, the number of flowers in a fig fruit influence the reproductive success in the pollinator. Therefore, both among- and within- species variation in characters of each mutualist can be shown to influence reproductive success of the other. This talk discusses the estimation of heritabilities of these characters that often influence the reproductive success of the mutualist, and the implications for the coevolution and continued stability of the mutualism.

## Phylogenetic relationships and molecular evolution in parasitic and mutualistic associates of figs

#### Edward Allen Herre and Carlos Machado

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We present phylogenetic analyses of all major taxonomic and ecological groups of fig-associated wasps based on sequences of their mitochondrial genes COI and COII. These wasps range from indispensible mutualistic pollinators to an ecologically diverse group of parasitic non-pollinators. Although the analyses support monophyly of the pollinators, the analyses also confirm recent suggestions that fig-associated wasps as a whole do not form a monophyletic group and indicate that figs have been colonized independently by several unrelated groups of chalcid wasps. Further, similar ecological strategies to exploit figs as a resource have evolved independently in several different lineages of fig wasps. Moreover, using calibrated genetic distances we can estimate the age the origin of the mutualism, as well as the timing of events relevant to the biogeographic distribution of the present groups of figs and their respective pollinators.

## PLENARY LECTURE

## Plant adaptation to insect pollinators: ecological factors and limits to specialization

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The adaptation of flowering plants to animal pollinators has been a recurrent theme in evolutionary biology ever since Darwin's pioneering contributions. The long-standing Darwinian research program in pollination biology has been characterized by the search for an adaptive value of floral traits in relation to pollinating agents. Seamless pursued for more than one century, this research program has been extremely successful in identifying spectacular plant adaptations to pollinators, and in proving that certain floral traits of some animal-pollinated actually represent adaptations to pollinating agents. Because of its historical roots and inherent biases, however, the program has failed to provide information on some critical quantitative aspects, e.g., How common are species whose floral traits have been predominantly shaped by the selective action of their current pollinating agents ? How much of the floral phenotype of an average animal-pollinated plant has arisen as a consequence of selection exerted by pollinators ? Increasing evidence indicates that adaptation of plants to pollinators is probably much less frequent than ordinarily assumed, and that the relative unspecialization of plants on animal pollinators is probably the rule rather than the exception in nature. This realization should promote a significant extension of research programs in pollination biology, from just seeking evidence illustrating plant adaptations to pollinators and identifying the selective mechanisms involved, towards incorporating a rigorous quest for explanations on why unspecialization is so widespread in nature. Although unspecialization may be adaptive in itself, its generality might also reflect the operation of a number of factors consistently limiting specialization. Among these, ecological, extrinsic factors (as opposed to genetic, intrinsic ones) seem to play an important role by limiting either (1) the occurrence of selection on plants by pollinators, and/or (2) the responses to selection when it occurs. The former category includes spatio-temporal variation in the interaction between plants and pollinators, context-dependence of pollinator pressures on plants, and the apparently universal decoupling of pollinator effectiveness and abundance. The second category includes the occurrence of small proportional variance in reproductive success attributable to variance in the interaction with pollinators, and the prevalence of site-specific effects (where the plant is) over individual-specific ones (how the plant is) as determinants of plant-pollinator interactions.

#### PRESIDENTIAL ADDRESS

## The colonisation of Europe after the Ice Age.

#### Godfrey M.Hewitt

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Along with molecular genetics, the study of paleo-climates has made great strides. Together they are allowing us to understand how both present processes and past history contribute to current biodiversity. Current evidence for orbitally forced climatic oscillations will be summarised, including Croll-Milankovitch cycles, Bond cycles and Dansgaard-Oeschger events. In particular the effects of the Pleistocene ice ages on species distributions will be considered, and in turn their possible effects on the genetic composition of populations and species genomes. Most information is available for the last ice age and Holocene period of warming following this glaciation, particularly from deep ice cores and from fossils in cores from land and sea (eg. pollen, beetles, foramens). Using the meadow grasshopper Chorthippus parallelus as an example, the effects of climatically induced range changes will be explored. Data is available from a range of attributes - song, morphology, chromosomes, allozymes, cuticular hydrocarbons, rDNA, mtDNA and ncDNA. These will be considered to assess genetic diversity and the structure of present hybrid zones, and along with pollen data across Europe to identify refugia and colonisation routes. Modern DNA techniques are allowing such studies of species genotypes across their range, and phylogeographies are accumulating for species in Europe and North America particularly. These detailed examples will be considered and compared to look for concordance of refugia, expansion routes, hybrid zone position and structure in Europe. The variation in extent of divergence within species, over several ice ages and among regions across Europe will be considered, as will rates of divergence and speciation. The general picture for Europe can be compared with that for North America and other parts of the globe using the data available.

## Female eyespan and variation in mating preferences in the stalk-eyed fly, Cyrtodiopsis dalmanni.

#### Andrew Hingle

### University College London

The exaggeration of male secondary sexual ornaments is driven by female preference for ornamented males. However, most empirical work focuses on the maintenance and cost of male ornaments. Little is known about female preferences and the factors which effect them.

Visual acuity in *C.dalmanni* is positively correlated with eyespan. Does variation in female eyespan explain any of the variation in mating preferences in this species? Here I present a thoroughly replicated study of variation in mating preference between large and small eyespan females.

#### **Epigenetic Inheritance in Prokaryots : Myth or Reality?**

## V. Grandjean\* and L.Hirschbein

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Epigenetic is defined as a reversible modification of genetic expression without any alteration in DNA sequence which is transmitted to the progeny (1). This type of regulation, which was considered for a long time exclusively reserved to eukaryotes, is also observed in prokaryotes (2,3,4).

First described by Hotchkiss and Gabor in *Bacillus subtilis*, protoplast fusion, has made it possible to bring the cellular content of two bacterial cells together into a single heterodiploid cell. Heterodiploidy is associated with chromosomal inactivation, leading to the formation of Noncomplementing diploids (Ncds).

Chromosome segregation and inactivation are independent parameters, since diploids carrying stably inactivated chromosomes give rise to haploid bacteria with loss of the inactivated chromosome. Consequently, Ncd clonal populations are heterogenous. In haploid Ncd derivatives, reversible (epigenetic) chromosomal inactivation can also affect large fragments of coding DNA regions. The inactivated state persists through cell division (between 20 to 40 generations).

The *spo* OA gene is required for the maintenance of the inactivated state, as well as for the transition between reversible and irreversible silenced chromosomes or chromosomal regions.

The inactivation of a coding DNA region correlates neither with an alteration of the nucleotide sequence nor with a specific base methylation. The transformation efficiency of silent markers is at least 100 times lower than that of DNA from cells expressing the same marker. Homologous recombination within silent DNA region decreases to 3% when compared with the homologous recombination within the expressed DNA region (17%). All together, these data strongly suggest that chromosomal silencing is most probably due to structural modifications of the bacterial nucleoid. Thus driving force in bacterial evolution and adaptation should included epigenetics silencing mechanisms

1) Holliday, R.(1994) Dev.Genet.15, 453-457.

- 2) Lynch, A.S., and Wang, J.(1995) Pro.Natl.Acad.Sci.USA 92,1896-1900.
- 3) Schnetz, K and Wang, J (1996) Nucleic Acid Res.24, 2422-2428.
- 4) Grandjean, V et al., (1998) Biol.Chem. 379, 553-557.

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## Spore killing in fungi

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In many ascomycetous fungi (like the genetic model species *Neurospora*, *Aspergillus* and *Podospora*) the products of a single meiosis are recognizable as ordered tetrads, linearly arranged in asci. This offers unique opportunities for the study of abnormal segregation patterns, since – unlike the situation in animals and plants - segregation distortion (meiotic drive) is directly connected to a clear phenotype. Meiotic drive will always show up as *Spore killing*: the production of asci containing only half the normal number of spores, the surviving spores carrying the driving genetic element. The population genetics of meiotic drive differs essentially in (haploid) fungi from diploid animals and plants, providing less opportunity for stable polymorphisms of driving and nondriving chromosomes.

This talk will review our recent work on Spore killing in *Podospora anserina*. In normal crosses of *Podospora anserina*, four binucleate spores are produced per ascus. These spores are heterokaryotic for markers that show second division segregation (SDS) and homokaryotic for those showing first division segregation (FDS, e.g. centromere linked markers). In a cross between a killer and a sensitive strain only spores that carry the killer locus are viable. Such a cross thus produces asci containing four viable spores that are heterokaryotic or two viable spores that are homokaryotic for the killer locus. Therefore, the frequency of killing depends on the chromosomal position (i.e. frequency of FDS). In the local *P.anserina* population of Wageningen (The Netherlands) which has been sampled from 1991-1997 almost 20% of the isolates are Spore killers. Sofar at least six different Spore killer types have been obtained that differ in the frequency of Spore killing and in the interaction with other killer strains. All other natural isolates found sofar are sensitive to Spore killing.

*Spore killers* are segregation distorters that violate the Mendelian rule of equal segregation of alleles and have been found in several ascomycete fungi. In normal crosses of *Podospora anserina*, four binucleate spores are produced per ascus. These spores are heterokaryotic for markers that show second division segregation (e.g. the mating type locus) and homokaryotic for those showing first division segregation (e.g. centromere linked markers). Spore killing in *P.anserina* is characterised by the abortion of two of the four ascospores in (part of) the asci. Spore killing can be discriminated from other genetic causes of ascospore abortion (e.g. lethal mutations, translocations). In a cross between a killer and a sensitive strain only spores that carry the killer locus are viable. Such a cross thus produces asci containing four viable spores that are heterokaryotic or two viable spores that are homokaryotic for the killer locus. Therefore, the frequency of killing depends on the chromosomal position (i.e. frequency of FDS). In the local *P.anserina* population of Wageningen (The Netherlands) which has been sampled from 1991-1997 almost 20% of the isolates are Spore killers. Sofar at least six different Spore killer types have been obtained that differ in the frequency of Spore killing and in the interaction with other killer strains. All other natural isolates found sofar are sensitive to Spore killing.

## Evolution of courtship interactions in Drosophila - complicated courtship or rape

#### Anneli Hoikkala

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The primitive mating pattern in Diptera is mating in flight; in most species of this order the mating, however, occurs on substrate. In some species the courtship rituals preceding copulation are very complicated, while in other species the males may mount the female without any preceding courtship. Conflict between the courtship interests of the two sexes may affect the direction in which courtship evolves. Males, which in many *Drosophila* species invest only sperm in progeny production, mate with as many females as possible. Females, on the other hand, mate only once or a few times during their adult life, and for them the quality of the mating partner is more important than the number of copulations achieved. The lower sexual drive of the females in comparison to that of males gives the males two evolutionary ways to achieve more matings: to evolve traits that raise female receptivity during copulation or to evolve traits enhancing forced copulations. Elaborate courtship rituals of the males and specific rejection and acceptance behaviours of the females enhance the females to exercise mate choice before mating (cryptic female choice). The passage of sexually antagonistic genes between the two sexes enables the males and the females to hold back each other's evolution. Also, characters like courtship rituals are in danger of being destroyed by random mutations unless natural or sexual selection functions to maintain their integrity.

## The impact of the environment on the epigenotype

#### **Robin Holliday**

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For many years it was believed that information can flow from DNA in the chromosomes to RNA and proteins, but not in the reverse direction. This is now known to be incorrect, because DNA may be modified by DNA methyltransferases, and that can change gene activity. Also, there are mechanisms to remove methyl groups from DNA. This opens up a number of possibilities with regard to environmental or other influences on the epigenotype, which can be defined as the sum of the genotype and those DNA modifications which influence gene activity. Many epigenetic changes are part of normal development, but others are abnormal, as in the emergence of tumours. At the moment, the routes by which environmental effects can influence the epigenotype are not well known, although evidence that they exist is well documented. Some examples of such influence will be discussed, as well as possible mechanisms whereby DNA modification is changed. The likelihood of these changes being transmitted through meiosis to the next generation will also be considered.

#### Detecting recombination among gene sequences: methods and applications.

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Determining the extent to which recombination shapes the genetic structure of populations is an area of growing importance. Here, we will first briefly review the different methods that have been developed for estimating the frequency of recombination among sets of sequences, and for detecting the break-points of specific recombination events, and discuss their respective strengths and weaknesses. A new maximum likelihood method for assessing the significance of recombination break-points is then presented. Finally, a number of methods of detecting recombination are applied to various RNA viruses previously thought to be clonal in population structure. For some these, including dengue virus, evidence for genetic exchange is presented for the first time. We suggest that as analytical tools improve, recombination will be an increasingly common observation among the genomes of RNA viruses.

#### Molecular evolution of the Soritidae, a group of large Foraminifera

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Soritidae are symbiont bearing, benthic foraminifera belonging to the order Miliolida. They constitute together with other representatives of large symbiont bearing foraminifera a major component of cenozoic carbonate sediments and are important biostratigraphic markers.

Soritidae include three different genera, the Peneroplinae, the Archaiasinae and the Soritinae. We sequenced the complete small subunit rRNA gene (SSU r DNA) for most species of each genus included in the Soritidae. Molecular phylogenetic trees of the Soritidae were compared to paleontological data and the hypothesis of a molecular clock was tested. According to our data, the rates of substituion are relatively constant within the Soritidae and correspond to the evolutionary rates of Miliolida in general, which represent a fast evolving group among foraminifera.

## Mutation versus natural and sexual selection

## D. Houle

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The difficulty in keeping a control population is a persistent obstacle to mutation accumulation experiments in some species. As an alternative I have been investigating the use of selection on populations of pooled mutation accumulation lines, that is, a reverse mutation-accumulation experiment. In principle, the advantage of this approach is that selection is often much stronger than mutation, and so the time course of a given amount of change will be much shorter in the selected, or reverse direction than in the mutation, or forward direction. Simulation results show that the time to the peak rate of change is very sensitive to the number of mutations that have accumulated between the lines. A second advantage of reverse mutation-accumulation is that it offers the opportunity to investigate the effects of varying the selection regime on the accumulated mutations. For example, an important question with sexual selection is the degree to which mating success reflects the overall genetic quality of the individual. The good genes theory predicts a tight relationship between naturally selected fitness and mating success, while other models suggest an arbitrary relationship. Preliminary results suggest that sexual selection does not discriminate among mutation-accumulation genotypes in *Drosophila melanogaster*, contrary to the good genes expectation.

## PLENARY LECTURE

#### What have DNA polymorphism data told us?

#### **Richard Hudson**

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What kinds of inferences have we been able to make aboute volutionary processes and parameters using molecular polymorphism data? With a focus on examples from Drosophila and humans, methods of analysis and specific conclusions will be reviewed. From a theoretical perspective, what can we expect to be able to extract from DNA sequency polymorphism data? Can we reliably make inferences about selection acting on specific genetic loci? Can we make reliable inferences about current or past population sizes? Can we reliably estimate mutation, recombination, or migration rates from polymorphism data? The difficulties and promise of using DNA sequence polymorphism data for such inferences will be considered.

## Rapid evolution of size and thermal sensitivity in Drosophila subobscura in North America

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Many laboratory studies show that flies have the genetic capacity to alter thermal sensitivity and size rapidly. However, whether this capacity is realized in nature is an open question. North American populations of *D. subobscura*, introduced from the Old World only 20 years ago, offer opportunities to monitor rates of evolution in nature. The introduced flies have evolved a latitudinal cline in wing size that is remarkably similar to the baseline cline seen in native Old World *subobscura*. Moreover, these flies have also evolved latitudinal clines in the sensitivity of fitness (Mueller's serial transfer) to temperature and density. For example, high-latitude populations of both native and introduced flies have reduced fitness at high temperature and at high density. In summary, several traits of introduced *subobscura* have already differentiated and appear to be converging on patterns seen in native, Old World populations. Thus, the genetic capacity of flies to evolve quickly is realized in nature, even on a geographic scale.

#### Mitochondrial DNA polymorphism of an ancient Japanese population in Yayoi period

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The Yayoi period, when the base of the traditional Japanese society was formed, extended roughly from 400 BC to AD 300. This culture, which emerged in the western part of Japan, was based on rice cultivation. Archaeological evidence shows a transition from the former hunting and gathering culture called the Jomon period to this culture. Further, there exists a clear difference in morphometric features between Yayoi and Jomon people. One strong hypothesis for the formation of Yayoi people is that a new ethnic group from Asian Continent migrated during the early fourth century BC and that immigrants from the Asian Continent had a significant genetic effect on the populations of this time in Japan, and they intermixed with the native Jomon people to form the Yayoi people. In this study, DNA was extracted from human bones recovered from a 2000-year old archaeological site located in northern Kyushu in southwestern Japan. Mitochondrial DNA sequences of 180 sites were determined for 33 individuals. These sequences were classified into 12 different haplotypes defined by 12 segregating sites. Phylogenetic and population genetical analysis were done using these data.

The study of morphological evolution and molecular evolution from the phylogenetic analysis of the pax gene families.

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Pax gene families have been identified from a broad range of invertebrate and vertebrate animals. Members of the Pax gene family encode transcryption factors containing a DNA binding paired domain which is involved in developmental control and the formation of the central nervous system (CNS). The family members are classified into six classes or subfamilies, depending on the presence of paired-type homeobox and octapeptide. For the example, Pax-6 genes are shown to be involved in early eye development. Therefore, it has been proposed that the various types of eyes evolved from a single eye prototype, by a pax-6 gene dependent mechanism. We constructed a phylogenetic tree using DNA and amino acid sequences of pax genes. The phylogenetically analysis suggested that the most gene duplication event of pax gene family occurred at very early evolution of animals before the parazoan and eumetazoan divergence. The gene duplication event in each sub family occurred on chordate lineage and completed before the fish tetrapod divergence. Our phylogenetic analysis also suggested the duplication of eyeless and toy was occurred the lineage of inverteblate. This suggests that a gene duplication event on particular lineage is related to its morphological evolution.

## A new approach to infer microsatellite evolution in vivo

#### Marianne Imhof & Christian Schlötterer

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Despite the importance of microsatellites for genetic analysis, their mutational mechanisms are not yet fully understood. A detailed study of mutational patterns requires many mutational events. Because microorganisms have short generation times they provide a good system to study evolutionary processes. A popular assay is to clone microsatellites into yeast or bacteria. Mutational events can be detected by frameshifts in a reporter gene. This approach, however, has certain limitations. Our goal was to establish a generalized method, which permits the analysis of microsatellites with their naturally occuring flanking sequence. Using our approach it is possible to calculate mutation rates and obtain the full mutational spectrum from the overnight culture of *E. coli*. The influence of repeat type, motif, length and the flanking region on the mutational behaviour will be presented and discussed.

#### Some evolutionary implications of social learning

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Whatever, the opposition to the inheritance of acquired characters, there has never been any doubt that many animals (and not just man) pass on to their offspring some of the behaviour that they learnt during their lifetime. This may include aspects of their food preferences, ways of finding and handling food, where to live, who their enemies are, and who would make a good mate. Although this type of socially learnt and transmitted behaviour is certainly a case of the inheritance of acquired characters, it has been accepted only as a *product* of evolution, and not as an *agent* of evolutionary change. I shall show that recognizing social learning as an agent of change can lead to (i) new evolutionary interpretations of fundamental behaviours such as parent-offspring relations; (ii) simple evolutionary explanations for behaviours such as adopting; (iii) a different and more sophisticated view of the evolution of the ability to learn.

#### Pulses of speciation in the sea

### J. B. C. Jackson and K. G. Johnson

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Extensive new paleontological data for diverse assemblages of tropical American reef corals, bryozoans and mollusks demonstrate that speciation and extinction over the past 10 million years were concentrated in pulses of less than 1 million years duration. Pulses occur in the Late Pliocene about 2.5 to 1.5 million years ago depending on the taxa involved. Rates of origination and extinction were at least three times greater during pulses than at any time during the preceding 8 million years or afterwards. Less than 10% of extant species of well-studied Caribbean clades originated during the past 1.5 to 2.0 million years so faunas are virtually identical throughout the entire Pleistocene and recent. A similar pulse occurred near the Oligocene-Miocene boundary about 25 million years ago but is not so well documented. If general, these results have important implications for phylogenetic studies based only on living taxa. Widespread occurrence of unresolved polychotomies in molecular or morphologically based phylogenies are most likely data that reflect the Late Pliocene pulse of speciation rather than methodological noise. Moreover, if molecular clocks are not independent of rates of taxic evolution, then rates of molecular evolution may vary over time within clades. These issues can be resolved only by combining molecular and paleontological studies of diverse recent clades with an excellent fossil record.

### Sex ratio distorters and sex role reversal

### F. M. Jiggins

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Sex role reversed mating systems in which females compete for males and males may be choosy are usually associated with males investing more than females in their offspring. We report that sex role reversal may also be caused by selfish genetic elements which distort the sex ratio towards females. Some populations of the butterflies *Acraea encedon* and *A. encedana* are extremely female biased because over 90% of females are infected with a *Wolbachia* bacterium that kills their sons as embryos. Many females in these populations are virgins suggesting that their reproductive success may be sperm limited. Females in these populations form lekking swarms at landmarks in which females exhibit behaviours which we interpret as being to solicit matings from males. Release-recapture experiments found that mated females tend to leave these swarms which supports the hypothesis that the reason female *A. encedon* swarm is in order to mate. This behaviour is a sex role reversed form of a common mating system in insects in which males form lekking swarms at landmarks and compete for females. Female lekking swarms are absent from less female biased populations, instead butterflies in these populations are associated with the larval food plant.

## Introgression between Quercus suber L. and Quercus ilex L. assessed by cpDNA polymorphism.

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Previous studies on chloroplast DNA (cpDNA) variation have shown an extensive introgression between different species of the genus *Quercus*, belonging to subgenus *Quercus*. This works presents a study of cpDNA variability in a Mediterranean oak (*Quercus suber*). By means of PCR-RFLP technique, polymorphisms in two fragments of the chloroplast genome were identified. The survey of 32 *Q. suber* populations from Spain, and of several *Q. ilex* populations, has shown an introgression between these two evergreen species belonging to different subgenera. This exchange is mostly unidirectional, since only "ilex" cytoplasm is found within *Q. suber*. A geographic pattern appears, as introgressed populations are found only in eastern Spain and in the north-west, where the species range is more fragmented. Furthermore, different haplotypes are found in the populations characterised by "ilex" cytoplasm, and high variability is shown in inland southern mountains (Sierra Morena). Possible mechanisms leading to actual situation will be discussed.
## Evolutionary and life history aspects of cryptobiosis

## K. I. Jönsson

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Cryptobiosis is the collective name for a quiescent ametabolic state of life utilized by some organisms, including both plants and animals, to overcome periods of unfavourable environmental conditions, in particular droughts and freezing. In some metazoans, tardigrades, rotifers, and nematodes, cryptobiosis may be entered repeatedly throughout the whole life cycle. Many studies, some of them performed more than two hundred years ago, have demonstrated a remarkable ability of cryptobiotic organisms to withstand extreme environmental conditions while in the cryptobiotic stage, including freezing to temperatures near absolute zero. I will discuss this apparent over-adaptation in the perspective of current adaptation theory. I will also discuss some life history aspects of cryptobiosis, in particular with respect to processes of senescence.

#### In vitro studies of competitive fitness between vancomycin resistant and sensitive Enterococcus faecium

## Pål Johnsen, Gunnar Skov Simonsen, Ørjan Olsvik and Arnfinn Sundsfjord

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Vancomycin resistant enterococci (VRE) have shown remarkable ability to persist without selective antibiotic pressure in both colonized hospital patients and at farms exposed to the glycopeptide growth enhancer avoparcin. Compensatory mechanisms leading to reduced cost of antibiotic resistance have been stated to be important for the persistence for resistant bacteria in antibiotic free environments. In the present study we wanted to examine the competitive fitness of isogenic vancomycin resistant and susceptible enterococcal strains before and after 1000 generations in serial transfer cultures with or without subinhibitory concentrations of vancomycin or avoparcin. Preliminary results suggest that VRE with newly aquired plasmid mediated resistance of the VanA type were outcompeted by the susceptible isogenic counterpart. The difference in competitive fitness between resistant and susceptible strains was unchanged after 1000 generations both in media with glycopeptides and without antibiotics. A considerable adaption to the medium was observed in all strains, and this effect was several times larger than the cost of resistance in terms of generation time. The levels of plasmid segregation and horizontal gene transfer were too low to influence the overall results of the competition assays.

The results may indicate that VRE can persist without selective antibiotic pressure due to environmental adaption and limited reversion to susceptibility in spite of the cost of vancomycin resistance.

## Is silk weaving in ants an hygienic behaviour?

#### Rebecca N. Johnson and Ross H. Crozier

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Weaving using larval silk is a unique behaviour found in only one of the 12 ant subfamilies, the Formicinae. Weaving appears to be associated with an arboreal lifestyle and the genera that exhibit this behaviour also lack a metapleural gland. This gland is thought to be the key diagnostic trait of modern ants differentiating them from other social hymenoptera. It is thought to serve an antibiotic function possibly required for living in the soil and it appears that arboreal weaver ants no longer require it. In addition, it appears that there have been parallel losses of this gland, probably at least four separate times. The population structure of one weaver in particular, *Polyrhachis doddi*, has been studied in detail giving insights into why some species adopt an arboreal lifestyle.

## Keystone species in community organization

#### F. Jordán

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Keystone species are the most important members of communities. They are considered as key players for various reasons, like the quantity of their biomass or the strength of their interspecific interactions. Despite the popularity and increasing actuality of the keystone concept, ecologists have two serious problems in keystone studies. First, we have no quantitative approach for characterizing species importance. Second, it is nearly impossible to predict key species in a community in an a priori way.

Here, we present a reliability theoretical approach for making quantitative predictions about the importance of species in a community. We analyze how important is the position of a point representing a species in a food web graph. From this point of view, a species should be considered as a keystone, for its position is very important in the energy/matter flow network of the community. We take into account both top-down and bottom-up interactions, but only the effects mediated by trophic links. We introduce keystone indices for analyzing how many species go extinct secondarily, following single, primary species deletions. High keystone indices characterize the keystone species of trophic flow networks.

We suggest, that a species considered as a keystone for its position in the trophic flow network may really have a large impact on others only if trophic interactions are of prime importance in the regulation of the community. If competition or other types of interactions dominate, our keystone indices are less useful.

We discuss the role of positional keystone species in community organization. Food webs seem to take shape by decreasing the number of keystone species during community assembly. In other words, trophic flow networks become more homogeneous as for keystone indices of the species.

#### Active pollination in the fig/pollinator mutualism: who decides which flowers are pollinated?

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Among plant pollinator relationships, the ones involving pollinating seed parasites may lead to extreme coevolution between partners. One of the most impressive product of this coevolution is active pollination, i.e. behavioural and anatomic traits aimed at pollinating purposely. It has evolved in at least three mutualisms: the *Yuccal Yucca* moth, the *senita* cactus/ *senita* moth and the *Ficus*/ agaonide associations.

*Ficus* species are pollinated either passively or actively. It has been suggested that active pollination allows the wasps to pollinate the ovaries in which they lay an egg thus inducing the development of the fig embryo and ensuring better larval nutrition. We tested this hypothesis by establishing on flowers of 6 different species of figs, including monoecious species and male and female figs of dioecious species, which flowers received an egg and/or pollen. We show that : 1) in passively pollinated figs, pollen is dispersed haphazardly within the fig, 2) in actively pollinated male figs (i.e. figs producing only wasps and pollen), pollinators do deposit pollen on the flowers in which they lay their eggs, 3) in actively pollinated monoecious and female figs (i.e. figs which are selected to produce seeds) pollinators do not have control over which flowers are fertilised because, stigmas are too densely packed. Their close physical contact can even result in lateral growth of pollen tubes. This probably increases fig seed production. Thus, over such a specialised trait as active pollination, there seems to be a conflict of interest between partners of the mutualism. This conflict may explain why active pollination has been repeatedly lost in the fig-agaonid mutualism.

Nuclear ribosomal ITS2 sequences are useful to resolve the basal relationships in the phylogeny of Timarcha (Coleoptera, Chrysomelidae)

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Attempts have been made to infer the phylogenetic relationships in Timarcha using mitochondrial DNA sequences (i. e. cytochrome oxidase II gene and partial 16S rDNA sequences). These markers allow a partial resolution of this phylogeny, resulting in poor phylogenetic signal at deeper nodes. Other approach for molecular phylogenetic inference has been the analysis of nuclear ribosomal internal transcribed spacer (ITS2) sequences. We have included in the analysis 97 ITS2 sequences from 29 taxa of Timarcha covering the three extant Palaearctic subgenera, and in most cases we have studied three or more cloned sequences for every taxon. These sequences are 525 bp long on average, and show a conserved pattern of substitution, but have regions of high variability, with insertion/deletion events and internal amplification of short repeats (2-3 bp). The range of interspecific nucleotide divergence is 0.2-13.0 (Kimura-2-parameter distance). For phylogenetic analyses all trees have been rooted with ITS2 sequences of T. metallica (average divergence:  $12.9 \pm 0.8$ ), the only included species of Metallotimarcha, that is considered the most plesiomorphic subgenus, and which is in accordance with the mitochondrial phylogenies. The ITS2 phylogeny result in a better resolution for the corresponding unresolved basal nodes of the mitochondrial phylogenies, whereas it cannot discriminate the relationships of closely related species as those included in the analysis belonging to the T. goettingensis complex (11 taxa) and their sister group (T. hispanica). This nuclear phylogenetic hypothesis does not give support for a distinction between the subgenera Timarchostoma and Timarcha s. str. as any of them appear as a supported monophyletic assemblage.

## From animal domestication to the Dead Sea Scrolls: evolutionary and ecology changes

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A shift of nomadic hunter-gatherers to sedentary communities was a major

Evolutionary event for modern man. This shift was associated with plant and animal domestication, and disrupted ecological balance. Human activity has caused marked genetic changes among the wild and domesticated species present in the region. Alterations in the wild species are due to natural selection and environmental pressures, whereas changes in the domestic species are due to human impact. It is assumed that domestication took place in small herds and that human selection and selective breeding have contributed to accelerated genetic change and reduces variability over time.

Recent improvements in methods of extraction and amplification of DNA have made it possible to recover genetic information from past extinct species and to reconstruct ancient population structures. This research compares and contrasts the rate of genetic change and variability within and between selected species of wild and domestic forms of *Capra* in the Southern Levant over the past 12,000 years. As distinct from methods commonly used to extrapolate genetic change over time, this research studies DNA in real time. The research is based on analysis of DNA sequences of modern and ancient Caprinea.

The modern samples are composed of primitive breeds of Capra species

from the Levant, and the past ruminant populations was sampled from archeological remains such as bones, teeth and skin from different sites and different periods. One unique sample from the Roman period are parchments of the Dead Sea Scrolls. Understanding the genetic changes in the domestic and wild *Capra* species in the Levant is important in the preservation and conservation of them and other threatened species.

## Helping vs. intraspecific parasitism: egg carrying in the golden egg bug

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Theoretically individuals are not expected to help each other if helping yields more costs than benefits and if the receiver is not a relative. Golden egg bug (*Phyllomorpha laciniata*; Heteroptera, Coreidae) females lay eggs on the backs of both female and male conspecifics. Eggs do not survive in nature unless carried. Bugs receive eggs voluntarily and involuntarily, and most eggs are not fertilised by the carrier. Only when male-male competition is intense males are likely to carry their own eggs. In those cases egg carrying can be regarded as passive paternal care. The costs and benefits of egg carrying have been evaluated experimentally. Egg carrying does not increase male mating success. In nature, bugs experience high predation pressure, and eggs carrying and (in most cases) lack of relatedness between the eggs and the carrier, I suggest the golden egg bug as the first known intraspecific parasite in which parasitism is not related to active parental care.

Genetic variation between alternate-year cohorts of Xestia tecta (Lepidoptera: Noctuidae) in Finnish Lapland

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Several species within the genus *Xestia* exhibit alternate-year flight; with different cohorts fiying in alternate years. Typically one cohort is abundant and other one rare. The population dynamics and typical 2-year life cycle of the two cohorts indicate that they are more or less isolated in time. Molecular markers can be used to estimate gene flow and migration among and between the cohorts. The aim of this study was to quantify the amount of gene flow among and between the different cohorts of *Xestia tecta*, in the same geographical area, as well as between cohorts in different geographical areas. The methods used were allozyrne electrophoresis and mitochondrial genome sequencing.

Molecular variation in *Xestia tecta* provides limíted evidence of genetic differentiation and isolation between the even and odd year cohorts in eastern. Finnish Lapland, and between the populations in westem Lapland. Substantial gene flow could explain the low levels of differentiation between the cohorts. Another hypothesis is that the current *Xestia tecta* populations are isolated remnants of a much larger ancestral population, and that they have become isolated from each other so recently that there has not been enough time for substantial differentiation to develop between them. Further intensive molecular and ecological studies will be necessary in order to fully explain the observed lack of genetic variation between the different cohorts of *Xestia tecta* 

Extreme levels of mitochondrial DNA sequence divergence among the populations of the gecko Cyrtopodion kotschyi in the Aegean Archipelago (Greece)

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The gecko *Cyrtopodion kotschyi* is an interesting model organism for studying the dynamics of evolutionary processes, since it is widely distributed in the hundreds of islands of the Aegean archipelago, which vary in size and isolation times. To reconstruct the phylogeography of this species a portion of the COI mitochondrial DNA gene was sequenced from several insular and mainland populations. The results revealed very high levels of genetic divergence among sequences from different islands, which in some cases exceeded 24%. This level of divergence, probably the highest ever found in intraspecies comparisons, raises question whether there exist cryptic species. The large evolutionary distances suggest long separation times of the island populations may also have experienced a rapid evolutionary rate due to the small effective size which, in turn, may has been caused either by bottlenecks resulting from geological events or simply by the inability of small islands to sustain large populations. An attempt to calibrate a molecular clock by using geologically dated sea barrier formation among islands and the mainland indicates a mitochondrial sequence divergence rate of 4% per million years, which is double the "universal" one. The phylogenetic analysis of the sequences is in accordance with the paleogeography of the area and supports a vicarian pattern of distribution.

## The evolution of genetic canalization under fluctuating selection

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If the direction of selection changes from generation to generation, the ability to respond to selection is maladaptive: the response to selection in one generation leads to reduced fitness in the next. Since the response is determined by the amount of genetic variance expressed at the phenotypic level, rapidly fluctuating selection should favor modifier genes that reduce the phenotypic effect of alleles segregating at structural loci underlying the trait. Such reduction in phenotypic expression of genetic variation has been termed genetic canalization. I support this argument with two- and multilocus models with alternating linear selection, and Gaussian selection with fluctuating optimum. A canalizing modifier gene affects the fitness of its carriers in three ways: (1) it reduces the phenotypic consequences of genetic response to previous selection; (2) it reduces the genetic response to selection, which is manifested as linkage disequilibrium between the modifier and structural loci; (3) it reduces the phenotypic variance. The first two effects reduce fitness under directional selection sustained for several generations, but improve fitness when the direction of selection has just been reversed. The net effect tends to favor a canalizing modifier under rapidly fluctuating selection regimes (period £ 8 generations). The third effect improves fitness of the modifier allele if the fitness function is convex and reduces it if the function is concave. Under fluctuating Gaussian selection, the population is more likely to experience the concave portion of the fitness function when selection is stronger. Therefore only weak to moderately strong fluctuating Gaussian selection favors genetic canalization. This study considerably broadens the conditions that favor genetic canalization, which so far has only been postulated to evolve under long-term stabilizing selection.

## Molecular phylogenetic study of endemic Lumbriculidae (Oligochaeta) from Lake Baikal (Russia)

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Lake Baikal is the largest, deepest and most ancient (28 MY old) of the all existing great freshwater reservoirs. Its fauna is characterized by the presence of highly speciose and endemic species flocks. The *Lumbriculidae* is one of the most important and diverse families of *Oligochaeta* in the lake. About one third of the world's known lumbriculid taxa inhabits the lake.

The present study attempts to obtain a general picture of the phylogenetic relationships among Baikalian lumbriculids. With this objective, we amplified and sequenced a 640 bp long fragment of the mitochondrial COI gene of 25 species representing all 6 Baikalian lumbriculid genera.

The analysis revealed a fairly good concordance between the phylogenies inferred from molecular and morphological data. The recent separation of some *Rhynchelmis* species in a distinct clade, as suggested by morphological data, is confirmed by molecular data and the genus *Pseudorhynchelmis* Hrabe (1982) is here revalidated. Moreover, our results comfirm the morphology based assumption that *Agriodrilus* and *Teleuscolex* are congeneric with *Lamprodrilus*.

One of the potential advantages of the molecular approach to phylogeny reconstruction is the theoretical opportunity to estimate the times of divergence using a carefully calibrated molecular clock. The amount of nucleotide substitutions between Baikalian taxa studied here suggests that the age of the Baikalian lumbriculids as a whole is comparable to the geological age of the lake (ca. 30 MY). However, the age of the most important clade, containing half of the modern species, is considerably younger (ca. 3 - 4 MY). Our results suggest that this group originated as a recent and monophyletic Baikalian radiation, and is therefore a true species flock. Its current diversity seems to be the result of a single radiation that gave rise to many of the contemporary species of lake Baikal. Although the overall phylogeny is well resolved, the relationships within this subgroup are not, in spite of the sufficient amount of the phylogenetic signal as estimated by the maximum likelihood mapping method. Possible mechanisms of explosive speciation and ecological circumstances which would favour such a pattern of diversification will be discussed. This work was supported by INTAS grant 94-4465 and Russian Foundation for Basic Research (project

98-04-49276a).

#### QTL Analysis; new solutions to old problems

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Most of the naturally occurring genetic variation of importance to animal and crop improvement, medicine and evolutionary biology, is multi-factorial in inheritance involving several genes plus a major input from the environment. The discovery of ubiquitous and naturally occurring molecular genetic markers in the late 80's has opened up the opportunity of identifying and locating the individual underlying genes, Quantitative Trait Loci (QTL), studying their effects and carrying out selective breeding or genetical analysis on the basis of individual QTL. In this talk, I will present the basic principles of analysis and try to describe some of the conclusions that are emerging from analysis of traits in plants. Marker analysis of segregating populations can result in poor accuracy of QTL location biased estimators. The causes of these problems and their possible resolution are explored such as the use of substitution lines or near isogenic lines to improve mapping accuracy when looking for candidate loci.

## From QTLs to genes: high resolution QTL mapping in mice

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It is widely held that further progress in the understanding of the genetic basis of quantitative variation will depend on identifying some of the contributing genetic factors. To this end we have been mapping quantitative trait loci (QTLs) that contribute to artificial selection responses in lines of mice divergently selected on body size. Analysis of reciprocal crosses between the high and low selection lines has suggested that the X chromosome contributed disproportionately to the selection response. QTL mapping experiments suggest that almost all of the X chromosome contribution is associated with a single QTL that changes body size by about 20%. Evidence from genetic analysis of the QTL so far points to the involvement of a single gene. We describe results from a progeny testing approach, to fine-scale QTL mapping that should give the resolution at which positional cloning of QTLs in mammals is feasible.

## The effect of a microsporidian sex ratio distorter on the reproductive behaviour of Gammarus duebeni

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Many horizontally transmitted parasites are known to manipulate their host's behaviour in order to increase transmission to other potential hosts, but little is known about the effects of vertically transmitted parasites. Since vertically transmitted parasites are passed on to the next generation via the gametes of infected females and therefore rely on host reproduction for their own transmission, we would predict that the parasite would be selected to increase infected female mating success. However, selection on the host may favour males which can differentiate between uninfected and infected females. Here we investigate the impact of a vertically transmitted microsporidian sex ratio distorter on reproductive behaviour and mate choice in the amphipod *Gammarus duebeni*. We found that male *G. duebeni* are prepared to guard uninfected females for longer than infected females. Evidence of male preference for uninfected or infected females, in choice tests, was not conclusive. Finally, we present a model to illustrate the consequences for both the parasite and the host.

## I DNA reveals evidence for benefits of group living in Bechstein's bats

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Female Bechstein's bats (Myotis bechsteinii) form groups during summer to raise their young. However, while maternity colonies are common in bats, little is known about their adaptive value. Whatever causes sociality in bats, ecological constraints or individual direct benefits should be reflected in the microgeographic genetic population structure of a species. We present an analysis of mitochondrial DNA in Bechstein's bats using three molecular markers, including a novel microsatellite which allowed for high individual discrimination. Comparison of marker variability within and between 10 colonies living in close proximity revealed little variability within each colony, whereas most colonies were clearly distinguished by colony specific mitochondrial haplotypes (Fst=0.68). Data suggested that Bechstein's bat colonies are populated by females belonging to one or maximally two matrilines and are socially closed groups, even in the apparent absence of microgeographic dispersal barriers. Group living in M. bechsteinii therefore appears not to be primarily caused by predator avoidance or social thermoregulation. In such cases individual group composition is not expected to be of prime importance and strict colony fidelity is unnecessary. The genetic population structure of the Bechstein's bat can be best explained by the hypothesis that females seek related and familiar cooperation partners.

## Criteria for selection of topologies

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Molecular phylogenetics is successful, mainly because parallel changes are much less likely at the molecular level compared with the morphological level. Because sites of DNA sequences can be regarded as sample data from a population, we can estimate evolutionary histories statistically. Inference of phylogenetic tress consists of statistical modeling of evolutionary processes and selection of topologies. Maximum likelihood estimation of phylogenetic topology can be accomplished by the adoption of an explicit model for the (proce) of sequence evolution. Evolutionary processes can be regarded as Markov processes. Not a few works on evaluation of reliability of estimated topologies were developed, including parametric/ non-parametric bootstrap, normal approximation and Bayesian approach. But, their statistical properties have not been (full) investigated theoretically. Here, we derive statistical distributions of maximum likelihood estimates of (inter) branch lengths and log likelihood ratios, with remarks on non- standard aspects of the statistical problem in topology selection. We also propose a simple alternative to the posterior probabilities of topologies which require heavy task of computation, and show the reason why it works.

# Estimation of the dispersal function of maize pollen in order to assess the risks associated with deliberate release of transgenes.

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The dispersal function of genes is an important factor in many genetical studies. Either in population genetics, when dealing with the advance of an advantageous gene, or in agronomy, when trying to assess the risks of an escape of a transgene outside of a field, the dispersal function, and more particulary the shape of its tail, is of principal interest. We propose here an estimation of the individual dispersal function of maize pollen. Two large scale field experiments have been realized in order to provide an estimation in field condition, including long distance dispersal. Different models for the individual dispersal function, based on Brownian Motions, have been developped taking into account the biology of the corn, especially the difference of height between male and female flowers. These models have proved to be efficient to explain the observed data, particularily the anisotropy due to wind direction. The estimations of the implied parameters are also in accordance with estimations of the meteorological and biological parameters acquired independently.

## Molecular phylogeny of tilapiine cichlid fishes: the origin of complex parental care (?) behavior(s)

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In the proposed study we present a new phylogeny of tilapiines (an assemblage of African and Levant cichlid fishes) based on molecular markers.

We sequenced the complete mitochondrial ND2 gene (1047bp) in 35 species, and a 340bp fragment of the cytochrome b gene in 27 species. Separate analyses were performed in order to test the monophyly of different tilapiine assemblages which were defined based on morphological characters. We present a wide taxa spectrum, including not only the so called "tilapiine-species", but also lineages of Lake Tanganyika, and West African species. Our molecular data set suggests that in contrast to morphological hypotheses from Regan (1920, 1922), Trewavas (1983), and Stiassny (1991) that the tilapiines are not a monophyletic group. We mapped the evolution of the parental care systems of the main groups of tilapiines, including the substrate spawning genus Tilapia, and the mouthbrooding genera Sarotherodon and Oreochromis, onto the ND2 phylogeny. The ND2 analysis confirms the hypothesis of Trewavas (1980) of a single origin of biparental, paternal and maternal mouthbrooders, and is in disagreement of the hypothesis from Peters & Berns (1978, 1982) which assumed a multiple independent origin of mouthbrooding species.

## Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites

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This study addresses within-population dispersal patterns among the species rich Lake Malawi cichlids, specifically among the rock-dwelling mbuna group. Relatedness values were calculated for 160 individuals belonging to two species from known locations in the field by screening 6 highly polymorphic microsatellite loci. Using a novel analysis technique that does not rely upon paternity exclusion, results from both species indicate that spatially adjacent females have higher average relatedness values than those separated by larger distances, but that this pattern is reversed in males. This thus provides firm evidence for male-biased dispersal within the Malawian cichlid flock.

#### Postglacial colonization of Fennoscandia by distinct phylogeographic lineages of the bullhead, Cottus gobio

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We used mtDNA and allozyme markers to study the colonization history of the bullhead Cottus gobio in northern Europe. This small fish lives in rivers and lakes of Europe; in the north it also inhabits the brackish coastal waters of the Baltic Sea. Sequencing and restriction analysis of a mitochondrial D-loop segment from c. 50 populations revealed a clearcut subdivision into an eastern and a western haplotype group in Fennoscandia. This division was concordant with the geographical pattern of strong allozyme differentiation at several loci. These data suggest that northeast of the Baltic Sea, Finnish lakes were postglacially invaded from Russia, whereas west of the Baltic another, western phylogeographic lineage colonized Sweden from the south. In brackish coastal waters the western lineage has, however, extended its range also to the eastern parts of the Baltic, probably replacing the other lineage with lower salinity tolerance. Contact zones between the two lineages are now found both in freshwaters north of the Baltic Sea, and between coastal and riverine populations along the Finnish coast. The observed molecular patterns and the colonization hypothesis accord with earlier views presented on the basis of morphological variation in the bullhead.

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#### Horizontal gene transfer: evidence and role in the evolution of prokaryotes

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Orthologous gene families that are conserved in diverse bacterial, archaeal and eukaryotic genomes typically show patchy phylogenetic distribution, which suagests that horizontal gene transfer and lineage-specific gene loss played a major role in evolution. Dístinguishing between these two types of events with confidence is not casy. However, combined analysis of patterns of phylogenetic distribution and tree topologies suggest parsímomous scenarios that favor horizontal transfer, differential gene loss or a combination thereof for individual gene families. Holizontal gene transfer appears to involve all functional categories of prokaryotic genes, with the possible exception of core components of translation and transcription, but seems particularly prominent among genes that encode DNA repair and signal transduction system components. Frequently, horizontal transfer seems to be accompanied by the elitnination of the original gene responsible for the respective function. Such events can be classified into two categories: i) non-orthologous gene displacement - replacement of a gene by, an unrelated or distantly related gene coding for a functionally similar protein, and ii) xenologous gene displacement replacement of a gene by an ortholog Iroín a phylogenetically distant lineages. These phenomena will be discussed using examples from a comparative study of DNA repair systems and a systematic analysis of the evolution of aminoacyl-tRNA synthetases. In spite of the prominence of horizontal gene transfer and differential gene loss, a clear phylogenetic signal still can be extracted Irom comparisons of entire protein sets from completely sequenced genomes. Phylogenetic trees produced by using parameters of the distribution of similarity, scores between likely orthologs to calculate evolutionary distances between genomes will be discussed.

#### Molecular evolution of Bov-B LINEs in vertebrates

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Since their discovery in family Bovidae, Bov-B LINEs, believed to be order-specific SINEs, have been found in all ruminants and recently also in Viperidae snakes. The distribution and the evolutionary relationships of Bov-B LINEs provide an indication of their origin and evolutionary dynamics in different species. The evolutionary origin of Bov-B LINE elements has been shown unequivocally to be in Squamata. The horizontal transfer of Bov-B LINE elements in vertebrates has been confirmed by their discontinuous phylogenetic distribution in Squamata (Serpentes and two lizard infra-orders) as well as in Ruminantia, by the high level of nucleotide identity, and by their phylogenetic relationships. The direction of horizontal transfer from Squamata to the ancestor of Ruminantia is evident from the genetic distances and discontinuous phylogenetic distribution of Bov-B LINE elements. The ancestor of Colubroidea snakes has been recognized as a possible donor of Bov-B LINE elements in Ruminantia. The timing of horizontal transfer has been estimated from the distribution of Bov-B LINE elements in Ruminantia and the fossil data of Ruminantia to be 40-50 My ago. The phylogenetic relationships of Bov-B LINE elements from the various Squamata species agrees with that of the species phylogeny, suggesting that Bov-B LINE elements have been stably maintained by vertical transmission since the origin of Squamata in the Mesozoic era.

## Analysis of color pattern variation in the zebra cichlids of Lake Malawi

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Color variation is ubiquitous among many closely related taxa of endemic rocky-shore (mbuna) cichlid fishes. Among allopatric populations of the common mbuna *Metriaclima zebra*, fishes possess either red or blue dorsal fins; *in situ* observations reveal subtle variations in color patterns, but these patterns are common and also geographically widespread. Similar color forms which are geographically distant could represent

members of discrete evolutionary lineages that dispersed during lake expansion. Alternatively, populations of similar color variants could have evolved independently in multiple regions. To address these ideas, we characterized color morphotypes from disjunct populations using three microsatellite loci. Analysis suggests that similar color phenotypes in this species complex do not originate in contiguous geographic areas. This suggests that the process of color differentiation, perhaps critical to speciation in this and other taxa, may not have occurred during recent bouts of lake level fluctuations. Consistent with this perspective, *in situ* observations do not suggest syntopic differentiation.

## QTL mapping of correlated traits and epistasis detection

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Two alternative concepts of the genetic basis of population differentiation are known. The 'gradual divergence model' assumes that adaptation and isolation processes are due to accumulation of many additive genes with small effects. By contrast, the 'genetic revolution model' postulates strong epistatic interactions of fitness genes. It is not an easy task to distinguish between these alternatives. Direct estimation of genomic distribution of epistatic effects may be of primary importance for such complicated issues as interaction of selection and linkage in polymorphism maintenance, evolving reproductive isolation, adaptation to stress, evolution of recombination, etc. Our analysis shows that joint treatment of correlated trait complexes may increase the power to detect epistasis and the accuracy of the parameter estimates. A complementary conclusion is also true: epistasis may be helpful in discriminating between alternative hypotheses about the trait(s) genetic control, e.g. in testing for the presence of two linked QTL vs. one QTL. Multiple trait analysis allows to address further questions on genetic architecture of fitness traits, e.g., testing for "linkage vs. pleiotropy", evaluating the dependence of epistasis on individual's genotype (phenotype) and ecological conditions, dissecting the phenomenon of canalization of gene action, etc.

# Incipient sympatric differentiation in Drosophila: a complex adaptive syndrome caused by strong microclimatic selection

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The opposite slopes of Lower Nahal Oren designated "Evolution canyon" at Mt Carmel, Israel contrast sharply due to large difference in solar radiation. We revealed significant adaptive differences in D. *melanogaster* genotypes between the slopes, partly confirmed for its sibling species D. *simulans*. The fitness complex involved oviposition temperature preferences, tolerance to thermal and drought stress and starvation, etc. This remarkable differentiation has evolved in spite of a very small inter-slope distance that could by far be surpassed by flies' migration. The direction of the revealed differences was exactly the expected one to result from adaptation to local conditions. A challenging question is how such a microsite differential selection for stress tolerance accompanied by behavioral differentiation (habitat choice and reduced migration rate) and reinforced by sexual isolation. Here we report new results on fitness-related traits and significant mate choice manifested by flies from both slopes of the canyon. This is the first demonstration of incipient sympatric differentiation caused by strong microclimatic selection involving stress tolerance, habitat choice and partial premating isolation.

### Fitness effects of single and multiple spontaneous mutations in the yeast Saccharomyces cerevisiae

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Spontaneous mutations can be easily obtained in yeast strains transiently deprived of mismatch repair. Fitness declines substantially when such mutations are accumulated. It appears, however, that the magnitude of genetic load depends not only on the effects of individual mutations, but also on their interactions. The present experiments are aimed at estimating the relative importance of additive and non-additive components of the mutational load. Fitness effects of single (or very few) mutations are studied in a collection of strains subject to brief spontaneous mutagenesis. Dominance effects are evaluated in diploids after back-crossing haploid mutants to their non-mutated haploid progenitors. Epistatic interactions are analyzed by crossing the load-free strains with the strains carrying multiple mutations and then estimating both the mean value and distribution of fitness among the progeny. The experiments are in progress but the already gathered data suggest that deleterious mutations act synergistically.

Could be the conflict between male and female the cause of melanotic tumor formation in *Drosophila melanogaster?* 

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The present author reported a unique type of melanotic tumor in the C104 strain of *Drosophila melanogaster*, which derived from a natural population in Szentendre, Budapest (Kosuda 1990; 1992; 1996). The turnors develop not at the larval stages but at the adult one, although most melanotic tumors develop at the larval stages. Their expression is also sexlimited and/or organ-specific. They ofien become visible in the abdomen of female flies only without unaided eyes Men they fully grow up. However, they can usually be detected under the microscope exclusively in the vicinity of spermatheca. The melanotic tumors are usually attached to either or both spermatheca and subsequently encapsulate them. Aging effect on tumor formation is also revealed, that is, the incidence of melanotic tumor formation increases as female flies get old, whereas turnors are not developd in young female flies just after eclosion (Kosuda 1990). In the present article, the author reports that a lot of gynandromorphs were found in the C-104 strain. The existence of gynandromorphs in this melanotic tumor strain strongly suggests that hernocytes of male part aggregate and encapsulate spermathecae developed in female body, after having recognized that spermatheca are foreign intruders to male.

#### Reverse endosymbiosis? Losses of organelles in evolution and ontogeny

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The endosymbiotic hypothesis for the origin of eukaryotic cell implies two contradictory processes. Mereschowsky nearly a century ago hypothesised not only the endosymbiotic origin of chloroplasts by the equation, Animal plus Chloroplasts (Cyanobacteria) = Plants, but also the reverse, Plants minus Chloroplasts = Animals. This anticipates organisms that through a loss of chloroplasts differentiate into secondary heterotrophs (animals). The first equation has been transformed into the now widely accepted endosymbiotic theory but until recently, the second equation was only speculative. Studying bleaching phenomenon in the mixotrophic flagellate *Euglena gracilis*, we have demonstrated the preferential sensitivity of the chloroplast to the action of xenobiotics. Bleaching in Euglena is connected with irreversible elimination of functional chloroplasts and can be considered as a process supporting Mereschkowsky s second equation. Recent molecular and biochemical data have documented the reductive dimension of cell evolution. A spectacular example is the persistence of residual, functional plastid genomes in nonphotosynthetic plants, some protists, bleached mutants of E. gracilis, and remarkably also in protozoan parasites of the phylum Apicomplexa. In many cases of secondary plastid endosymbiosis, the process whereby a protist engulfs a eukaryotic alga, genomic extinction of the nucleus has happened repeatedly. Molecular data indicate that the common ancestor of all extant eukaryotes contained mitochondria. Subsequent evolution has been reductive, not acquisitive (with the exception of the plastids). The primitive taxa that lack mitochondria, collectively called Archezoa, lost the original organelle or modified it into hydrogenosome. On the other hand, the Aposymbiosis Theory of Carcinogenesis (Schwemmler 1993) proposes that carcinogenesis is ontologically a return to the embryonic phase. In a formal phylogenetic sense, carcinogenesis is a reversal of symbiogenesis; the functional loss of the organelles (mitochondria) which were once respiratory symbionts.

#### SINE Families as Markers of Mammalian Phylogeny

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Short interspersed element (SINE) families can be used as reliable markers of host evolution. SINE families are preserved in the genome for time exceeding periods of families and orders radiation. SINEs seem to have no physiological functions and therefore are not influenced by convergent evolution. We have developed a phylogenetic test based on binary qualitative character — the presence or absence of specific SINE families in the genomes of different species. SINE families are detected by hybridization and PCR of the genomic DNA. B2 and 4.5S1 RNA-related elements were found in only three (Muridae, Cricetidae and Spalacidae) out of nine tested rodent families. The presence of DIP element only in the genomes of jerboas (Dipodidae) and birch mice (Zapodidae) indicates close relation between these families. Dimeric B1-dID SINEs are abundant in the genomes of dormice (Gliridae) and squirrels (Sciuridae) but absent from the myomorphous rodent genomes (Muridae, Cricetidae, Spalacidae, Dipodidae and Zapodidae) suggesting dormice relation to squirrels rather than to the myomorphous rodents. ID elements are specific for all tested rodent families (15) but not for other mammalian orders. These data strongly support the recently disputed monophyly of Rodentia. Now we have isolated four SINE families from the insectivore genomes and the phylogenetic conclusions are forthcoming.

## Physiological and genetic consequences of high temperature stress in Drosophila

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Heat shock proteins (Hsps) and other molecular chaperones perform diverse physiological roles. One is to facilitate organismal thermotolerance, of which the functional consequences are concentration and developmentally dependent in *Drosophila melanogaster*. Too little Hsp70 limits tolerance, while too much restricts larval growth. Early pupae and adults, however, show no such constraints on survival. To determine the generality of an Hsp70-thermotolerance relationship, Hsp70 concentration and the increase in survival to stress were assayed at a range of temperatures in intact larvae and adults of two related temperate species, *D. melanogaster* and *D. simulans*, and in the desert species, *D. mojavensis*. Larvae of *D. melanogaster* and *D. simulans*, and in the desert species, *D. mojavensis*. Larvae of *D. melanogaster* and *D. simulans* respond similarly to heat; they express Hsp70 maximally at 36-37°C, and tolerance of heat shock increases by 1.5-2°C after the Hsp70-inducing heat pretreatment. By contrast, *D. mojavensis* expresses Hsp70 only at higher temperatures and pretreatment increased thermotolerance much less, although this species tolerates much higher temperatures. Critically, the temperatures that maximally induce Hsp70 often failed to induce thermotolerance in either *D. simulans* or *D. mojavensis*. These results suggest that the stress response has not necessarily evolved to compensate for the thermal environment, and that regulatory control may be both complex and varied among even related species.

The role of life history traits and temporal heterogeneity in the ecology and diversity of six neotropical *Drosophila* communities

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Theoretical studies have shown that life history traits can play a considerable role in the ecology and diversity of natural communities through effects on e.g. interspecific competition and the role of predators. Recently, two models were developed that linked life-history trade-offs and temporal variation to community ecology of (tropical) insects living on patchy, ephemeral resources. The first model relates a life-history trade-off and temporal hetero-geneity to competitor coexistence. It predicts a positive relationship between temporal hetero-geneity and the diversity of life history strategies in a community. A second model relates differences in life history traits between parasitoids and their hosts to the role of top-down control in (tropical) host populations. This model predicts a reduced top-down control in temporally varying environments. In this study, we tested the predictions of both models in a field study on *Drosophila* communities in Central Panama. At six locations we measured temporal patterns in resource abundance, patterns in composition of the *Drosophila* comm-unities, and the impact of parasitoids for a period of one-year (20-45 generations). Trends in the data are consistent with the predictions of both models, confirming the potential roles of both life history trade-offs and temporal roles of both life history in determining local community patterns.

## Development of insecticide resistance in Danish populations of the housefly Musca domestica (L.)

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Resistance of insects to insecticides is one of the major challenges facing applied entomologists, but presents excellent opportunities for the study of the fundamental aspects of evolution in an environment strongly altered by man. The understanding of this evolutionary process is important for the development of pest management systems to avoid or delay resistance.

Monitoring of resistance in Danish field populations of houseflies related to the use of insecticides for fly control has been performed regularly since 1948 by biological assay and has recently been combined with biochemical and molecular tests.

Insecticide resistance is caused by metabolism, changed target site sensitivity, altered penetration and behavioural changes. We have focused on metabolism by general or specific esterases, glutathione S-transferase and P450 monooxygenases. We have implemented a method to detect mutations in the pyrethroid targeted Na-channel protein, and are defining haplotypes of the organophosphate target acetylcholinesterase. The refined methods of resistance detection will enable us to define resistance genotypes or haplotypes for which fitness parameters can be determined. This approach towards a population genetical view, can provide us with information on more than a theoretical level, on how to predict and manage resistance problems and give excellent possibilities of fundamental studies of the evolutionary process.

Comparative study of microsatellite variation in the Alpine marmot (*Marmota marmota*) and in the endangered species *M. vancouverensis*.

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As revealed by allozyme studies, genetic variation is strongly reduced in Alpine marmots (*M. marmota*) from Austria and Germany. 10 highly polymorphic microsatellite loci were used to investigate whether this genetic depauperation is restricted to the eastern part of the distribution area or if it also affects the core region in the Central Alps of Switzerland and France. To estimate the impact of founder effects and genetic drift, 5 reintroduced populations from Austria and the Spanish Pyrenees were included in the study. The data indicate a clear differentiation between the autochthonous populations from the Western Alps and those from the Eastern Alps. The reintroduced populations show a heterogenous pattern of variation depending on the source population and the successive population history.

*M. vancouverensis* is a North American species that has experienced a dramatic decline of the population size down to 70 individuals over the past 10 years. To save this highly endangered species from extinction, a recovery program has been started. For this purpose it would be helpful to have appropriate genetic markers to avoid inbreeding and loss of variability. Thus the 10 microsatellite loci isolated from the genome of *M. marmota* were also tested in *M. vancouverensis*. However, only two of these loci showed variation. This finding indicates that the gene pool of *M. vancouverensis* is depauperated, at least compared to that of *M. marmota*. The work was supported by the FWF (project P11840-GEN).

## Relationships between some East Asian vertebrates inferred from cytochrome b sequences

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Molecular markers such as cytochrome *b* gene of mtDNA proved to be useful not only for phylogenetic reconstructions but also for population analysis and revealing intraspecies' variation. In Far East Asia many populations are isolated in islands and semiisolated in the borders of their species' ranges. We studied several terrestrial animals by using partial and full sequencing of cytochrome *b* gene in purpose to understand their evolutionary history. For the moles *Mogera wogura* subdivision is substantial in the Japanese islands; it is more significant between islands than within each island, while in the motherland almost no difference was found. Then, differentiation of 4 *Mogera* species inhabiting the Islands may be explained by their consecutive settling. For the crows, we discovered 2 distinct lineages of *Corvus corone orientalis* with the border in central Sakhalin island and somewhere in the East Siberia. However more western Siberian populations of *C.corone orientalis*, all *C.cornix* and *C.c.corone* from Europe belong to the same lineage. Such kind of subdivision does not correspond to the morphological differentiation. Minor interpopulation variation in *C.macrorhynchos* came to light, with the borderline also in Sakhalin island which confirms subspecies division. In the both latter cases secondary contact could be assumed due to different ways of range's populating, via South or North. Thus, using some molecular markers, together with knowledge about morphological characters and historical biogeography, can clear up ways and tempos of species' evolution.

## Nucleotide variation at the Chalcone Isomerase locus in Arabidopsis thaliana

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In inbreeding, colonizing species the lack of effective recombination and the possibility for efficient selection and drift may produce different patterns of genetic variation compared to outbreeding species. To investigate the nature of nucleotide polymorphism in a natural selfing species, the *Chalcone isomerase (CHI)* gene region was sequenced in 24 worldwide ecotypes of *Arabidopsis thaliana* (L.) Heynh. and in one ecotype of *Arabis petraea*. This locus codes an enzyme that is involved in the first steps of flavonoid biosynthesis, and therefore in the synthesis of compounds conferring protection against UV-light. The level of nucleotide variation was low (qTOTAL=0.005, qSIL=0.007) compared to other studied regions in *Arabidopsis*. The neighbour-joining tree of the ecotypes was bifurcated but not as clearly as in the other regions in *Arabidopsis*. The minimum number of recombination events observed with the four-gamete test was three, which is high in the light of the highly selfing reproduction mode of *A. thaliana* and the low number of polymorphic sites in the sample. Negative Tajima's *D* and the distribution of pairwise nucleotide differences at *CHI* suggest that *Arabidopsis* population is expanding or that there has been a recent selective sweep. Comparison of silent polymorphism and divergence at the *CHI* region and at the other gene regions so far studied revealed in some cases a significant deviation of the direct relationship predicted by the neutral theory. Different selective scenarios that can account for the observed patterns of variation will be discussed.

#### Importance of propagule size and genetic variation for colonization success

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Understanding the factors determining colonization success and risk of extinction have become increasingly important in population ecology and conservation biology. The probability of local extinction is suggested to decrease with increasing population size. Similarly, propagule size is known to influence colonization success. Ecological and genetic mechanisms, and also environmental and demographic stochasticity can expose small populations to extinction. The importance of genetic variation in colonization success has remained untested. To test the importance of genetic variation for colonization success, we introduced mated waterstrider (Aquarius najas) females of various numbers and origins in spring into 90 streams devoid of this species. Propagule size and its genetic diversity were manipulated by introducing 2, 4, 6, 8 or 16 females from either one or two original populations. The number of origins of introduced waterstriders simulated the genetic diversity of the propagules. Successful colonizations were counted on two occasions in autumn and the colonization success was compared between the treatments. Both the greater size of the founder population and the larger number of origins improved colonization success. This result is in accordance with a more common idea of a higher risk of extinction in smaller populations. According to our result this idea can be applied to founder populations as well. Moreover, in the same model colonization success was highest among populations that originated from two different origins. The result indicates that the probability of a propagule to survive in a new environment depends not only upon the amount of colonizating individuals but also upon the amount of genetic variation (e.g. amount of different origins of individuals) available for selection.

#### Does the immunocompetence handicap principle work in Panorpa vulgaris scorpionflies?

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Good genes models of female choice rely on sufficient genetic variability in male viability. Host-parasite coevolution may create such genetic variability. According to the "Immunocompetence handicap hypothesis", males with superior immunocompetence should be able to increase resource allocation to sexually selected ornaments. If immunocompetence is heritable, females selecting highly ornamented males may thereby increase parasite resistence in their offspring.

We studied the immunocompetence of *Panorpa vulgaris* scorpionflies (Mecoptera: Panorpidae). In this insect, cryptic female choice is based on saliva secretions produced by males during mating. Saliva secretion is a Zahavian handicap, serving as an honest quality indicator. We examined whether saliva secretion is an immunocompetence handicap. Thus, it was expected that males producing more salivary masses have offspring of superior immunocompetence. Furthermore, we analysed if the immune traits studied (the hemolymph lysozyme titer and the phagocytic activity) are heritable and sexually dimorphic.

In accordance with the expected trade-off between immunocompetence and investment into sexually selected ornaments, female *P. vulgaris* possess a more powerful immune system than males. The immune functions studied are heritable — a necessary condition for the immunocompetence handicap hypothesis. As predicted, the immunocompetence of offspring varied in accordance with the different capabilities of fathers to produce salivary secretions. However, these genetic effects were rather weak and differed between male and female offspring.

## Speciation over basic niche borders among endemic cichlids of Lake Malawi

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Variation in endemic cichlid species flock in Lake Malawi was studied from muscle fatty acid content, microscopic morphology of scale surface and enzyme electrophoresis. The analysis of fatty acid composition confirms, that niches in studied species are established and stabile. In addition to clear foodweb traces, fishes in similar niches possessed large biochemical differences, because of endogenic components. Scale fine morphology utilising scanning electron microscopy grouped species across niche types. Enzyme electrophoretic variation allowed the grouping of species based on genetic identities. The results suggest, that although niche is a conservative character, fundamentally new niches have been invaded several times during the evolution of species flock. Single basin structure offers no strict geographical barriers for allopatric speciation, but lake sediments reveal that seemingly homogeneous environment is in fact historically heterogenous. Niche switces may result from sympatric speciation under released competition, following local fish kills recorded in the sediment data.

## Physical map based on RAPDs in the cactophilic species Drosophila buzzatii

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*Drosophila buzzatii* is a cactophilic species of repleta group of *Drosophila* commonly used in population genetic studies. The lack of polymorphic molecular markers makes it difficult to unravel the molecular basis of the quantitative genetic variation observed for some metric characters (i.e. body size and development time). We are constructing a physical map based on random amplified polymorphic DNA markers (RAPDs). We have screened 85 10-mer primers and found 153 polymorphic and reproducible markers. These RAPDs were mapped by *in situ* hybridisation to polytene chromosomes of *D. buzzatii*. We found that 73 RAPDs gave a unique signal, 45 RAPDs gave no signal, and the rest gave two or more signals. Thirty-eight markers were sequenced and span a total of 28 kb. These markers were compared against DNA sequence databases to look for any similitude with existing sequences and for any new coding sequence.

#### The effect of Epigenetic inheritance on the evolution of multicellularity

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Epigenetic markers play an important role in the process of differentiation in multicellular organisms. In early evolution of multicellular organisms, the separation of genetic and epigenetic inheritance may have been weaker. We present a model for the evolution of a regulatory gene network in multicellular organisms. In this model cells evolve to react to the environment and interact with other cells. Using this model we examine the effects of resetting vs. not resetting the epigenetic markers between successive generations. We examine the evolutionary stability of mechanisms for removing epigenetic markers.

Role-reversal of mitochondrial DNA and the phylogeography of populations of mussels (*Mytilus galloprovincialis*) in the Eastern Mediterranean and the Black Sea.

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Genetic markers offer a potentially very powerful tool for studying aspects of population biology of the organisms. Interpretation of their variability may explain the phylogeographical relationships among populations. The distribution of allelic variants of the genetic markers has been influenced from the past history of the populations, the population size, the migration rate and the natural selection. Genetic markers are chosen that are not affected by natural selection in most situations.

We have used three genetic markers to study the structure and the evolution of the populations of the Mediterranean mussel *Mytilus galloprovincialis* in the Black Sea and the Eastern Mediterranean: mitochondrial DNA, allozymes and nuclear DNA markers. Although allozymes and nuclear DNA markers are inherited biparentally, mtDNA in animals is transmitted maternally. Mussels of the genus *Mytilus* are the exception of the rule. Females curry a type of mtDNA (called F) which transmit to both their daughters and sons. Males appear heteroplasmic for one F molecule (from their mother) and one M molecule that have inherit from their father and they can transmit it only to their sons. This special mode of mtDNA inheritance has been termed as Doubly Uniparental Inheritance (DUI) and results in to two different mtDNA lineages; one F, that transmitted through females and one M, that transmitted through males. From time to time an F molecule enters to the M lineage and is transmitted paternaly. This phenomenon has been termed as masculinization.

For the present study seven mussel populations were sampled between 1995 and 1997. These include one population from the Black Sea (Sevastopol), three from Aegean Sea (Halastra, near Thessaloniki; Megalo Pefko, near Athens; and Faros, near Heraklion, Crete), one from Ionian Sea (Cephalonia Island), and one from the Adriatic Sea (Venice lagoon). One more population from the Atlantic coast of Spain (Galicia) was studied for comparison. All individuals sampled were scored for five allozyme genes by means of starch electrophoresis. MtDNA variation was scored by a PCR-RFLP assay targeted to the cytochrome oxydase III gene (with 5 restriction enzymes) and 16s ribosomal RNA gene (with 3 restriction enzymes). Allele and haplotype frequencies were estimated, as well as gene, haplotype and nucleotide diversities. Mitochondrial RFLP profiles were used to construct evolutionary trees reflecting the phylogeny of the mitochondrial genomes, based on distance and maximum parsimony methods.

13 mtDNA restriction patterns have been found for the F lineage and 11 for the M lineage. All the Black Sea haplotypes have also been found in the Mediterranean, which indicates that the two populations have the same origin. Examining the haplotypes heterogeneity there is not significant difference among the Eastern Mediterranean populations. However the Black Sea population is significantly different from the Eastern Mediterranean populations indicating barrier in gene flow between the two marine basins.

As expected from the DUI, all the females were homoplasmic (except of one) and most of the males were heteroplasmic. Among the males from all the populations there were some that appear to curry only the F mtDNA haplotype. These apparently homoplasmic males can be either truly homoplasmic or carry a second M type, newly masculinized F, which is identical with the F that comes from their mother.

One of the main differences between the Black Sea population and the populations from the E. Mediterranean was that a great proportion of the Black Sea population males are heteroplasmic for two types which both belong (in terms of sequencing) to the F lineage. That means that the phenomenon of masculinization is more widespread in the Black Sea than in Mediterranean or the Atlantic. Until now the masculinization has been observed in other species of the *Mytilus* genus in low proportion.

Analysis of the haplotype and nucleotide diversity has shown lower diversity in the Black Sea population. Allozyme data also support this result. Reduced diversity could be a result of marine circulation which prevent the genetic variability originated in the Mediterranean to enrich the Black Sea population. It can also be due to a historical event like a bottleneck.

#### The life, death, and resurrection of "the inheritance of acquired Characters"

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For most of recorded history, the idea that acquired characters are inherited has been taken for granted. It began to be serious 1y doubted in the second half of the 19 th century, but was stiR defended by most biologists, including Darwin. Gradually, the weight of opinion shifted until, by the mid-20th century, the befief that acquired characters cannot be inherited became almost a dogma. Now opinions are beginning to shift again. I shall discuss some of the background to these changing opinions, and try to see the extent to which they have been the result of new observations, new experiments, and new biological ideologies.

## **Experimental Tests of Genetic Code and Ribozyme Origins**

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*In vitro* selection, or directed molecular evolution, provides the means to probe evolution from the simplest of building blocks—random RNA sequences, but it also provides a window into the most basic principles of the evolutionary process. I will discuss experiments ranging from the construction of small RNA catalysts with multiple functions to the recapitulation of stereochemical interactions that influenced the genetic code's organization in early evolution.

Through *in vitro* evolution, we discovered what may be the world's smallest RNA ligase ribozyme (Landweber & Pokrovskaya, *PNAS*, 1999). This RNA is unusual in its requirement of only *two* unpaired nucleotides, and this extreme simplicity suggests that it would have undoubtedly arisen in early evolution. More surprisingly, the catalytic RNA also *contains* a smaller self-cleavage motif originally found in the *Tetrahymena* group I intron. This makes it a "dual catalytic RNA"–promoting both cleavage at one site and ligation at another. As the second activity arose as a byproduct of selection for ligation, we interpret it as a spandrel in the design of an RNA enzyme. The emergence of this unexpected pair of reactions in a single RNA suggests that similar catalytic structures can arise under surprisingly simple conditions and that multiple catalytic modules can evolve from very small pre-existing parts.

Most theories for the origin of the genetic code require specific recognition between nucleic acids and amino acids at some stage of the code's evolution. *In vitro* selection of RNA molecules (aptamers) that bind amino acids now allows us to search for motifs that interact directly with the amino acid. Studies of arginine (Knight & Landweber, *Chemistry & Biology*, 1998) provide the strongest support for an intrinsic affinity between any amino acid and its codons. This suggests a role of chemical determinism in choosing the codon assignments for this amino acid and rejects the "frozen accident" hypothesis.

## DNA sequence polymorphism in natural populations: causes, associations and implications

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The forces shaping DNA sequence polymorphism and divergence will be discussed in light of recent empirical and theoretical investigations of the interaction of linked selection, mutation and genetic drift. The site frequency spectra of DNA sequence polymorphisms at loci in Drosophila genomic regions of low crossing over per physical length exhibit a skew toward rare variants. The recombination in the phylogenies of the haplotypes is not part of available theoretical predictions. The theoretical challenges of recent, genome-wide surveys of DNA sequence polymorphism will be considered.

Linkage disequilibrium between DNA sequence polymorphisms and phenotypic effects in candidate genes maybe used to localize and characterize the population genetic basis of quantitative genetic variation. Recent attempts to apply this approach to Drosophila bristle variation have achieved success in that intermediate frequency polymorphisms have been associated with quantitative variation in both sternopleural and abdominal bristle numbers in a natural population. The implications of these results for theoretical models explaining the maintenance and divergence of quantitative genetic variation will be discussed, as will prospects for more advanced experimental designs.

## Natural selection for reduced cost of heat-hardening in Drosophila melanogaster

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A variety of stressors induce the heat-shock response. The heat-shock response involves the production of specific heat-shock proteins (HSPs) and serves to reduce the harmful effects caused by stress. A short term non-lethal high temperature stress induces the heat-shock response and results in heat-hardening. Heat-hardening leads to increased stress resistance but also does impose a cost in terms of reduced fecundity.

To examine whether the cost of heat-hardening is genetically variable, we selected for reduced cost of hardening by '

## Assessment of genetic variability in Lathyrus using molecular markers

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Lathyrus is a member of tribe Viciae in the Fabaceae family. All the species under study belong to the section Lathyrus exepted *L. ochrus* which belongs to the section Clymenum (Kupicha, 1983). *L. sativus* L. is a pulse cultivated since Neolithic, from south of Europe to India, through north Africa, Ethiopia and the Middle East. It is particularly important in India where the culture occupied 1.6 millions hectares in 1981. *L. cicera* L. is generally considered as one of the ancestors of *L. sativus* (Jackson et al, 1984). It has been use as a forage in Europe. *L. latifolius* L. is an ornamental perennial species, similar to sweet pea (but perennial). *L. sylvestris* L. is related to *L. latifolius* and is supposed to hybridized with it (Davies, 1958). It is equally perennial. It grows wild in western and northern Europe. Inproved cultivars have been selected for forage purpose. *L. ochrus* L. is a mediterranean species, which can been used as forage.

Our objective is to establish at the molecular level, using RAPD markers, the phylogeny of these species taking into account polymorphism at the species level. To this purpose we have focused our study in species belonging to the same taxonomic section, last species (*L. ochrus*) being a control. Then we have selected two populations of different geographical origins per each species. The sample is composed of 135 individuals distributed in groups of 18 individuals for *L. sativus* (Ethiopia and Tunisia), *L. cicera* (Portugal and Tunisia), *L. ochrus* (Tunisia), *L. sylvestris* (France), 12 individuals for *L. sylvestris* (Hungary), 10 individuals for *L. latifolius* (France) and 5 individuals for *L. latifolius* (Hungary).

Kupicha F. (1983) The infrageneric structure of *Lathyrus*. Notes Roy. Bot. Gardens Edinb, 41: 209-244. Jackson M.T. and Yunus A.G. (1984) Variation in grass pea (*Lathyrus sativus*) and wild species. Euphytica 33: 549-559.

## High genetic load explains segregation distortion and marker-associated heterosis in bivalve mollusks

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Inheritance studies with marine bivalve mollusks often detect departures from Mendelian segregation. Discrepancies appear in late larval stages but are especially marked at juvenile or adult stages; they occur in random-bred progenies but are striking in inbred families. The loci affected vary from cross to cross. These deviations from normal Mendelian segregation interfere with standard methods of linkage or QTL mapping. One hypothesis for widespread distortions of Mendelian inheritance is background selection against deleterious mutations, which could result from the very high fecundity of bivalves. If so, we expect minimum expression of genetic load, thus minimum segregation distortion, at the earliest developmental stages. We examine segregation of 19 microsatellites loci in early swimming trochophore larvae (6 hrs old) from nine F2 or F3 hybrid families of *Crassostrea gigas*. For several microsatellite loci, there is evidence for non-amplifying ("null") alleles; but taking null alleles into account, we find that segregation ratios are Mendelian in 98% of the cases. Juveniles (2-3 months old) from the same crosses show segregation distortion in 20% of the cases. In most cases, this is due to selection against the IBD (identical by descent) homozygote genotype. This can be explain by tight linkage of our marker loci to nearly lethal, recessive genes. A map-based approach indicates that there could be up to 15 lethal genes per individual genome. This evidence for large genetic load in bivalves supports Zouros' associative overdominance hypothesis for correlations between multilocus allozyme heterozygosity (or somatic aneuploidy) and growth rate.

## Behavioural variation among migration forms and populations in the brown trout

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Aquatic organisms are expected to show high levels of interspecific variation owing to their limited dispersal ability across watersheds. The brown trout (*Salmo trutta*) occurs in three forms that differ in their migration behaviour. In the lake-run brown trout and the sea trout young migrate to lakes or sea, respectively, after 2-5 years in the river and after maturation return to breed in their natal river. The resident form spends its whole life cycle in the stream. The three forms are known to differ in several life history traits, but evolutionary theory suggests that different forms may differ also in their behaviour. For instance, resident fish populations are expected to be more aggressive than migratory populations. We studied behavioural variation among Finnish trout populations. The traits selected for the study were aggressive behaviour, foraging activity, and antipredator behaviour in response to chemical cues from a fish predator. The study fish originating from four lake-run, three sea-run and three resident populations were brought to common environment as eggs. Behaviour of individually-marked fish from each population was screened in aquarium experiments and the growth rate of the fish was monitored for eight months onwards. The results imply that the trout populations differ significantly in aggressive than lake-run and resident populations. At population level, there is a positive correlation between the amount of aggressive behaviour and growth rate.

## On the evolution of cheating in mutualisms

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The formal framework of adaptive dynamics makes it possible to examine how complex, intricate ecological interactions evolve. Mutualistic associations have a special interest, because they appear to be vulnerable to invasion by mutants that cheat. Such mutants gain the benefits of their partner without providing anything in return and have the potential to destabilize mutualisms. Yet cheaters are known to exist in a range of mutualistic associations, including plant/pollinator systems. This paper applies the techniques of adaptive dynamics to the evolution of specialist plant/pollinator associations to determine the consequences of mutations that lead to cheating.

## Adaptive dynamics in multidimensional trait spaces: Darwinian demons and canonical convergence stability

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Over the long term, evolutionary change consists of a sequence of successful mutant invasions. Models of adaptive evolution often have the property that change is guided by – but not fully determined by – fitness. In a given situation many different mutant phenotypes may have a fitness advantage over the residents, and are thus potential invaders, implying that the mutational process plays an important role in deciding which particular invasion will take place. For multidimensional trait spaces, an evolutionary analysis of several traits considered together differs from separate analyses of single traits in two basic ways. There may be fitness interactions between traits – so that natural selection on one trait depends on other traits – and there may be inter-trait genetic correlations, for instance because of pleiotropic mutations. These phenomena can have a profound influence on evolutionary stability in multidimensional trait spaces. I will make two points regarding this influence. First, if we are willing to contemplate any conceivable mutations, adaptive evolution from nearby any point in trait space to nearby any other point (and back) will typically be possible. In such a case, there will be no convergence stable points in the trait space. Second, for more realistic situations, where mutational genetic variation can be characterized by a constant or slowly varying covariance matrix, I will introduce the concept of canonical convergence stability and present a purely fitness-based stability criterion, involving the Jacobian of the selection gradient.

## Phylogeographic analysis of species and populations of the Macrostomida from three major faunal regions

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The Macrostomida are a morphologically well-defined group among free-living Platyhelminthes. Several species were described with almost cosmopolitan distribution. We chose morphologically closely related representatives of the Macrostomidae, showing enigmatic differences in the structure of their nervous system. In order to test whether these species are really as closely related as suggested by taxonomy, or whether their different nervous organization reflects a much more ancient split, we compared the levels of genetic divergence both, on the intraspecific level, as well as among species using ribosomal DNA sequences of the ITS region.

Microsatellites and allozymes: two complementary views on the selection between marine and lagoon habitats in the sea bass.

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The interpretation of genetic population structure depends crucially on the assumption of the selective neutrality of genetic markers. One consequence is that all neutral markers should be affected in the same fashion by drift and migration whereas selection may influence loci differently. Indeed, selection could constitute a force able to strongly influence dispersal and gene flow. Such selective processes are particularly likely in the case of marine organisms which could be subject to environmental fluctuations at the time of their recruitment. In the sea bass (Dicentrarchus labrax), an euryhalin an euryherm marine fish able to colonise estuaries and lagoons during its life cycle, several studies have suggested the possible occurrence of selection on some enzymatic loci which were also involved in acclimation to freshwater and in the differentiation between marine and lagoon samples. In the context of these studies we analysed 19 samples of sea bass on 6 microsatellite loci. Eight of these samples were already analysed on allozyme markers in a previous study. On the base on the comparison of the datasets available on the two types on markers on the Mediterranean area, and using an original method invoking structural hypotheses, we tested the hypothesis that some loci in D. labrax exhibit patterns of allele frequencies caused by adaptation to different environments. This study showed firstly that microsatellite markers displayed a lower Fst estimates than those observed with the 18 allozyme loci. Moreover, despite microsatellite loci reflected geographical proximity, allozymes were more correlated with ecological parameters. The conclusions of our study put a crucial question of the genetic load in sea bass regarding to the high number of loci suspected to be under selection.

#### Local transposition in Drosophila transgenic lines of hobo elements

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Transgenic lines with complete *hobo* element were obtained from Hikone line. These transgenic lines were studied along generations to determine the evolution of the structure of the element (complete or deleted), the number of insertion sites, their localization on the polytene chromosomes and the possible appearance of new rearrangements. In these lines, transposition was estimated by the level of *hobo* insertions and excisions at different generations.

During the 80 first generations, we demonstrate that *hobo* transposable element invades all chromosomes in euchromatin. The *hobo* distribution varies between larvae, within a line at a given generation. This implies excisions and insertions at random. Nevertheless, some insertions hotspots have been found. The number of insertions remain low (<10) and the hybridization signals were unique at each insertion site, except for one line (about 20 at G80). Then, in that line, at five different loci located on both autosomes, double, and even triple, hybridization signals were detected and maintained over the following generations.

These results could be explained by two transposition mechanisms. Until G80, the increasing number of *hobo* insertions may be the result of a random transposition, with excision and insertion in all loci. Then, after G80, in one line, a regulation of the transposition may appear, without excision in some loci.

## Codons Usage: host genes versus transposable elements

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Degeneracy of the genetic code implies that the majority of amino acids are coded by more than one codon. It has been demonstrated that a bias generally exists in the use of codons for a given amino acid. Thus, a given codon can be preferentially used. In bacteria, and particularly in *Escherichia coli*, such a bias, correlated with the expression level of genes and with the tRNA abundance, has been reported.

Multivariate analyses can be used to study the codons bias in sequences. This allows us to discriminate each sequence by the frequency of triplets utilization. It is then possible to compare different sequences and to check whether the same set of codons or not is used. A comparison between codon usage of transposable elements and host genes, based upon a Factorial Correspondence Analysis (FCA), was mainly done in *Drosophila melanogaster* and few other *Drosophila* species. This allows us to discuss the *P* element horizontal transfer between *Drosophila melanogaster*, and more generally the use of the codon usage to detect horizontal transfers of transposable elements.

## What the comparison of homologous domains tell us about the structural evolution of transposable elements ?

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Comparisons of homologous domains of transposable elements belonging to different families or classes frequently show the existence of conserved regions. The regions may have two origins. First, they can derive from the same ancestral element. Second, they can be due to a convergence.

The first hypothesis is probably the right explanation when the conserved regions are longer than 20 amino acids. In this case, the similarities observed can be used for phylogenetic analyses and then to propose a model of evolution of the domain considered. Such work was done for several domains:

1 - the transposase / integrase of class II transposons and LTR retrotransposons and retroviruses;

2 - the gag domain of LINEs and telomeric elements,

3 - the envelop (env) gene of LTR retrotransposons and retroviruses.

These comparisons partially published (Capy et al., 1996 and 1997) added to those of Xiong and Eickbush (1990) and McClure (1991) allow us to propose a general model of evolution of transposable elements. In this model, it is suggested that:

1 - integrases of LTR retrotransposons and transposases of class II transposons containing the DDE signature may share a common ancestor;

2 - elements with no DDE signature showing similarities with resolvases and/or topoisomerases may have a different origin;

2 - telomeric elements (TART and Het-A) probably derive from LINEs like elements;

3 - weak similarities were detected between env genes of LTR retrotransposons and retroviruses.

## Diet-dependent female choice for males with "good genes" in a soil predatory mite

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Female choice for mates with "good genes" presupposes that some males have better genes than others<sup>1</sup>. Yet, this type of mate selection causes genetic variability to disappear by selection against inferior males. This paradox may be resolved when substantial variability is maintained at selection-mutation balance. Alternatively, populations exhibit genetic polymorphisms maintained by frequency-dependent selection or heterozygote advantage. Here we show that (1) a local population of soil predatory mites exhibits genetic variation in prey preference for two prey species, that (2) hybrids between selected preference lines are superior or inferior in reproductive success depending on prey diet composition, and that (3) females mate disassortatively when hybrids are superior, but switch to assortative mating otherwise. Thus, mate choice varies with diet and is tuned to incorporate "good genes" in the offspring, *i.e.* genes that promote reproductive success of the offspring on the same diet as that experienced by their parents. In this way, hybrid success and mate choice act together in either maintaining or eliminating genetic polymorphism in local populations.

## Mitochondrial DNA divergence of transpacific species across the "Eastern Pacific Barrier"

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The "Eastern Pacific Barrier" (EPB), 5400 km of uninterrupted deep water between the central and eastern Pacific, constitutes the greatest marine obstacle to the dispersal of shallow-water organisms. Most shallow water genera are represented by different species in the eastern and the central Pacific. However, some species are found on both sides of the EPB. These "transpacific" species are considered by "dispersal" biogeographers as evidence of invasions through the barrier, whereas "vicariance" biogeographers think that transpacific species are morphologically conservative remnants of previously continuous distributions. We compared mitochondrial DNA nucleotide sequence from the two sides of the barrier in 15 species of shorefishes and in 4 species of sea urchins. The results indicate that in most cases central and eastern Pacific populations of transpacific species are very similar, indicating recent gene flow. In the fantail pipefish *Doryhamphus excisus*, however, the genetic differences are much greater; this appears to be one case of a morphologically conservative complex of allopatric species, because the mtDNA differences between central and western Pacific populations are even grater than those between central and eastern Pacific. In the sea urchin genus *Echinothrix*, one species, *E. diadema*, shows complete panmixia across the EPB, while the other, *E. calamaris*, is characterized by distinct clades on each side of the barrier. Thus, the EPB acts as a haphazard filter. It has resulted in speciation in many groups, but it also permits passage of larvae from time to time.

## Genetic bases of foxtail millet domestication in the context of comparative mapping in cereals

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Domestication of most species of cereals has involved a common set of traits such as non-shattering, increasing seed weight, simultaneous flowering and ripening. The small genome size of foxtail millet (2C=1 pg) makes this species particularly attractive for comparative genome studies. The objective of our study was to map the genetic factors controlling the domestication syndrome in this species. An AFLP linkage map of foxtail millet using an F2 population derived from an interspecific cross between the cultivated form (*Setaria italica*) and its wild progenitor (*S. viridis*) was constructed. Several major domestication QTLs were tagged on this genetic map. Furthermore we tagged QTLs for the same traits in F3 families of a previously mapped *S. italica* x *S. viridis* cross (Devos *et al.*, TAG 96:63-68, 1998). Results showed that the majority of genetic factors were localised on restricted regions of the genome. We will discuss the evolutionary implications of our study in the context of comparative mapping of domestication genes in the grass family.

## Resistance and Tolerance in Rapid Cycling Brassica

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The study of the adaptive defenses of plants against natural enemies has focused on the ability of plants to avoid damage (plant resistance). Increasing attention is being given to the plants' ability to sustain damage with little reduction in fitness (plant tolerance), and to the existence of trade-offs between these two different defensive traits. This study examines the existence of a genetic correlation between resistance and tolerance among 15 half-sib families of Rapid Cycling *Brassica rapa*. Resistance was assayed as the complement of leaf damage incurred by larvae of Pieris rapae, and tolerance as the reduction in fitness due to fixed degrees of simulated damage.

#### Methods for Testing the Molecular Clock Hypothesis

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The molecular clock hypothesis has continued to be a central issue in molecular evolution. As the molecular clock concept has been widely used in the dating of evolutionary events, it is important to test whether a global clock concept is valid, especially in the dating of deep divergences such as the eukaryote-prokaryote split. We shall review some of the methods proposed in the literature and then present a new method for the nonstationary case, in which the GC content is not at equilibrium but has changed significantly among lineages. As will be seen, this is a difficult case and the application of an inappropriate method can be misleading.

#### Restricted female dispersal within and between populations of the ant Formica exsecta.

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One important issue in social behaviour is to understand what factors may favour a shift from single-queen to multiple-queen colonies in ants. It has been suggested that low dispersal success of founder queen might be one important factor allowing the evolution of multiple-queen colonies (polygyny) and the ensuing decreased relatedness among colony members. The aim of this study was to quantify female dispersal in a polygynous population of the ant *Formica exsecta*. In this species queens have to either parasitized the nest of other *Formica* species (*Serviformica*) or infiltrate an established colony of their own species to become reproductives. Genetic (microsatellite) analyses of nine populations in the Swiss jura mountains revealed that (i) colonies generally contain several queens and (ii) nestmate workers are only distantly related. To estimate female dispersion rate, we determined the distribution of mtDNA RFLP markers. We found five different haplotypes and an AMOVA analysis showed that 80% of the variance in haplotype distribution was explained by differences between populations (st=0.97, p<0.001). A detailed analysis of the three populations containing more than one haplotype showed strong isolation by distance with most nests containing a single haplotype. These data indicate

extremelly limited gene flow by females between populations and also among nests of the same population.

## Cryptic species within the Herring Gull Larus argentatus/cachinnans complex

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Traditionally the Herring Gull has been regarded as a circumpolar ring species consisting of a chain of interbreeding subspecies. However, recent evidence of limited or no interbreeding in areas of contact between distinct taxa called this hypothesis into question. We investigated the mitochondrial population genetics of eight forms within the complex, concentrating on taxa distributed in the southern portion of the Palearctic (*L. michahellis, L. atlantis, L. cachinnans, L. barabensis, L. mongolicus, L. heuglini, L. taimyrensis* and *L. graellsii*). The following questions were addressed: 1) To what extent are the taxa genetically differentiated? 2) Are there barriers to gene flow between geographically neighbouring forms? 3) What can mtDNA tell us about the population history of taxa within this group?

Domain I of the mitochondrial control region (420 bp) was sequenced in 452 individuals from 18 breeding populations. We identified 49 variable sites and a total of 79 haplotypes. Molecular analysis of variance revealed significant interpopulation differentiation and identified three clear barriers to gene flow: (1) between *graellsii* and *atlantis* in the NE Atlantic, (2) between *michahellis* and *cachinnans* in the western Black Sea and (3) between *barabensis* and *mongolicus* in the Central Asian steppes. Central Asian *barabensis* were indistinguishable from *heuglini*, indicating that the obvious plumage differentiation between them must be very recent. Mean pairwise sequence divergence between taxa ranged from 0.2% (*heuglini* vs. *barabensis*) up to 3.1% (*cachinnans* vs. *michahellis*). The haplotype genealogy revealed a monophyletic *michahellis/atlantis* clade as sister group to all other taxa. *L. cachinnans* s. str. appeared paraphyletic in the gene tree with a deep split between two clades, indicating a relatively long history of large population size. All other taxa had shallower branching patterns. The minimum spanning network showed excellent congruence between geographic and genetic population structure.

#### Rapid Parasite-Mediated Natural Selection in Daphnia

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Parasite-host coevolution may be at the heart of some of the most important issues in evolutionary biology including the maintenance of sexual reproduction and genetic polymorphism. Central to any hypothesis concerning disease and evolution is the notion that host genotypes differ in their susceptibility, and thus parasitic infection is borne disproportionately by susceptible members of the population (=parasite-mediated natural selection). My work on *Daphnia* and their microparasites combines field and laboratory studies to test these assumptions and ascertain if parasite-mediated selection is a prevalent force in nature. As a first approach, I sought to determine if genetic variation for resistance could be detected with simple genetic markers (allozymes). I detected clonal variation for infection in 12 of 25 populations studied. These results suggested the potential for natural selection, but did not explicitly demonstrate it because such field data can not control for multiple confounding factors. To circumvent this problem, I have conducted laboratory experiments on *Daphnia magna* infected with the castrating bacterium *Pasteuria ramosa*. I compared the susceptibility of those clones that were infected at the time of collection to those that were healthy when collected. The results showed that infection was naturally prevalent in the genetic subset of individuals which are more susceptible. Thus I was able to link genetic variation for resistance to the natural distribution of a parasite that has substantial fitness costs for its host, and hence provide an example of parasite-mediated selection in natural *Daphnia* populations.

## Thermal stress and evolution.

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Data from our lab on the evolution of stress resistance are reviewed concentrating on *Drosophila* as a model organism and on extreme temperatures as environmental stress. In general ample genetic variation for stress resistance is found within and among populations and with and without a prior exposure to non-lethal temperatures (acclimation). For both low and high temperature stress a rough correlation between the climate of origin and thermal resistance is apparent. Acclimation at a non-lethal temperature led to a significant increase in survival after heat shock lasting over several days but a cost of expressing the "heat-shock response" was identified in that increased survival after acclimation was accompanied by reduced fertility. Studies of heat-shock proteins showed that the expression of Hsp70 in adult flies is greatly increased by acclimation and correlated with survival rate. Relative survival of different life stages varied among populations indicating that different mechanisms or genes at least in part are responsible for or are expressed at different developmental stages. Phenotypic variation and its genetic component as well as fluctuating asymmetry (FA) of quantitative characters were studied under extreme temperatures and generally an increase of variation and FA was found under stress. Possible mechanisms and evolutionary implications of this result are discussed.

## How many beneficial mutations are needed to stop Mullers Ratchet?

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Recent observations of mitochondrial DNA in pedigrees revealed surprisingly high mutation rates. To reconcile these levels with significantly lower expectations based on phylogenetic analyses, hotspots and long-term removal of mutations by weak selection have been invoked. The latter, however, would imply an increased genetic load. Together with recent estimates of slightly deleterious mutation rates in the human genome this may seem to endanger long-term survival.

Our simulations of such populations have shown that biologically meaningful sets of parameters exist which do lead to extinction, if only deleterious mutations, selection and drift are considered. However, this may be avoided by advantageous mutations. These may compensate directly for specific deleterious mutations or may lead to new capabilities improving fitness. Furthermore, compensatory adaptation in quantitative traits may prolong time to extinction or even prevent deterioration of absolute fitness at all.

Different distributions of mutational effects and other parameters are explored by stochastic computer simulations in order to find the critical frequency of advantageous mutations necessary to stop Mullers Ratchet.

## Syntrophy, massive gene transfer, and the chimeric origin of eukaryotes

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That eukaryotes descend from a common ancestor with archaea is the most recent version of the classical model for the origin of eukaryotes (a prokaryote-to-eukaryote transition). This idea emanated from the first rooted universal phylogenetic trees, where the root lay in the bacterial branch. However, contradictions showing eukaryotes and bacteria as sister groups appeared with the use of additional protein markers. More recently, comparison of complete genome sequences have indeed confirmed that eukarvotic genomes have a mixed heritage. Informational genes (DNA replication, repair, recombination, transcription, translation) are more closely related to archaeal homologues, whereas operational genes (metabolism, transport, etc.) are more similar to their bacterial counterparts. In this context, two new chimeric models for the origin of eukaryotes have been put forward, the hydrogen hypothesis1 and the syntrophy hypothesis2. Both propose that eukaryotes arose through a metabolic symbiosis (syntrophy) mediated by interspecies H2-transfer between bacteria and methanogenic archaea, and that mitochondria were initially anaerobic. However, whereas in the hydrogen proposal only one type of bacterial partner is involved (a-proteobacteria) which, in the way of becoming mitochondria, originated eukaryotes, in the syntrophy model, two distinct types of bacterial partners are engaged. These are sulfate-reducing d-proteobacteria, natural symbiotic partners of methanogens in most present and fossil anaerobic environments on the planet, and methanotrophic a-proteobacteria (future mitochondria), which would recycle methane in such assemblages. Over a long symbiotic life, a progressive bacterial-to-archaea transfer and replacement of non-informational genes occurred, which would explain the mosaic nature of eukaryotic genomes. 1 Martin, W. & M. Iler, M. (1998) Nature 392:37-41.

2 Moreira, D. & Lúpez-García, P. (1998) J Mol Evol 47:517-530.

#### DNA topology and thermal stress in hyperthermophilic archaea

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Changes in DNA supercoiling, mRNA and protein conformation, and alteration of membrane lipids appear essential components of the regulatory network which accounts for the general response to stress. In particular, a transient change of DNA topology associated to thermal stress seems a current theme in all organisms. Hyperthermophilic archaea, growing optimally above 804C, do not escape this rule. As in mesophilic bacteria, DNA linking number (Lk) increases during heat shock and decreases during cold shock. Despite this analogy, plasmid DNA topology and proteins that regulate DNA topology are essentially different. By contrast to bacteria, eukaryotes and mesophilic archaea, whose DNA is negatively supercoiled, hyperthermophilic archaea possess relaxed to positively supercoiled plasmids. This correlates with the presence of the hyperthermophile-specific reverse gyrase, which creates positive supercoils. We have studied the response to thermal stress at DNA topological level in Sulfolobus islandicus (kingdom Crenarchaeota), which contains the two plasmids pRN1 and pRN2. In addition to reverse gyrase, the most likely regulators of DNA topology in Sulfolobus are the archaeal-specific topoisomerase VI (Topo VI), a powerful decatenase also able to relax positive and negative supercoils, and the small DNA-binding protein Sis7 (Sso7/Sac7 homolog). We analyzed plasmid topological changes during heat shock (80 to 85-874C) and cold shock (80 to 654C) in parallel to levels of reverse gyrase, Topo VI and Sis7. We did not detect significant quantitative changes in these proteins. However, global reverse gyrase activities in crude extracts were strongly dependent on temperature. Additionally, we detected an enhanced thermoresistance of reverse gyrase activities after prolonged heat shock, which was dependent on heat shock protein expression. We propose a model where reverse gyrase, Topo VI, Sis7, and the archaeal chaperonin play an analogous role to topoisomerase I, gyrase, HU and DnaK in mesophilic bacteria.

## Morphological transformation and mosaic transition: example of lagomorph teeth

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Lagomorphs (hares, rabbits and pikas) share a peculiar teeth morphology, used in the taxonomy and phylogeny of the group. The four main cusps of the lower p3 are differently connected to each other. The observed connectivity patterns (CPs) occupy only part of the morphospace of all possible 4, 3 and 2 connection types. Seven out of the eleven theoretically possible CP are observed, of which only three are relatively frequent in the observed samples, about 200 taxa and thousands of specimens. From all the non-observed cases, a morphological restriction appears: the connection between the two posterior cusps is fixed.

The morphological diagnosis of each lagomorph taxon usually includes a single CP. Most of the rarely observed CPs are individual variations within a taxon. The documented cases of succession between two taxa usually involves uniform morphological transformation within a single CP, rarely a change between two CPs. When it is the case, transition occurs through a mosaic of CPs different from the origin and the target ones.

## Sequence variation of 5S rDNA among several bivalve molluscan species

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Genes encoding 5S ribosomal RNA (5S rDNA) have been cloned and characterized from many eukaryotes. Usually they are organized into one or several clusters of tandem repeats consisting of coding sequences separated by nontranscribed spacers. However, for species of bivalve molluscs, information about the sequence of 5S rDNA is limited to the coding region of three species from different famillies. In this study, the whole 5S rDNA repeated unit of three other bivalves, also from different famillies, *Cerastoderma edule, Chlamys varia* and *Mytilus galloprovincialis*, was amplified by PCR and sequenced. In *C. edule* and *C. varia* PCR amplification yielded a single band of 545 and 455 bp respectively, but two main bands of 258 and 775 bp in *M. galloprovincialis*. The results obtained indicate that coding region displays a length ranging from 118-120bp while spacer region ranges from 139-656bp. Alignment of the coding region sequence of all six species shows a maximum of ten different nucleotide positions. No differences were observed between *M. galloprovincialis* and *M. edulis* nor between *C. edule* and *Calyptogena magnifica*. In contrast, the nontranscribed spacer differs substantially among all four sequences obtained and an alignment is almost impossible when *M. galloprovincialis* sequences are included.

## Satellite DNA in the ant Formica cunicularia (Hymenoptera, Formicidae)

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Digestion of total nuclear DNA of the ant *Formica cunicularia* with *Sau*3A and *Alu*I and subsequent agarose gel electrophoresis has shown the presence of highly repetitive DNA yielding the typical ladder-like banding pattern. This satellite DNA is organized in a tandem repeat of monomers of 129bp.

Like satellite DNAs of other genera of ants and other Hymenoptera, it is AT rich (57,4%) and posesses several A or T rich runs as well as some short direct and inverted subrepeats.

The average pairwise sequence divergence between monomers is 16.12%. The monomer sequences do not bear any similarity to other repeat DNAs in the sequence data banks.

Restriction analysis with methylation sensitive enzymes (*Hpa*II-*Msp*I and *Sau*3A-*Nde*II-*Dpn*I) strongly suggests that this DNA is undermethylated.

Hybridization experiments were perfomed to test the possible existence of a repetitive sequence similar to the cloned in *Formica cunicularia* in other species of the genus *Formica*. Interspecific sequence similarities between *F. rufibarbis*, *F.selysi*, *F. sanguinea*, *F. fusca* and *F. cunicularia* were detected by Southern analysis. However the results of Southern analysis in *F.gagates* showed a lack of sequence similarity. Further comparative molecular studies of the repetitive sequences of theses species might provide insight about the evolution of the genome in the genus *Formica*.

## Phenotypic plasticity in the egg-sac building strategy of a desert spider

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A phenotypically plastic trait is adaptive if it enhances the organism's functioning and increases its fitness in a particular environment. Polyphenism provides a simple case for studying the effects of plasticity and genetic stability on behavioral traits. Populations of the Negev desert spider *Benoitia lepida* (Agelenidae) exhibit two relatively distinct strategies of egg-sac building which vary in their frequency of occurrence with elevation. One strategy is to attach the egg-sac to the top branches of shrubs. This occurs at high frequencies in populations above 850 m above sea level. The other strategy, suspension of each egg-sac by a thread above the sheetweb, occurs primarily below 850 m. Other characteristics of egg-sac structure and placement vary in a partially correlated manner with elevation.

We show that this geographic difference in strategy in not entirely genetically stable, but also responds adaptively to environmental factors. We performed reciprocal transfers of spiders from two populations in the Negev at different elevations: one at Sede Boqer (556 m), where the 'hanging' strategy predominates, and one at Borot Loz (987 m), where the 'attached' strategy predominates. We determined the degree to which the source environment (genetic stability) and the change in elevation (environmental change) affected the egg-sac building strategy. If the change in strategy is adaptive then the behaviour of relocated spiders should shift in the direction of that of spiders at the new site and their reproductive success should be similar to that of spiders at the new location.

We found that the source site significantly affected most of the egg-sac characteristics, while the new site had a smaller effect. The interaction between the new site and the source site affected some variables, indicating a possible polymorphism in the phenotypic response to the environment. The direction of change was as predicted by the hypothesis of adaptive plasticity, but spiders that changed strategy with relocation had lower reproductive success. It is possible that the choice of strategy is affected also by previous experience of the females before relocation.

Additional sperm siring haploid cells in mosaic haploid-diploid bivalve embryo's: possible connection with non-standard heterozygosities and mitochondrial inheritance?

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Bivalves are well known for some unresolved problems that arise during population studies. Allozyme data show unexplained heterozygote deficiencies and multilocus heterozygosity is often correlated with fitness substitutes. The doubly uniparental mitochondrial inheritance in mussels is a major exception to the rule of maternal inheritance. We carried out a cytological study of pre-hatching embryonic development in the marine bivalve *Macoma balthica* to look at aneuploidy, which has been proposed as a possible cause of heterozygote deficiencies in bivalves. We examined embryo's from nine pair crosses at ages ranging from ten minutes to fourteen hours. The haploid chromosome number was found to be nineteen, which is common for the family Tellinidae. We found no evidence for aneuploidy. Most cells were diploid es expected, but we encountered individuals that additionally contained a substantial fraction of haploid cells. Such mosaic individuals were present in every cross and at every age, at a frequency that varied from 3 to 30 %. We can exclude the possibility that the haploid cells originate from a polar body or in some other way from the two initial gametes. Moreover, polyspermy is very common. Therefore we suggest that one or more additional sperm cells despiralize in the young embryo and start the haploid cell line. We discuss the importance of this mechanism for the heterozygote deficiency phenomenon and for the debate on why organels usually inherit uniparentally.

## Spontaneous deleterious mutation: results from worms, water fleas, and microbes.

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Mildly deleterious mutation has been invoked as a leading explanation for a diverse array of observations in evolutionary genetics and molecular evolution, and is thought to be a significant risk of extinction for small populations. However, much of the empirical evidence for the deleterious-mutation process derives from studies of Drosophila melanogaster, some of which have been called in to question. A broad array of data from mutation-accumulation experiments with the nematode Caenorhabditis elegans, the water flea Daphnia pulex, and the microbe Escherichia coli will be reviewed. Collectively these studies support the idea that most mutations have only mildly deleterious effects on fitness, while suggesting that significant differences in genomic deleterious mutation rates exist among species, with some perhaps having lower rates than those commonly assumed to occur in Drosophila. A long-term (250 generation) experiment with C. elegans also provides the basis for obtaining direct estimates of the mutation rate at the molecular level, using large-scale sequence analysis. Results for microsatellite loci and the mitochondrial genome indicate surprisingly high rates of change at the nucleotide level.

#### Estimation of Quantitative-genetic Parameters in Natural Populations.

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Because the genetic properties of populations can depend substantially on the environmental background and because many organisms cannot feasibly be grown in controlled laboratory settings, there is a need for methodology that will allow the estimation of quantitative-genetic parameters (e.g., heritabilities and genetic correlations) from observations on individuals in undisturbed settings. As pointed out by Ritland, a key to achieving such measures is the reliable estimation of relatedness among individuals with molecular markers. A recently developed method allows the efficient and simultaneous estimation of both the one-gene and two-gene coefficients of relationships, thereby providing a means for estimating both the additive and dominance components of genetic variance/covariance. The insight that can be gained when molecular and phenotypic information are jointly available will be discussed, as will the limitations of this approach. Particular attention will be devoted to the estimation of genetic correlations. A surprisingly simple approach that does not even require knowledge about the degree of relatedness will be outlined.

## Intra- and Interspecific Molecular Variation in the Coelopidae

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The genetics, ecology, mating behaviour and evolution of seaweed flies of the family Coelopidae have been studied for over 20 years. In particular, *Coelopa frigida* has proved a useful model organism in the study of sexual selection. Virtually all the variance in male size, a character strongly selected by females, is attributable to an inversion system on chromosome I. Studies of *C.frigida* are being increasingly extended to other species of *Coelopa* and related genera. There is thus a need, in application of the comparative approach to these data, for an understanding of the evolutionary relationships between species and the nature of intraspecific variation. This study uses the mitochondrial gene cytochrome oxidase II to look at molecular variation within *C.frigida* in Britain and Sweden, which exhibit two extremes of habitat. These experiments have revealed a pattern of large scale geographical sturcture, plus a substructure characterised by unique haplotypes endemic to islands. From the between species data, congruent phylogenies have been obtained for the family using the mitochondrial marker and the nuclear gene elongation factor 1-alpha.

## RAPD specific patterns and their polymorphisms in the Drosophila buzzatii cluster.

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The great differentiation found with the use of different genetic markers in the populations of the Drosophila species included in the buzzatii cluster and the intriguing aspects of its speciation process, led to the present study. The amplification of the genomic DNA with three different primers was done in three strains of D. buzzatii, two of D. seriema, two of D. koepferae, one of D. serido type B and one of D. serido type D. As outgroups, one strain of D. mulleri and one of D. simulans were used. Strain-specific and species-specific DNA fragments generated by the different primers produced a characteristic pattern of RAPD bands that allowed to recognize the different strains and species. The largest coefficient of variation was obtained in the D. buzzatii strains followed by D. seriema strains. D. koepferae and D. serido types B and D strains were less polymorphic, except the strain of D. serido type B and D. koepferae for the primer 69. The strain of D. serido type D, unlike the others, presented a high number of monomorphic bands for all the primers used. The present RAPD data for the strains of D. buzzatii and D. seriema are the first evidence for the existence of a vast stock of unknown nuclear polymorphism segregating in those populations. The level of RAPD polymorphism found in the strains studied was remarkably higher than that observed in studies of esterases performed in the same strains. The Similarity Index and the Cluster Analysis confirmed the relationships obtained using other markers in the same strains, reinforcing the idea of a differentiation between the strains of D. serido types B and D and the other species in the cluster. However, the strain A55 (D. serido type B) from Brazilian cerrado showed to be closer to D. koepferae of the Argentinean Chaco. This finding was not observed with any other marker. The RAPD assay showed high resolution and efficience to reveal new polymorphisms not detected by other genetic markers, to document the variability within and among populations and also for taxonomic purposes.

## Evolution of integration rate of clonal plants

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Clonal plants are a major part of terrestrial and continental vegetation. The transport system of many of the clonal plants are integrated, but many of them lose their connects later. The genetic individuals, called genets consist of several potentially independent physiological individuals, called ramets. According to the intensity of resource transfer between ramets , there is a continuous scale of the integration strategy. There are two extreme types of genets: the splitter, whose ramets don't integrate at all, and the integrator, whose ramets are totally integrated, creating one giant organism. We try to describe the evolution of the clonal plants integration strategy depending on the rate of environmental fluctuation. We use stochastic cell-automaton, mean-field modelling and adaptive dynamics methods, like PIPs to inspect the genets behaviour under different levels of environmental fluctuation. Our results suggest that low levels of environmental change give way to the splitter genet to control all good-quality patches in the matrix, and thus it becomes an ESS. But as the rate of fluctuation grows, the splitter loses its patches, while the integrator is less affected. At very high rates of changes the integrator strategy becomes evolutionary stable. At middle levels of fluctuation, there is an intermediate attracting strategy and coexistence of extreme types becomes possible. Only the temporal component of the effects of fluctuation can be explained by mean field approximation methods, while spatial components, which are responsible for coexistence, are to be studied furthermore.

Strong population structuring in marine species with high dispersal capabilities: the case of European anchovy (Engraulis encrasicolus)

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Marine species with high dispersal capabilities in the adult and /or premature stage usually exhibit very little population structuring. We report here the case of European anchovy (Engraulis encrasicolus), a small pelagic fish with pelagic eggs and larvae, which in sharp contrast to the expected pattern was found to present strong population structure. A previous study using RFLP analysis of mitochondrial DNA variation has revealed that two distinct groups of haplotypes (phylads A and B) coexist but with proportions significantly different among major basins [Magoulas et al., Mol. Biol. Evol. 13(1): 178-190, 1996]. Recently more samples from almost the whole distribution area of the species were analyzed. The results indicated a population structure even more complex than previously thought. In the Black Sea phylad A is present almost exclusively. In northern Aegean Sea phylad A predominates with a proportion of 0.85. In the Ionian Sea, the Tyrrhenian Sea, the Gulf of Lions and the Bay of Biscay the proportions of this phylad drops to 0.40. In northern, central and southern Adriatic its proportion is even less: 0.15. Quite unexpectedly, in three samples taken from the seas intervening between the Gulf of Lions and Bay of Biscay (that is between two areas dominated by phylad B) the proportions of phylad A ranged between 0.85 and 0.95. Thus the population structure of this species is characterized by the co-existence of the two clades, the long distance gene flow (as evidenced by the occurrence of the same haplotypes over the whole distribution area of the species) and the large genetic differences between the basins. A possible explanation for this pattern is that two subpopulations were isolated in the past, subsequently extensive dispersal took place during some time period(s), while recently local genetic drift occurred because of restrictions to gene flow due to hydrographic forces.

## Evolutionary branching and the evolution of anisogamy

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Anisogamy, the existence of dimorphism in gamete size, is a general feature of many sexually reproducing organisms. Parker, Baker and Smith (1972) proposed a model which to date forms the main basis for understanding the evolution of anisogamy. This model is based on the assumption that the fitness of a zygote is size dependent, and that the number of gametes produced trades off with their size.

The purpose of the present study is to reinvestigate and extend the model of Parker et al. by analyzing the problem of the evolution of anisogamy using the framework of adaptive dynamics (Geritz et al. 1998). We extend the results of Parker et al. by demonstrating that size dependence of zygote fitness can lead to a gamete size dimorphism through evolutionary branching. In contrast to previous models, where the evolution of anisogamy required a certain minimal variation in gamete size between different genotypes, gamete size is treated as a continuous, quantitative character in our model. Evolution of anisogamy then depends on the underlying quantitative genetics, and in particular on the degree of recombination between the loci determining gamete size. Assuming genetic variation for recombination rates and using numerical simulations, we show that natural selection promotes the evolution of low recombination rates and, finally, anisogamy.

Geritz, S. A. H., Kisdi, É., Meszéna, G., and Metz J. A. J. (1998). Evol. Ecol. 12, 35-57

Parker, G. A., Baker, R. R., and Smith, V. G. F. (1972). J. theor. Biol. 36, 529-553

## Preliminary allozyme study on the genetic divergence in the bivalve *Mytilaster minimus* from a polluted brackish environment and adjacent marine sites

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The genetic relationships among individuals of the bivalve *Mytilaster minimus* (Poli) from a polluted brackish-water environment and adjacent marine sites were studied by allozyme electrophoresis. Data obtained on 200 individuals at 19 presumptive loci show relatively high levels of within-population genetic variability. A general departure from Hardy-Weinberg equilibrium was detected due to a general deficit of heterozygotes. The presence of various private alleles indicated a marked genetic divergence between lagoon and marine samples. Nei's genetic distances ( $\pm$  standard error) ranged from  $D = 0.0042 \pm 0.022$  to  $0.2764 \pm 0.1327$ . Weir and Cockerham's *F*-statistics pointed out a high species genetic structuring, with lagoon samples genetically divergent from the marine ones ( $2 = 0.306 \pm 0.101$ , p < 0.001 by permutation test). Furthermore, a minor genetic substructuring was observed within the total of lagoon samples ( $2 = 0.033 \pm 0.012$ , p < 0.001). Genetic divergence between marine and lagoon populations may result from random genetic drift acting independently within each population in a background of reduced gene flow (estimated number of migrants per generation, Nm = 0.567). The adaptive strategies of *M. minimus* do not result in a general reduction of genetic variability in populations colonising unpredictable environments, as previously hypothesised for many brackish-water species; rather, adaptation should be regarded as the result of microevolutionary factors, such as genetic drift and/or natural selection which may favour alternative alleles in different habitats.
### Tracking evolution of aposematic signalling in the novel world

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Any evolutionary studies are badly hampered by a lack of experimental ways to test past events such as the origination of aposematism. Aposematism refers to conspicuous warning signals in noxious or otherwise unprofitable prey. The problem to study initial evolution of aposematic signalling is that even naïve predators have shown to have inherited avoidance against any common warning colours. We have developed a technique of using totally artificial prey with artificial signals on the artificial landscape to study selection pressures that would have excisted when very first warning signals evolve against totally naïve bird predators. The first experiment in the novel world demonstrated clear benefits for grouping of the conspicuously signalling unpalatable prey. However, secondary evolution of similar signals in other species was equally possible among solitary prey. In the second experiment, we tested the possibility that cospicuous signal evolved gradually even among solitary prey. The weak signals were hardly learned to be avoided by predators, but on the other hand weak signals did not suffer any costs of being conspicuous. Thus, the possibility remains that cost-free step-wise mutation over the range of weak signals could accumulate under neutral selection to produce effective strong signals.

### Costs and benefits of iridoid glycosides in Plantago lanceolata

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Secondary plant compounds can play an important role in the survival of plants under natural conditions. They can act as defence chemicals involved in plant-environment interactions. We study benefits and costs of the iridoid glycosides catalpol and its precursor aucubin in the ribworth plantain, *Plantago lanceolata*. Iridoid glycosides are monoterpene derivates that can occur in two forms: a glycone moiety, generally deterrent against generalist herbivores, and an aglycone moiety, the product of an enzymatic conversion, generally with antimicrobial activity. In *P. lanceolata*, these compounds can constitute up to 15% of the dry weight of the reproductive tissue. Deterrence of generalist herbivores by aucubin and catalpol is well documented. We study their role in defence against generalist herbivores and the fungal pathogen *Diaporthe adunca*.

In vitro experiments showed that the effect of iridoid glycosides on fungal growth strongly depends on the chemical form in which the iridoid glycosides are present. Whereas the aglycone moiety of aucubin and catalpol strongly reduced the growth of the fungus *D. adunca*, the glycone moiety of aucubin actually enhanced fungal growth. Plants induced iridoid glycosides as a response to fungal infection, and genotypes differed in the strength of the induction. A four-generation selection experiment for high and low levels of iridoid glycosides was performed to study fitness costs of these compounds, i.e. fitness reduction of high-iridoid lines in the absence of the fungus. There was a strong response to selection. We discuss both benefits of iridoid glycosides, i.e. differences in susceptibility to fungal attack and damage by a generalist herbivore between high and low selection lines, their costs, and the environmental dependence of costs.

### Phylogeny of dinoflagellates by the rRNA 5.8 gene sequencies

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Different hypotheses on the evolutive relationships among dinoflagellates have been obtained based on the analysis of morphological characters of both extant species and fossil cysts. More recently, molecular approaches are being used to test phylogenetic relationships among the different genera, which only partially support the ones obtained with morphological data.

We have analyzed 5.8S sequences of more than 30 dinoflagellate species belonging to 5 different orders (Gonyaulacales, Gymnodiniales, Peridiniales, Prorocentrales and Thoracosphaerales). Notwithstanding the limited length of this gene, we obtained distance and parsimony trees with the same main topology as those obtained with 18S sequences (Saunders *et al.*, 1997), thus confirming the possibility of using 5.8S sequences for phylogenetic reconstructions in dinoflagellates. Our analyses support the close phylogenetic relationships between *Thoracosphaera heimii* (Thoracosphaerales) and the phototrophic peridinioids that form calcareous cysts. However we were not able to resolve the phylogenetic relationships among other species of the same order Peridiniales as well as among the orders Gymnodiniales, Peridiniales and Prorocentrales. Within the Gonyaulacales clade, the species of the genus *Alexandrium* group in a well supported clade and are all characterized by the presence of a peculiar signature AAGAA at position 42-46, which differs from AAGGG present in all eucaryotes as well as in the other dinoflagellates.

### The effect of parents' food types on sex-specific roles in parental care: patterns and possible mechanisms

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Recent studies on birds have tested how parents allocate the food between themselves and their young. Until now the effect of food consumption by parent birds on their food delivery to their young, as well as other parental activities, has not been tested. We have shown that parent orange-tufted sunbirds *Nectarinia osea* will consume nectar, whole arthropods and liquidized arthropods from artificial feeders. However, they will only feed their young with whole arthropods. This provided a unique opportunity to experimentally manipulate the food eaten by parent sunbirds independent of that fed to their offspring. We hypothesized that parents invest in their current young according to the quality of food that they themselves consume. Breeding pairs with two or three chicks were provided with feeders containing: water (control), sugar solution or liquidized mealworms mixed with sugar solution. We examined parental time budgets in detail to test, by supplementing parents with different food types, whether and how we were able to cause changes in their levels of parental care. As food quality increased (from water up to sugar solution mixed with liquidized mealworms): 1) Parents (especially females) increased their food delivery of whole arthropod prey to their young 2) only males increased their nest guarding effort. Nestling food intake and growth increased with increasing food quality and decreasing brood size. We conclude that increased food quality from self-feeding allows parent sunbirds the extra effort to invest more heavily in their current young.

Outlook to Future Biomonitoring: Development of a New Method for Meiobenthology, based on rRNA Signatures

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Sediments in marine and freshwater as well as soil act as links between atmospheric, terrestrial and aquatic realms and may therefore control many ecological processes operating outside their bounderies. They harbor astonishingly diverse biotic assemblages, but there is little known of the extent of biodiversity in them. Land use practices, altered hydrological processes, and contaminated soil and water all threaten the biota of these critical ecological zones. More knowledge is needed to make ecological inferences on the soil and sediment biota over broad geographic ranges or to determine if a few taxa control key ecosystem processes.

For this purpose we are developing a new method to speed up the identification of meiobenthic organisms in freshwater sediments. We collected sediment samples from different lakes in Southern Germany and used an improved protocol to concentrate all organic material thereof and to extract the whole genomic DNA. From this pool of DNA as well as from known single specimens we amplified D3 to D5 expansion regions of the large ribosomal subunit (28 S rRNA), cloned and sequenced it or sequenced it directly. Allocation of the random sequences to particular species by phylogenetic methods resulted in a database of rRNA signatures representing the majority of the benthic inhabitants.

This database can be used to create DNA arrays which should allow qualitative and quantitative determination of species composition in a given community by hybridization techniques. As species representation can fluctuate widely under different ecological conditions, this may become a test for monitoring ecological changes in lakes.

#### Ancient asexual scandals

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Ruling evolutionary theory holds that fully asexual strains are doomed to early extinction. At least two animal groups (bdelloid rotifers and darwinulid ostracods) seem to defy this dogma; and for this they were called *ancient asexual scandals* (Judson & Normark, 1996). Whereas the bdelloids have received ample attention, Darwinulidae have remained virtually unknown, this in spite of the fact that the lineage has survived at least 100, maybe even 200, millions years without sex. One representative, *Darwinula stevensoni*, has persisted for at least 20 millions years without sexual reproduction. We argue that this ancient asexual has managed to escape mutational load, as well as Müller's ratchet, by a combination of several life history characteristics, including a general purpose genotype and efficient DNA-repair. Persistent and obligate asexuals also have to escape the theoretical effects of the Red Queen. We suggest several ways in which this could happen, and argue strongly against the importance of parasites as examples of Red Queen evolution, especially with regard to the survival of asexual lineages.

Phylogenetic relationships of leeches (Euhirudinea) and leech-like worms (Acanthobdellida and Branchiobdellida) among the Clitellata (Annelida) derived from 18S rRNA sequences

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The phylogenetic relationships of leeches and leech-like worms among the Clitellata is investigated using a data set with published and new 18S rRNA gene sequences of 14 taxa representing 9 families. In addition, two Aphanoneura and one mollusc are included. Three different alignments are considered and the possible influence of departures from the rates constancy among sites are evaluated by maximun likelihood analyses using a gamma-model of rate heterogeneity. Maximum likelihood estimates of the shape parameter a of the G-distribution are very low, whatever the alignment considered, suggesting that phylogenetic reconstructions taking into account the rate heterogeneity among sites are likely to be the most reliable. Our analyses show that among the Clitellata, the leeches and branchiobdellids are significantly faster evolving lineages, while there is no departure from rate constancy between Acanthobdella and oligochaetes. Branchiobdellids and leeches are considered as a monophyletic assemblage in all cases. Phylogenetic reconstructions produce mostly unresolved trees so that the phylogenetic position of the latter assemblage toward the oligochaetes is still ambiguous. In contrast, a strong support is obtained for a grouping between Acanthobdella and the oligochaete family Lumbriculidae, supporting the inclusion of the former taxon among the Oligochaeta. As recent histological and ultrastructural characters strongly reaffirmed a close relationship between Acanthobdellida and Euhirudinea, this suggests that long branches impede the resolution of phylogenetic relationships of leeches and leech-like worms among the Clitellata.

Parallel evolution of aphids and their endosymbionts: a molecular approach to the phylogeny of the *Aphidoidea*.

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Aphido constitute a monophyletic group within the order *Homoptera* (i. e, superfamily *Aphidoidea*). The *Aphidoidea* originated in the Jurassic about 150 my. ago from some aphidiform ancestor whose origin can be traced back up to about 250 my. They exhibit a mutualistic association with intracellular bacteria (*Buchnera aphidicola*) related to *E. coli*. This association is obligate for both partners. The 16S rDNA based phylogeny of *Buchnera* from four aphid families showed complete concordance with the morphology-based phylogeny of their aphid hosts which pointed to a single original infection in a common ancestor of aphids some 100-250 my. ago followed by co-speciation of aphids and *Buchnera*. This study concentrates on the molecular phylogeny of the hosts including representatives from 6 aphid families including the *Lachnidae*. We present results based on the full sequence of the ATP-6 mitochondrial gene. Although our data do not allow to establish definitive evolutionary relationships among the different aphid families, some traditionally accepted groupings are put into question. In particular, the *Lachnidae* and the *Aphididae* which from morphological data are considered to be recently evolved sister groups, do not seem to be as closely related as usually accepted. We have also incorporated a representative from the Lachnidae to the 16S rDNA based phylogeny of *Buchnera*. Finally we discuss our results in the light of the proposed parallel evolution of aphids and their endosymbionts.

### Rates of movement of transposable elements in Drosophila melanogaster

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We estimated the rate of transposition and excision of 11 element families (2244, pogo, opus, jockey, mdg-1, 297, 1731, roo, copia, 17.6 and 412) in a set of 200 replicas of a wild type 2nd chromosome extracted from a natural population of Drosophila melanogaster, that have been undergoing spontaneous element movements for 116 generations. During this accumulation period, the replicas were maintained heterozygous in the male line in order to avoid selection against insertions with recessive deleterious fitness effects. At generation 116 they were made homozygous, and element movements in euchromatin were scored by *in situ* hybridization. We detected 27 transpositions of elements belonging to 7 out of the 11 families and 1 excision event. The pooled transposition rate per element per generation is 1.11 x 10-4 in accord with theoretical predictions for equilibrium. As in other studies, copia is the most active family with a rate of 4.03 x 10-4, 6.9 times higher than the average rate for the other families. The estimated excision rate is 3.81 x 10-6, two orders of magnitude smaller than that of transposition, in agreement with the hypothesis of selection against element proliferation. Although elements were randomly distributed along the ancestral second chromosome, two observations suggest non randomness of new insertions: 11 out of the 13 insertions mapped on 2L are located in the distal half of this arm, and 5 out of the 7 new roo sites are clustered in a small region of 2L which represents only 9% of chromosome 2 euchromatin. Nearly 50% of the surviving lines after the accumulation period were found to carry recessive lethal mutations on the second chromosome, as expected with a rate of 0.005 lethal mutations per second chromosome per generation in males, as proposed elsewhere. Our data suggest that the total rate of transposition per haploid euchromatic genome would be of the order of 0.12 and that element transpositions could account for a maximum of 60% of visible mutations. Transposition rates within lethal lines did not differ from viable lines, and no excision events were detected within them.

# Evolutionary implications of the frequent horizontal transfer of mismatch repair genes

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Darwinian evolution is the selection of the fittest variants generated by mutation and recombination. Until recently, it has generally been assumed that mutation rates were minimal, because most mutations are either deleterious or neutral. However, natural populations of *Escherichia coli* and *Salmonella* exhibit highly variable mutation rates. The strongest characterized mutators, which represent about one percent of the natural isolates, carry defects either in the methyl-directed mismatch repair (MR) genes or in the *mutT* gene. During adaptation, these mutators may generate favorable mutations counterbalancing the deleterious mutation load. However, at the adaptive peak, selective pressure will favor lower mutation rates. Because MR gene defects stimulate homeologous recombination, they could facilitate MR restoration by horizontal transfer. Here we show that relative to housekeeping and *mutT* genes, MR genes exhibit a high exchange rate among *E. coli* natural isolates. We find that the hyper-rec phenotype level of MR- alleles, measured in the laboratory, correlates at 92% with the MR gene mosaicism extent. These results indicate a mechanism of recurrent losses and reacquisitions of MR functions expected to accelerate bacterial evolution.

### Does plasticity evolve during the adaptation to a novel, stable environment?

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The evolution of plasticity, though deserving considerable attention in Evolutionary Biology, has been poorly studied in empirical terms. A wild population is adapted to an unstable, heterogeneous environment. When it is brought to the lab, it is placed in a novel, stable environment, with predictable changes in selective pressures and reaction norms and loss of genetic variability for costly plasticity mechanisms. The studies with populations in the lab for many generations may cause an underestimation of the evolutionary potentialities of plasticity. An important approach will be to characterize the evolutionary trajectories of reaction norms of populations previously adapted to an unstable environment -eg. a`wild' one-throughout the adaptive process to a novel, stable environment- e.g. a laboratory one. We have started a project of laboratory adaptation in which we founded laboratory populations of Drosophila subobscura from a wild one (W). This five-fold replicated study uses as controls five replicates of an established population sampled from the same region, already at the 90 lh generation (B). We are analysing periodically the reaction norins of these populations, as a function of nutrients and densities, in several life-history traits, both at the juvenile (viability and developmental time) and adult phase (fecundities and starvation resistance). Assays done during the first 11 generations give indications of differential plasticity between B and W populations, though the degree varies between the generations assayed, between traits, and between environments. In general recently introduced populations present smaller sensitivities to environinental changes than established populations. These findings will be discussed in the light of theoretical models on the evolution of plasticity.

#### The phylogenetic relationships of mysticete whales as revealed by the analysis of SINE alleles.

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The phylogenetic relationships of mysticete whales have recently received considerable attention. Past studies that have sought to reconstruct these relationships using molecular data, have used mitochondrial sequences exclusively. These studies have included analyses of homologous portions of the control region, 12S and 16S ribosomal genes, and cytochrome *b* genes. Ambiguous portions in the phylogenetic tree, including the placement of fin, humpback, blue, and gray whales, consistently lack robust bootstrap values. Through the use of SINE data we are seeking to more clearly understand the phylogenetic relationships among the mysticete whales. Several SINE loci have been isolated and analyzed phylogenetically (8 loci isolated in previous studies, plus those isolated for this study), resulting in former phylogenetic ambiguities becoming more clarified. The analysis of these SINE data, in conjunction with mtDNA data, have allowed us to more conclusively determine the phylogenetic relationships of SINE allele fixation.

# Investigating the local adaptation of ticks (Ixodes uriae) in a multi-host seabird colony.

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Recent theoretical work has shown that the degree of local adaptation in parasites and their hosts depends, in part, on their relative levels of dispersal. This work predicts that if parasites disperse more than their hosts, parasites will be locally adapted to their host population and hosts will be locally maladapted to their parasite population. If, however, relative dispersal is higher in the host, the reverse may be true. We tested this hypothesis using the ectoparasite *Ixodes uriae* and its seabird, host species. As this tick is closely associated with the host nest substrate and likely depends on its host for dispersal, we expected this parasite to have lower dispersal levels than its host. We examined intraspecific local adaptation in this system using a cross-fostering experiment of kittiwake (*Rissa tridactyla*) nestlings among infested breeding cliffs where relative fitness measures of hosts and parasites were, compared between resident and nonresident chicks. We also determined whether there was any evidence of interspecific local adaptation within a single multi-host colony by exchanging parasites of kittiwake and, puffin (*Fratercula arctica*) hosts. Results and their implications are discussed in a host-parasite coevolutionary framework.

### Molecular phylogenies for gene families using unaligned sequences

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Likelihood based methods are widely accepted as the best for inferring phylogenetic trees. In the past computational issues have limited their use, but modern methods of stochastic simulation have extended the range of problems they can address. In addition, recent advances in Bayesian modelling allow us to directly quantify the uncertainty associated with an inferred tree. We plan to extend these developments with particular emphasis on the gene tree problem. When estimating gene trees, some regions of the gene may have insertion and deletion events which may be difficult to align and will not be modelled adequately by standard likelihood methods. In practice, this data is often omitted despite the information contained in the pattern of gaps and insertions. We aim to improve phylogenetic tree inference methods by explicitly modelling these insertions and deletions. Markov Chain Monte Carlo (MCMC) will be used to sample tree space to find the most likely trees. We plan to include the alignment step in our model, so that the end result will be a procedure that samples from alignments and trees simultaneously.

### Molecular evolution of B-lactamases

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The inactivation of β-lactam antibiotics by β-lactamases is the main mechanism by which bacteria resist β-lactamas. Shortly after the introduction of penicilllins and cephalosporins into the clinic β-lactamase producing isolates became prevalent, but the number and variety of β-lactamases remained fairly steady for over 20 years. After novel β-lactam molecules, such as cephamycins, carbapenems, monobactams, oxyimino β-lactams, clavams and sulfones, entered the clinical arena, the number and variety of β-lactamases increased at an accelerated rate. Between 1989 and 1995, the number of recognized β-lactamases more than doubled and now exceeds 200. New functional groups, such as plasmid-determined extended-spectrum β-lactamases that hydrolyze oxyimino-β-lactams and chromosomally encoded class A carbapenemases, emerged. In some cases these novel β-lactamases surfaced only in limited geographic areas. Together with PBPs, the targets of penicillin action, the β-lactamases form a superfamily of penicillin-recognizing enzymes. New data on the evolutionary relationships of PBPs and different β-lactamase classes, coupled with new understanding of their three dimensional structure, has provided insights into how these enzymes have evolved in clinical settings. The exact relationship between antibiotic usage patterns and selection for specific resistance mechanisms remains, however, a mystery. Without better understanding of the processes that determine the evolution of resistance mechanisms in clinical isolates, we may not be able to forestall a return to a "preantibiotic era".

# Population structure of the African Grey Parrot Psittacus erithacus: a search for informative DNA markers

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The African Grey Parrot *Psittacus erithacus* is widely distributed in the lowland forests of Central and West Africa, including the islands of Bioko and Príncipe. This species shows a high phenotypic diversity throughout its range, making it an appropriate model to study the role of ecological divergence in speciation. We used samples from Príncipe island and Gabon populations to investigate the suitability of different molecular markers to address questions of population structure and gene flow. The polymerase chain reaction (PCR) was used to amplify fragments from the mitochondrial DNA cytochrome-b and control region, the seventh intron of the b-fibrinogen nuclear gene, and microsatellite loci. The markers that were informative in the African Grey Parrot are presented. Preliminary results of genetic differentiation between Príncipe island and mainland populations and their conservation implications are discussed.

### Phylogenetic analysis of Drosophila class I and II transposable elements

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*Gypsy* and *bilbo* are class I transposable elements (TEs), which mobility is achieved through an RNA intermediate by the *reverse transcriptase* that they encode. *Gypsy* belong to the LTRs-flanked retrotransposons group or retrovirus-like, while *bilbo* lacks of LTRs, that is why is called LINE-like. TEs class II or DNA mobilised by a *transposase* are represented by *P*, the best characterised of this elements.

TEs sequences from *Sophophora* radiation species group were obtained using three pairs of PCR primers flanking: a conserved region of *P-element transposas*e gene, a *bilbo reverse transcriptase* preserved sequence and a region comprising from *reverse transcriptase* gene to a less conserved *env* region in the case of *gypsy*. The outcome TEs phylogeny is in general congruent with the species phylogeny, indicating a predominant vertical transmission, from generation to generation. *P-element* shows clear indications of four horizontal transmissions between species belonging to the groups: *melanogaster-willistoni; obscura-saltans* and *willistoni; willistoni-obscura; obscura-Scaptomyza* genus. These fates are not so evident in *bilbo* and *gypsy*, elements mobilised by a *reverse transcriptase*. The influence of the transposition mechanism and host influence on TEs evolution is discussed. The stronger sex weakened as well? Late-acting inbreeding depression in both male and female function of an hermafroditic plant.

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Inbreeding depression is an important selective force in the evolution of plant reproductive systems. In order to estimate the level of inbreeding depression, the complete life-cycle of the progeny should be screened. Most studies have been restricted to survival and growth in early life-stages. If generative life-stages have been included, often only the female function of flower and seed production have been considered. Inbreeding depression in the male function as siring success of the plant has received little attention. We will present data on the inbreeding depression in pollen performance, siring success and seed production in *Echium vulgare*. The production of seeds per flower was declined by 35 to 40% in plants derived from selfing. Pollen viability and rate of pollen tube growth were both lower for pollen from plants derived from selfing than for pollen from plants derived from selfing that for both lower for pollen from selfing. Inbreeding depression values for male and female functions were not correlated. Both functions must therefore be considered when calculating inbreeding depression. Presentation preferably in Symposium no. 1. (Molecular population genetics).

### Male-female conflict and the management of giant sperm in Drosophila bifurca

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Evolution has usually favored the production of a large number of tiny sperm. They are simply considered as paternal genes carriers representing a very small energetic investment, but endowed also with a very small paternity insurance. Numerous studies have demonstrated that such gametic strategy has been developed in response to intense sperm competition. The present report highlights another gametic evolutionary solution, which insures very high paternal insurance of fertilization and minimizes the postcopulatory female choice, *i.e.*, sperm gigantism. It has been studied in the Drosophilidae where more than 50% of the species analyzed until now have sperm longer than the body size. Sperm competition in female and sperm management by male were studied in *D. bifurca*, which has the longest sperm in the animal kingdom (about 6 centimeters).

Our study reveals an unusual reproductive strategy in which sperm rather than eggs are the limiting resource. Males partition their sperm stock among a maximum of 5 consecutive copulations with virgin females in one day, transferring a decreasing amount of sperm (from 62 to 9). From the second successive mate, they transfer less sperm than the number of ova they could fertilize (44). This situation favors female remating in order to replenish their storage organs. Such a behavior insures fertilization of all mature ovarioles in one time. Normally, female copulation with fully sexually mature virgin male give rise after 5 days to a laying of a first batch of about 44 fertile eggs. Then, female becomes receptive for another mate or, without males, lays successive batches of sterile eggs each 8 days until her death. When polyandry is observed, the second male transfers less sperm than if it was the first one. Sperm competition is thus very limited in this species. The sperm partitioning among mates is allowed by the peculiar morphology of male seminal vesicles in *D. bifurca*, which store sperm in single file. This unusual morphology in Drosophilids can be seen as a 'pea shooter' delivering sperm one by one.

We conclude that this partial re-establishment of isogamy by an increase in sperm size and a decrease in sperm number coincide with a particular sexual conflict between males whose fitness depends on the fragmentation of their sperm stock, and females whose fitness depends on the sperm number transferred during each copulation. The reproductive strategy associated with giant sperm gives to the male a weapon, which seems to be very powerful against the female control of paternity. Sperm gigantism represents an evolutionary 'cul-de-sac' in which selection has probably been so intense that sperm competition no longer exists, and individual sperm insurance is extremely high, an outcome improbable in the theory of anisogamy. One possible way for female to equilibrate the sexual conflict would to influence its offspring quality by premating choice, which should now be tested experimentally.

### The detection of clonal evolution in Taraxacum: a question of scale.

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Though traditionally assumed to have a high potential for asexual reproduction via apomixis, triploid individuals of *Taraxacum* from Northern Europe have signatures of sexual reproduction. Due to the excellent possibilities for dispersal, we could not refute that the genetic exchange originated in Southern Europe, where diploids occur. The chloroplast genome of section *Naevosa* that occurs primarily in Scandinavia is monophyletic and distinct from all sympatric dandelions. If only sexual reproduction had occurred among triploid dandelions, no sexual generations are expected among individuals of the *Naevosa* clade. This is exactly what has been found among the Norwegian individuals. Among the Danish, British, and Norwegian *Naevosa* plants however, a strong signal for sexual generations separate the individuals. If the sexual reproduction has occurred in NW Europe, i.e. without involvement of diploids, models of apomictic reproduction and geographic parthenogenesis are impaired because "facultative" asexual reproduction of triploid dandelions have not yet been incorporated.

### Spatial and temporal lethal-gene allelism in American colonizing populations of Drosophila subobscura

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About twenty years ago *Drosophila subobscura*, a typically Palearctic species, colonized both North and South America. The study of lethal genes in the O chromosome of this species has revealed certain aspects of this process. The aim of the present study has been to follow the evolution of the American populations of *D. subobscura*. The lethal-gene content of the population of Centralia (Washington) was analyzed. The frequencies of lethal and semilethal genes were  $16.9 \pm 4.6$  and  $6.2 \pm 3.0$ , respectively and the intrapopulational allelism was studied. Interpopulational allelisms were examined using lethal genes from populations separated in space and time from Centralia. The intrapopulational allelism of Centralia was  $0.122 \pm 0.036$ , but the interpopulational allelisms between Centralia and Gilroy I (California) and between Centralia and Bellingham (Washington) were even higher ( $0.155 \pm 0.032$  and  $0.153 \pm 0.024$ , respectively). All these cases of allelism are due to the complete association between a lethal gene shows that it is found in a significantly higher frequency than expected, suggesting that the O inversion, to which the lethal gene is completely associated, has a heterotic effect. The significant latitudinal clines of this inversion, its frequency higher than expected in inbreeding experiments and its significantly higher segregation in recombination studies support this hypothesis.

### Adaptive emergence of reproductive isolation

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Can reproductive isolation emerge by selection for assortative mating during speciation process?

Evolutionary branching was observed in frequency-dependent clonal selection models at convergent stable but evolutionary unstable singular strategies. It was suggested that this result may generalise for sexual organisms, as well, because the disruptive nature of selection at the branching strategy promotes selection for reproductive isolation. We investigate this issue in a population genetical model as simple as possible.

In our model, there are two independent loci, an ecological one and a mating strategy one. Lotka-Volterra type competition is supposed between the ecological genotypes. Evolution on the mating choice locus is followed by invasion analysis.

By and large, it is true that heterozygote inferiority selects for reproductive isolation while heterozygote superiority selects for random mating. However, the process of emergence of reproductive isolation is sensitive for the strength of competition between the genotypes.

Diversity of the ecological locus is lost during the process of isolation if the competition between the homozygotes is too strong and the selection is not symmetric enough.

Evolution stops at an intermediate assortment value if competition between the heterozygote and the homozygotes is too week, because the number of heterozygotes becomes low at low assortment and they are no longer inferior.

We conclude that adaptive emergence of reproductive isolation is a feasible process in well defined situations but the branching type singularity alone doesn't ensure this to happen.

### Heritability estimates of two metric traits by different methods in two Parus species

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Metric traits, such as body size may have effects on the fitness of idividuals and thus are under selection. Consequently, it is important to determine the heritability of these traits to predict the effect of selection. In this paper we compare the results of 5 different methods of estimating heritability farsus length and body weight. Our data were collected on *Parus major* and *P. caeruleus* in 1988 and 1989, We estimated  $h^2$  based on female-offspring, male-offspring and mid-parent-offspring regressions and from a full-sib analysis in both years. Further in 1989 we carried out a cross-fostering experiment (half of the sibs were exchanged between two nests of the same age) and calculated  $h^2$  from a 2x2 factorial nested ANOVA design. The obtained  $h^2$  values varied between the two years and the two sexes. The mid-parent-offspring regressions gave the most balanced results. The full-sib analysis seemed to overestimate heritability of both traits only in *P.major*. The  $h^2$  value calculated on the basis of the cross-fostering experiments corresponded well with the  $h^2$  estimation obtained from the female-offsring regressions in both species in both years. Our results suggest that those heritability estimates should be accepted when similar results are obtained by different methods.

### Patterns and processes in the evolution of the East African adaptive radiations of cichlid fishes

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The species flocks of cichlid fishes in the largest East African Lakes, Victoria, Malawi and Tanganyika, are well-known examples of adaptive radiations and explosive speciation. These species assemblages are the most species-rich and the most diverse, morphologically, ecologically and behaviorally among vertebrates. Phenotypic and genotypic data sets are expected to provide concordant phylogenetic information about these species assemblages, since both share identical evolutionary histories. Molecular data however have some advantages for phylogeny reconstruction over morphological data, such as the ability to discover parallel evolution and analogy which tends to be more difficult and potentially misleading in morphological data sets. Our understanding of the phylogenetic relationships among East African cichlid fish species flocks has increased dramatically during the last 10 years since the invention and application of the polymerase chain reaction which hughly facilitated the collection of molecular data for molecular phylogenetic, phylogeographic and population genetic research on cichlids. Phylogenetic analyses of recent molecular data in the context of the geological history of the East African lakes helped to elucidate some aspects of the evolutionary history and the evolutionary processes that might have lead to the origin of these extraordinary fish faunas. Here, I will attempt to review and summarize some of these advances and insights that were made both in terms of phylogenetic patterns as well as evolutionary processes in the last decade through the use of molecular data. I will also highlight the unexpected findings that sometimes resulted, point out which avenues of research are still unexplored and suggest where future work might yield further interesting insights in the origins of the adaptive radiation of the East African cichlid species flocks.

# Patterns and processes of speciation in fishes from freshwater and marine environments -a preliminary comparison

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With the advent of the polymerase chain reaction and "universal" primers for mitochondrial genes a comparative data base for the most commonly used molecular markers accumulated. The most commonly used mitochondrial markers for freshwater and marine fishes are the large ribosomal (16S) gene, the cytochrome b , gene, and the control region or D-loop. This "metric" of homologous genes and gene regions permits comparisons among population genetic and phylogeographic studies of different species of fishes. There are pronounced differences in the nucleotide diversity index and other measures of intraspecific variation between species suggesting that population parameters such as effective population size and the age vary strongly between species. Comparisons of studies from freshwater and marine fish species that are based on molecular markers will be used to investigate whether phylogenetic relationships, through 'phylogenetic constraints' are causing consistent patterns of genetic variation and whether mechanisms of speciation might also be taxon specific.

### Stage-dependent decisions in a parasitic copepod practising environmental sex determination

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Evidence is accumulating about the way strategic decisions over an organism's lifetime may depend on its state and on external circumstances. In the parasitic copepod *Pachypygus gibber*, sex is environmentally determined when the free-living infective stage (Copepodid 2) enters the host, the sea squirt *Ciona intestinalis*. Whereas in a rich trophic environment the copepodid 2 develops into a typical male or into a typical female (both are unable to swim and must remain inside the host), in poor trophic conditions it develops into an alternative free-living stage able to swim and to leave the host, the atypical male. Thus this copepod life cycle is characterised by two fundamentally different free-living stages. We conducted an experimental study to compare the priority decisions of the copepodid 2 and of the atypical male in their habitat selection behaviour. We showed that while copepodid 2's are mainly attracted by chemicals released by the host into the water, atypical males only respond to female and typical male cues. We discuss the adaptiveness on this behavioural difference in light of the ecological constraints met by the different stages of *P. gibber*.

### Molecular phylogeny and evolution of mitochondrial genes in terrestrial isopods.

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*Oniscidea* is a very large and diversified group of crustaceans. This sub-order of *Isopoda* includes only terrestrial species which is unique among *Crustacea* phylum. More than 4000 species are recorded living in various environments from semi-aquatic to arid habitats, all over the World. Some cladistic analyses have been recently proposed based on morphological characters, but they lead to contradictory results. Debates among authors concern essentially the position of two families of *Oniscidea* : *Tylidae* and *Ligiidae*, considered alternatively as primitive or recently derived. Other crucial points are the relationships between terrestrial and different aquatic isopods, and the origin of the group i.e. whether it is or not a monophyletic clade.

In order to avoid problems of morphological adaptive convergences, two mitochondrial genes (coding for CO1 and for 16S rRNA) have been chosen to build a molecular phylogeny of Oniscidea sub-order. Trees have been constructed from partial sequences of each gene and from a total data matrix containing all characters. Similar results are found with all data-sets and favoured an ancient divergence of both *Tylidae* and *Ligiidae* families. A paraphyletic origin of terrestrial isopods could be compatible with our results.

Moreover, the structure of mt rRNA of terrestrial seems to be very special for terrestrial isopods. By comparing with known secondary structures, specific deletions have been found for sequences of terrestrial isopods. Secondary structures have been determined and compared in several species of aquatic and terrestrial isopods.

Life history variation in a species flock: Phylogenetic perspectives on linking early ontogenetic morphology with brood and embyro sizes in *Lavigeria* gastropods from Lake Tanganyika, Africa

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Species flocks, by definition, include clades of closely related, sympatric species endemic to a delimited geographic region. Their existence challenges standard allopatric models of divergence and maintenance of species boundaries, and alerts us to the potential influence of other biological characters that may bolster divergence in sympatry. Lake Tanganyika, the oldest and deepest of the African rift lakes, harbors species flocks in numerous taxa, including several highly divergent, marine-convergent gastropod clades. These provide important comparisons with other diverse taxa such as the cichlid fishes in these natural laboratories of evolution, because 1) gastropods are ecologically central as they are the major benthic grazers in the rocky littoral zone; 2) gastropods are sympatric with other diverse taxa, thus provide comparison tests for hypotheses of extrinstic speciation mechanisms such as paleo-allopatry; 3) gastropods exhibit similar species-flock like variation, with some fuzzy species boundaries and hypervariable taxa, (implying retained ancestral polymorphism or hybridization), and other taxa clearly delimitable; 4) gastropod shells are fossilizable, leading to potentially deeper temporal perspectives, and include a record of ontogeny from the juvenile to the adult as a result of accretionary growth. The most diverse gastropod clade in Lake Tanganyika is Lavigeria (Cerithioidea: Thiaridae) including a minimum of twelve species of brooding gastropods, and two species of egg-layers. As we suspect that life history influences divergence for this group, we have documented differences in brood and embryo sizes at the species and population level for several ovoviviparous species in Tanzania. Life history differences correlate with morphological differences in the early ontogenetic shell (i.e. the protoconch and early teleoconch) which allows an extended comparison of variation across the full range of distribution of this clade using museum collections. Finally, we analyze the changes in life history in phylogenetic context by mapping these characters on a COI and 16s-ND1 mtDNA sequence phylogeny of this clade.

### Penis fencing in marine flatworms: pre-programmed escalation and the thin line between war and peace

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Pseudocerotid flatworms transfer sperm by hypodermic injection using 1 or 2 stylet-shaped penises (Michiels & Newman 1998, *Nature 391: 647*). Because individuals are hermaphrodites, all can stab and be stabbed. The overall chance of either happening is always 50%. Because receipt is costly, individuals attempt to maximise the gain (stabbing a partner) over the cost (being stabbed), resulting in escalated contests in which a mixture of attack and defence mechanisms is employed.

Observations on 5 *Pseudoceros* species (w. 1 penis) and 5 *Pseudobiceros* species (w. 2 penises) revealed that the degree of aggression and the damage inflicted are positively related with the likelihood that sperm transfer is unilateral. Sexual interactions range from peaceful, reciprocal, frequent mating to extremely aggressive hit-und-run tactics in which animals loose large parts of their body due to a unique sperm transfer mechanism. This unexptected mosaic in such closely related species suggests that the chance

This unexplected mosaic in such closely related species suggests that the chance

origin of a new defensive or offensive trait can force a population of hermaphrodites like these to accept a peaceful compromise or engage in a violent war.

### **Evolution of Individuality and New Levels of Fitness**

### Richard Michod

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The evolution of multicellular organisms is the premier example of the integration of lower levels into a single, higher-level individual. Explaining the transition from single cells to multicellular organisms is a major challenge for evolutionary theory. In this paper I provide an explicit two locus genetic framework for understanding this transition to a new unit of fitness in terms of the increase of cooperation among cells and the regulation of conflict within the emerging organism. Heritability of fitness and individuality at the new level emerge as a result of the evolution of organismal functions that restrict the opportunity for conflict within and ensure cooperation among cells. Conflict leads—through the evolution of adaptations that reduce it—to greater individuality and harmony for the organism.

# Genetic evidence for the effects of Pleistocene glaciations on the phylogeography of MacGillivray's warbler, a neotropical migratory bird.

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The genetic structure of MacGillivray's warbler (*Oporornis tolmiei*) was examined throughout its breeding range in western North America, including an isolated population in NE Mexico. Analysis of mtDNA sequence from the cytochrome *b* gene and the control region revealed marked differentiation between the NE Mexican and the USA populations, with sequence divergence in cytochrome *b* averaging 2.1% (range 0.9-2.8%). Patterns of mtDNA variation within the USA populations were consistent with expectations of a Pleistocene population expansion over the northern part of the range following a period of low female effective population size as indicated by the presence of a single widespread ancestral haplotype, little genetic subdivision, a star-like phylogeny of alleles, and a Poisson-shaped mismatch distribution. By contrast, mtDNA patterns in the NE Mexican population showed high levels of nucleotide and haplotypic diversity and a geometric mismatch distribution, as expected for a refugial population in long-term stable demographic equilibrium. Southern refugial populations unaffected by Pleistocene glacials have the potential to reveal historical patterns of genetic variation and provide crucial insights into general phylogeographic patterns of temperate North American bird species. Moreover, these refugial populations may harbor large proportions of a species' genetic diversity and evolutionary potential, and deserve further study.

# The role of predation in driving evolutionary trends: tests using Neogene muricid gastropods from tropical America.

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Predation has long been viewed as an important agent of natural selection. However, the role of predation in generating evolutionary trends that may span many millions of years remains poorly understood. Marine gastropods belonging to the family Muricidae provide an excellent group that can be used to explore this question. Muricids exhibit a wide array of shell architectural features that aid in resisting shell-crushing predators, including well-developed spines and shell thickenings. Moreover, muricids are diverse and well represented in the Cenozoic fossil record, permitting the documentation of evolutionary patterns. In this study I document patterns of morphological evolution in specific clades of tropical American muricids and use these to test the hypothesis that predation was a major driving force in morphological evolution. Cladistic analyses of the subfamily Muricinae were performed to provide the phylogenetic framework necessary to further interpret morphological trends.

Preliminary analyses of these data reveal complex patterns of morphological change. *Haustellum* and *Siratus*, which are among the most strongly ornamented muricines in tropical America, occupy relatively derived positions on the cladograms. Furthermore, the most derived members within these taxa are also the most heavily ornamented and are stratigraphically the youngest as well. While simple directional trends are not apparent at the subfamily level, the presence of trends in the most ornamented clades within the subfamily does suggest that predation was indeed an important agent of morphological evolution.

# Differences in the evolutionary outcome induced by dynamics of coinfection and superinfection in Vesicular Stomatitis Virus.

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The studies about evolution of viral virulence have focused on computing the evolutionarily stable level of virulence favored by tradeoffs within a host, by intra-host mutation of the virus and by competition for hosts. The evolution depends on the type interaction between disease strains, such as single infection (infection by one strain) coinfection (simultaneous infection by two strains) and superinfection (where an already-infected host is infected by another strain). The VSV populations are highly polymorphic, during the course of an infection viral variants may be generated that have some competitive advantage over the strains that initiated the infection, so that we can simulate the interaction between strains as interaction between different isolated viral quasiespecies employing an *in vitro* cell system. Our results demonstrated that coinfection leads to an higher virulence level than that found in the single infection model. Although, superinfection tends to lower virulence level in superinfection is similar to a single infection model. Although, superinfection tends to lower virulence than coinfection model, this result is in disagreement with the theoretical models about superinfection, but in these models it is supposed that a more virulent parasite can infect and "take over" a host that is already infected by a less virulent parasite strain.

# Population genetics and temperature reaction norms in a geographically widespread zooplankter, *Daphnia* magna.

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Evidence for temperature adaptation was inferred from changes in the optima and shape of temperature reaction norms for somatic growth rates. Ex-ephippial clones from eight populations across Europe were grown under standardised conditions at six temperatures (17-32°C). Clones from the same population exhibited significant variation in somatic growth rate and temperature reaction norm. However, although population mean growth rates were significantly different, the average population temperature reaction norm was parallel for all populations, with no significant difference in shape or the temperature range for optimal growth,  $23^{\circ}$ C -  $26^{\circ}$ C. Thus, local adaptation appears to have occurred, but probably in response to a factor other than temperature. Possibly, such a pattern may result from the nature of intermittent populations where diapause can be utilised to entrain the planktonic stage of the life-history within a range of temperatures.

Allozyme electrophoresis was used to genotype all ex-ephippial hatchlings from each population. Patterns of population genetic differentiation will be discussed in comparison to the geographic distance and ecological variation, represented by characteristics such as growth rate, body size and clutch size.

### Breeding structure of fig associated wasps

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Fig wasps have played a central role in our understanding of sex ratio evolution (Hamilton 1967, Herre 1985, 1987, Frank 1985). Predictions and tests of local mate competition are based on assumptions about the breeding structure of the population. So far the breeding structures of various fig wasp species have been inferred from the number of foundresses found in the fruits. We developed microsatellite markers to directly determine the parameters of the breeding structure predicted to influence sex ratios. We used multilocus genotypes of individual wasps, to estimate inbreeding coefficients of several species collected in the Republic of Panama. These genetic data allowed us to determine the exact relationship between inbreeding coefficients and the observed foundress numbers and sex ratios, both for pollinating and parasitic species, and thus to conduct precise quantitative tests of adaptation.

### Relating phylogenetic patterns to short term selection experiments on butterfly wing patterns

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Lab selection experiments on eyespot morphology in one species of *Bicylus* butterflies have shown that there is plenty of additive genetic variance for size and color composition and that these traits can change rapidly. Although selection was done on only one eyespot, correlated responses in all other eyespots were observed. A molecular phylogeny of 54 species of the butterfly genus *Bicylus* was used to test specific hypothesis of eyespot morphological evolution. Given the high additive genetic variance for size and colour composition found for one species, we tested whether there was high lability of these traits across the whole genus. Also, we tested whether the presence of eyespots and/or change in their relative sizes was, in contrast, more constrained by phylogenetic history.

### Contrasting levels of nucleotide diversity at the avian Z and W sex chromosomes

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The neural theory of molecular evolution states that in absence of selection, the mutation rate should generally be the driving force. It is consequently assumed that levels of nucleotide diversity (intraspecific polymorphism) in neutral DNA sequences should be governed by the local mutation rate, a hypothesis which lacks empirical support. Recent studies of sex chromosomes have provided evidence for a higher mutation rate among males than females. Thus in birds, the Z chromosome, which spends two-thirds of the time in male germline, evolves faster than the female-specific W chromosome. We show now that levels of nucleotide diversity are drastically higher on avian Z chromosomes than on W chromosomes. In fact, no intraspecific polymorphism whatsoever was observed in about 2,3 kb intron sequence from a total of 83 W chromosome copies of four different species. In contrast, the average pairwise nucleotide diversity (*B*) between Z chromosome introns was  $1.4x10^{-3}$ . We argue that this cannot be explained by selective sweeps on the W chromosome, but is most likely due to the lower mutation rate of females. This supports the idea that the degree of genetic variability at neutral loci is determined by the local mutation rate. Speciation events within the catfish genus Hypostomus (Loricarfidae) relate the colonisation history and ancient patterns of neotropical river systems.

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The catfish genus *Hypostomus* (Loricariidae) is distributed in all tropical south American freshwaters, from northem Argentina to Panama. All members of this genus are sedentary, short distance swimmers, and their preferred habitats are strearns and small rivers with running waters where they live stuck to the substrate. Due to this way of life, speciation events can mainly be linked to river disjunctions followed by new connections to neighbouring rivers. The knowledge of *Hypostomus* evolutionary history would allow the reconstruction of ancient patterns of neotropical river systems and their colonisation history.

The phylogeny of *Hypostomus* species belonging to all main neotropical drainages was inferred using DNA sequences of the mitochondrial D-loop region. Our analyses show that this genus is paraphyletic as it includes representatives of some closely related genera. However, four main clades have been identified, each one revealing different aspects of the history of tropical south American rivers and their colonisation.

# Extinction is more than a field of bullets: simulating the loss of evolutionary history due to anthropogenic extinctions

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In 1997, Nee and May (Science 278:692-694) presented provocative evidence that a single round of random extinction on randomly evolving clades removed only a small proportion of the extant evolutionary history. Maximizing the amount of history retained through judicious choice of the taxa to cull allowed only a marginal improvement. For comparison we investigated the effects of plausible nonrandom extinction on plausible nonrandom trees. Previous consideration of tree shape suggests that the probability of speciation may differ across lineages at any time and may be heritable across lineages through time. We simulated such trees and then subjected them to various sorts of culling. When the probability of present-day extinction was correlated with a character which shows phylogenetic inertia (and most aspects of the extended phenotype do show some such inertia), the amount of evolutionary history removed by extinction increased somewhat. When the probability of present-day extinction was made positively correlated with past diversification rates (species living in the tropics may be an example) the amount of evolutionary history removed first increased slightly as rate variation increased and then diminished to almost the minimum possible. When present-day threat and past diversification success were negatively correlated (large-body size may be an example) the amount of total evolutionary history removed increased steeply with increasing rate variation. For our model of exponential diversification, increasing the variation among lineages in speciation rates also increased the maximum amount of history which could be retained. Taken together, these results suggest that the amount of extant evolutionary history lost through anthropogenic extinctions might be both more substantial (bad news) and more manageable (good news) than May and Nee first suggested.

### Deciphering the early evolution of eukaryotes using new analysis methods

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Because the most ancient eukaryotic fossils are difficult to interpret and morphological data from extant species are not always phylogenetically discriminatory, the prevailing model of early eukaryotic evolution is almost entirely based on comparative sequence analysis, particularly of ribosomal RNA. This model of eukaryotic phylogeny shows several early-emerging protist lineages, mostly amitochondriate, which are considered as living relics of the progressive assembly of the eukaryotic cell. This implies a step-by-step evolutionary process. However, contradictions in phylogenies obtained using other markers, and the finding of genes of unequivocal mitochondrial origin in the genomes of these amitochondriate protists, question the validity of the current paradigm. We have analysed this problem using a new method (the Slow-Fast) that allows extracting the most reliable phylogenetic information, which is contained in the slowest-evolving positions. These positions keep much more information than the fast-evolving positions, which are strongly affected by mutational saturation. Misleading results are usually obtained when fast-evolving positions are included in the analyses, since they are more abundant and overwhelm the information of the slow-evolving ones. Our results clearly demonstrate that all the early-emerging taxa actually evolve fast, and consequently appear misplaced at the base of the tree by a long branch attraction artefact. Since, depending on the markers, the fast-evolving taxa attracted to the base are not always the same, this also explain the contradictory phylogenies. Phylogenetic evidence suggests that the emergence of all major groups took place during a short time span (a radiation). In fact, this model fits all available data more accurately than the classical step-by-step model. As a result of their rapid diversification, the relative order of the eukaryotic groups is very difficult to infer. The use of rare events, such as shared insertions or deletions, or gene fusions, will be of great value for this task.

# Consistency between vertebrate codon usage and dinucleotide preferences is reduced in (G+Q-rich sequences

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Vertebrate genomes can be divided into compartments of homogeneous GC-content (isochores). We contemplate three interesting findings. First, the vertebrate codon usage follows the composition of the isochore in which the genes reside (Aissani et al., 1991. J. Mol. Evol. 32, 493-503). Second, there is high degree of concordance between vertebrate codon usage and dinucleotide preferences (the discrepancy between the observed and the expected frequency of nearest neighbouring bases) (Nussinov, 198 1. J. Mol. Biol. 149, 125-131). Third, dinucleotide preferences differ in genes of varying GC-content (Gutiérrez et al., 1993. J. Mol. Evol. 37, 131-136).

One can speculate on the causal relationship(s) between base composition, codon usage and dinucleotide preferences. Since codon usage and dinucleotide preferences both changes with different GC-content, one might speculate whether they origin from the same underlying mechanisms. A prerequisite for this common cause would be a constant level of consistency between codon usage and dinucleotide preferences regardless of the GC-content. Consistency between codon usage and dinucleotide preferences was calculated for sequences from *Homo sapiens* (human) and *Xenopus laevis (Xenopus)*, sorted according to their GC3-content (the GC-content of the third codon positions).

We find that the level of consistency between codon usage and dinucleotide preferences decreases with increasing GC3-content in both species. Since codon usage follows the regional GC-content very closely, it seems unlikely that the GC-enrichment and the preferences for dinucleotides are facilitated by the same mechanism.

Evidence for multiple selective sweep effects in association with the In(2L)t inversion in Drosophila melanogaster.

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The hitchhiking model of population genetics predicts that an haplotype associated with an advantageous mutation on a linked locus can replace haplotypes from the same locus previously established at a neutral mutation-drift equilibrium. The lower the recombination rate, the larger the hitchhiking effect. Inversions, since they strongly inhibit recombination between chromosomal types, are useful to reveal selective sweeps. Sequence variation was recorded at three loci located on the left arm of chromosome II of *D. melanogaster* in an African population in association with the In(2L)t inversion.

At the Supressor of Hairless (Su(H)) gene, two haplotypes (one in each chromosome arrangement) made up two third of the sample; this low haplotype diversity departed significantly from neutrality in an haplotype test. Closer to the inversion breakpoint the vacuolar ATPase (Vha) locus showed lower polymorphism and high divergence with D. simulans. This discrepancy in the polymorphism over divergence ratio between the two genes departed from neutrality, as revealed by the HKA test. Though these data support recent selective sweep effect at Vha and Su(H) locus, in the region located between these two genes, the sequence variation of the Sos gene shows no similar effect. It is thus hard to determine whether this results from one selective sweep event associated with the inversion or from two independent selective sweep events. Two hypotheses can be put forward : either a single event associated with the inversion produced two selective sweeps or two independent selective sweep events occurred.

### The evolution of agriculture in ants

### Ulrich G. Mueller

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Cultivation of fungi for food originated about 50 million years ago in fungus-growing ants (Attini). The subsequent evolutionary history of this agricultural symbiosis was inferred from phylogenetic and population-genetic patterns of 553 cultivars isolated from gardens of "primitive" (phylogenetically basal) fungus-growing ants. A phylogeny for 57 representative ant-cultivated fungi and 36 closely related free-living fungi, combined with population-level (RFLP) and AFLP fingerprinting analyses, indicates that:

a) fungus-growing ants succeeded at domesticating multiple cultivars during their evolutionary history;

b) some domestications occurred recently in evolution, and some extant ant lineages may still domesticate novel fungi on occasion;

c) single ant lineages farm a diversity of cultivars;

d) ants are capable of switching to novel cultivars, even though cultivars are normally vertically propagated through the transfer of clonal inocula from parent to offspring nest;

e) cultivar clones are shared occasionally between distantly related ant species, probably via lateral transfer between ant colonies.

These results demonstrate remarkable evolutionary convergence between ant and human agriculture and reveal an unexpected complexity in these nonhuman agrarian societies. Domestication of free-living fungi continued following the origin of fungus-growing behavior, and, along with cultivar exchange between ant species, may have persisted for 50 million years of ant evolution as a means (i) to replace cultivars after accidental or pathogen-driven loss of gardens, (ii) to respond to environmental changes by acquiring cultivars with novel features, or (iii) to capitalize on strains that were improved while associated with other ant lineages. If exchanges occur frequently among ants, as population-genetic patterns suggest, the history of ant agriculture may have been characterized by the same rapid lateral spread of cultivars that has shaped the history of human agriculture.

### Dynamic genetic structures of invaded Amphipod and Dreissena populations

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A rapid invasion is supposed to be accompanied with genetic impoverishment via the founder effect. Depending on the mode of dispersal, a patch-like distribution of the residual genetic variation can persist for many generations. We tested these hypotheses by investigating the genetic structure of the Central European invaders *Dikerogammarus* spp., *Corophium curvispinum* and *Dreissena polymorpha* by allozyme electrophoresis and mtDNA sequencing. These riverine species are well suited to study invasion processes, because the routes and tempi of invasion can be reconstructed via public databases. The genetic structures appeared to be out-of-equilibrium with some patch-like patterns. The temporal dynamic of genetic mixing is exemplified with *Dreissena* across a recently opened canal.

### 3D-visualization of morphological structures and gene expression patterns in development

# Johannes Streicher, Markus A. Donat, Wolfgang J. Weninger, Bernhard Strauss, and Gerd B. Müller

### Integrative Morphology Group, Department of Anatomy, University of Vienna, Austria

A future integration of genetics, development, and phenotypic evolution requires the development of appropriate tools for three-dimensional representations of genetic events in pattern formation and morphogenesis. Here we present a highly automated method for the combined 3D-visualization of gene expression signals and morphological structures from serial sections of whole-mount in-situ-hybridized embryos. For a demonstration of the method, we have reconstructed mouse embryos stained for the neuronal marker gene Scg10. Drill holes introduced into a permanent embedding medium prior to sectioning serve as external markers for automatic, macro-driven congruencing (realignment plus rectification) of the digital images captured from microscopic sectional views. Segmentation of the gene expression signals and the boundaries of morphological features is subsequently performed by another macro. Additional morphological features are segmented semi-automatically. From this protocol result stacks of binary images containing the gene expression patterns and the desired morphological structures. Reintegration of all sectional representations of a series is then performed on a workstation using a commercially available software package. In addition to the advantage of obtaining three-dimensional representations of complete gene expression patterns, which can be easily viewed from all angles, the Scg10-models show that high resolution reconstructions reveal new aspects of gene expression topography that cannot be seen by conventional visualization methods such as whole-mount or single-section *in-situs*. In addition, the 3D-models can be made universally accessible in www-databases.

### Epigenetic constraints in morphological evolution

### Gerd B. Müller

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Developmental constraints are often perceived as representing merely a limiting factor in phenotypic evolution, or, in more generous accounts, as the cause of certain biases on the production of variant phenotypes. This paper will argue that developmental constraints have a more active role in evolution by causing morphological innovations and providing the organizational basis for homology. The emphasis will be on epigenetic constraints, a particular class of developmental constraints comprising those constraints that arise from the non-programmed components of developmental systems. These are influential both in primitive and advanced forms of development, but, as evolution proceeds, the prevailing epigenetic factors change fundamentally. While physical and generic tissue properties represent the major epigenetic components of primitive development, conditional inductive interactions among the constituent tissues predominate in advanced development. Eventually, the new interactions arising from these constraints become secondarily captured and routinized by genetic circuitry, which serves to channel and reinforce the epigenetic templates. In this scenario the generative factors in morphological evolution are distinct from those ensuring heritability and variation.

### Homeotic duplication of the pelvic body segment in anuran tadpoles

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Homeosis, the ectopic formation of a body part, is one of the key phenomena that prompted the identification of essential selector genes in development and highlighted their role in evolution. However, homeotic transformations of the same order of magnitude as seen in insects are rarely observed in vertebrates. Here we report the capacity of retinoic acid to induce the homeotic duplication of a whole body segment in vertebrate axial regeneration. Treatment of tail-amputated anuran tadpoles (*Rana temporaria*) with retinoic acid results in the generation of a pelvic body segment at the mid-tail level, including vertebral elements, pelvic girdle elements, and limb buds. These results are in contrast to the "one way" rule (Einbahnstrasse), which predicts that in normal development only homeotic transformation into more caudal structures is possible. Based on the current concepts relating retinoids, homeobox genes, and developmental patterning in vertebrates, we conclude that in dedifferentiated, regenerating blastemata retinoids can also induce an anteriorization of the expression of homeotic genes in axial development, leading to the respecification of a rostral body segment at a distant caudal level.

#### Population biology of carried and invasive isolates of Streptococcus pneumoniae

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The population structure of *Streptococcus pneumoniae* in a sample of 134 carried, antibiotic susceptible isolates was examined using a DNA based version of multi locus enzyme electrophoresis: multilocus restriction analysis (MLRA) - involving RFLP analysis of PCR products generated from 9 loci of house keeping genes located around the pneumococcal chromosome. Antibiotic susceptible carried (throat or nasopharyngeal) isolates from Oxford and Manchester (UK) and from an HIV positive cohort Nairobi, Kenya, showed an epidemic population structure. Twelve carried clonal groups each with different serotypes, were identified at both locations within the UK. Three of these carried clones identified within the UK were found to possess identical RTs (restriction types) to several invasive isolates from either Spain or Uruguay, indicating that these particular carried clones are also associated with cases of invasive disease. As expected from previous studies, the population of 53 invasive, mainly penicillin resistant isolates was also found to be at linkage equilibrium. Serotype switching among RTs was identified among 13% of clusters that possessed two or more members. A single non-typable isolate from an HIV seropositive patient in Kenya, although included within this study on the basis of possessing typical pneumococcal phenotypes for bile solubility and optochin susceptibility, and being positive for previously believed robust diagnostic tests, was clearly genetically isolated from the typical pneumococci included within this study.

### Multilocus molecular evolutionary analyses

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Nucleotide substitution rates differ both among species (lineageeffects) and among genes (locus effects). In order to explain the mechanisms behind these rate differences, it is necessary to determine if lineage and locus effects alone are sufficient to explain the observed heterogeneity in substitution rates. Relative ratio tests allow for investigation of lineage X locus interactions, where, for example, gene A may evolve quickly in species 1, but slowly in species 2. Several versions of relative ratio tests are discussed, and applications to chloroplast and mitochondrial data are presented.

### Neutral theory and DNA sequence variation in humans

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The neutral theory of molecular evolution is an excellent model in part because it is mathematically tractable and makes a number of explicit testable predictions. Statistical analysis of DNA sequence variation within and between species allows us to infer where and how selection may be acting at the molecular level. For example, neutral theory predicts that the ratio of polymorphism within species to divergence between species will be the same for different genes, while selection may lead to an uncoupling of polymorphism and divergence. In regions of the genome with reduced recombination, selection at one site may reduce levels of variability at linked neutral sites as a result of background selection against deleterious mutations or genetic hitchhiking associated with the fixation of adaptive mutations. Neutral theory also makes clear predictions about the frequency distribution of polymorphisms in a population at equilibrium. Skews in the frequency distribution may be a sign of population effects (e.g. bottlenecks) or of locus-specific effects (e.g. selection), and these effects may be teased apart by comparing variation at multiple loci. Here I evaluate some of these predictions of neutral theory in light of nucleotide and microsatellite variability in regions of the human genome experiencing different rates of recombination. Comparison of genetic and radiation-hybrid maps reveals significant heterogeneity in recombination rate in different genomic regions and shows that recombination is suppressed near the centromeres of most chromosomes. Both nucleotide diversity and variance in repeat size for microsatellites vary by more than one order of magnitude among loci. There is some evidence for reduced genetic variation in low-recombination regions. Different loci show different patterns in the frequency distribution of polymorphisms. Together, these data indicate that selection plays an important role in shaping genetic variation in some regions of the human genome.

An extension of the Cheverud and Routman's model of physiological epistasis to more than 2 loci: Effects on the release of additive variance after bottlenecks.

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Since the mid-eighties, there has been growing attention on the role of epistasis and dominance as sources of additive genetic variance after a bottleneck. Numerous experimental results showing an increase in genetic variance after founding events have been interpreted as a confirmation that epistasis can be a genetical basis of evolutionary changes in the context of small and subdivided populations. This finding has helped in renewing interest in Wright's shifting balance theory.

Our main concern is the discrepancy between models and reality. Models are generally based on either two or an infinity of loci. However, QTL analyses show that the number of loci underlying quantitative traits is usually larger than two but still reasonably low. We therefore implemented the Cheverud and Routman's model of physiological epistasis up to 4 loci. Increasing the number of loci is expected to have consequences on the increase in additive genetic variance, since the rate of fixation depends on the number of genes. Indeed, we show that increasing the number of loci delays the release in additive variance, just as increasing the size of bottleneck does. This results depend however on the nature of epistasis (additive by additive, dominance by dominance or additive by dominance epistasis). Our results also demonstrate that when allele frequencies are explored in the initial infinite population later on subjected to consecutive bottlenecks, a decrease in additive variance is on the average observed, associated with a very large variance for additive variance.

### Coevolution, or lack of it, between lycaenid butterflies and ants.

### David Nash

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The butterfly family Lycaenidae is unusual in that most of its members have some sort of symbiotic association with ants. These symbioses range from facultative mutualisms, in which sugar-rich food rewards are provided to ants in exchange for protection against predators and parasites to obligate mutualisms involving more complex food rewards, and parasitic interactions, where lycaenid larvae manipulate ants into tending them against the ants' best interests. Lycaenid caterpillars, pupae and adults show complex adaptations to their association with ants, including unique secretory organs, modified body form, specialised stridulatory organs and modified behaviour. The associations between lycaenid butterflies and ants have often been taken as paradigms of the adaptive coevolution of distantly related organisms.

However, the ants that associate with lycaenid butterflies do not show many obvious adaptations to these interactions. Most lycaenid-tending ants are morphologically unspecialised and have a wide dietary breadth. The behaviours involved in lycaenid-tending and protection are also very general, being largely indistinguishable from those involved in brood care and colony defence.

In this presentation I will review the evidence for coevolution and coadaptation of lycaenids and ants, and examine the consequences that the rather one-side adaptation of lycaenids to associate with ants has had on the evolution of lycaenid-ant interactions.

### Effect of inversion polymorphism on linked nucleotide variability

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Recombination is a main factor determining nucleotide variability in different regions of the genome. Chromosomal inversions, that are ubiquitous in Drosophila, are known to reduce and redistribute recombination, and thus their specific effect on nucleotide variation may be of chief importance as an explanatory factor of different levels of DNA variation. In spite of that, no theoretical study dealing explicitly with the effects of inversions on the nucleotide variability of linked regions has yet been worked out. We use the coalescent approach to help to fill up this vacuum. First, we develop analytical expressions to predict nucleotide variability in old inversion polymorphisms which have reached the mutation-drift equilibrium. The effects on nucleotide variability of a new arrangement appearing in the population and reaching a stable polymorphism are then studied by computer simulation. We show that inversions modulate nucleotide variability in a complex way. The establishment of an inversion polymorphism is a partial sweep that eliminates part of the variability in the population. This is followed by a slow convergence to the equilibrium values. During this convergence, regions close to the breakpoints have much lower variability than central regions. However, at equilibrium, regions close to the breakpoints have higher levels of variability and differentiation between arrangements than regions in the middle of the inverted segment.

# Evidence for two persistent lineages of the blood retrotransposon during the evolution of the Drosophila melanogaster species complex

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Generation of new copies of mobile elements by retrotransposition is expected to be a very error-prone process, due to the lack of proof-reading repair activity of RNA polymerase and reverse transcriptase, and the possibility of recombination during reverse transcription, if two different RNA genomes are packaged into the same virus-like particle. These factors promote diversification of LTR-retrotransposons. If a retrotransposon is highly adapted to its intracellular environment, most of the new variants will be eliminated as a consequence of interelement selection within the genome, because of the restriction in copy number increase imposed by natural selection at the organismic level.

We have chosen the *blood* retrotransposon in the *D. melanogaster* species complex as a model system to investigate the effect of intragenomic selection on the variability of retrotransposon families. PCR was used to amplify the *blood* 5' untraslated region from the four species of the complex. This approach revealed discrete size variants within and among species. Phylogenetic analysis of DNA sequences indicates that the two most abundant size variants represent different *blood* lineages, which diverged prior to the split of the complex. The short size lineage seems to be the most active in *D. melanogaster* (all the known mutations caused by *blood* insertion involve elements belonging to this lineage), but it is absent in *D. sechellia*. The long size lineage is present in the four species of the complex. Analysis of divergence among elements within the same lineage from different species suggests that both lineages have been subject to selective constrains during their evolution, in a sort of competition over a significant period of time.

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The evolution of thelytoky in honeybees (*Apis mellifera*): the impact of the mode of worker reproduction on dominance hierarchies among laying workers and on cell construction

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It has been argued that the frequency of queenloss is a constraint in the spread of genes for thelytoky. However, this does not imply that thelytoky does not affect other behavioral traits of workers. The impact of the mode of worker reproduction on reproductive dominance among laying workers and on brood cell construction in queenless colonies was studied in honeybees (Apis mellifera). Seventy colonies were sampled across a transect through the natural hybrid zone between A. m. capensis with thelytokous worker reproduction and A. m. scutellata with arrhenotokous worker reproduction. The colonies were dequeened and debrooded. A high proportion of colonies absconded or died (N = 44). For 26 colonies, the ratio of worker vs. drone brood cell construction was estimated and the sex of the laving worker offspring was determined. Laying workers produced only female offspring in pure A. m. capensis colonies and only male offspring in pure A. m. scutellata colonies. 42.1% of the hybrid colonies produced exclusively female offspring and not a single colony produced only male offspring. This shows a significant advantage (p<0.001) for thelytokous reproducing workers to become reproductively dominant. However, in 57.9% of the hybrid colonies drone and worker offspring was simultaneously reared to the adult stage, suggesting that reproductive dominance is not exclusively determined by the mode of worker reproduction. All colonies with female worker offspring built queen cells supporting the idea that the primary function of thelytoky is to replace lost queens. Pure A. m. capensis colonies produced exclusively worker brood cells, whereas pure A. m. scutellata colonies produced only drone brood cells. Within the hybrid zone colonies produced either both types of brood cells or exclusively worker cells according to the mode of laying worker reproduction present in their colonies. In all colonies where laying workers produce male offspring drone cell building can also be found. This may indicate a central role of the spatial distribution of surrogate queens in the colony on the sort of cell built and on reproductive dominance among workers.

# Estimates of genetic and phenotypic variance in *Drosophila buzzatii* under nutritional stress - a comparison of estimation methods

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Most organisms occasionally experience environmental stress. The capability of stress influencing adaptations and natural selection and the importance for evolutionary processes, has recently gained broad interest. Experiments have shown an ambiguous pattern and there has been a controversial discussion on whether genetic and phenotypic variance are increased under environmental stress. For the model organism *Drosophila buzzatii* I estimated genotypic and phenotypic variance under a gradient of nutritional stress conditions using the parent-offspring regression and isofemale line method.

### Estimation of Population Parameters and Recombination Rates from Single Nucleotide Polymorphisms (SNPs)

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Some general likelihood and Bayesian methods for analyzing Single Nucleotide Polymorphisms (SNPs) are presented. An efficient method for estimating demographic parameters from SNPs in linkage equilibrium is derived. The method is applied in the estimation of growth rates of a human population based on 37 SNP loci. It is demonstrated how ascertainment biases, due to biased sampling of loci, can be avoided by appropriate conditioning when calculating the likelihood function. Second, a Markov Chain Monte Carlo (MCMC) method for analyzing linked SNPs is developed. This method can be used for Bayesian and likelihood inference on linked SNPs. The utility of the method is illustrated by estimating recombination rates in a human data set containing 17 SNPs and 60 individuals. Both methods are based on assumptions of low mutation rates.

### The evolution of polyandry: multiple mating and female fitness in insects

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Males of most animal species can increase their fitness by mating with many mates, whereas female reproductive success is limited by the number of eggs she produces. This suggests that male fitness generally increases steadily with mating rate, while one or a few matings are sufficient for females in order to maximize their reproductive success. Contrary to these predictions, however, females of the vast majority of insects mate multiply. We performed a meta analysis of 122 experimental studies addressing the direct effects of multiple mating on female fitness in insects. The results of these analyses clearly show that female insects gain directly from polyandry in terms of increased lifetime offspring production. Despite an overall negative effect of remating on female longevity in species without nuptial feeding, the positive effects of remating (increased egg production rate and fertility) more than outweighs this negative effect for moderate mating rates. The average potential direct net fitness gain of polyandry for females was as high as 30-70%. Therefore, the near ubiquitous occurrence of polyandry in insects does not present a paradox or a problem, and observations of monandry, though rare, are much less well understood. However, our results also support the existence of an intermediate optimal female mating rate in insects in general, beyond which a further elevated mating rate is deleterious for females. The existence of such optima implies that sexual conflicts over the mating rate should be very common and persuasive in insect, and that antagonistic coevolution between the sexes plays a key role in the evolution of mating systems and in the evolution of many reproductive traits. We discuss the evolution of nuptial feeding in light of our findings, and suggest that nutritional ejaculates may be the result of such sexually antagonistic coevolution. Future research should abandon the prevailing dualistic view of polyandry as a dichotomous phenomenon, as either existing or not, and instead should aim at gaining a quantitative understanding of the evolution of female mating rates.

### Colonisation patterns of a polyploid plant on heavy metal soils in Scandinavia

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Few plant species are adapted to grow in serpentine soils. These natural heavy metal soils are extreme habitats due to high concentrations of nickel, deficiency of plant nutrients and dry conditions. *Cerastium alpinum* (Caryophyllaceae) is one of the most characteristic plants on serpentine in Scandinavia. It is a polyploid and hermaphroditic alpine plant, which also grows outside serpentine. *C. alpinum* belongs to a species complex and shows great variation in morphology within and between populations. To study the colonization pattern of *C. alpinum* we are here investigating the genetic differentiation among populations. We studied twelve serpentine and twelve non-serpentine populations located in Finland, Norway and Sweden by starch gel enzyme electrophoresis. Since the enzyme patterns of polyploid plants are in general complex, we analyzed the enzyme phenotype frequencies rather than the exact genotypes of eight polymorphic loci. In addition, we analyzed the allele frequencies for three of the populations in Norway and western Sweden are in general genetically similar, but differ from the Finnish and eastern Swedish populations. The Finnish and eastern Swedish populations showed similar phenotype and allele frequencies. This suggests two independent colonization events of Fennoscandia following the Ice Age: one eastern and one western. *C. alpinum* has therefore been able to repeatedly colonize serpentine irrespective of genetic background.

Evolution of gall morphology and host plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae)

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The nematine sawflies that induce galls on willows (Salix spp.) offer a good model system for the study of evolutionary questions. There are over 200 nematine galler species, most of which are mono- or oligophagous. The species can be separated into 7-8 different groups based on the type of gall that they induce.

It has been suggested that the different gall types evolved gradually in the following sequence: (1) Leaf folders; (2) Leaf blade gallers; (3) Apical leaf gallers; (4) Basal leaf gallers; (5) Petiole gallers; (6) Stem gallers; and (7) Bud gallers. We tested the hypothesis by reconstructing the phylogeny of 5 outgroup and 31 ingroup species using sequence data (678 bp) from the mitochondrial Cytochrome b gene. Maximum parsimony and maximum likelihood analyses resulted in essentially the same phylogeny with high support for important branches.

The results show that: (1) The galling species probably form a monophyletic group; (2) True closed galls evolved only once, via leaf folders; (3) All gall type groups are mono- or paraphyletic; (4) Similar gall types are closer on the tree than would be expected by a random process; (5) There is an apparent trend from the leaf edge towards the more central parts of the host plant; and (6) Many willow species have been colonized several times, which excludes the possiblity of parallel cladogenesis between willows and the gallers.

Many of the patterns in the evolutionary history of nematine gallers have also been observed in earlier studies on other insect gallers, indicating convergent evolution between the independent radiations.

# Identification and phylogenetic relationships in Spanish Barbus species inferred by RAPD-PCR markers

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The Genus Barbus (Pisces: Cyprinidae), a freshwater group widely distributed throughout the Iberian Peninsula, have controversial taxonomy and systematics due to morphological similarities and allopatric distributions of its species. On the other hand, the RAPD-PCR method has been used succesfully in identification studies of different organisms, including fishes.

Thus, ramdom amplified polymorphic DNA (RAPD-PCR) analysis has been applied to eight Spanish species of the Genus Barbus. Ten random 10-mer were used to assay inter and intraspecific variation in 233 specimens. Diagnostic bands have been found that can identify unambiguously the different Barbus species. Moreover, a total of 270 markers were analyzed that allow us the establishment of the phylogenetic relationships among the different species. In summary, RAPDs are very useful markers for identification purposes as well as for phylogenetic studies, specially in those groups with controversial taxonomy.

### Phylogenetic relationships in four species of insect pests

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Insect pest species constitute a very serious problem in countries such as Spain with temperate climate and high level of agriculture practices. Recently, molecular genetic techniques are being used to analyze insect pests population structure. Any approaches that might help us understand global and local insect pests population structure would be very important in evaluating existing, or devising new, management strategies. Thus, we applied the polymerase chain reaction (PCR) to generate random amplified polymorphic DNA (RAPD) to four insect pest species, namely, Ceratitis capitata, Bactrocera oleae, Lyriomiza huidobrensis and Bemisia tabaci. Each individual was scored for the presence or absence of every amplification product, and data entered into a binary matrix. Cluster analysis, using the UPGMA method was performed and a dendrogram was produced using NTSYS program. All ten individuals from each species clustered together. The RAPD data indicated that B. tabaci is the most different of the four studied species, and that, surprisingly enough, L. huidobrensis is closer to B. oleae than C.capitata is.

# Phylogeography of the Western Palearctic Yellow wagtails (Motacilla flava L)

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The Yellow wagtail-complex (*Motacilla flava* L) consists of a large number of races, parapatrically distributed from Europe and North Africa in the west to Alaska in the east. Inter-race variation is discontinuous, though virtually confined to the head-region of the male plumage. The phylogeny of the Yellow wagtails is unclear, largely due to the current lack of molecular genetic data. From the overall morphological similarity and the parapatric distribution it seems reasonable to assume that the Yellow wagtail complex is fairly young, perhaps consisting of incipient species. The mode of diversification is traced by relating the male plumage variation to the pattern of distribution in the Western Palearctic, and by comparing the present distribution with palaeoclimatological maps based on data from the last ice-age onwards. Although preliminary inferences can be obtained in these ways, molecular markers make the chain of evidence complete. Nine races of Western Palearctic Yellow wagtails were analysed by means of microsatellites and the mitochondrial ND2 and ND6. The resulting phylogenies were compared to the palaeoclimatiological maps and the pattern of plumage variation.

# Historical and contemporary colonization of novel environments by hybrid Onopordum thistles

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We present data confirming the isolation of and subsequent evolution of hybrid lineages from parental species of the Eurasian thistle genus *Onopordum*. Contemporary patterns of genetic diversity in Australian (alien) and historical patterns from European (native) *Onopordum* both indicate that hybridization has played a significant role in the evolution of these thistles. Adaptation to novel environments, such as may have been found when *Onopordum* colonized Australia from Europe, or recolonized Europe after glaciation, may be promoted by the transfer of genes between lineages and assortment of these genes under different selection regimes.

### Near neutrality in the interactive systems

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The meaning of near neutrality is investigated by the pattern of DNA sequence variation, and by simulations based on the interaction models. Average and variance of DNA sequence divergence were examined. Many patterns of average divergence agree with the nearly neutral prediction, but there are cases that are not in accord with the prediction. The latter may be related to the shift of isochore structure of chromosomes. The large variance of the number of substitutions is often observed in comparative studies of DNA sequences. The result of simulations indicates that the change of population size has a large effect on elevating the variance of evolutionary rate for nearly neutral mutations.

# Determination of phylogenetic relationships among cetartiodactyls: hippopotamuses are the closest extant relatives of whales

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Analysis of the insertion of SINEs has proved to be a powerful method for the determination of phylogenetic relationships (Shedlock andOkada, BioEssays, in press, 1999). In a previous study (Shimamura et al., Nature 388, 666-670, 1997), we showed that cetaceans, hippopotamuses and ruminants form a monophyletic group by characterizing retropositional events of a SINE unit during the evolution of species of Artiodactyla and Cetacea (i.e. Cetartiodactyla). We have now isolated and characterized ten additional loci that represent sixteenretropositional events and that appear to define phylogenetic relationships among cetartiodactyls and to clarify the origin of whales. Analysis of four of the loci demonstrated that cetaceans and hippopotamuses form a monophyletic group that excludes ruminants. Analysis of two lociconfirmed the monophyly of pigs and peccaries, and analysis of another locus indicated that chevrotains are the most basal species amongruminants. In addition, one locus provided evidence that, among cetartiodactyls, camels diverged first. Thus, cetaceans appear to be deeplyembedded within Artiodactyla. This conclusion prompts serious reconsideration of the possibility that mesonychians might, in fact, represent the ancestors of modern whales.

### Allozymes for the discrimination between two oak species and their hybrids

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Mixed stands of cork oak (*Quercus suber*) and holm oak (*Quercus ilex* ssp. *rotundifolia*), that cover large areas in Portugal, are potential sites of hybridism between these two species. This hybridism, though infrequent, might concur to economical loss due to a supposed relationship between the proportion of holm oak genome in the cork-producing trees in such stands and a reduced quality of the cork. This study reports the enzyme activities extracted from oak leaves that appear to allow a discrimination between the two species and allow to identify hybrids between them. The trees in three mixed stands as well as a few spontaneous hybrids were individually studied and their progenies collected and grown in a nursery. Pure stands of both species, including plants grown from a germplasm collection representative of the whole natural distribution of *Q. suber*, were used as reference. Current results on monomorphic and polymorphic enzyme activities will be presented and discussed.

# Biometric survey of cork oak families representative of the whole species natural range

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An international collaboration was set up to sample cork oak (*Quercus suber*) germplasm from provenances in the seven Mediterranean countries representative of the natural range of the species. Most of this germplasm was grouped by families and was germinated and grown in fairly homogeneous conditions in a commercial nursery in Portugal. Height and branching of the whole plants, as well as area, width-by-length ratio and margin indentation of early leaves were evaluated, and the variances and some covariances analysed. The plants were 10-month old, and 15 were sampled per family, 5 families per provenance. Significant differences among families (within provenances) were found for all characters, but not for all provenances in each character; moreover, such significance among families was apparently independent between characters. However, ANCOVA revealed interdependence between height and branching, as well as between leaf area and leaf margin indentation in several provenances. By grouping neighbouring provenances as geographic groups, nested ANOVA indicated that variation among provenances (within geographic groups) for the leaf characters appeared to be significant in several groups, except for the leaf width/length ratio. A parallel analysis of allozyme variation is underway, from which further detail of the phenotypic variation within this sample of the cork oak germplasm is expected. Germplasm collection and growth were part of Project FAIR 1 CT 95 (EU).

# Genetic neighborhood size in the seaweed Ascophyllum nodosum (Fucales)

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Ascophyllum nodosum is a dominant seaweed along many rocky intertidal communities along northem European coasts. Next to the kelps, fucalean taxa such as Ascophyllum are the largest macrophytes and provide important habitat for fish and invertebrates. Using both nested-hierarchical sampling and spatial autocorrelation, we determined the genetic neighborhood size of populations of A. nodosum at Roscoff, France. The analysis is based on six polymorphic microsatellite loci and 350 individuals. Strong genetic structure at small spatial scale was found and is consistent with demographic models based on longlived individuals, low recruitment and many sib matings. Understanding the underlying genetic structure of natural benthic populations over a range of spatial scales can reveal how the causes of structure may change with scales. This investigation is a first step.

Microsatellite analysis of stock structure in the commercially important teleost Orange Roughy (*Hoplostethus atlanticus*).

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The potential of microsatellites as a tool in revealing stock structure was investigated in this study of the commercially important Orange Roughy *Hoplostethus atlanticus*. Previous genetic and non-genetic studies have not been able to clearly distinguish population structure within the global distribution of this species. It was hoped that as microsatellites have revealed population structure in many species not apparent from earlier allozyme or mtDNA analysis that they may help clarify stock composition within the Orange Roughy fisheries. 8 microsatellite loci were screened across 10 populations (total N=932) from the global range of the teleost and all were highly polymorphic (16-45 alleles).

Estimates of genetic differentiation between the locations (Fst) were relatively low even over large geographic distances (South West Pacific to the North Atlantic). They were however significantly positive, indicating population differentiation. Pairwise comparisons of allele frequency distribution yield further evidence for spatial variation. The situation for the Orange Roughy may be more complex than previously thought. This result may have significance for stock management. Our populations were assigned according to the different management zones and some of these areas do not contain large aggregations of fish. This means that trawling over a large area could increase the chance of collecting more than one population/stock. Hence, we have an opportunity to investigate the relationship between management zones and the extent of the fish populations.

### Phenological variation in populations of Lythrum salicaria along a latitudinal transect

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In plants with a wide latitudinal distribution, differences in the length of the growing season are expected to result in spatial variation in selection on phenological characters. In this study, we examined population differentiation in phenology and morphology in the self-incompatible perennial herb *Lythrum salicaria* along a latitudinal gradient from southern to northern Sweden. To test the hypothesis that the *L. salicaria* populations have become genetically differentiated in terms of phenology, we grew seeds representing 33-63 maternal families from each of 15 populations, depending on population size, in a common garden at Umeå, northern Sweden. We then scored eight characters related to vegetative and reproductive phenology. In addition, to examine whether among-population differentiation in phenology is paralleled by among-population differentiation in floral characters, we also scored ten floral characters on each plant. There was significant variation in both phenology and floral morphology among the *L. salicaria* populations sampled. Phenological characters varied predictably along the latitudinal gradient: Northern populations started to flower earlier, grew for a shorter period, produced winter buds earlier, and had a lower probability of flowering in the first year than the southern populations. In contrast, flower morphology varied significantly among population, but did not differ consistently among different geographical regions. The adaptive significance of population differences in phenology and morphology is currently examined in field experiments.

# Genetic differentiation in resting egg banks of a rotifer species complex in Spain

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Here, we present the first exploration of the genetic diversity of the rotifer species complex *Brachionus plicatilis* in inland and coastal lakes in Spain with the novel approach of using its resting egg banks. Hatchlings from resting eggs of 58 sites resulted in 434 clones, which were screened using four polymorphic allozyme loci. A high level of genetic polymorphism was found consisting of 43 composite genotypes which were clustered into six well differentiated groups, often found in sympatry with low or no hybrids between them. Mating behavior experiments supported the pattern of genetic differentiation. Some groups had restricted geographical distributions, and show a preference for habitat type. Our results confirm patterns found in other zooplankters and suggest that classical taxonomy has underestimated biological diversity in rotifers, since the occurrence of additional sibling species in this complex seems very probable.

# Investigating the details of a symbiotic interaction: unraveling chemical variation in an antibiotic gland secretion of the leafcutter ant Acromyrmex octospinosus

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The metapleural gland, located at the posterolateral corners of the thorax, is an organ found only in ants. The function attributed sofar to the secretion produced by this gland is that of antibiotics for the protection of the ant's body surface and the nest against microorganisms. As leafcutter ants depend obligatorily on a highly vulnerable clonal fungus one would expect that they might have evolved very powerful antiseptic secretions. Where previous studies have reported on 2 chemical compounds in the metapleural secretion of *Acromyrmex* ants, we were able to detect an additional 20 major substances in workers from two lab colonies and two colonies sampled directly in the field by use of a polar column on a GC-MS. A function related to defense against microorganisms could be attributed to most of these newly detected substances based on literature surveys and our own biotests. In general ants need to be able to adapt to rapidly evolving diseases and the genetic variation required for such responses has been hypothesized to be generated by high queen-mating frequencies. Indeed leafcutter ants of the genus *Acromyrmex* seem to have the highest queen mating frequency sofar reported in ants as revealed by microsatellites developed during this study. To test wether there is a genetic component to the variation in the composition of the metapleural gland secretion in *Acromyrmex octospinosus*, reflecting a general ability to cope with varying challenges of infectious fungal or bacterial strains, the metapleural gland secretion of individual workers from different patrilines has been analysed in detail.

### Mating tactics and countertactics of males and females in the blue-footed booby

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In high density areas, breeding pairs of *Sula nebouxii* in Isla Isabel, Mexico, perform intra and extra-pair copulations. During the 1995-1997 breeding seasons we investigated: (1) which is the effect of density of breeding pairs over the mate guarding tactics in males and over the extra-pair activity in females (32 focal pairs)?, (2) how males respond to experimentally increased uncertainty of paternity (17 experimental and 17 control pairs)? and (3) which is the behavioural context of egg dumping in females (6 cases)?. (1) Males increased the intra-pair courtship rate, but not the intra-pair copulations rate, with an increase of potential rivals in the vicinity. This behaviour occurred during, but not before the supposed fertile period (1-5 days before laying) of their social mate. Females increased their extra-pair activity before but not during their own supposed fertile period with the increase of potential extra partners. (2) 41% of the experimental males with increased uncertainty of paternity (induced by an artificial separation from their mates), but not the controls, retaliated their social female's potential promiscuity by destroying the first egg laid. (3) All 6 females that dumped eggs copulated with more than one male; two were paired and by dumping their egg may have avoided the infanticidal behaviour of their social mate, and 4 were unpaired and obtained a mate or a territory in the site where the egg was dumped. Tactics and countertactics to maximize individual's reproductive output may be constrained by the behaviour of the social mate.

Genetic differentiation and relationship between geographical and genetic distance based on microsatellites among Danish Brown trout (*Salmo trutta*)

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The population structure in Brown trout from thirteen Danish rivers was studied, employing eight polymorphic microsatellite loci. The rivers were distributed among four geographical regions, the Karupaa river system situated on the west coast of Jutland, the Gudenaa river system running out on the east coast of Jutland, the southern part of Zealand and, finally, the island of Bornholm, situated in the brackish waters of the Baltic sea. Significance in the correlation between genetic and geographical distance was found when data were analysed according to the infinite allele model, whereas only a weak correlation was observed when assuming a stepwise mode of mutation. From these four regions the island of Bornholm was chosen for deeper investigation of genetic variation on a temporal scale, since the special conditions, as brackish water and extremely low water levels in the rivers during the summer period with periodical local extinction as a result, predicts structure of its own. To study the dynamics of this system and compare present day variation with variation a collection of scales ranging back to 1940 from fish stemming from five different rivers, three large and two small, were analysed with seven of the eight microsatellite loci.

### Genetical and environmental bases of a sexual polymorphism : aphally in snails

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The evolution of mating systems can be studied through sexual polymorphisms - situations in which different sexual types coexist. Few such studies have been conducted in animals when compared to plants (the most famous example is gynodioecy). Aphally is a sexual polymorphism that occurs in animals only, and will be considered here in the fresh water snail Bulinus truncatus. Regular hermaphrodites, referred as to euphallic individuals, coexist within populations with aphallic individuals which are deprived of the male copulatory organ. Both types can self-fertilize, though aphallic individuals can outcross only as females. The determination of aphally appears to be both genetic and environmental (Shrag and Read, 1992; Doums et al., 1996), but the respective part of each aspect has to be specified. For this reason we conducted an experiment in B. truncatus in order to analyze genotypic reaction norms. It was conducted using 40 lines that have been maintained under pure selfing over more than 10 generations. The reaction norm of aphally ratio (frequency of aphallic individuals) was studied over three temperatures (19, 25 and 30°C) for these lines. We also investigated whether resource reallocation occurs in aphallic, that is whether the energy not spent in the phallus can be reallocated in another fitness function (e.g. fecundity). The aphally ratio was found to increase with temperature, though variation was found among lines. A significant genotype-by-environment interaction was also detected, meaning that the sensitivity to temperature can be selected. A significant reallocation was also found, though for a single fitness attribute (growth) and a single temperature (30°C). The results are discussed in the context of environmental threshold model (Roff, 1986). Doums, C., P. Brémond, et al. (1996). "The genetical and environmental determination of phally polymorphism in the freshwater snail Bulinus truncatus." Genetics 142: 217-225.

Roff, D. (1986). "The evolution of wing dimorphism in insects." Evolution 40: 1009-1020.

Schrag, S. J. and A. F. Read (1992). "Temperature determination of male outcrossing ability in a simultaneous hermaphrodite." <u>Evolution</u> 46: 1698-1707.

### Microsatellites reveal paternity in the flying squirrel Pteromys volans

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The eastern flying squirrel *Pteromys volans* is an aboreal rodent that is resident in old, mixed boreal forests. The westernmost populations of this species in Europe, occurring only in Finland and other Baltic countries, have declined dramatically during the 20th century. This appears to be due mostly to habitat fragmentation caused by the large scale landscape changes that have resulted from intensive forest management. In Finland the flying squirrel is classified as a declining species that needs to be monitored. Females are extremely site-tenacious, and occupy small territories that may be included within the home ranges of one to a number of males. In turn the home ranges of males may encompass sites occupied by one or more females. Because habitat fragmentation is thought to be a primary cause of the decline of this species, knowledge of the mating system is essential for the development of management practices. To investigate paternity in the flying squirrel, we have developed a number of polymorphic DNA microsatellite markers for this species. Recent results, using the microsatellites to determine the paternity of juveniles whose mothers were visited by a number of males during the breeding season, will be presented.

### Egg size in freshwater salmonids - what is the significance of the male?

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Egg size is an important trait in the early life history of fish. It clearly affects hatchling size, and thus has far-reaching consequences for the further performance of an individual. Within a single species, there is considerable variation in egg size both between populations and among females, as well as in different reproductive seasons. Traditionally, egg size has been considered an entirely maternal characteristic, and the possibility for paternal effects on egg size have been often neglected in studies of early life history.

We studied egg size in four freshwater salmonid species: salmon (*Salmo salar* m. *sebago*), brown trout (*Salmo trutta* m. *lacustris*), Arctic charr (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*). Except lake trout they are all native to the Finnish fish fauna, but nowadays most stocks are dependent on continuous restocking with hatchery fish. Salmonid eggs reach their final size several hours after fertilisation as a consequence of swelling. We studied final egg size from several fertilisation matrices in each species. The matrices were created by crossing six females each with six males producing 36 full-sib-half-sib families. By excluding the effect of initial egg size from the analyses, we show that the male has a statistically significant effect on the egg swelling and thus on the final size of the egg. Our results suggest that the genetic contribution of the male in the offspring traits may be expressed at very early stages of development.

#### Evolution and divergence of dual inheritance systems

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The systems enabling the generation and transmission of phenotypic states have recently been called *epigenetic inheritance systems*. It has been previously proposed that these systems have a substantial role during speciation. Divergence of isolated populations may be first triggered by the accumulation of (heritable) phenotypic differences that are later followed and strengthened by genetic changes. Using a simple theoretical framework, I examine the evolution of a quantitative trait specified by dual (genetic and epigenetic) inheritance systems (see also Pál (1998) *Proc.Roy.Soc.London.B.* **265**,1319-1323). Using the adaptive landscape metaphor, I address the question how selection acts on epigenetic variability to optimize genotypic performance.

At first, I discuss the "exploratory" behavior of an epigenetic inheritance system on a one peak adaptive landscape. If a trait is far from the optimum, than it is advantageous to induce heritable phenotypic variation. Conversely, if the genotypes get closer to the peak, it is more favorable to canalize the phenotypic expression of the character. This process would lead to *genetic assimilation*. Next it is shown, that the divergence of heritable epigenetic marks acts to reduce or to eliminate the genetic barrier between adaptive peaks. An epigenetic inheritance system can increase the probability of transition from one adaptive state to another. A corollary of my thesis, that evolution can proceed through suboptimal phenotypic states without passing through a deep adaptive valley of the genotype. Therefore, speciation may be first triggered by the accumulation of (heritable) phenotypic differences that are later followed and strengthened by genetic changes. Accordingly, epigenetic inheritance systems enable a localized search at the phenotypic level, guiding the genetical system to new optima.
### Postglacial loss of genetic variation in ringed seals of the Baltic Sea and Lake Saimaa

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The ringed seal *Phoca hispida* colonized the Baltic Sea basin c. 10000 BP following deglaciation, and may have remained isolated from the large main Arctic population since then. Parts of the Baltic population were subsequently further isolated into emerging Fennoscandian lakes, and now survive as landlocked subspecies in Lake Saimaa and Lake Ladoga. The Saimaa seal is seriously threatened, with some 200 individuals left. We assessed traces of population history in genetic variation of the Arctic, Baltic and Lake Saimaa ringed seals. In

terms of microsatellite heterozygosity or mtDNA D-loop haplotype diversity, the Baltic seals showed only slight reduction (2%) from the high variability in the Arctic population. However, D-loop sequence genealogies reveal a clear difference, the Arctic population containing many old mitochondrial lineages, only a few of which are retained in the Baltic; this means 20% lower nucleotide diversity (0.033 vs. 0.026). The lacustrine Saimaa seals have drastically reduced variation: 70% lower microsatellite heterozygosity, 80% lower nucleotide diversity. Discounting mutation, the loss of nuclear diversity would correspond to a long-term N=350 in the Saimaa population. The remaining variation corresponds to 1.5 nuclear genomes of the ancestral population, and evidently only one ancestral mtDNA lineage survives in the lake.

#### Conservation of satellite DNA in species from the genus Messor (Hymenoptera, Formicidae)

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Satellite DNA has been characterized in three spanish species from the genus *Messor:M. structor, M.barbarus* and *M.bouvieri*. All species show the presence of a satellite DNA organized in a tamdem repeat of monomers of 79 bp. The sequence analysis of 12 cloned including 28 monomeric units reveals very high intra-and interspecific sequence similarity.

Like satellite DNAs of other insects it is A-T rich and presents direct and inverted internal repeats. Restriction analysis of the total DNA with methylation sensitive enzymes (*Hpa*II-*Msp*I and *Sau*3A-*Nde*II-*Dpn*I) strongly suggests that theses DNAs are undermethylated in the three analyzed species.

Phylogenetic analysis separates the monomeric sequences into two clusters but into whitin the clusters, satellite clones are not grouped species-specifically. Such high sequence conservation could be related to preservation of satellite DNA curvature and with to homogenization processes, such as unequal crossing-over and gene conversion.

### Identification and application of polymorphic microsatellites loci in the genus Limonium (Plumbaginaceae)

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In this work we present the characterisation and application of microsatellite loci as suitable molecular markers for the population analysis of species in genus *Limonium*. Many endemic species of this genus can be found in the Iberian Peninsula and Balearic Islands, with a high incidence of endangered taxa. This genus presents two well defined groups of species, apomictic (obligately asexual) and sexually reproducing species. Our goal is to study the genetic variation in populations of species from both groups in order to compare the patterns of variation found in species with both breeding system, which could be useful in designing conservation measures.

Eighteen primers have been developed for SSRs on *Limonium narbonense* a sexual tetraploid species of presumably hybrid origin. All but one of these microsatellite loci has shown polymorphism with a range of genetic diversity values from 0.5 to 0.9 across 30 individuals from five different populations of *L. Narbonense*. We will present a preliminary analysis of genetic population structure in these populations with 14 of these SSR loci.

Also, conservation of these loci has been examined in other 14 species from the genus *Limonium*, showing a low-cross species transferability.

Moreover, no variation has been found in a genetic analysis using three *a priori* polymorphic microsatellites loci in four populations of *L. Rigualii*, an endangered and endemic species from Mediterranean coast of the Iberian Peninsula.

We discuss the reason that might explain this low success in across species transferability of SSR loci as polymorphic molecular markers.

# The evolution of developmental mode and diet diversification in cone snails: a study in molecular paleobiology.

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Cone snails comprise a genus of predatory gastropods that paralyze prey with a powerful neurotoxin by injection through a hollow harpoon-like tooth. The genus has been remarkably successful, with over 500 described species and a variety of life history, developmental and ecological features. A molecular phylogenetic view of the genus, based on mtDNA sequences, nuclear introns and the sequences of a diverse array of conotoxin genes, allows a reconstruction of evolutionary patterns leading to the current species diversity. We show that developmental mode evolves quickly. Species with non-planktonic larvae have evolved numerous times, and do not cluster in monophyletic groups. By contrast, evolution of dietary specialization is rarer. Particular feeding guilds like fish eaters and mollusc eaters are monophyletic and have existed since at least the middle Miocene. Fish eaters comprise two separate phylogenetic lineages with distinct radular teeth, and may have evolved twice from worm-eating relatives. Prey specialization is shown to be an ancient feature of the genus, and all 4 major feeding modes have survived the mass extinctions of the late Miocene. Dietary specialization is associated with major shifts in conotoxin genes., and fish eating, mollusc eating and worm eating cone snails show tremendous variation in toxin gene. The genes for the conotoxins display a rapid rate of genomic duplication as well as the fastest rates of amino acid evolution known for any eukaryote gene. The diversity of diet shown in this genus may reflect the rapid duplication and diversification of the conotoxin gene family.

# Gene flow and host race formation in the waterlily leaf beetle *Galerucella nymphaeae* (Chrysomelidae: Coleoptera)

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Galerucella nymphaeae is a herbivorous beetle living on four different host plants: *Nuphar lutea*, *Nymphaea alba* (both Nymphaeaceae), *Rumex hydrolapathum* and *Polygonum amphibium* (both Polygonaceae). We have previously demonstrated that beetles living on Nymphaeaceae are bigger and darker, have larger mandibles and lay larger eggs but less per clutch than beetles originating from Polygonaceae. We also have shown that beetles exhibit feeding and oviposition preference for their natal host and larvae survive better on their natal host. While morphological, life history and fitness traits clearly differ, different types of beetles are readily intercrossable, with fertile offspring in F1 and F2. Together these results suggest that host race formation is going on in *Galerucella nymphaeae*.

Here we present data about gene flow within and between host plants, based on RAPD analysis, suggesting that the observed differences lead to reproductive isolation between the types. The results are complemented by a phylogenetic inference based on ITS1-sequence analysis and are discussed in the light of host race formation.

Family structure in *Abies nebrodensis* (Lojac.) Mattei and differentiation from related *Abies* species using allozymes and chloroplast microsatellites

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Abies nebrodensis (Lojac. Mattei) (Sicilian Fir) is now extremely scarce and represented by only one relic population of 29 individuals occurring in a limited area in Sicily (Italy). Taxonomic boundaries between this species and the other closely related Abies species are not clear due to the overlapping morphological characteristics of the individual members of the genus. The morphological traits of A. nebrodensis have been said to be intermediate between A. alba (Mill.), A. numidica (De Lann.) and A. cephalonica (Loud.). In the present study we used allozymes markers to study the genetic structure of seven natural populations of A. alba, A. cephalonica, A. nebrodensis and A. numidica. Furthermore, we used chloroplast microsatellites (cpSSRs) to assess the level of chloroplast DNA variation in four natural populations of A. alba, A. nebrodensis and A. numidica. The aim of the study was: to compare the level of polymorphism detected with allozyme and cpSSR markers; to test if cpSSRs were suitable markers for examining variation among related Abies species; to study the family structure in the A. nebrodensis population; and finally to provide new information about the taxonomic position of A. nebrodensis. Results from both analyses indicated that all the species clearly differentiate from each other and provide support for the classification of A. nebrodensis into a separate taxonomic group. The cpSSR analysis revealed a high level of polymorphism in the Abies species studied. However, due to the hypervariability observed at the microsatellite loci, we concluded that cpSSRs might not be so useful for examining variation among species closely related, like the Abies species analysed in the present study. However, cpSSRs were very informative as markers for studying the family structure of the A. nebrodensis population and revealed that individuals sharing the same paternal parent were closely located in the population.

#### Galapagos Hawks: Genetic Studies of Variation in Mating Behavior

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The Galapagos hawk (*Buteo galapagoensis*) is the only diurnal raptor on the Galapagos, where they inhabit nine islands. Their mating system varies from standard pairs on some islands to polyandrous groups comprising single females with multiple males on others. The polyandrous populations represents the most extreme example of this unusual mating system in birds. We are investigating variation in mating behavior and morphology between islands, using genetic markers to understand the reproductive dynamics of the mating system and differentiation between islands. Genetic evidence based on minisatellite DNA fingerprinting suggests that, within polyandrous groups, cooperating males are not closely related, and paternity is distributed randomly, as predicted by behavioral observations. Populations on Santa Fe, Santiago, Espanola, and Isabela (at Alcedo) are strongly differentiated. The genetic variation between islands far exceeds that within islands, some of which appear practically clonal using DNA fingerprinting. F values range from 0.14 between Santiago and Isabela, large and centrally located, to 0.89 between the smaller and more remote islands of Santa Fe and Espanola. Ongoing work includes sampling the remaining four islands sustaining undisturbed populations, developing molecular techniques to confirm sex, investigating history of ancestry of populations by mitochondrial sequence data, and study of resource base associated with monogamy and polyandry.

#### Cladistic analysis of morphological and molecular characters of Mastus (Gastropoda, Pulmonata, Enidae).

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The genus *Mastus* with a circum Mediterranean distribution is a highly differentiated land snail in the Aegean Archipelago. However, the use of different sets of diagnostic morphological characters during the last decades has led scientists to contrasting results that are even more contradictory in the case of Crete, where the number of *Mastus* species according to different authors, varies from four to fourteen.

Consequently, the use of overall similarity approaches along with a variable and dubious set of characters proved to be inadequate for studying *Mastus* differentiation, making urgent the need for using a more efficient and robust analysis tool and re-evaluating the characters used. A similar outcome was observed for *Albinaria*, another land snail genus that differentiates strongly in the Aegean region. However, in the case of *Albinaria* cladistic analysis of morphological and molecular characters gave an uplift in the study of the genus phylogeny and the evolutionary processes leading to differentiation were partly revealed.

In this work a cladistic approach based on molecular characters along with a more extensive set of morphological characters already used in phenetic approaches, is implemented for the first time in the genus *Mastus*. The outcome of this study is presented and the taxonomic significance of the characters used and the evolutionary history of the genus in the Aegean region are discussed.

# Offspring growth in a drumming wolf spider - effects of father size and sexual attractiveness

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Female choice behavior has gained wide theoretical and empirical interest within the theory of sexual selection. We investigated consequences of female choice on offspring growth by comparing the effects of male attractiveness to the inherited effects on growth. As a study object we used a drumming a wolf spider, *Hygrolycosa rubrofasciata*. Females of this species are choosing more actively displaying males and male display activity, i.e. drumming rate, is correlated with male viability both in laboratory and in field. Previous results indicate, that there are slight indirect benefits of female choice in terms of increased survival of the offspring. We followed reproductive success of the females mated to males differing in their phenotypic quality and growth of the offspring. There is huge variation in male size and the resemblance of offspring to their fathers in body mass was relatively high. Male display status did not contribute to offspring mass in any observable manner. Developmental time of the male offspring was affected by male sexual status, even if this was not the case within female offspring. On the other hand, only within the female offspring developmental time was negatively affected by weight at maturation; the larger they were at age of age of 145 days, the sooner they maturated. Male mating success does not seem to be affected by male sexual attractiveness. Instead, the sexes differ greatly in their growth pattern.

# Searching For Genetic Founder Effects in Tree Species on the Krakatau Islands in Indonesia.

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The vegetation of the Krakatau islands was completely destroyed during the infamous 1883 eruptions; thus creating a rare opportunity to study genetic effects of population founding as species colonized the islands. The islands are situated half way between Java and Sumatra with the nearest mainland forests being 40 km away. All colonists of the islands must have arrived by air (wind, birds and bats) or by water.

This project aims to examine whether there were any effects of founding on population genetic structure (AFLPs) and whether the processes involved in colonization can be determined.

Four secondary forest tree species have been chosen for study; *Dysoxylum gaudichaudianum*, *Ficus fistulosa*, *F. pubinervis* and *Oroxyllum indicum*. Comparative sites were sampled on the Krakatau islands, Java and Sumatra. The Ficus species are early colonists of high seed dispersal vagility whereas both *D. gaudichaudianum* and *O. indicum* are later colonists with a much reduced dispersal vagility.

Analysis of molecular variance (AMOVA) shows very little differentiation of the Krakatau populations to those of the mainland sites. This is further supported by the fact that the number of rare bands in Krakatau populations is not significantly different from mainland sites and in fact some mainland populations have significantly fewer bands. The effects of dispersal mode, colonization time and colonization processes on population structure will be discussed.

#### Microsatellite variation in Palearctic and colonizing populations of Drosophila subobscura

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Dinucleotide repeats are highly variable markers, very abundant in the genome of animals and plants. They have been used in several genetic studies and proved to be useful to analyze variability and genetic struture between populations of the same species. Thus, they are ideal markers to study variation in colonizing scenarios. *Drosophila subobscura* is a well studied Palearctic species that colonized North America two decades ago. A partial genomic library of this species was used to isolate 80 dinucleotide repeats because few sequences having microsatellites were available in GenBank. The mean number of perfect repeats in this species is higher than that found for other *Drosophila* species, and the number of repeats in the clones ranges from 5 to 36. In the present work we study the microsatellite variation in the area where the species was originated and compare it with the level of variation of the recently colonized area. Ten perfect repeats have been chosen to survey variation in four European and two North American populations. The four European populations, distributed along a North-South latitudinal gradient are: Århus (Denmark), Montpellier (France), Barcelona (Spain) and Málaga (Spain). In North America the species is highly abundant along the west coast; the two populations used are Bellingham (WA) in the north, and Fort Bragg (CA), in the south of its distribution range.

# Low levels of nuclear genetic variability in the endangered Mediterranean monk seal after a population bottleneck.

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Genetic data have become essential tools for understanding the biology and ecology of natural populations. Of special interest is the analysis of levels of genetic variability because of its attributed importance in the persistence of populations over time. We report here the first description of nuclear genetic variability in the only remaining sizable colony of the Mediterranean monk seal, Monachus monachus, located at Cabo Blanco in the Atlantic ocean, whose estimated size during the study period (1994-97) was 317 individuals. This population was formerly distributed widely in the area and was abundant enough to sustain commercial harvesting. In this study, we surveyed 39 microsatellite loci, isolated in five related pinniped species, in a sample of 52 pups. Only 15 loci were polymorphic, with a maximum of 3 alleles detected. Three loci appeared to be X-linked. No departures from HWE were detected and no genetic structure was found between the two caves which contain animals. Relatedness analysis showed that reproduction was not dominated by a small number of succesful males. We use three different tests based on allele frequency data to show that the colony has recently lost genetic variability, most likely as a consequence of the great reduction of population numbers. We also estimated pre-reduction N, using a method based on the pattern of variation in alleles, at 5850 individuals. Thus the estimated reduction in population size was  $\sim 90\%$  with an average heterozygosity reduction of 70%. The reduction in variability may have had an effect on the severity and outcome of a mass mortality event which affected the colony two years ago. Further research is needed to clarify the role of genetic variability on the current and future demographic trajectory of this colony, since a low reproductive rate (40%) and still-born pups have been observed. This raises the question of whether inbreeding depression is affecting the colony.

Comparative Phylogeography of two Iberian Lizards, Lacerta lepida and Lacerta schreiberi

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A study of the phylogeography of two lizard species of Iberian Peninsula was carried out. They show marked differences in ecological tolerance. *Lacerta schreiberi* has isolated populations in the galleries of rivers and streams of southern mountains, occupies lowland rivers in the centre of its distribution and also forest habitats in the northern limit. In contrast the larger *Lacerta lepida* shows a much wider ecological tolerance, occupying typical Mediterranean habitats in southern Iberia but also occupying northern and high altitude habitats, the French South and Atlantic coast, and North Italy.

A fragment of 650bp of Cytochrome b gene of the mitochondrial DNA was sequenced for both species Fifty-one samples of *Lacerta lepida* from 26 populations and 44 samples from 21 populations of *Lacerta schreiberi* were scored. Microsatellites results were obtained for 13 populations *L. schreiberi*.

For both species the results show an unexpected pattern of genetic differentiation with no relation with present ecological and physical barriers.

The genetic distributions are better explained by a history of colonisation from glacial refugia, but do not fit with the pattern of coastal refugia that had been anticipated. Instead there is strong evidence of inland refugia. A second surprising finding was the high degree of genetic differentiation between regions. For *Lacerta lepida* this suggests an unexpectedly ancient fission of the population which appears to date back to geological events leading to the isolations of the betic mountain system. These findings lead to re-evaluate the systematic and the conservation strategy for both species.

#### Genetic evaluation of the systematic of Liolaemus archeforus group from Argentina

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Recent studies have subdivided the former species of *Liolaemus archeforus* into six different species: *L. archeforus, L. gallardoi, L. zully, L. sarmientoi, L. escarchadosi, L. tari, using on morphological characters and the evolutionary species concept. These species each show a high degree of colour variability usually with two distinct forms.* 

To help interpret this variation, mitochondrial DNA sequence data was obtained in order to construct a molecular phylogeny. A fragment of 306bp of the cytochrome b gene was sequenced, from three species each divided into two colour forms, comprising a total of 24 samples.

The molecular phylogeny showed that *L. sarmientoi* is a monophyletic group well differentiated from both *L. tari* and *L. escarchadosi* (6-7% of sequence divergence), strongly supporting its previous classification as a distinct species. *L. tari and L. escarchadosi* cluster together with very little differentiation despite the fact that they are both monophyletic. We did not detect genetic differentiation between the colour forms in any species.

The systematic of this group could be further elucidated by extending the genetic survey within these species and to the other three.

# Maintenance of altruistie behaviour in non-equilibrium populations: a study of unicolonial ants

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Several invasive ant species have populations dominating extended habitats by a high density of socially connected nests. In each nest several queens are reproducing and workers from neiglfbouring nests show no aggression but are freely exchanged. The existence of such `unicolonial' populations raises two significant problems to, evolutionary biology. First, workers seem to, violate Hamilton's rule by altruistically raising offspring unrelated to themselves. Thus, unicolonial populations should be prone to, invasion by `cheater' mutants inducing queens to, produce predominantly sexual offspring. Consequently, the social structure should break down and unicoloniality would only be an evolutionary transient phenomenon. Second, unicoloniality is found in invasive species where populations are rapidly expanding following colonisation events. The genetic structure of such populations is far from equilibrium. It is, however, currently unclear how this affects the estimation of genetic relatedness among nestmates and of F-statistics for quantifying gene flow within and between populations. The existence of a genetic substructure of unicolonial populations may decrease the probability of `cheater' mutants to spread and facilitate the maintenance of altruistic worker behaviour. In this study we investigated the social and genetic structure of a recently established population of the Argentine ant, *Linepithema humile*, using information from five variable microsatellite loci. Furthennore, the effect of population foundation and expansion on estimates of F-statistics was studied by simulations. This allowed to, deterinine both (1) whether unicolonial populations are genetically structured, thus conforming to theory, and (2) to what extent non-equilibrium conditions in expanding populations lead to biased measures of such substructure.

#### Genetic variation in chaetognaths: first results on the neritic Sagitta setosa and the oceanic S. lyra.

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The pelagic environment is often regarded as homogeneous and speciation rates of plankton are considered to be slow. To increase our understanding of speciation in the ocean, genetic variation and population structures of marine plankton need to be studied. Although levels of genetic variation have been described for several planktonic crustaceans, little is known about genetic population structures of other planktonic taxa, like chaetognaths.

Samples of the neritic chaetognath *Sagitta setosa* Müller, 1847 from the North Sea and the estuary region of 'Zeeland' (the Netherlands) and of the oceanic *S. lyra* Krohn, 1853 from both sides of the Alboran front in the western Mediterranean Sea were examined using allozymes and Random Amplified Polymorphic DNA-markers (RAPDs) as indicators of genetic variation and differentiation. Seven loci encoding seven enzymes were resolved for five population samples of *S. setosa* after an initial survey of 19 enzyme systems. Four loci were polymorphic and revealed a total of 18 alleles, which were found indicative of high levels of genetic variation. The oceanic *S. lyra* appeared less polymorphic, since only one enzyme, out of 14 enzymes tested, was polymorphic for this species. Allozyme data did not provide any evidence of genetic heterogeneity of *S. setosa* over the sampled area. In addition, levels of gene flow were high and genetic distances low between different population samples. This indicates that *S. setosa* from the North Sea and the estuary of 'Zeeland' are part of a single breeding population. The observed variation in morphological characters in these areas are therefore suggested to be ecophenotypical. The RAPD-technique generated many polymorphic markers in both species. However, no population sample specific diagnostic markers were revealed and no clustering of population samples was observed. These observations lend further support to the hypothesis that *S. setosa* and *S. lyra* are not genetically structured within the sampled areas.

### Patterns of life history diversification in yucca moths

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The evolution of species interactions can cause further diversification by creating new resources. I use the association between yuccas and yucca moths as a model to discuss patterns and mechanisms of serial diversification in specialist pollinator and herbivore lineages. I will present data on diversification and character evolution in yucca moths, focusing on the origin of cheater moth species that depend directly on the activities of their mutualist ancestors.

The history of the yucca - yucca moth association is elucidated with the aid of new molecular data. Phylogenetic analyses are used to test hypotheses concerning the number of origins of cheater species, and an association between the evolution of cheating and variation in pollinator oviposition habit. Mechanistic hypotheses for the evolution of cheating will be explored further.

# The evolution of passive dispersal: A comparative study of seed morphology in aquatic plants

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The evolutionary ecology of dispersal, mainly among terrestrial plants, has received extensive attention during the past decade. Aquatic plants, although broadly assumed to rely on seed dispersal by animals (waterfowl), have hardly been studied. Aquatic plants occupy island-like habitats across large geographic areas and only a few species are wind dispersed. Various dispersal syndromes have been defined based on different morphological features, such as hairs, surface structure, seed size and shape. However, the adaptive significance of these morphological features has not been rigorously tested.

We tested whether the evolution of seed characters, reported to be dispersal-related, is constrained by phylogenetic relationships. In a second step we used a hierarchical analysis to disentangle the effects of dispersal mode, habitat and life-history characteristics. The analysis is based on more than 200 species of pondweeds and other aquatic plants. Seed images extracted from the literature and from field samples were obtained and subjected to digital image analysis. Quantitative data (morphometry) were standardised using Fourier transformation and PCA. In addition we compared morphological characters, ecological attributes and phylogenetic distances by means of matrix and multivariate analyses.

# High genetic differentiation among the south-western populations of the European sculpin, *Cottus gobio*, lineage (Pisces, Cottidae).

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Protein electrophoresis was used to describe the level of genetic differentiation between one peculiar species of sculpin described from a single river in South France, *Cottus petiti* (Bacescu and Bacescu-Mester, 1964), to other nearby populations of *Cottus* sp. The allozyme variability observed revealed a much more complex pattern than initially expected: levels of differentiation suggest the presence of several rather than one distinct taxa (EPPE et al. in press). However, it appeared obvious that (1) the number of populations examined should be significantly increased to gain a more comprehensive understanding of the degree of divergence within and across the drainage basins, and (2) other molecular markers should be investigated to validate the allozyme patterns observed. This poster presents an overview of the allozyme data set together with results of Cytochrome b sequencing on a larger set of populations from France, Belgium and Italy.

# A high frequency of cryptic deleterious mutations in C. elegans

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Several important evolutionary questions, including the evolution of sex and recombination and the magnitude of mutation load, require knowledge of genomic rates of deleterious mutations and distributions of their effects. The extent to which deleterious mutations with very small phenotypic effects contribute to these phenomena has however been unknown, since mutations with very small effects may not be detectable by phenotypic assays in the laboratory. We have measured the effects on fitness-related traits of induced mutations in the nematode *Caenorhabditis elegans* using a system for which the number of point mutations, the majority of which must be deleterious in natural conditions, since protein coding DNA sequences are strongly conserved. In reproductive output assays of the lines, only ~1.4 mutations per line were detectable, and had large deleterious effects of ~24%. A maximum likelihood (ML) analysis suggests that the distribution of fitness effects of new mutations is discontinuous, with an additional large class (comprising >95) of deleterious mutations which have no detectable effect on fitness in the laboratory. These mutations, though cryptic, are significant for mutation load and the maintenance of sexual reproduction.

#### Do male noctule bats disperse randomly ?

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Microchiropterans are small-bodied, nocturnal, volant mammals which are difficult to survey with classical methods such as capture-recapture or telemetry. The population biology of many bat species is, for this reason, still fragmentary. In the noctule bat (*Nyctalus noctula*) the problem is compounded as in addition it is a tree-dwelling and migrating species. An analysis of mtDNA sequences has shown that most female noctules are philopatric for the colony where they were born. Females migrate each year to hibernating colonies following migration routes which direction is constant throughout Europe, and copulations take place during fall migration. The geographic origin of the males that females meet during migration is unknown but determines the amount of gene flow between nursing colonies.

The aim of this study was to work out how male noctules disperse. Using data on eight microsatellite loci from thirteen nursing colonies sampled all over Europe (with about twenty bats sampled per colony), I compared mitochondrial with nuclear DNA partition of genetic varaibility which revealed tremendous differences between male and female dispersion rates. Then, I conducted a fine analysis of population structure on the microsatellite loci. The overall population structure was, although very low, highly significant. It was not possible to detect any pattern of isolation by distance or a trend for males to disperse along migration routes. To summarize, male noctules seem to disperse at very high rates, in all directions and on large distances, *i.e.* randomly. Using simulations, I finally tested whether random male dispersal would be consistent with the significant population structure observed in the nuclear data set.

### Where is the root of the universal tree of life?

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The currently accepted universal tree of life based on molecular phylogenies is characterised by a prokaryotic root and the sisterhood of archaea and eukaryotes. The recent discovery that each domain (bacteria, archaea, and eucarya) represents a mosaic of the two others in terms of its gene content has suggested various alternatives in which eukaryotes were derived from the merging of bacteria and archaea. In all these scenarios, life evolved from simple prokaryotes to complex eukaryotes. We argue here that these models are biased by overconfidence in molecular phylogenies and prejudices regarding the primitive nature of prokaryotes. We propose instead a universal tree of life with the root in the eukaryotic branch and suggest that many prokaryotic features of the information processing mechanisms originated by simplification through gene loss and non-orthologous displacement.

# Male versus female mediated gene flow in red grouse (Lagopus I. scoticus)

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Many species show considerable sexual dimorphism in the degree of natal philopatry. In birds, females tend to disperse, whereas males remain close to their natal area. Such patterns of asymmetric philopatry may result in genes with diparental and uniparental transmission exhibiting different patterns of overall population structure. Here we examine differentiation between red grouse populations from NE Scotland using microsatellite and mitochondrial polymorphisms. Significant differences in microsatellite allele frequencies were apparent at a localised scale (<10kms), with genetic divergence increasing as a function of geographic distance. In contrast, minimal divergence was detected using mitochondrial sequence analysis. Such patterns may appear consistent with extensive female mediated gene flow, but it is difficult to reconcile how effective female dispersal does not generate panmixia at both mitochondrial and nuclear loci.

We use simulation models to highlight that under certain ecological scenarios the effective size of the nuclear genome can be smaller than the mitochondrial, and the patterns of divergence we observe are plausible, and relate to differential movement of male and female grouse.

# Evolution of phenotypic plasticity to light in Arabidopsis thaliana

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A phylogenetic and quantitative genetic approach was used to investigate the evolution of phenotypic plasticity in Scandinavian accessions of *A. thaliana* and closely related species. Plants were exposed to long and short photoperiods. Variation for plasticity was found for 5 of 8 traits. Phylogenetically independent contrasts showed the coevolution of 2 (of 10) plasticities and 6 (of 15) across-treatment means. One (of 3) across-treatment means coevolved with their respective plasticities. Phylogenetically informed ANOVA contrasts revealed that character means evolved faster than character plasticities (as judged by the number of significant contrasts for the two classes of traits). Results are currently being compared with the response of the same accessions to light quality (shade avoidance) to determine if the two types of plasticity constrain each other's evolution.

#### Reproductive strategies in female diamondback moths, Plutella xylostella.

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Insects that are long-lived as adults, and have limited time intervals when they find suitable substrates for their progeny, often have their reproductive activities kept under tight hormonal control. In contrast to this, it has been suggested that insect species with short-lived adults are physiologically ready to mate soon after eclosion, with little flexibility in the onset of sexual maturation. The diamondback moth is a polyphagous species that feeds on cruciferous plants. Although it is short-lived at the adult stage, it faces variable host-plant quality and availability and therefore should delay reproductive activities when host-plant are not present. Thus, we test the hypothesis that the diamondback moth has evolved life-history strategies that provide for flexibility in the onset of reproductive activities depending on the presence or absence of host-plants. Our results show that heavier females, reproductively capable upon eclosion, began calling (release of a sex pheromone) within the first scotophase and had numerous mature oocytes. Light females, which are often associated with poor host-plant quality or crowding of the immatures, displayed flexibility in the onset of reproductive activities (calling behaviour and oocyte maturation).

#### Phylogeography of the coral reef fish, Acanthurus triostegus, in the Pacific

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The Indo-Pacific area has been recognised as the most diverse biogeographic area among marine ecosystems. This diversity shows gradient with higher diversity in the Indonesia-Philippines area and decrease of species richness going East in the Pacific islands. Three major theories (center of origins, center of accumulation, and center of overlap) have proposed mechanisms that lead to higher diversity in the Indonesian-Philippines area. Up to now, classic biogeography based on species richness is unable to distinguish the most likely model among the three. The life cycle of most coral reef fishes is made of two distinct phases : benthic adults and juveniles which are restricted to the reef area and pelagic larvae evolving in the ocean. As a result of the fragmentation of the coral reefs, species can colonise new habitats only through the pelagic stage.

We investigate genetic approach as a new tool that could give evolutionary perspective in biogeography. The rationale of such an approach is that genetic diversity has been found to be correlated to species richness. A total of 725 *Acanthurus triostegus* issued from 18 locations spread out in the Pacific were analysed for isozymes polymorphism. Highest heterozygosity values were found in the eastern Pacific sites (Polynesia and Clipperton) and the lowest value was also issued from the eastern Pacific (Marquesas). Four major groups were separated using a neighbour-joining algorithm on non-biased pairwise Nei's genetic distances : two groups with eastern Pacific sites and two groups with central Pacific sites. Such pattern is opposite to the commonly mentioned center of origin hypothesis and suggests that Polynesia was the center of dispersal of *Acanthurus triostegus*.

New estimates of the age-specific properties of spontaneous mutations that affect mortality rates in *Drosophila melanogaster*.

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Age-specific effects of spontaneous mutations on mortality rates in *Drosophila* are inferred from three large demographic experiments. Data were collected from inbred lines that were allowed to accumulate spontaneous mutations for 10, 19 and 47 generations, and estimates of age-specific mutational variance for mortality were based on data from all three experiments. Estimates were obtained using a model developed for the genetic analysis of age-dependent traits (the character process model). In this theory, the analogs of variance components for standard traits are continuous covariance functions for age-dependent traits. Both within and among generation analyses suggest that the input of genetic variance is greater for early life mortality rates than for mortality at older ages. In females, age-specific mutational variances ranged over an order of magnitude from  $5.96 \times 10^{-3}$  at week 2 post-eclosion to  $0.02 \times 10^{-3}$  at week 7. The male data show a similar pattern. Mutational correlations among mortality rates at different ages tend to increase with the accumulation of new mutations.

Drosophila resistance genes against parasitoids : a gene-for-species concept

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Drosophila melanogaster larvae react against eggs of hymenopteran parasitoid wasps by surrounding them with a multicellular melanotic capsule. The genetic determinism of this response had been studied using susceptible (non forming capsule) and resistant (forming capsule) strains. Differences in the encapsulation response to *Leptopilina boulardi* involve a single gene, *Rlb*, with two alleles, the resistant one being dominant. Differences in the encapsulation capacity of *D. melanogaster* against *Asobara tabida* are also explained by a major segregating locus, *Rat*, with a dominant resistant allele. These data clearly demonstrate that natural adaptations can have a simple genetic basis.

Both *Rlb* and *Rat* have been assigned to the second chromosome which raised the question as to whether the same gene works against the two wasp species. This is unlikely because *Rlb* confers specific protection against *Leptopilina boulardi* and is probably involved in parasitoid recognition. However, these genes could be part of the same cluster, as often shown in the case of plant resistance genes to pathogens. Our recent studies have demonstrated that *Rlb* and *Rat* are separate genes, *Rlb* being localized at 2-86.7, while Rat is located near the centromere. They are about 35 cM apart which demonstrates that *D. melanogaster* known resistance genes to parasitoids are not organized into a cluster.

This work was allowed by the acquisition of avirulent strains of wasps, a situation rarely encountered in the field. Using the avirulent strain of *L. boulardi*, we determined the occurrence of the resistance phenomenon in European populations. The encapsulation rates range from 42.4 to 77.7 with only one population highly susceptible. The question of the selective pressures explaining this high resistance level remains opened. Another part of our work was to precise the genetic and molecular location of *Rlb*, in order to clone this gene, to determine its function and its frequency in the field. Using strains bearing deletions, we demonstrated that resistance to *Leptopilina boulardi* is conferred by the 55C; 55F3 region with the 55E2-E6; F3 region particularly involved. A detailed physical map has been obtained.

### Imprinting is for sex not conflict

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The conflict theory of genomic imprinting predicts that imprinted genes are growth enhancing when paternally expressed and growth suppressing when maternally expressed. The expression pattern of autosomal imprinted genes generally fits these predictions. However, the conflict theory cannot easily account for the pattern of X-linked imprinting in humans and mice. This has led to the proposal of a novel hypothesis that X-linked imprinting has evolved to control sex specific gene expression in early embryos. The hypothesis links paternal X-imprinting (i.e., paternal copy silencing) to random X-inactivation and the retention of Y-linked copies, and links maternal X-imprinting to escape from random X-inactivation and the loss of Y-linked copies. The hypothesis offers a good explanation of the existing data on X-imprinted genes.

#### Intraspecific phylogeny and distribution of sexual and parthenogenetic planarians (Schmidtea polychroa)

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In the hermaphroditic planarian *Schmidtea polychroa* (Platyhelminthes, Tricladida), sexual and parthenogenetic biotypes are known. Parthenogenesis is sperm-dependent, which means that sperm is used only to initiate egg development. Sexuals and parthenogens can be found in allopatry or in sympatry. Parthenogens occur over a wide geographic range in Europe, while sexuals seem to be absent in areas north of the Alps. Genetic data from nuclear markers (allozymes, microsatellites) indicate that sexuals and parthenogens can hybridize. Hybridization is possible because parthenogens, having originated from hermaphroditic sexual ancestors, continue to produce sperm. High genotypic diversity among parthenogens in mixed populations suggests that hybridization results in independent origins of new parthenogenetic lineages.

We report sequence data from a 450bp fragment of the mitochondrial COI gene from sexual and parthenogenetic populations. Our study sites comprise parthenogenetic populations from Central Europe, and mixed populations from North Italian lakes and Central Italy. We found 20 different haplotypes that can be assigned to 3 main clusters, one of which was restricted to Central Italian populations. In parthenogenetic populations north of the Alps, several similar haplotypes from one cluster were found, while in North Italian lakes, haplotype diversity was very high. There we found several haplotypes from two main clusters that have diverged by about 5% of nucleotides. None of the clusters is restricted to sexuals or parthenogenetic lineages that originated from coexisting sexuals, and distantly related ones that colonized the area independently from the coexisting sexuals.

#### Gradual or saltatory evolution of satellite DNA in the genus Pimelia?

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Genomic DNA of 29 species of the genus *Pimelia* was digested with restriction enzymes and the DNA fragments analyzed by agarose gel electrophoresis. In all species, characteristic ladders of multimeric bands of satellite DNAs were obtained. Southern analysis showed a minimum of 60% similarity among the different monomeric units and the presence of only one major species-specific satellite DNA. Sequence analysis of the monomeric units suggests the presence of at least seven different satellite DNA families in the genus *Pimelia* (PIM357, PIM502, PIM509, PIM512, PIM515, PIM513, and PIM705). All sequence variants have a presumably common strech of 310 bp with 60% similarity, being the remaining parts of the sequences family-specific. Sequence phylogenetic relationships are difficult to establish among the more divergent families, which could be explained by a saltatory type of evolution. However, the family PIM357, presents transition stages produced by homogenization-fixation patterns predicted by molecular drive (gradual evolution). The tracts of gene conversion and sequence rearrangements seem to be the main factors altering the sequence organization of the PIM357 monomeric unit.

#### Evidence for a sexual monogamy in the mound-building mouse, Mus spicilegus.

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Contrary to the house mouse, *Mus musculus domesticus*, the mound-building mouse, *Mus spicilegus*, was poorly studied and there is no information on the characteristics of the mating system in field conditions. The house mouse mating system is polygynous/promiscous in commensal populations and polygynous in feral populations. Previous ethological studies of *M. spicilegus* in laboratory conditions showed that this species presents several behavioural characteristics which could lead to a monogamous system (Patris 1998; Patris & Baudoin 1998). In order to test the hypotheses of social and sexual monogamy in this species we studied 14 experimental groups of 4 to 6 individuals in outdoor enclosures during the period of reproduction (May to September 1998). We recorded the spatial distribution and behaviour of mice and the characteristics of reproduction. In parallel we used microsatellite loci in order to genotype parents and their offspring produced during this period. Results (1) confirm the hypothesis of a social monogamy in these experimental conditions and (2) show that the mating system corresponds to a sexual monogamy. Genetical data fit totally with predictions made from behavioural data. This study is the first description of a monogamous system in one species of the genus *Mus*.

#### Expression in a Teleost Fish: Fundulus heteroclitus

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Populations of Fundulus heteroclitus from different thermal environmentsvary in the transcriptional regulation of the lactate dehydrogenase-B gene(Ldh-B). Populations from the north expressed 2-fold more Ldh-B in their livers than southem populations. Using a novel in vivo method for thestudy of gene regulation, we have shown that this difference is the result a mutation in the glucocorticoid binding site. To further test this possibility, we subjected fish to, various handling stresses and injected others with cortisol. Stress and cortisol treatment elevated Ldh-B transcription and plasma cortisol levels of southem populations to, the levels observed in northem populations under resting conditions. Togetherthese results indicate that Ldh-B transcription in Fundulus populations sensitive to, stress and mediated by glucorticoid levels.

Genetic variability in native and introduced meadows of the seagrass *Halophila stipulacea* from the Red Sea and Western Mediterranean

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Halophila stipulacea (Forssk.) Aschers. (Hydrocharitaceae) is a dioecious seagrass that colonized the Mediterranean basin probably following the opening of the Suez Canal (1869). Since the end of the last century natural meadows have been reported in the Eastern side of the basin and only recently along the Northern coast of Sicily (Western Mediterranean). In order to investigate the level of genetic divergence between original and introduced meadows, we examined the polymorphism of RAPD markers and rRNA ITS1 region in four meadows, of which two are located in the Red Sea and two along the Sicilian coast (Vulcano Island and Oliveri-Tindari coastal lakes). Overall genetic diversity was high and, unexpectedly, no substantial differences were found between the two geographical areas in the levels of within-meadow genetic variability. Genetic substructuring was present within the Vulcano meadow, which was sampled at different depths. Exclusive RAPD markers were present in the two areas, suggesting genetic divergence between Mediterranean and Red Sea populations. The same phylogeographical trend was confirmed by ITS1 sequence analysis. We conclude that (i) genetic variability is comparable between original and introduced *H. stipulacea* meadows and (ii) Western Mediterranean meadows are genetically distinct from the Red Sea ones.

# Spatial heterogeneity can resolve the paradox of the lek

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Although much attention in recent years has been paid to temporal, genetic, and phenomenological solutions to the paradox of the lek, little effort has been placed on understanding the implications of spatial heterogeneity for sexual selection. Spatial heterogeneity can maintain heritable variation in fitness, and can therefore maintain female choice of mates of high genetic quality. Female choice is most likely to evolve when migration is of intermediate strength. Once female choice has evolved, the species is more likely to add new habitats to its niche, thus increasing selection for female

#### A genome-wide departure from the neutral model in natural populations of Drosophila

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A selectively neutral, panmictic population at statistical equilibrium can adequately account for a number of features of polymorphism data. Here, we report a genome wide, systematic departure from the neutral expectation for single nucleotide polymorphisms in natural populations of *Drosophila melanogaster* and *D. simulans*. Either the effective population size of the two species is much smaller than previously believed, or both species exhibit greater intralocus linkage disequilibrium (non-random association of alleles on chromosomes) than predicted by the standard neutral model. Possible explanations for an excess of linkage disequilibrium include variation in recombination or mutation rates, certain forms of selection, and population subdivision. The non-uniform spatial distribution of mutations seen in the data is shown to have little effect on our measure of linkage disequilibrium. We also demonstrate that a simple two island model of population subdivision does not account for the observations. While more complex demographic models cannot be ruled out, these findings raise the possibility that natural selection has acted on some if not many of the loci considered.

#### The role of balancing selection in the maintenance of single-locus polymorphism

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Since natural selection requires variation to act, the amount of genetic variation in a given population is of central theoretical and experimental importance. This amount is estimated by the genetic variation present in current populations. Electrophoretic studies of natural populations reveal that ten to twenty percent of all loci have multiple alleles. These multi-allelic loci may be the result of the accumulation of unselected mutations (neutral theory) or of balancing selection (selectionist theory). The neutral theory views selection as primarily eliminating variation, whereas the selectionist theory views selection as often maintaining variation. Therefore, our view of selection and evolution depends upon the question of how multiple allelic systems evolve.

To address whether balancing selection increases genetic variation, we examined two models: one in which selection varies over time in a cyclic fashion, the other in which selection varies in the two sexes. We explored these models for a single multi-allelic locus to explore more generally the effect of balancing selection on the maintenance and construction of multi-allelic systems. To do so, we constructed two computer models. The "fitness-space" approach examines the proportion of all possible fitnesses capable of maintaining different sized allelic systems. The proportion of possible fitnesses is greater in balancing selection models. The "constructionist" approach examines the ease in reaching this portion of possible fitnesses, our research suggests that balancing selection models. Thus, in contrast to previous hypotheses, our research suggests that balancing selection may not increase the amount of variation present in natural populations.

Adaptive changes of migratory behaviour in response to global warming: a quantitative genetic study in the blackcap (Sylvia atricapilla)

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In the last three decades, global temperature has been increasing at an unprecedented rate. It has been hypothesised that this environmental change will drive a selection process by which migratory populations should gradually evolve towards residency. Moreover, we expect changes in migration distance and intensity, and in the timing of breeding and migration.

Drawing on the data on migratory activities of more than 700 blackcaps from a migratory population, we assessed the potential of migratory traits for adaptive evolutionary change, and predicted the trajectory and rate of response to selection caused by climatic changes. We found adaptive phenotypic plasticity in the onset of migratory activity, and high phenotypic variation, moderate to high heritabilities, and favourable genetic correlations among all migratory traits. These characteristics may in concert lead to very rapid and flexible responses to changes in the environment, favouring longer or shorter migration distances, and a different timing of migration. Moreover, we demonstrated a significant trend for a decrease of the intensity and consequently, of the amount of migratory activity over the last 10 years. Furthermore, there was a trend for a delay of the onset of migratory activity. In a multivariate quantitative genetic model, we identified the onset of migratory activity as the prime target of selection. This delay of the onset of migratory activity was most pronounced in birds born late in the season. Thus, selection on the timing of migration will differentially affect birds born at different times of the season, thereby facilitating adaptive changes of the reaction norm.

# Trade-off between mate search and foraging can stabilize simultaneous hermaphroditism in animals

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In animal kingdom, hermaphroditism is largely restricted to lower invertebrates, and is extremely common in certain phylogenetic groups. This has inspired a search for selectionist explanations for evolutionary stability of hermaphroditism. In studies of hermaphroditic mating systems the concept of trade-off has always been central, usually focusing on the trade-off between reproduction through male versus female function. We studied the consequences of another type of trade-off to mating system evolution, the trade-off between time allocation to feeding and mate search. The model shows that simultaneous hermaphroditism will be evolutionarily stable when 1) searching for mates is time-consuming, 2) active search and foraging exclude each other and 3) population densities are reasonably high to allow some chance encounters between individuals. This model can be applied to all free-living invertebrate hermaphrodites, which have limited sensory and locomotive abilities and feed on low-energy resources.

# omparative phylogeography of four small mammal taxa with different ecological requirements in the Central African tropical forest.

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The Central African forest exhibits a high species richness which is thought to be the result of speciation events associated with forest fragmentation during the Pleistocene arid phases. Some conserved forest patches may have acted as "refuges" for the forest fauna which diverged in isolation and then expanded. In this study, we investigated the effects of the Quaternary climatic and environmental changes on the mammalian fauna. Two molecular markers, 16s rRNA and Cytochrome b mitochondrial gene fragments (for *H. stella* only), were selected to reconstruct the phylogeography of the taxa. One can assume that the ecological preferences of the species have influenced the present distribution of the populations in combination with the paleo-environmental changes. Hence, four widely-distributed and abundant species with different ecological requirements were chosen ; one shrew (Insectivora, Soricidae) and three murid rodents (Rodentia, Muridae). The shrew : *Sylvisorex johnstoni* and two of the rodents : *Hylomyscus stella* and *Stochomys longicaudatus* are typical forest dwellers ; whilst *Lophuromys sikapusi* inhabits the savanna and forest-savanna margins.

Specimens were trapped at 14 typical or peripheral forest sites in the following countries: Cameroon, Central African Republic, Popular Republic of Congo, and Gabon. Additional specimens from the Democratic Republic of Congo and Côte d'Ivoire were included whenever available.

Our results indicate that the phylogeographic patterns differ among the species according to the interplay of ecological filters and evolutionary factors that will be discussed.

### Parental effort and immune responsiveness in the blue tit

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A major task in current life history research is to understand the mechansims behind life history trade-offs. For example, how is it that current reproductive effort is at conflict with future reproduction? We here test one potential mechanism, namely if there is a physiological trade-off between parental effort and immune defence. We manipulated brood sizes in blue tits and measured the ability to produce antibodies upon a challenge with diphteria-tetanus vaccine. Birds raising reduced broods mounted a stronger response to diphteria than birds raising unmanipulated broods, but there was no statistically significant difference between groups in the response to tetanus. This finding lends support to the hypothesis that somatic maintenance, in the form of defence againts infectious parasites, trades off against parental effort.

# Temporal variation in the genetic structure of host-associated populations of the small ermine moth *Yponomeuta padellus* (Lepidoptera, Yponomeutidae)

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Temporal changes in allele frequencies were studied in host-associated populations of the small ermine moth *Yponomeuta padellus*. At one site, populations from three host plants (*Sorbus aucuparia*, *Amelanchier lamarckii*, and *Crataegus* spp.) were sampled annually during a four-year-period and analysed with 20 polymorphic allozyme markers. At two other sites, allele frequencies at 5-6 enzyme loci of *Y. padellus* populations from two different host plants were also tested for consistency over a 13-year-period. Significant allele frequency changes occurred in the short-term analysis, whereas allele frequencies remained relatively stable through time in the long-term analyses. Furthermore, allele frequencies of *Y. padellus* populations from *Crataegus* spp. were relatively stable compared to the other host populations. The role of the agents responsible for the observed patterns is discussed.

### The birth-and-death process and the evolution of the Cecropin multigene family in Drosophila

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In *Drosophila melanogaster* the *Cec* locus is a compact cluster of genes involved in the immune response. The *Cec* cluster has been cloned and sequenced in *D. subobscura*. Unlike in *D. melanogaster*, in *D. subobscura* the cluster is split in two regions that map in different locations of the O chromosome. These two regions have been named *Cec99C* and *Cec83B* according to their cytological location. *In situ* hybridization on polytene chromosomes of different species of the *obscura* group suggests that the split of the cluster occurred after the separation of the *melanogaster* and *obscura* groups, but prior to the separation of the *D. pseudoobscura* and *D. subobscura* lineages. The *Cec99C* region contains one *Cec* gene, one pseudogene and the remains of another gene. The *Cec83B* region contains six *Cec* genes, which are the result of the recent duplication and inversion of a fragment including three genes arranged in tandem. Estimates of sequence divergence between the different copies of the split in two separate clusters. The duplication-deletion process has been the main force involved in the evolution of this family in *D. subobscura*, while other processes such as gene conversion have had a minor contribution in the evolution of the *Cec* family in this species. Comparison of the *Cec* genes in species of the *melanogaster* complex, in *D. virilis* and in *D. subobscura* indicates that the birth-and-death process plays an important role in the evolution of this multigene family.

# Neutrality, selection, and the evolution of protein-coding DNA: the importance of the distribution of selection coefficients

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The traditional dichotomous arguments of either neutrality or selection aremisguided; the real question concerns the proportion of genes in a genomethat are consistent with neutrality or selection. We should view genomes as collections of genes which are predisposed to different modes of selection. In a sense the genome exhibits "niche partitioning" of genes with different selection coefficients (negative purifying selection, neutrality or near neutrality, positive Darwinian selection). We present empirical data from nuclear and mitochondrial protein coding genes which illustrate these patterns. Using the McDonald/Kreitman test, we show that virtually all mitochondrial genes exhibit a pattern of excess amino acid polymorphism (relative to divergence), but that nuclear genes show a broad distribution of McDonald/Kreitman patterns: some genes show excess amino acid divergence, while others show excess amino acid polymorphism. This difference between mitochondrial and nuclear genes is highly significant. Simulations by my colleague Dan Weinreich show that the dominance relationship of selected mutations can play an important role in this nuclear-mitochondrial dichotomy. We are investigating how the linkage relationships of different genomic regions interact with dominance patterns to modulate the opportunity for selection on individual loci. The interaction of selection, dominance and recombination alter the ways in which the "niche partitioning" of selection coefficients in a genome is realized.

#### The evolutionary dynamics of male-killers and their hosts

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Male-killing bacteria are cytoplasmic sex ratio distorters which cause sex-limited pathogenesis of their insect hosts. Male killing is thought to be adaptive for the bacteria because only female hosts can transmit it. Also, the killing of male hosts by their bacteria can augment the fitness of female hosts carrying clonal relatives of those bacteria. Here we consider the evolution of male-killers and their hosts and attempt to explain observations of multiple male-killers in natural host populations. First we show that such male-killer polymorphism cannot be explained by a classical model of male-killer. We then show that more complicated models incorporating the evolution of resistance in hosts can explain male-killer polymorphism. However, this is only likely if resistance genes are very costly. We also consider the long-term evolutionary dynamics of male-killers, and show that there is no reason to suppose that male-killer transmission efficiency will necessarily increase over time.

Comparative molecular organization of the Muller's element *E* between two distantly related *Drosophila* species: *D. melanogaster* and *D. repleta* 

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Comparison of the gene arrangement on the chromosomes between distantly related species allows us to infer the course of genome evolution. *Drosophila* species are particularly suitable for such comparative studies because DNA clones from one species can be mapped by *in situ* hybridization to the polytene chromosomes of other species. Using this technique, we have constructed a physical map of the *D. repleta* chromosome 2, which is homologous to chromosome arm 3R of *D. melanogaster* (Muller's chromosomal element *E*). The map bears a total of 93 nonredundant molecular markers and includes the precise localization of 61 protein-coding genes and the tentative localization of another four. The comparison of gene arrangement in Muller's element *E* between *D. melanogaster* and *D. repleta* shows an extensive reshuffling. Using a likelihood method, we have estimated the number of fixed inversions that differentiates the two species as  $146\pm26$ . Since these two species belong to different subgenera, *Sophophora* and *Drosophila*, respectively, and diverged some 40-60 myr ago, the evolution rate is 1.2-1.8 inversions fixed per myr. Despite the extensive reshuffling, the order along the chromosome of the 70 effective markers (those localized in separate chromosomal sites) is not completely independent in the two species (non-parametric correlation coefficients are statistically significant). This result is unexpected if breakpoints of fixed rearrangements are distributed at random.

# Frontera: Conditions for the Simulation of Boundary Pattern Evolution

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Connectedness is a mark of organisation in living organisms. When two or more organic structures interact they form boundary patterns that can be recognised at all levels of morphological organisation (e.g., atoms form molecules, cells form tissues; bones form skeletal compounds; etc.) Boundaries are particular active sites where conditions can emerge for the appearance of patterns, which could ultimately be a source for innovations in evolution. Theoretical approaches to simulate boundary patterns are a good starting point to understand processes underlying the emergence of form. Frontera is a new software that uses Cellular Automata models to simulate boundary patterns and Graph Theory to formalize and describe their properties. Under different constraint conditions Frontera render patterns that simulate aspects of naturally emergent connectivity designs (e.g., seriality; symmetry; branching). Realised and possible boundary patterns can be mapped out on the morphospace of connections, providing a way to understand how different constraints contribute to morphological variation. Different simulations of boundary evolution are presented as well as a discussion concerning the relation between the constraints imposed to the Cellular Automata and the resulting pattern disparity.

# Natural hybridization between *Salvelinus malma* and *S. confluentus*: reproductive and ecological fates of hybrids

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Salvelinus confluentus and S. malma are migratory freshwater salmonid species with parapatric distributions. In sympatric areas, where S. malma adopts a small-bodied resident life history, extensive natural hybridization occurs between the two species, yielding a variety of hybrid classes morphologically indistinguishable from parental individuals. The current study uses one mitochondrial and three nuclear markers for the examination of 1100 juveniles from 26 sites in five tributaries to a single watershed. Nuclear analysis showed that 8% to 16% of individuals are of hybrid origin. Hybrids are found in all five tributaries and the proportion of hybrids increases as either parental species becomes more prevalent at a site. The asymmetry of the initial cross (S. malma male by S. confluentus female) and subsequent backcrosses are predictable based on species and hybrid body sizes, spawning times, and mating tactics, and is supported by the consistent presence of S. confluentus mtDNA in hybrids. Both static cohort (four age classes, 1998) and dynamic cohort (fry 1997, yearlings 1998) analysis revealed an increase in proportions of hybrids over time, and the presence of multiple hybrid classes indicate that hybrids are both viable and fertile. Pure parental individuals, however, form the majority of individuals, and there is no evidence that the two species are collapsing into a hybrid swarm.

# The mode and tempo of freshwater fish colonisation across the Isthmus of Panama based on molecular markers: which routes were available?

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We present a molecular appraisal of the dynamics of colonisation of lower Central America by 5 South American derived lineages of fresh water fish. All lineages are members of 4 genera belonging to families generally thought to have had no historical potential to disperse through marine waters. As a consequence of their assumed physiological intolerance to marine waters they are restricted to dispersion events resulting from geographically and temporally sporadic connections between freshwater drainage basins. The occurrence of such inter-drainage exchange events are intimately related to the (well studied) geological development of the Isthmus since its emergence 3.1-3.5 Ma, consequently studies of such fish are considered to permit strong inference regarding the terrestrial evolution of this important faunal exchange corridor. Phylogenetic hypotheses are based on mitochondrial DNA markers from 400+ individuals sampled across Central and South America. Our molecular results indicate that the Central American histories of the four genera are complex but can be tied to events associated with or post dating the development of the Panama isthmus. We show that many lineages with restricted geographic distributions now demonstrate significant genetic divergence over modest geographic distances, whereas other lineages distributed across much larger geographic areas exhibit markedly less divergence. Our results suggest that the modes of historical dispersal available to Central American colonisers may in the case of some lineages have included marine routes not available to others, and as a consequence rapidly accelerated their geographic dispersion. The observation that congeneric lineages may exhibit extreme variation in their potential to disperse via marine waters is explored as are the phylogeographic and ecological implications for freshwater zoogeography as a whole.

### Evolution of the Amylase gene family in drosophilids : focus on Amyrel, a distant relative.

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"Populations, génétique et évolution " CNRS Gif sur Yvette - France

Amylase enzymes have been well studied for more than 40 years because of their very important metabolic function which is easily detected. Most organisms studied so far have several copies of the *Amy* gene. The members of this gene family have undergone various evolutionary phenomena such as : concerted evolution among closely located copies, strong divergences leading to pseudogenes, changes in the regulation of genes. Amylase is now among the best models to understand the evolution of gene families.

In Drosophilids, we found recently a very divergent copy although active, that we named Amyrel.

This copy was first detected by PCR in a few species of the *Sophophora* subgenus but an extensive survey over a large number of species indicates that its origin is as ancient as that of *Drosophilidae*. The structure of *Amyrel* is strikingly different from *Amy* : it lacks the ancestral intron in position 177 but has an intron in position 655 never detected in any other amylase gene. Moreover, the level of divergence between *Amy* and *Amyrel* raises 40% for nucleic as well as protein sequences. A detailed analysis of *Amy* and *Amyrel* sequences shows that the two types of genes have different codon usage and that *Amyrel* seems to have evolved significantly faster than *Amy*. Using RT-PCR, we showed that the temporal expression of *Amyrel* is restricted to L2-L3 larval stages while *Amy* is active from L1 to adult stages (except pupal stage).

The biological function of *Amyrel* is still questionable. We are presently assaying *in vitro* expression experiments on *Amyrel* to study the corresponding protein. We hope that biochemical informations would help explaining evolution of this particular copy and its maintaining for more than 50 million years in the *Drosophila* phylum. *Amyrel* is another example of the capacity of duplications to create novelty.

Morphological, genetic and ecological differentiation of the planktonic foraminifer *Globorotalia truncatulinoides* in the South Atlantic

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The planktonic foraminifer *Globorotalia truncatulinoides* was restricted to tropical-subtropical environments until 300 kyr when it colonized colder south Atlantic environments in two succesive waves. In sediments, morphological variations have been described in association with this colonization and with modern environmental gradients.

In order to understand the biological significance of these variations, patterns of morphological and genetic differentiation of G. *truncatulinoides* have been studied in plankton samples along a transect of in the South Atlantic within the temperature gradient experienced by the genus.

A Fourier analysis of the foraminifer outline was used to quantify morphological differences. A geographic differentiation occurs along the transect, opposing conical tests in warm waters to lenticular tests in cold waters. A relationship between size and shape suggests that heterochronical processes and change in life history traits could explain this differentiation. Genetic analysis of ribosomic DNA on specimens from the same transect show a clear differentiation of two groups, each being further differentiated in two sub-groups. The distribution of these genotypes fits the morphological and environmental patterns, with the transition between the two main groups being coincident with the morphological main variation and a change of water masses.

These results suggest that the morphological variability is due to a genetic differentiation rather than ecophenotypy. Coincidence of genetic, morphological and ecological transitions suggests that colonization of colder and nutrient-rich environments has been allowed by fixation of adaptations such as changes in life-history traits by reproductive isolation.

Morphological and physiological variability of the coccolithophore *Calcidiscus leptoporus* in plankton populations and culture experiments

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*Calcidiscus leptoporus* is a world-wide distributed species of coccolithophore, a group in which the algal cell is surrounded by calcite platelets, the coccoliths. Morphological variations of *Calcidiscus* coccoliths are known from Holocene sediments according to geographic parameters. *Calcidiscus* coccoliths assemblages are characterized by bimodal distribution with a dominance of small coccoliths in cold to sub-tropical waters, shifting to a dominance of large coccoliths in tropical warm-waters. The biological significance of this variability is not known and can be interpreted as ecophenotypy or mixing of genetically different populations.

In order to understand the significance of these biogeographic variations, morphological variability within populations and individuals and variations with environmental parameters on living coccospheres have to be considered and compared to results on Holocene assemblages.

Seasonal variability and relationship between morphology and temperature in plankton samples will be estimated, to determine if the different morphotypes co-occur in living populations or if bimodal fossil assemblages correspond to succession of the different morphotypes trough the year.

Study of cultures will then allow to compare levels of variability of monoclonal populations with plankton samples and thus assess the potential genetic heterogeneity of the natural populations. Besides, cultures at different temperatures, showing physiological differences in growth rate, should show if the "large" and "small" morphotypes are due to ecophenotypic variations or genetic differences. Together, studies of plankton samples and cultures experiments should finally allow a paleobiological interpretation of the morphological variations in the fossil record.

#### Developmental variations and pollen morphology evolution.

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The pollen grain is the haploid organism produced by flowering plants as the male gametophyte. It is composed of two or three cells surrounded by a complex multilayered wall that represents its external morphology. Apertures are openings the pollen wall, permitting exchanges, pollen tube germination, and preventing pollen burst by accomodating pollen volume variation. Flowering plants exhibit an enormous range of variations in aperture number and distribution.

To elucidate the potential effects of development on the evolution of this character, we performed a developmental study of the ontogenetic events that are involved in aperture site definition for low aperture number (that are the more widespread pollen morphs). This study, based on theoretical modeling and experiments, proposes a general system for aperture number and distribution determination that apply at the scale of Angiosperms. In particular, it has been possible to relate variations in morphology to particular developmental sequences.

Consequences of development in pollen morphology evolution are various. i) Developmental constraints apparently delimit the total amount of diversity at any taxonomic level within Angiosperms. ii) Comparisons between the different developmental sequences indicate differences in their ability to be modified. iii) Development could lead to the production of particular morphologies potentially suboptimal. This poses the question whether development is not an evolutionnary force comparable to genetic drift.

### Conflict over colony growth in eusocial Himenoptera

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Social insects provide striking examples of elaborate cooperative behaviour, yet life within colonies also entafis conflicts. For example, workers and queens typically have, different sex ratio optima, causing a potential intra-colony conflict over sex allocation. Here, we expand the framework of sex ratio conflicts by integrating life-history parameters and show that a potential conflict can arise among colony members over investment in colony growth (worker production) versus colony reproduction (production of new queens and males). The occurrence of this conflict depends on whether the number of eggs in the colony is limited. When the number of female eggs available for raising is limited, worker production has be traded off against production of new queens. Here, conflict arises because the workers favour smaller, but more fernale-producing colonies than the queen. No trade-off between worker and queen production is imposed if egg number is not limited and consequently no queen-worker conflict arises. We fiHffier show that, whether or not egg number is limited, fernale larvue are in conflict with other colony members over colony investment decisions. This is because larvae can increase their inclusive fitness by developing into new queens even if this significantly decreases overall colony productivity. The extent of the conflicts between colony members is influenced by the genetic structure of colonies and our models make predictions that allow to determine which party (queen, workers, or larvae) is in control of caste determination in social Hymenoptera.

#### Preliminary results in a molecular phylogeny of the tribe Valerianeae Höeck (Valerianaceae Batsch.)

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Valerianeae Höeck is the most important tribe within the family Valerianaceae, due to the quantity of its species and its broad geographical distribution. To test the relationships between different members of this tribe we have used the intergenic chloroplast region located between the ATPb and the rbcL genes as genomic marker for 25 species of this tribe. As show the results, the main evolution of this intergenic region is due to changes of the type 'indels', but there are also substitutions as evolutionary events which are combined with vast zones of deletions in some studied taxa. As a consequence, we compare the method of Barriel (1994) to codify the different combinations of indels and substitutions with traditional ones (missing values, fifth state). The preliminary results show **Fedia** Gaertner (3 species) and **Valerianella** Miller (3 studied species) as sister-groups, as well as the monophyly of the genus **Centranthus** Graebner (4 species), and of the whole of the american studied species of the genus **Valeriane** L. (7 species).

Experimental Evolution of 'Transcription-Impaired' and 'Transcription-Competent' Rifampin-Resistant *E. coli:* Functional Compensation? Enhanced Resistance? Or Reversion? What are the Outcomes of Secondary Adaptation?

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Rifampin [rif] is a potent antibiotic that targets the transcriptional apparatus of prokaryotes, inhibiting mRNA initiation and ultimately effecting bacterial cell death. Among the bacterial pathogens against which rif is used as clinical therapy (eg. *Mycobacterium tuberculosis, Staphylococcus aureus, Neisseria meningitidis*), resistance can nearly always be attributed to acquired amino acid substitutions in the beta subunit of RNA polymerase (RpoB). In the interest of understanding the evolutionary consequences of resistance, we pose the question, "if transcription is of pivotal importance for efficient cellular function, then do mutations that diminish rif-binding and impair transcription have large collateral effects on fitness?" Stated differently, is there a fitness burden to rif-resistance and if so can we trace the cost directly to transcriptional defects?

In laboratory settings, the frequency of conversion to rif-resistance is relatively high as multiple different RpoB mutations can generate resistance. The resultant drug-resistant clones are not, however, equivalent. Derived mutants of *E. coli* K12 exhibit a spectrum of phenotype with respect to fitness 'cost' and level of resistance. We have exploited this variation to explore *in vitro*, i) the primary effects of rif-resistance mutations on fitness (e.g., resistance level, transcriptional impairment, cost) and, ii) the nature of secondary adaptations to the primary resistance lesion (e.g., what is the trajectory of evolution for resistant clones? compensation? reversion? or enhanced resistance?

Additionally, we have looked at how the genome responds to strong selection on a single locus (RpoB). Most mutants resistant to rif are at a fitness disadvantage relative to their drug-sensitive ancestors. We have allowed 'low-fitness' (and 'high-fitness') RpoB mutants to evolve (with and without drug-selection pressure) in order to evaluate whether or not evolved increases in fitness compartmentalize within transcriptional apparatus, or spring from more generalized 'adjustments' in the background genome.

# Gene flow among populations of the Lake Tanganyika rock cichlid Ophthalmotilapia ventralis along a coherent coastline

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To determine gene flow among Tanganyikan species *Ophthalmotilapia ventralis* we analyzed mitochondrial DNA variation in different populations along the southern lake shore. We selected five habitats each seperated by a distance of about four kilometers.

Rock habitats were also segregated by mud shores and river estuaries. For each population 30 individuals were characterized based on genetical methods. Our data emphasize the influence of species-specific ecological characteristics on gene flow over barriers or distances.

# Aminoacyl-tRNA Synthetases as Markers of the Evolution of the Genetic Code

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Aminoacyl-tRNA synthetases (ARS) catalyze the specific aminoacylation of tRNA molecules with their cognate amino acids, a crucial step in the process that translates genetic information to protein sequence. Each enzyme is specific for one amino acid and its cognate tRNAs. All extant ARS can be structurally divided into two distinct classes, that evolved from two single ancestors. The universal sequence conservation for most extant ARS suggests that the evolutionary events that generated these enzymes took place before the establishment of the three phylogenetic branches of life (Bacteria, Archaea, and Eukarya). However, recently found examples of non-universal ARS suggest that important aspects of genetic translation were settled more recently than initially thought.

These findings include the discovery of the first case of class switch among ARS. It has been found that, in a small number of organisms, the canonical enzyme lysyl-tRNA synthetase (LysRS-II, a class II ARS) is replaced by a different lysyl-tRNA synthetase (LysRS-I) (1). In another case of non-canonical distribution, Glutaminyl-tRNA synthetase (GlnRS) is absent in most bacterial species, where its function is replaced by glutamyl-tRNA synthetase (GluRS) and a transaminase enzyme (2). A recent realization regarding the evolution of these enzymes is the widespread existence of ARS-like proteins. These molecules, which are completely uncharacterized, are homologous to discrete domains of ARS, but their distributions are not universal (3). The functional and structural evolution of extant aminoacyl-tRNA synthetases and ARS-like proteins will be discussed. The analysis of the evolution of these molecules is beginning to provide us with information about the process of appearance of the main phylogenetic branches of the tree of life. Results concerning the evolution of alanyl-tRNA synthetase, and its implications for the evolution of early eukaryotes will be presented.

1. Ibba, M., Morgan, S., Curnow, A. W., Pridmore, D. R., Vothknecht, U. C., Gardner, W., Lin, W., Woese, C. R., and Soll, D. (1997) "A euryarchaeal lysyl-tRNA synthetase: resemblance to class I synthetases" *Science* **278**(5340), 1119-22.

2. Lamour, V., Quevillon, S., Diriong, S., N'Guyen, V. C., Lipinski, M., and Mirande, M. (1994) "Evolution of the Glx-tRNA synthetase family: the glutaminyl enzyme as a case of horizontal gene transfer" *Proc.Natl.Acad Sci.USA* **91**, 8670-4.

3. Ribas de Pouplana, L. (1999) "Aminoacyl tRNA synthetase –like proteins. New additions or remnants of the past ?" *Trends Biochem. Sci.* In press.

# Haplotypic diversity of maritime pine (Pinus pinaster) in Portugal revealed by cpSSR

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Six polymorphic chloroplast microsatellites were used to evaluate levels of genetic variation within and among twelve populations of *Pinus pinaster* from the distribution range of the species in Portugal. Thirty-two haplotypes were found, with 47% of them being specific for single populations (rare haplotypes). The analysis of cpSSR variation detected a low degree of population divergence. The differentiation among populations based on the IAM (infinite allele model) estimator was very low (=0.023), but significantly different from zero. The similar parameter based on the SMM (stepwise-mutation model),  $R_{,}$  was not significantly different from zero, indicating that the populations differ in their haplotypic frequencies but not in the size of their alleles. Overall, high haplotypic variation within populations was detected. Using the SMM estimator, mean genetic distance of individuals within populations,

, the populations were divided into two groups. The first group contained five populations mainly from the central part of the country and they possess, in general, a high effective number of haplotypes. Among them, two populations were divergent from almost all the others, based on the pair-wise Nei's distance (*Ds*). The results indicate that no geographic genetic pattern can be found in Portuguese populations of maritime pine. The history of expansion of the species range in Portugal during the last century, mainly due to human activity, and the extensive gene flow among populations might explain these results.

#### Colonization patterns and biogeography in the Canary Islands: the emerging picture

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The Canary Islands are a volcanic archipelago located in the Atlantic Ocean, at 100 km from the Northwestern coast of Africa. The origins of the archipelago are controversial, although the most recent revisions favour the hypothesis if being the result of a hot spot volcanism. The seven main islands are roughly arranged in a straight line, representing a gradient of both time of origin and proximity to the mainland. The Canarian Archipelago is usually included in the Macaronesian biogeographic region which comprises several volcanic island groups in the Notheastern Atlantic Ocean. Besides the Canaries, they are the Azores, Madeira, Selvagens and Cape Verd Islands.

Cases of insular evolution and adaptive radiation are very frequent in volcanic islands, and the Canarian Archipelago harbours a flora and fauna that is extremely rich in endemisms (between 50 and 70% of the species). In the last few years, and in the context of the so-called comparative method, several papers have addressed the

subjects of species diversification and island evolution in the Canaries within a phylogenetic framework. Based on the results obtained in these works, we try to infer a general pattern to allow the assessment and understanding of the processes involved in the generation of biodiversity in this archipelago.

#### What can extant Bilateria tell as about the organization of the bilaterian stem species?

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The aim of this talk is to portray the interdependence of phenotypic characters in a model of the bilaterian stem species. The following plesiomorphous phenotypic characteristics will be addressed: cellular tissue organization, monociliated epidermal cells, protonephridial cyrtocytes, basiepithelial nervous system, digestive cavity, occurence of acoelomate, pseudocoelomate and coelomate condition of the body cavity during ontogenetic development.

The review of these characteristics points to the necessity for studying (with molecular techniques) both larvae and adult organisms in the many extant Lower Bilateria featuring a biphasic life cycle.

#### Distribution of Wolbachia strains in populations of the cherry fruit fly Rhagoletis cerasi

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Crossing experiments between populations of the European cherry fruit fly *Rhagoletis cerasi* L. (Diptera, Tephritidae) showed patterns of unidirectional incompatibility. Females of northeastern populations crossed with males from southwestern populations did not yield viable eggs whereas the reciprocal cross resulted in normal numbers of offspring. Populations were screened by PCR using *Wolbachia* specific primers. All populations were found to be infected by *Wolbachia*, an endocellular proteobacteria which can cause cytoplasmic incompatibility in insects. Sequencing and PCR-RFLP revealed the presence of two different *Wolbachia* strains, *w*Cer1 and *w*Cer2 in all individuals of southwestern populations, whereas northwestern populations were only infected by *Wolbachia* wCorf of an Australian population of *Drosophila simulans*.

# Hybrid zones and the genetic architecture of a barrier to gene flow between two sundflower species

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Genetic analyses of reproductive barriers represent one of the few methods by which theories of speciation can be tested. However, genetic study is often restricted to model organisms that have short generation times to are easily propagated in the laboratory. Replicate hybrid zones with a diversity of recombinant genotypes of varying age offer increased resolution for genetic mapping experiments and expand the pool of organisms amenable to genetic study. Using 88 markers distributed across 17 chromosomes, we analyze the introgression of chromosomal segments of *Helianthus petiolaris* into *H. annuus* in three natural hybrid zones. Introgression was significantly reduced relative to neutral expectations for 26 chromosomal segments, suggesting that each segment contains one or more factors that contribute to isolation. Pollen sterility is significantly associated with 16 of these 26 segments, providing a straighforward explanation of why this subset of blocks is disadvantageous in hybrids. In addition, comparison of rates of introgression across barrier to introgression is due to chromosomal rearrangements. These results demonstrate the utility of hybrid zones for identifying factors contributing to isolation and verify the prediction of increased resolution relative to controlled crosses.

# Differences in feminizing patterns produced by *Wolbachia* endosymbionts in woodlice: the result of a Red Queen process ?

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*Wolbachia* are maternally inherited bacterial endosymbionts. They induce feminization in the woodlice *Armadillidium vulgare* (terrestrial isopod). This symbiotic relationship has the following characteristics : (i) The microorganisms reverse the putative males in functional females. Males are therefore individuals that escape *Wolbachia* infection. (ii) Due to the dynamics of the infection, genetic females have disappeared from infected populations, and all infected females found in the wild are genetic males feminized by the symbiont. (iii) Infected females transmit the infection to about 90% of their offspring, and therefore produce broods with 90% daughters. (iv) *Wolbachia* prevent the efficiency of the androgenic hormone, the molecule responsible for male sex differentiation (the female phenotype is not affected by the injection of this molecule).

We recently found that numerous woodlice species from different families are infected by feminizing *Wolbachiae* endosymbionts. However, in most species studied, the feminizing pattern differs in two ways from the "*Armadillidium* pattern": males can harbour the symbionts, and infected females are masculinized after the injection of androgenic hormone (*Wolbachia* does not prevent the efficiency of this molecule)

To explain these differences, we propose an evolutionary scenario based on the Red Queen hypothesis. The selection of host genes that counteract the symbiont feminizing effect could have been followed by the selection of symbiont genes that overcome host resistance. The differences in feminizing patterns between hosts could reflect different levels of this hypothetical evolution.

# Effect of sib competition on observed inbreeding depression in self incompatible species *Arabis petraea* (L.) Lam.

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We have studied the effect of sib competition on inbreeding depression in mainly outcrossing species, Arabis petraea (L.)Lam.. Populations of self-incompatible plant species could be expected to have high levels of inbreeding, but such populations have been rarely studied. Abiotic and biotic environment have been found to have an effect on observed inbreeding depression. Increased inbreeding depression has been found in stressful conditions (Dudash 1990), including intense competition (Schmitt and Ehrhardt 1990). As density increases, enhancing intraspecific competition, fitness differences between siblings may become more pronounced. Intraspecific competition increases inbreeding depression if competitive ability correlates negatively with the level of inbreeding. Competition between siblings has been considered as one mechanism promoting outcrossing over selfing in populations with mixed mating system (McCall et al. 1989). The Arabis petraea seed material used in this study originated from Karhumäki, Russia. Twelve maternal plants were each crossed with two paternal plants. Within the resulting twenty-four families crosses between siblings and unrelated plants were conducted. Seeds with four different levels of inbreeding were produced: outcrosses (F = 0), half-sib crosses (F = 0,125), full-sib crosses (F = 0.25) and selfed seeds (F = 0.5). During the spring and the summer 1998 ninety-six crosstype-family combinations were grown in greenhouse conditions. Plants were grown in different densities: one, two or four plants per pot. We found significant inbreeding depression only in biomass measures in two plants per pot treatment. Increased competition reduced all fitness measures at every level of inbreeding. However, the inbreeding level of competing individuals had no significant effect on the character means. The results will be presented and discussed in our poster.

#### The quest for the first bilaterian from 18S rDNA sequences. Acoel flatworks as the likely earliest bilaterian.

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The quest for the first bilateral organism and its subsequent radiation remain the main unsolved questions in comparative embryology and evolution. The mos accepted hypothesis, based on the argument of increasing levels of complexity along evolution, sees the acoelomates as the simplest bilaterians from wich the pseudocoelomate first and, later on, the more complex coelomates evolved. The alternative hypotesis considers the first bilaterians as complex organisms, likely segmented and coelomate, being pseudocoelomates and acoelomates groups derived by simplification.

Molecular methods of phylogenetic inference, namely 18SrDNA sequencing, have been instrumental to rule out severa simple animal groups (e. g. nematodes, rotifers, and platihelmints among others) as potential candidates to this basal position. Nonetheless, when acoel flatworms, traditionally classified as an order of the Platyhelminthes, are included in this kind of analysis, they always branch after the diploblasts, indicating they might be primitive tripoblatic animals. However, since all acoels sequenced so far show rate of nucleotide substitution 3-5 times greater than those of most other Metazoa, their branching at the deepest base of the trees is likely to be artefactual. To overcome it,complete 18S rDNAs from 18 acoel species were obteined, and non-fast evolving acoels compared to non-fast evolving species of other metazoans. Results show that acoels do not belong to the Platyhelminthes but represents the extant members of the earliest divergent Bilateria, an interpretation also supported by recent studies on the embrionic cleavage pattern and the nervous system structure. Potential pitfalls of molecular methods and ways to overcome them will be briefly discussed.

# Chromosomal contribution to adult body size in latitudinal clines of Drosophila melanogaster

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Latitudinal variation in body size in *Drosophila melanogaster* occurs throughout the world. An understanding of the underlying genetics is crucial for a full explanation of this phenomenon. A first step in this process is to determine the contribution of each chromosome to variation in body size. Here, I report on studies in parallel of flies from two continents (South America and Australia), testing whether latitudinal variation in body size in a pair of independent clines has the same genetic basis. On both continents, the largest effect on body size is localised to chromosome three which may suggest that the same gene or genes of major effect are being selected for in each cline. In addition there are effects on body size that are significant but of small magnitude. The chromosomal origin of these effects differs between the continents which indicates that the two clines are not genetically identical.

#### The Evolution of Genetic Architecture.

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To make long-term predictions using present quantitative genetic theory it is necessary to assume that the genetic variance-covariance (**G**) matrix remains constant. However, **G** can be altered by two processes, selection which tends to cause varying divergence among the elements of different matrices and drift, which also causes matrices to diverge but remain proportional to each other. The assumption of a constant **G** is predicated on the hypothesis that selection is sufficiently weak that mutation can replace variation lost due to selection. This assumption can only be justified by empirical demonstration that the **G** matrices estimated from natural populations are not significantly different. In this seminar I 1) Review the methods available to detect variation among matrices, 2) Present two examples, one in which significant variation in genetic architecture over time has been observed, and one in which proportional variation between two species was detected, 3) Argue that the primary question is not one of hypothesis testing but rather interval estimation to address the question of how divergence among **G** matrices is related to phylogeny.

# Behavioral and morphological basis of incipient speciation between sympatric ecotypes of an intertidal snail

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On exposed rocky shores in Galicia, two ecotypes of *Littorina saxatilis* can be found at different shore levels. These forms differ in many phenotypic and genetic traits and they show assortative mating where they meet in sympatry, although some hybridization occurs. We estimated mate choice coefficients (sexual isolation) in every mate combination from the mating pool, providing new information about the mate choice mechanism, and then used multiple regression to find those morphological traits causing the observed pattern in sexual isolation. Mate choice coefficients are partially caused by a micro-scale morph aggregation in mid shore, but when they are corrected for this effect, those pairs which involved at least one hybrid form mated randomly. Thus, mate choice is also caused by the interactions between pure ecotypes. A significant amount of the sexual isolation (assortative mating corrected for environmental effects) is explained in terms of morphological diversity (r<sup>2</sup> of the model = 41.2%). This morphological diversity includes both shell and penis measurements. Furthermore, a direct role of penis morphology (number of mamilliform glands and penis width) can be shown independent of the striking shell differences between ecotypes. This supports previous suggestion that an anatomical incompatibility in copulatory characteristics may contribute to the sexual isolation between these ecotypes. The proposed mechanisms contributing to sexual isolation and the traits involved suggest that reproductive isolation has evolved in these populations indirectly by natural selection, adapting each ecotype to its particular ecological niche.

Evidence for introgressive hybridization at microsatellite loci between two marine fishes (Sebastes sp.) from the North Atlantic.

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While relatively common for terrestrial and freshwater organisms, evidence for extentive introgressive hybridization is scarce in marine organisms. In this paper, we provide evidence for such a phenomenon between two economically important fishes from the Northwest Atlantic; S. fasciatus and S. mentella are respectively found in allopatry south and north of a zone of sympatry that extends in the Gulf of St.Lawrence.Using 8 microsatellites loci, we documented the extent of genetic divergence among 12 populations; 4 of S. fasciatus, 4 "allopatric" populations S. mentella and 4 "sympatric" populations S. mentella from the zone of sympatry. All estimates of genetic divergence (pairwise Fst, Fst, D) were congruent in showing little divergence among populations within S. fasciatus and S. mentella found in allopatry. In contrast, a pronounced differentiation was observed between these 2 groups. However, populations of S. mentella within the zone of sympatry were less genetically differentiated from S. fasciatus than were allopatric populations of S. mentella. This pattern was also confirmed by a Factorial Correspondence Analysis (FCA) based on individual multi-locus information. A detailed analysis of allelic composition also showed an admixture of both S. fasciatus and S. mentella specific alleles in S. mentella found in sympatry. Altogether, this study provided evidence for pronounced introgressive hybridization between the two species when found in sympatry, and suggested that introgression may be unidirectional, from S. fasciatus into S. mentella. Further analyses are under way to assess whether this phenomenon is of ancient or recent origin.

#### Developmental constraints in the evolution of the human face

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The discovery of homologous Hox genes as responsible for substantially different phenotypes has revived the interest on morphological evolution, since the final result of developmental processes need to be explained in a phylogenetic context. This new interest on morphology overlaps with the long standing biological theories rooted in internalist perspectives, and gives a refreshed insight into the "form and function" debate. In spite of these advances, however, current evolutionary theory preponderantly approaches the evolution of form as an adaptation problem.

The morphological evolution of the human face, from which a large amount of background information is available, is a good case for discussion of these matters. Simply stated, two different patterns emerge in the evolution of *Homo* in the last million year, associated with an increase in brain volume. On one hand, modern human cranial topology, grossly defined by a relocation of the face below the forebrain and anterior cranial base. On the other hand, the evolutionary differentiation of Neanderthals. In this latter case, a unique development of facial prognatism characterise the morphological evolution of this human group. A variety of functional reasons have been proposed for explaining this modification, favouring either adaptation to cold environment or masticatory functions (e.g. heavy use of the anterior dentition). In this paper, I will explore the processes underlying the development of facial morphology, and how interactions between brain and cranial base development constraint the phenotypic results arising in the evolution of the human face.

#### The theoretical basis of measures of kin selection in subdivided populations

#### F. Rousset and S. Billiard

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Some basic kin selection models are reformulated as stochastic mutation-selection-drift processes in finite subdivided populations. All genetic parameters are defined as expectations under this process, specifically as functions of probabilities of identity in state. A measure of kin selection is defined which in some cases is very similar to previously used "fitness" measures. It does not really qualify as a "fitness" measure and, in contrast to earlier assumptions, this measure is not supposed to give the direction of selection on a deviant allele given any particular allele frequency in the population. In fact it does not, particularly for rare alleles. Rather, we show that it gives the first order effect of selection on expected allele frequency under mutation-selection-drift equilibrium, which is a global measure taking into account the effects of selection at all gene frequencies. Techniques for evaluating such a measure and evolutionarily stable strategies are available, as well as generic definitions of relatedness parameters measurable using genetic markers.

#### Phylogeography and cryptic species in a cosmopolitan echinoderm

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*Amphipholis squamata* is a hermaphroditic, brooding britle star (Ophiuroidea) with an extremely wide distribution. It has been reported world-wide, except for extreme polar regions and occurs from the sublittoral to several thousand meters depth. Due to the absence of free-living larvae, and presumably therefore low dispersal, this species was chosen as a model to investigate world-wide marine phylogeographic patterns. We analysed 2000 bp of DNA sequence of 16S mtDNA, COI mtDNA and 18S DNA from thirty *A. squamata* populations world-wide. Genetic diversity and divergence within and among populations are high, with genetic distance between some populations attaining the highest intraspecific levels reported in the scientific literature. Based on our data we propose that A. *squamata* is composed of a complex of several cryptic species. Phylogenetic analysis of the data results in a well supported tree with four highly divergent clades corresponding to 1) northern temperate hemisphere locations, 2) southern temperate clades are sister groups resulting in a bipolar distribution pattem, which has been reported in a number of other widely distributed marine invertebrates. Specimens from depth are highly divergent suggesting that depth is an important barrier to gene flow, possibly more so than horizontal distance.

#### The role of Hox genes in establishing segment-specific bristle patterns in the legs of Drosophila

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Genes of the *Hox* clusters provide a molecular framework for the diversification of segments in arthropods and vertebrates. Individual *Hox* genes are expressed in staggered domains along the antero-posterior body axis. Their differential expression causes cells that would otherwise be equivalent to adopt different developmental fates.

To understand how segment diversification can occur under the spatial control of Hox genes one needs to determine at what steps in the developmental process Hox genes directly control segment morphology. We have studied how specific bristle patterns are generated from identical segment ground plans in the 2nd and 3rd leg of the fly *Drosophila melanogaster*. These differences include the absence of specific macrochaetes from the third leg: the sternopleural macrochaete, the edge bristle and the apical bristle are missing. The Hox gene Ubx is needed for these differences because in the absence of Ubx function the bristle pattern of the third leg is completely transformed to that of the second leg.

We have followed the development of sensory organs in the leg discs to identify points of divergence between the 2nd and the 3rd leg.

We have induced Ubx- clones at different times in development to assess when Ubx acts to repress the development of bristles in the 3rd leg.

We are trying to identify additional factrs that account for the selective elimination of some but not all macrochaete precursors expressing high levels of UBX protein.

Comparative phylogeography and population structure in an endemic cichlid lineage from Lake Tanganyika

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Large-scale lake-level fluctuations in the Pleistocene are thought to have heavily influenced the evolution of the endemic cichlid species flocks of Lake Tanganyika. Phylogeographic data based on mitochondrial DNA (mtDNA) sequence variation from 95 specimens collected from 66 localities were used to assess the influence of these historical events on evolutionary patterns and processes in the Eretmodini, an endemic tribe of rock-dwelling cichlids. The high degree of intra-lacustrine endemism and the pronounced phylogeographic structuring of the observed eretmodine mtDNA lineages can be partly explained by the influence of these major lake level fluctuations that split up the single lake basin of Lake Tanganyika into three isolated sub-basins. Our results thus support the hypothesis that the current genetic structure is strongly affected by changes in lake level due to past climatic changes. In addition, we also quantified the genetic population structure of two eretmodine lineages along the southern Congo shore in order to investigate the extant of population subdivision on a microgeographic scale. Using both, mtDNA control region sequences and six microsatellite loci, we found a significant genetic differentiation between test populations. Our results show that contemporary gene flow is limited between populations and suggest that genetic divergence along patchy rocky habitats is an additional force in shaping the distribution patterns found in eretmodine cichlids. Such high degrees of population subdivision may help to understand more about the evolutionary mechanisms responsible for the explosive speciation found in cichlid species flocks.

# Queen size dimorphic ants: a life history syndrome with consequences for population structure ?

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Ants' reproductive strategies can be divided into independent modes of colony establishment and dependent colony founding in which young queens seek assistance from existing colonies, related or unrelated. The coexistence of two female reproductive morphs that only differ in size in some ant species (queen size dimorphism) can be taken as explicit evidence that the two reproductive options coexist in these species long enough for selection to shape morphology. As populations generally vary in the balance between the two morphs, and the resulting life histories differ in dispersal, profound effects for the population fine structure are to be expected.

The North-American ant *Leptothorax rugatulus* has been found queen-dimorphic over a wide geographic range and its relative abundance makes it a good model organism. Collection data indicate strong, consistent differences in morph frequency between populations. The morphology of a colony's queens and its social type is strongly correlated: large queens prevail in monogynous colonies, while most of the small queens are found in polygynous colonies. After providing some evidence for different reproductive tactics, we will present the results of a comparative study of population fine structure using microsatellites as genetic markers. We compare three populations that differ in their morph frequencies and social colony structure. In conclusion, the presented results will be discussed in the context of the evolution of dispersal polymorphisms and alternative reproductive tactics in social insects.

#### Signal selection in a desert lily

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Plants frequently display their flowers on long flower stalks to advertise them to their pollinators. We sought to determine whether such advertisements constitute reliable signals; a signal must be costly otherwise all plants regardless of quality and benefit to potential pollinators would invest in such signals. The Negev desert lily *Pancratium sickenbergeri* (Amaryllidaceae) is a suitable species to test this concept. In the fall the plant produces a tall flower stalk. The optimum height of the flower stalk is likely to be the result of costs and benefits for the plant, where the benefit curve is the result of pollination and the cost curve is the result of herbivory and allometric growth. There is a strong positive correlation between flower stalk height and the probability that it will be eaten by the dorcas gazelle *Gazella dorcas*. The large flower produces abundant nectar and pollen and is visited by moths, butterflies, bees and syrphid flies. The benefit of a tall stalk is shown by the significant positive correlation between stalk height in this species appear to be a reliable signal to pollinators that has resulted from the costs inflicted by herbivory.

Reconstruction of the evolution of the AP68 microsatellite locus in 11 Primate Platyrrhine species (Cebus albifrons, Cebus apella, Saimiri sciureus, Saguinus oedipus, Saguinus geoffroyi, Cebuella pygmaea, Aotus lemurinus., Alouatta seniculus, Lagothyix lagotricha, Ateles fusciceps and Ateles belzebuth).

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The reconstruction of the gene tree of the AP68 marker is not in agreement with the phylogenetic tree of the Plathyrrine, because some selective pressures might be affecting it. Many of the species studied were fixed for an alleleof 168 pb (S. oedipus, S. geoffroyi, A.lemurinus and L. lagotricha). Cebus apella was fixed for an allele of 166 pb, while C. albifrons presented, in higher frequencies, also this same allele. This group of primates so similar is composed by Callitrichinae, Cebinae and one Atelinae species. Cebuella pygmaea was fixed for one allele of 176 pb In general, the other Atelinae showed more polymorphism and higher alleles. This is the case of A. fusciceps (179 pb), A. belzebuth (171, 174, 177 and 179 pb) and Alouatía seniculus (193 and 196 pb). The sizes of the alleles found for this last three species are noteworthy smaller than those reported by Ellsworth and HoeIzer (1998) for Alouatta senículus (262-268 pb) and Ateles geofroyii (240-242 pb). This means that the evolution within these Atelinae is substantially higher than in the other species analyzed. Saimiri sciureus do not amplify for this marker, which means that this species lost this DNA segment. This should be an indication that the original size of this microsatellite in the Platyrrhine was about 168 pb, because it is not-parsimonious that independently six Platyrrhine species reached the same allele size. This also indicates that some background (purifying) selection should be actino on this marker in these genera, because it is in a region of low recombination with continual input of deleterious mutations which reducing neutral variability at loci linked, as should be the marker in question. On the other hand, in some genera as Aloualta and Ateles this background selection is not present or, there might even be direct, or hitchhikina effect, for the fixation of diverse alleles by adaptative positive selection.

Differential phylogenetic results among seven Colombian Primate species using seven microsatellite loci in function of the genetic distances used: The advantages of the 8pi 2genetic distance versus other genetic distances for the reconstruction of Primate phylogenies and calculation of time of divergence among the seven species studied

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Seven Primate species (*Cebus albifrons, C. apella, Saimiri sciureus, Alouatta seniculus, Lagothrix lagotricha, Ateles* fusciceps and *A. belzebuth*) were studied for 7 microsatellite loci (AP40, AP68, D5SI 17, D17S804, D5S 111, D6S260 and D14S51). Various multivariate analyses were carried out to analyze the phylogenetic relationships between these 7 species, using the four classical genetic distances of Nei, Cavalli-Sfórza and Edwards, and Prevosti, and xx2, specifically created to work with microsatellite loci. The first are based on an infinite allele mutation model, while the second is in agreement with a step-wise mutation model. For a comparison, we used the phylogenetic results of Scímeider et al., (1996), Horovitz et al., (1998) for molecular data, and of Rosenberger (1984), for morphological data. The xx2 distance showed more consistent phylogenetic results than the other genetic distances. With the Nei's distance one inconsistence was the association of *Lagothriz* with *Cebus* and *Saimiri*, and with the Prevosti's distance, the relationship of *C.apella* with *Ateles*, being stronger than with C. *albifrons*.

In contrast, the 8W distance generated a phylogenetic tree much more similar to those shown by other phylogenetic analyses, carried out by the previously authors quoted. The time of divergence found between certain species-pairs were in years: *Cebus albifrons-C. apella* 2.8x106; *Ateles fusciceps-A. beIzebuth*, 3x105; *Cebus-Saimiri*, 5.6x106; *Cebus-Lagothrix*, 21.5x105; *Cebus-Ateles*, 19.6x106; *Saimiri-Ateles*, 16.2x106, and *Lagothrix-Ateles*, 4106, in agreement with those calculated by Schneider et al., (1993).
Evolution of a regulatory domain involved in the synthesis of aromatic amino acids: characterization of this domain in the endosymbiont of aphids *Buchnera aphidicola* 

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Buchnera aphidicola is a Proteobacteria that maintains an endosymbiotic association with aphids. Due to the low nutritional quality of the plant sap diet of aphids, the proposed role of the bacteria in the symbiosis is provide aphids with essential amino acids. In fact, genes involved in the biosynthesis of leucine and tryptophan have been amplified by means of their transfer to plasmids (1,2). Phenylalanine is another essential amino acid that seems to be overproduced by the endosymbiont, although no gene amplification via plasmid has been found. In bacteria, the main biosynthetic pathway comprises three reactions, the second of them catalysed by prephenate dehydratase (coded by the pheA gene). This protein contains a regulatory domain at the C-terminus whose main function is the feedback inhibition of the protein by phenylalanine. We have sequenced a region of the genome of Buchnera aphidicola (host: Acyrthosiphon pisum) which includes the gene pheA. A multiple alignment of Buchnera protein with other of eubacterial, arqueobacterial and eukaryotic origins have shown the presence of several changes in the regulatory domain of Buchnera that probably have made insensitive the protein to the allosteric control by phenylalanine. In order to demonstrate this statement, a site-directed mutagenesis study has been started to confirm that these changes produce the desensitization of this protein to the inhibitor concentration. In addition, we show that this domain is also present in some unrelated proteins, the aromatic amino acid hydroxylases. A phylogenetic analysis of this domain in the two kind of proteins has been performed, indicating a very old domain transfer event.

1. (Bracho, A. M., Martinez-Torres, D., Moya, A., and Latorre, A (1995). J. Mol. Evol. 41, 67-73.

2. (Lai, C. Y., Baumann, L., and Baumann., P. (1994). Proc. Natl. Acad. Sci. USA 91, 3819-3823.

# Maintenance of a genetic polymorphism by heterozygote advantage: studies on prey prefrence in soil predatory mites.

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In a previous article we showed that a local population of the soil predatory mite, *Hypoaspis aculeifer*, harbours genetic variation in preference for two prey species: the bulb mite, *Rhizog1yphus robini*, and the copra mite, *Tyrophagus putrescentiae*. Here, we show that in terms of population growth rate the bulb-mite-preferring line outperforms the copra-mite-preferring line irrespective of whether it is reared on copra mites or bulb mites alone. Hence, there is no evidence for a trade-off in reproductive performance. However, hybrids outperform the selected lines when fed on copra mites, but have intermediate reproductive success when fed on bulb mites. On a mixed diet of the two prey species hybrids also outperform the selected lines. Thus, rather than trade-off relations, heterozygote advantage explains the maintenance of genetic variation in prey preference in the laboratory culture, as well as at a small spatial scale in the field.

To investigate the likelihood of hybridization, mate choice of the selected lines was analysed experimentally. It was found that mate choice of the selected line is assortative on a prey diet where this line is superior in reproductive success, but when hybrids are superior, disassortative mating predominates. Thus, diet-dependent switches in mate choice are implicated in the maintenance or breakdown of genetic variability within local populations.

## Sex biased introgression in flycatchers revisited - genetic pitfalls

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Previous genetic analyses of the closely related collared flycatcher (*Ficedula albicollis*) and pied flycatcher (*F. hypoleuca*), suggested high divergence of mitochondrial DNA (mtDNA) based on restriction fragment comparisons (RFLP) but similarity of nuclear DNA. These birds hybridize to some extent with female hybrids exhibiting higher levels of sterility than male hybrids. Hence, the different signals from the nuclear and mitochondrial markers were ascribed to sex biased gene flow, i.e. introgression of nuclear DNA only, through fertile male hybrids. Here, allopatric and sympatric flycatchers are compared using seven microsatellite loci and direct sequencing of mtDNA. Clearcut, but moderate genetic differentiation of the two species is reported for both types of markers. Moreover, a comparison of allopatric and sympatric populations of the two species suggests low rates of nuclear introgression, ruling out introgression as the main explanation for allozyme similarity. It is suggested that the lack of allozyme differentiation of the two species is caused by stabilizing selection. The discrepancy in estimated sequence divergence of mtDNA is explained, at least in part, by RFLP's overestimating sequence divergence because the same insertion/deletion is counted as a separate mutation for each restriction enzyme used.

#### Gene network evolution: developmental constrains, entretchement and flexibility

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Neo-Darwinian theory has a low predictive capacity in morphological evolution because does not include in its theoretical framework the interactions between genes that generates morphological variation firom molecular variation. In this work we use gene networks capable of pattern formation over cells in space that differ in the relationship between genotype and phenoúype (i.e.we can correlate molecular and morphological variation) to explore properties that can be used to discriminate in which evolutionary contexts may a developmental system. exhibit one network or another. Such networks reflect emergent mechanisms (like in reaction-diffusion models) and more hierarchic mechanisms providing a new tool to evaluate their relative importance. Emergent non expansive networks gíves the maxímum number of patterns (and they are more complex) both for mutations and alterations of initial inductions (heterotopies). Thus they can be more often involved in the generation of new forms. However this flexibility produces a high mutational cost that prevents the combination of such networks with others and thus the more stable hierarchic networks may replace them, except perhaps in late development. The high homeostatic capacíty of expansive emergent networks favours them. at early phases of development. Further evolutionary implications are studied.

## Comparative phylogenetic analysis among major Tanganyikan Cichlid-Lineages

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Lake Tanganyika, the oldest of the East African Lakes, harbors the ecologically, morphologically and behaviorally most complex flock of cichlid fishes. The formation of the major lineages happened in a very short period of time. Thus, evolutionary reconstruction is difficult. We analysed the phylogenetic relationship among 54 Tanganyikan species by using two mitochondrial gene segments (the entire control region with 895 bp and 402 bp of the cytochrome b). After testing for the influence of different selective constraints the weighting regimes were optimized by estimating the relative mutation frequencies in regions of high and low variation for the control region, as well as for first, second, and third positions of amino-acid-tripletts in the cytochrome b. Then a branch-length-test was performed as to identify taxa of uneven mutation rates and to exclude those taxa in the following analyses. We used parsimony-, neighbor-joining-, and maximum-likelihood-methods including standard statistics. The outcoming topologies from parsimony- and neighbor-joining-analysis were absolutely identical. The maximum-likelihood-tree was in agreement. Our results suggest the Tylochromini, Trematocarini, Bathybatini, Tilapiini, Eretmodini and Lamprologini as the seedings-lineages of Lake Tanganyika that colonized the lake after its formation. The remaining lineages arose within a very short period of time by way of a truly explosive speciation event.

# Plastid DNA sequences and secondary metabolites help to reconstruct the phylogeny of Aurantioideae (Rutaceae)

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The plastid *atpB/rbcL* spacer has been sequenced for 20 genera (44 species) of subfamily *Aurantioideae* representing all subtribes and three other *Rutaceae* genera as outgroups. The tree resulting from these sequences plus a partial set of plastid *rps16* intron sequences is in good agreement with data from phytochemistry: carbazoles are mainly confined to tribe *Clauseneae*, they dominate in *Clausena* and *Bergera*, occur in *Micromelum*, and coexist with highly characteristic S-containing amides in *Glycosmis*. In contrast, polyoxygenated flavones and prenylated coumarines dominate in tribe Citreae, in which carbazoles are lacking. Phytochemical, plastid DNA, and other data support the transfer of *Murraya* s.str. (excl. of *Bergera*) and *Merrillia*, from *Clauseneae* to *Citreae*. Available results support the generally accepted circumscription of the subfamily but indicate considerable changes with respect to the "natural" grouping of genera as proposed in the classical study of SWINGLE & REECE (1967). Redefined, tribe *Clauseneae* include genera with a predominance of plesiomorphic characters, whereas features of tribe *Citreae* are increasingly apomorphic. Subtribes *Triphasiinae*, *Balsamocitrinae* and *Citrinae*, the economically important "true citrus fruit trees" (i.e. *Eremocitrus*, *Clymenia*, *Poncirus*, *Fortunella*, and *Citrus*) is well supported by the molecular data.

## Effects of genetic heterogeneity in vertical transmission on symbiont survival and distribution.

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Genetic heterogeneity in interspecific interactions can play a critical role in the coevolution of the species involved. We have conducted an analytical and numerical investigation of the effects of genetic heterogeneity in the vertical transmission of a symbiont, for the baseline case with no other evolutionary forces present. We introduce interspecific disequilibria in cross-species studies, to quantify nonrandom associations between host genotypes and alleles, and symbiont absence or presence (partitioned according to symbiont strain when applicable). We use this novel coevolutionary approach to delimit how vertical transmission rates affect the symbiont's genetic variability, survival, prevalence, and distribution across host genotypes. We have considered two scenarios: (a) polymorphic symbiont and uniform vertical transmission (all host genotypes transmit the symbiont to their offspring at equal rates), and (b) monomorphic symbiont and differential vertical transmission (different host genotypes transmit the symbiont at a different rate). In the first scenario, maintenance of different symbiont strains is possible only when they have equal transmission rates, and this rate is >0.5. Differential transmission, as compared to uniform vertical transmission: (i) increases the overall chance of symbiont survival from 50% to almost 60% when transmission rates and gene frequencies are generated at random from uniform distributions; (ii) dramatically reduces the minimum average vertical transmission rate at which the symbiont can survive from 0.5 to 0.008; and (iii) readily creates permanent host-symbiont disequilibria de novo, whereas uniform transmission can neither create nor maintain such associations. Heterozygotes are a bridge of symbiont transmission between the homozygotes. In consequence, heterozygotes are slightly more likely to carry and maintain the symbiont in the population, and on average are more randomly associated with the symbiont than homozygotes. Simple evolutionary forces can therefore create substantial nonrandom associations between two interacting species, which has implications for issues as diverse as coevolution, speciation, and vaccination programs.

# Nucleotide variation in the olfactory-specific genes OS-E and OS-F of Drosophila melanogaster and D. simulans

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Odorant binding proteins (OBPs) are low molecular weight secreted proteins that have been proposed to bind, and solubilize, hydrophobic odorants and pheromones across the vertebrate olfactory mucus and insect sensillar lymph. Although the specific function of these molecules in olfaction is still unknown it has been proposed that they could play a role in olfactory coding.

In *Drosophila*, two of theses genes, the olfactory-specific genes OS-E and OS-F, are arranged in tandem in the same genomic region with similar intron-exon organization. DNA sequence variation in the OS-E and OS-F genes has been analyzed in order to infer the evolutionary forces shaping nucleotide variation in these genes. Due to the putative role of odorant binding proteins in the recognition system between individuals and/or in odorant discrimination, variation at these genes might reflect the action of the natural selection. In the present work we have analyzed nucleotide variation in nine lines of *Drosophila melanogaster* and also in one strain of *D. simulans*. The region surveyed (~4.8 kb) includes the coding regions of the *OS-E* and *OS-F* genes as well as their intergenic region.

Elongation factor-la introns as molecular markers for recovering phylogenetic relationships among putative sibling species in European populations of genus Pauesia (Hymenoptera:Braconidac:Aphidiinae)

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Elongation fáctor-lx (EF-lx) is a highly conserved nuclear protein coding gene that has proved to be phylogenetically informative at low taxonomic levels, specially by the presence of fast evolving sequences (introns) therein. Hence, we investigated the utility of two EF-lx introns for the phylogenetic analysis of closely related taxa and their efficiency for detecting geographic variation among them by using the species of genus Paucsia as a model system. Three putative species complexes had previously been drawn within this genus using rnorphological data, but both their monophyly and species composition have been questioned and many populations are not referrable to described species. In particular, our study analyzed the extent of the EF-1 a differentation at the former levels by sequencing approximately 800 bp, including two introns. Dealing with introns, the main associated problem is to establish accuratly hypotheses of character hornology. So, we inferred phylogenetic trees for 35 sequences of Pauesia (plus 3 outgroups) by performing 72 alignments under different gap-change ratio parameters. Trees were constructed using neighbor-joining, parsimony and maximum-likelihood methods. All of the multiple sequence alignments procedures yielded the same basic structure for the estimate of the phylogenetic relationship among the taxa. However, the placement of some taxa was sensitive to the alignment procedure used. The multiple alignments from the different procedures varied greatly in length, but aligned sequence length was not a good predictor of the similarity of the resulting phylogenetic trees. In'general, results supported the postulated groups and allowed to clarify the relationships among most of the taxa.

## The mycorrhizal symbiosis: Selection pressures and molecular evolution in a 400 million-year old symbiosis

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The mutualistic mycorrhizal symbiosis between 80% of plant species and the arbuscular mycorrhizal fungi (AMF; Class: Zygomycete) has existed since plants colonized land about 400 million year ago. Theoreticians have predicted that mutualistic symbionts are not subject to either selection pressures favouring the evolution of a sexual life history or evolution of specificity and that they will evolve slowly. Recent evidence from ecological studies on the effects of AMF on plant fitness and effects of plant species on AMF life history traits indicate that indeed selection pressures which would favour specificity exist. In the second part of this presentation, I will show data from molecular studies on the genome organization of AMF that give us a clue to evolution of these fungi. The data indicate that owing to their unusual life history and in the absence of recombination, AMF have possibily evolved to habour a genetically diverse population of nuclei within individuals. Most of the molecular data presented concern the multi-copy ribosomal gene family and the data also indicate that the process of concerted evolution my not be acting on this gene family in the AMF. The consequences of the molecular evolution of AMF will be discussed in relation to the evolution of specificity in the mycorrhizal symbiosis.

## Phylogeny and Biogeography of the Family Triacanthodidae (Tetraodontiformes, Pisces)

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A variety of pioneering studies performed utilizing phylogenetic systematic techniques seem to suggest that the vast majority of speciation processes in terrestrial and freshwater taxa might be due to vicariant events. By contrast very preliminary work on marine organisms seems to indicate that different modes of speciations might be predominant in the sea, perhaps due to important differences in the reproductive biology of many marine organisms. More phylogenetic hypothesis are badly needed in order to test these preliminary results for marine organisms. For this purpose a phylogenetic systematic analysis of the family Triacanthodidae (Tetraodontiformes, Teleostei) is being conducted. The evolutionary interrelationships of these deep benthic fishes are reconstructed with the use of morphological characters, obtained through the examination of the osteology and the external features of two fossil species from the Oligocene and twenty-two extant species. Once a phylogenetic hypothesis is available, and the biogeographical distributions of both present and fossil taxa are known, it may be possible to hypothesize which modes of speciation might have been responsible for the present composition of this family and its distribution. The results of this study are presented and discussed.

## Geophysiological modelling of the evolution of marine ecosystems

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Living organisms evolve within ecological associations (ecosystems, landscapes, biomes, the biosphere) that have a biological component and a physico-chemical component. Until recently, the attention of ecologists has been mainly directed towards understanding the effects that the interactions between the biological components of ecosystems have on the dynamics of populations and communities. Such interactions (competition and predation) have been thought to be the main cause for the observed organization of ecosystems. However, we believe that to better understand the dynamics of ecosystems, greater attention should be directed to the methods in which the physico-chemical environment interacts with the living organisms. Theoretical work, based on the development of Lotka-Volterra models shows how deeply organisms and environment interact and influence each other, and how important it is to take into consideration ecological associations as "wholes", and not just as sums of independently functioning pieces.

## Postglacial colonisation routes of European hedgehogs

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European hedgehog populations belonging to *Erinaceus europaeus* and *E. concolor* have been investigated by mitochondrial DNA analysis. The distribution of these species covers most of Europe, with *E. europaeus* in the west and *E. concolor* in the east. Their ranges meet with some overlap in central Europe.

A previous Cytochrome b phylogeny has shown a considerable divergence between genomes occurring in different regions of each species range. A western and an eastern clade have been identified within both *E.europaeus* and *E. concolor*. The geographical structuring of the four lineages from west to east across Europe implies that the southern European peninsulas acted as Pleistocene refugia, from which northen Europe was colonised.

A detailed analysis of the pattern of divergence and of the geographic partioning of haplotypes across northern and central Europe is presented and implications for postglacial colonisation routes are discussed.

The fine scale geographical substructuring in the derived and refugial populations is also being investigated using Cytochrome b and Dloop sequences, and the preliminary results are presented.

### Nucleotide variation at the Adh locus in outcrossing Arabis petraea/lyrata compared to selfing A. thaliana

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The mating system is a major determinant of the distribution of genetic variation in plant populations, but it is correlated with other life history characteristics that can also influence genetic diversity. We have examined nucleotide variation of the outcrossing *Arabis petraea/lyrata* by SSCP analysis and sequencing, and compared our results to those found earlier for the selfing of *Arabidopsis thaliana*, by Innan et al. (1996) and Bergelson et al. (1998). The species are close relatives, with non-synonymous divergence 1.2 %, synonymous 15 %, comparable to *Drosophila* sibling species. Worldwide, the nucleotide diversity ( $\pi$ ) is similar in the two species, 0.0057 and 0.0068. The within population diversity is much higher in *A. lyrata* (0.003). Of the total variation, 66 % is between the North American *A. lyrata* and the European *A. petraea. Arabidopsis* lacks such geographic structuring. The North American *Arabis lyrata* had an excess of alleles at intermediate frequencies (Tajima's D = 2.3, P < 0.05). *A. petraea/lyrata* results suggest that the species wide nucleotide diversity of *A. thaliana* has not been reduced by background selection. In addition to the mating system, weediness and associated frequent founder events in *A. thaliana* may account for the contrasting patterns of variation.

#### Balancing selection in a subdivided population

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Self-recognition systems such as the major histocompatibility system (MHC) in manunals and, selPincompatibility (SI) in plants are extremely polymorphic systems in terms of the number of alleles and the amino acid diversity observed. We investigated through simulations the influence of population subdivision (the island model) on pattems of diversity at loci under different models of balancing selection chosen to represent different self-recognition systems. For all models we found that genetic differentiation is much reduced when compared to expectations for a neutral locus. The number of alleles and in particular the nucleotide diversity can be much reduced by subdivision compared to a pamnictic population the same total size. We added recombination to the models in order to investigate diversity around a locus under balancing selection. The results show that when genes are sampled at random from the population, subdivision decreases the genomic region around the locus where diversity is elevated and consequently that balancing selection is harder to detect from pattems of nucleotide diversity in a subdivided population. The results are discussed in relation to published sequence data from self-recognition systems.

Molecular analysis of the *GLABROUS1* locus in *Arabidopsis thaliana* indicates the presence of two diverged allelic classes which are not associated with the distribution of trichomes

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*GLABROUS1* (*GL1*) is a *myb* homolog with a central role in trichome initiation of *Arabidopsis thaliana*. We studied trichome distribution and the molecular variation of *GL1* in 26 ecotypes. Substantial sequence variation was detected in a 3 kb fragment which includes the complete coding region of the *GL1* locus ( $\pi = 0.01$ ). Phylogenetic analysis of *GL1* indicated the presence of two diverged clades among the 26 ecotypes. A similar distribution of polymorphism has recently been described for other *A. thaliana* loci and was associated with a balanced polymorphism. We present evidence that the polymorphism pattern at *GL1* is not caused by a balanced polymorphism. However, neither a simple neutral explanation nor directional selection fits the dataset entirely. Phenotypic analysis detected substantial variation in trichome density among the ecotypes studied, but no correlation between the two molecularly defined clades of *A. thaliana* ecotypes and their trichome phenotype was observed. We propose that more information about population history and outcrossing rates of *A. thaliana* is needed before patterns of molecular variability can be used to infer selection.

Mate guarding reduces sperm competition in the red firebug *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae)

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The red firebug *Pyrrhocoris apterus* (L.) is a common Palearctic heteropteran species feeding mainly on linden seeds. Observations of marked individuals in the field showed that females commonly mate with a number of different males. Since sperm of all mating partners of a female is usually stored in the female's spermatheca, sperm competition should be an important aspect in the firebugs' mating behaviour.

The sperm utilization pattern of doubly mated females was determined by use of a genetic marker. The mechanism of inheritance of this marker is well known. On average, the second male to mate fertilized the larger proportion of eggs ( $P=59\%\pm29\%$  SD).

With last-male sperm precedence copulatory mate guarding could help to avoid or reduce sperm competition. Indeed, even though sperm transfer ceases after about 2 to 3 hours, some bugs remain in copula for up to 2 days in the field. Anchor-like clasping structures on the male external genitalia suggest that males can maintain a strong grasp on the female which may allow them to control the termination of copulation. In the laboratory the duration of copulation varies systematically with the operational sex ratio. The duration of copulation increased from a median duration of 7 hours with an even or female biased sex ratio to 15.3 hours with a male biased sex ratio. This suggests that males prolong the copulation as a post-insemination guarding tactic under conditions of intensified competition for females.

## Evolution and speciation in ancient lake ostracods - differences and resemblances

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Ostracods, small bivalved crustaceans, form a significant part of the endemic, benthic fauna in ancient lakes. Up to 90% of ostracods are endemic to Lake Baikal (20 to 30 myr old) and up to 95% are endemic to Lake Tanganyika (12 to 20 myr old). We have compared the most extensive ostracod radiations of both lakes, the Baikalian *Cytherissa*-flock comprising 50 (sub-) species in one genus and the Tanganyikan *Cyprideis*-flock with c. 20 species in 6 genera. Since both flocks are closely related, they offer an unique opportunity to compare patterns of evolution and speciation amongst the two oldest lakes in the world.

A combined methodological approach, using DNA sequencing of nuclear and mitochondrial regions as well as morphological analysis, reveals significant differences between the two flocks. The *Cytherissa*-flock appears to be a rather young fraction of the Baikalian fauna, having originated 3 to 5 myr ago, when the modern, oxygenated abyss of the lake formed. Phylogenetic reconstructions show a multiple origin. The monophyletic *Cyprideis*-flock, in contrast, is considerably older with an age of 5 to 8 myr and could most likely endure drastic lake levels changes during its history.

### The origin and evolution of male-killing Wolbachia

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A detailed phylogenetic analysis of *ftsZ* and *wsp* DNA sequences is used to investigate the origin of male-killing *Wolbachia*, previously isolated from the 2-spot ladybird, *Adalia bipunctata*, and the nymphalid butterfly, *Acraea encedon*. The two genes are found to differ as to their utility for phylogenetic analysis. Sequence variation is here correlated with phylogenetic information content. Both genes additionally show significant rate heterogeneity between lineages which, in most cases, seems to give rise to homoplasy. Consequently, only a limited number of clades can be inferred with confidence. With respect to the origin of male-killing, the two genes nevertheless prove to be informative, although they consistently produce contrasting results. This contrast indicates genetic exchange between symbiont strains through recombination. In addition, *A. bipunctata* is found to be host to two recently diverged strains of male-killing *Wolbachia*. These show increased substitution rates for both genes. Moreover, the *wsp* gene which codes for an outer membrane protein is shown to be subject to positive selection in these taxa. These findings are postulated to be the product of high selection pressures due to the persistence of antagonistic host-symbiont interactions in this ladybird species. In conclusion, our study demonstrates that a detailed phylogenetic analysis, including characterisation of the dynamics of DNA sequence evolution, can serve as a valuable basis for our understanding of the evolution of *Wolbachia* bacteria.

## Interspecific hybridization in Hyalodaphnia: Ancient lineages versus contemporary gene flow

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Zooplankton species of the genus *Daphnia* form interspecific hybrids and backcrosses in lakes all across Europe. Lakes may contain three species and all three of their interspecific hybrids. Ecological studies show that under certain environmental conditions, interspecific hybrids exhibit a selective advantage compared with parental species.

In order to determine the genetic differentiation between species involved in such crosses, *12S*, *CO1* and *ITS* DNA sequences were obtained and analyzed using phylogenetic methods. Species represent evolutionarily old lineages that diverged during the Mesozoic. This phenomenon of high sequence divergence but low reproductive isolation raises several questions concerning the mechanisms that allow interspecific hybridization without melting species gene pools.

In order to differentiate ecological and genetic processes which are responsible for interspecific hybridization, ecological differentiation and reproductive isolation of species and hybrids was investigated. Studies of species and interspecific hybrid abundances and 11 lake characteristics revealed associations of taxa and environmental conditions. Genetic analyses of field populations further indicate that backcross clones have lower reproductive success than parentals. This differential reproductive success and the ecological associations of hybrids and parental species are responsible for the reproductive isolation of species despite contemporary interspecific hybridization. Low levels of backcrossing and occasional gene flow between species, however, indicate the potential for the establishment of introgressed recombinants and reticulate evolution.

Discrimination of erypfic Southern African *Culicoides* species of the Imicola complex (Diptera: Ceratopogonidae), based on arbitrarily primed DNA fingerprínting

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In the Old World *Culicoides imicola is* the only vector of Affican horse sickness virus (AHSV), and the major vector of bluetongue virus (BTV). The Imicola group, or complex, is one of at least ten groups in the World that make up the subgenus *Avatitia Fox 1955*. Currently, the Imicola group is represented by seven morpliologically described, and three undescribed, species; all are restricted to the Old World. While each possess unique eco-ethological features, most of the species are difficult to identify morpliologically. In addition, species complexes raise the problem of vector competence.

We used a RAPD approach (namely, the AP-PCR amplification procedure after WeIsh and McCIelland, *Nucleic Acids Res. 18: 7213, 1990*) to discriminate seven putative species of the *Culicoides imicola* complex froin Southem AfricaStatistical analyses of the RAPD data were computed using the RAPD package of Black. IV (Black, W.C. IV (1995) *Methods in Molecular Biology, vol. SO, Species Diagnostics Protocols: PCR and 0ther Nucleic Acid Methods, pp. 3955.* Humana Press, Totowa, NJ). The relationships between individuals, populations and/or species were assessed by the Neighbour-joining method of cluster analysis on the values of the pairwise dissimilarity matrix, and by Principal Coordinate Analysis (PCA). The estimations of the variation auributable to the clifferencies among populations, within species and among individuals within populations were evaluated by AMOVA.

The RAPD results support the specific status of the seven morphological taxa of the C. *inicola* complex. Comparisons between the morphological and molecular phylogenies are presented.

## Sympatric speciation by sex ratio selection?

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We discovered and investigated a Lake Victoria cichlid with a complex color polymorphism that apparently represents one original species and two incipient species, all of which are sympatric. Laboratory breeding experiments demonstrated that the genetics do not completely explain the pattern of color variation in nature. Mate choice experiments show that males of the incipient species exhibit mating preferences against the original species, and males and females of the original species exhibit strong mating preferences against the incipient species. Male mating preferences might evolve because of sex ratio selection. We observed strong sex-ratio distortion in certain matings between original and incipient species. These matings are avoided in mate choice experiments. The observed mating preferences appear to restrict gene flow and exert disruptive sexual selection between the original and incipient species, but the species we studied do not differ in morphology or ecology from the original species, but the species in the other species pairs differ in morphology and ecology as well as color and mating preferences. This implies that color polymorphism, when associated with mate choice polymorphism, can be an incipient stage in sympatric speciation, and that disruption of gene flow by mate choice precedes morphological and ecological differentiation.

# Nucleotide variation at the yellow gene region in four different chromosomal arrangements of Drosophila subobscura

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An approximately 5.7 kb region including the *vellow* (v) gene was sequenced in 46 lines of D. subobscura sampled in two different natural populations: Riba-roja (Catalunya, Spain) and Bizerta (Tunisia). In this species, the y gene maps at section 2B of the A(=X) chromosome separated from the centromere by more than one euchromatic section. Therefore, the strong reduction of the recombination rate in the y gene region of D. melanogaster (due to its telomeric position) is not expected in D. subobscura. In addition, the y gene is located very close to one of the breakpoints of the A1, A6 and A5 (common to A7) inversions of segment I (sections 1 to 7) of the A chromosome of D. subobscura. Consequently, nucleotide variation at the y gene has been analyzed in four different chromosomal classes for segment I: Ast (Ast+A2 arrangements), A1, A2+6 and A2+3+5+7 (sex-ratio arrangement). Nucleotide diversity estimates for the whole region studied within these classes are: 0.0062, 0.0046, 0.0002 and 0.0046, respectively. The Ast chromosomal class exhibits the highest level of nucleotide variation, which is similar to that found at other gene regions studied in this species. Thus, the strong reduction in variation detected in D. melanogaster is not present in D. subobscura. This result is consistent with the change in the recombinational environment of the y gene region between both species. The four chromosomal classes are genetically well differentiated. Both Ast and A1 gene arrangements seems to be rather old. In contrast, the low variation within A2+6 indicates that this is a much more recent gene arrangement despite it reaches very high frequencies in the Bizerta population. Surprisingly, A2+3+5+7 lines form two well differentiated clusters in the gene genealogy. This result is due to the presence of different polymorphic sites that segregate at intermediate frequencies in complete linkage disequilibrium within this chromosomal class. Possible explanations of this result will be discussed.

## Nucleotide variation at the Acph-1 gene region in a Tunisian population of Drosophila subobscura

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Nucleotide variation in an approximately 2.1 kb region including the acid phosphatase-1 (Acph-1) gene was analyzed in 45 isochromosomal lines of D. subobscura isolated from a natural population sampled in Bizerta (Tunisia). Lines differ in their chromosomal arrangement for segment I of the O chromosome: 21 are O3+4+8, 21 O3+4+23 and three O3+4. Nucleotide diversity estimates for the whole region studied within each arrangement are: 0.0121, 0.0095 and 0.0130, respectively. The three gene arrangements are genetically well differentiated, which indicates that the Acph-1 gene is a good marker of these arrangements due to its location very close to one of the breakpoints of inversion 3. However, genetic exchange between arangements was also detected. Gene conversion tracts were identified in different O3+4+8 and O3+4+23 lines. Genetic differentiation analysis between arrangements was extended to different Ost and O3+4 lines from a previously studied spanish population. All comparisons including the Ost lines show the highest level of differentiation. The location of the Acph-1 locus relative to the breakpoints of the inversion loop present in the different heterokaryotypes explains this result. A total of 22 replacement polymorphisms have been detected in the ACPH-1 protein: 10 within O3+4+8, 11 within O3+4+23 and 1 within O3+4. All these polymorphisms, except one present in the O3+4+8 arrangement, are singletons. A null allele was also detected in a O3+4+23 line. This allele has a 16 bp deletion in exon III that causes a frameshift mutation. In addition, a marginally significant (P=0.06) and a significant (P=0.03) excess of nonsynonymous polymorphisms is detected within O3+4+8 and within O3+4+23, respectively, when the McDonald and Kreitman's test is applied using D. guanche in the interespecific comparison.

#### Spontaneous chromosomal alterations in two populations of Chironomus riparius in the surroundings of Turin.

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In the German, Russian and Bulgarian natural populations of *Chironomus riparius* (syn. *C. thummi*), spontaneous inversions in salivary gland polytene chromosomes were rarely observed. In contrast, in larvae of two populations (Santena and Moncalieri) from the industrialised area surrounding Turin, 52 different types of inversions (both inherited and somatic) and 5 different types of deficiencies were found. Fifty percent of the locations of boundaries of inversions in chromosomes from the Santena larvae and 33 % of those from the Moncalieri larvae coincide with location of clusters of two repetitive DNA elements called *Alu* and *Hinf*. Clusters of these two repetitive elements occupy 34 out the 722 heterochromatic bands present in the *C. riparius* chromosomal set (i.e. 5 %). Thus nearly half of the spontaneous breaks occur not randomly in a very small portion of the genome. Since *Alu* and *Hinf* elements are composed by 70-80 % of AT repeats, they can represent potential weak points where inversion breaks are more likely to occur. In sediments of the area near Turin some heavy metals (Cr, Cu and Cd) are present in a concentration higher than that observed in unpolluted sediments and thus they could increase the frequency of chromosomal breaks.

# On the Evolution of the Structures in the Standard Genetic Code as an Outcome of Code-Message Coevolution I

## David H. Ardell and Guy Sella

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Shortly after the standard genetic code was discovered [1], Woese [2] and others [1][3][4][5][6] noticed regularities in its organization, and it was suggested that these regularities are useful in minimizing errors from mutation and translation. It was claimed that the effect of errors in assigning amino acids resulting from mutation and misreading are reduced by having the code's organization promote the substitution of similar amino acids in the event of error. In 1968, Crick [7] argued against the plausibility of selection for error-correcting codes. Firstly, changing an existing code implies a large loss in fitness since it makes the messages that evolved with that code useless. Secondly, a code that expresses many amino acids is useful even if it is not error correcting; therefore, code-message coevolution is prone to freezing on a random expressive code. A more systematic quantitative estimate of the "quality" of the code was done recently [8][9], indicated that the code is extremely good in error correcting. We present a framework for studying the coevolution of codes and messages. Following Woese's [2] concept of statistical proteins, the fitness of a code with a genetic message is evaluated through the fitness of the protein distribution it produces as a result of sloppy translation; where the genetic message distribution for a given code is the outcome of the mutation selection balance. Revisiting Crick[7], we derive an invasibility criteria determining which code variation may enter a given message population. Using these invasibility dynamics, we study code-message coevolution with codon and amino acid spaces with simple topologies. With these examples we are able to explain how error-correcting codes result from local evolutionary principles; we are also able to explain other structural characteristic of evolved codes such as redundancy patterns and specific choices of amino acids.

- 1. Nirenberg M. Jones O. Leder P. Clark B. Sly W. Pestka S. (1963) Cold Spring Harbor Symp Quant Biol 28:549-58
- 2. Woese C. (1965) Naturwissenschaften 60 : 447-59
- 3. Sonneborn T. (1965) in Bryson V. Vogel H (eds) Evolving genes and proteins. Academic Press, NY pp 377-97
- 4. Zuckerkandl and Pauling (1965) Evolving Genes and Proteins, Academic Press, NY pp. 97
- 5. Goldberg AL. and Wittes R. Science 153:420-24
- 6. Epstein C. (1966) Nature 210 (5031) : 25-28
- 7. Crick F. (1968) J Mol Biol 38:367-79
- 8. Shimizu M (1982) J. Mol. Evol. 18:297
- 9. Knight R.D. and Landweber L.F. (1998) Chemistry & Biology 5(9):R215-R220
- 10. Wong JTF (1975) Proc Natl Acad Sci USA 72(5):1909-12
- 11. Taylor F. and Coates D. (1989) BioSystems 22:177-87
- 12. Di Giulio M (1997) J. Theor. Biol. 187:573-581
- 13. Ardell, D.H. (1998) J Mol Evol 47:1-13
- 14. Freeland and Hurst (1998) J. Mol. Evol., 47(3):238-248

# On the Evolution of the Structures in the Standard Genetic Code as an Outcome of Code-Message Coevolution II

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Using the code-message coevolutionary model presented in I, we study the effects of different errors in mutation and translation on the structure of a code resulting from evolution, with realistic codon and amino acid spaces. First, we study how the interplay between the strength of selection and the magnitude of mutation affects the evolution and final structure of codes. We find that there exists a transition in mutation-selection parameters where the number of amino acids encoded drops dramatically. We refer to this transition as the encoding

catastrophe. An intuitive account as well as a systematic study of this phenomenon are provided. Then we turn to the mutation structure, focusing on transition-transversion mutational biases, and showing how local evolutionary principles induces a block structure in the code and how the degree of covariance of this structure varies with evolutionary parameters. Varying the bias parameter within ranges taken from the literature[1][2][3][4] we also study the behavior of different error-correction and code expressivity measures. A transition to error-correcting is observed as the bias is increase, and we explain this transition in terms of the encoding catastrophe. Then we introduce positional misreading, in a parameter range taken from the literature[5][6], and study its systematic effect on code structure as a result of the local coevolutionary dynamics. Finally, the combination of mutational biases and positional misreading is studied and many of the structural characteristics of the SGC, such as error-correcting, redundancy patterns and positional organization characteristics found in studies of the SGC [7] [8], are reproduced. In these studies, the evolutionary shaping of the code is the outcome of local evolutionary principles, and not an optimization principle acting on the final code. We conclude with some comments on future directions.

- 1. Collins DW (1994) Genomics 20: 386-96
- 2. Kumar EN (1996) Genetics 143 : 537 -48
- 3. Moriyama EN, Powell JR (1997) J Mol Evol 45 : 378-91
- 4. Morton BR (1995) Proc Natl Acad Sci USA 92: 9717-21
- 5. Davies J, Jones D & Khorana H (1966) J Mol Biol 18: 48-57
- 6. Parker J (1989) Microbiol Rev 53(3): 273-98
- 7. Ardell, D.H. (1998) J Mol Evol 47:1-13
- 8. Freeland and Hurst (1998) J. Mol. Evol., 47(3):238-248

## Specialization does not mediate coexistence in a mycophagous insect community, competitor aggregation does

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Resource specialization is often thought to he at least part1y selected by the pressure of competition with other species. The ensueing resource partitioning would reduce interspecific interactions relative to intraspecific interactions and thereby stabilize the coexistence of competitors that are limited by similar resources.

We analyze a dataset comprising 60 insect taxa breeding in 66 types of mushrooms. We find that the insects in this conununity are resource limited and that most species are highly specialized. flowever, differential use of resource types does not reduce interspecific interactions because specialization is. essentially random with respect to other species. Consequently specialization does not stabilize coexistence and it cannot be the result of selection by interspecific competition.

We fffid that intraspecific aggregation over mushrooms does cause the reduction of interspecific competition relative to intraspecific competition required for stable coexistence. This is in agreement with the "Aggregation model of coexistence", that has been claimed to explain diversity in patchy insect communities. Our study is the first to show that aggregation rather than resource partitioning stabilizes coexistence in a community including this many resource types.

We speculate on the evolutionary reasons for specialization and aggregation.

## Cost of reproduction and ageing

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Reproduction has been shown to increase mortality (the "cost of reproduction"). Because females are in general selected for lower mating frequencies than are males, both mating itself and effects afterwards can be a source of evolutionary conflict between the sexes. However it is possible that females may evolve some level of resistance to the harmful effects of mating. I will discuss the results of a series of experiments examining the effects of evolutionary change in lifespan on the resistance to the cost of mating in female *Drosophila melanogaster* which have been selected for age at reproduction. By manipulating egg-laying and exposure to males (levels of reproduction), I have been able to examine the effects of egg-production, courtship and mating on the role of the cost mating in the extension of lifespan.

## Patterns of relationship among Arabidopsis ecotypes

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We are examining genetic relationships among approximately 250 Arabidopsis thaliana ecotypes using AFLP (Amplified Fragment Length Polymorphism) markers. Our intent is to place the ecotypes into a geographic/phenotypic context from which future evolutionary studies and QTL mapping experiments may be planned. Preliminary analyses have shown that the phylogenetic signal contained in the AFLP data is weak, presumably due to recombination and recent human-induced migration. We have therefore devised an AFLP-based method to assess the frequency and distribution of *Tat1* retroelement insertions in the different ecotypes, as this information will likely minimize homoplasy. Based upon the *Tat1* position and sequence data, we discuss phylogeny and patterns of relationship among *Arabidopsis* ecotypes.

## Is genetic leakage between apomictic flatworms a form of pseudosex?

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The freshwater simultaneous hermaphroditic flatworm, *Polycelis nigra*, is characterized by two reproductive biotypes; sexual individuals are diploid, and apomictic (pseudogamous parthenogenetic) individuals are polyploid (typically 3n). Aneuploidy, in the form of 3 different supernumerary (B) chromosomes, is common to apomictic individuals but completely absent from sexuals. Using both karyotypic and molecular genetic (AFLP) markers, we have shown that one of these (B1) appears to leak from sperm to egg nucleus during parthenogenetic crosses. This may represent a mechanism through which some genetic information is exchanged between otherwise asexual individuals. This process, which could have been initiated by B1 in the form of genomic parasitism, may secondarily benefit B1 carriers since limited genetic exchange may help counteract some of the negative aspects associated with apomixis.

## The Evolution of Microsporidian Sex Ratio Distorters

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Maternally inherited parasites are selected to bias the sex ratio of their hosts towards females, the transmitting sex. We are investigating the evolutionary origins of sex ratio distorters within parasites of the protozoan Phylum Microsporidia. Some microsporidia are feminizers, that is, they convert genotypic males into fully functional phenotypic females, and other microsporidia are male killers, that is, when in a female they transmit vertically, but when in a male they kill the host and transmit horizontally.

We present a study of the molecular phylogeny of transovarially transmitted microsporidia in amphipod crustaceans, which we have used to address the following questions. What is the diversity of microsporidian sex ratio distorters? How many times have feminization, male killing and transovarial transmission evolved within the microsporidia?

Isolation by distance, oceanographic barriers to gene flow and secondary contact between Atlantic and Mediterranean populations: new evidence from microsatellite DNA studies of the cuttlefish *Sepia officinalis*.

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The area of sea between the western Meditteranean and eastern Atlantic has for some time been recognised as an important phylogeographical area for marine species. Secondary contact between species isolated on either side of the Straits of Gibraltar by sea level and other environmental changes during glacial periods, barriers to migration caused by present oceanographic conditions, and isolation by distance effects have been shown to have distinct effects on population structuring and genetic differentiation in animals as diverse as annelids, fishes, crustaceans, cephalopods and bivalve molluscs.

We present data for 7 microsatellite loci from 6 samples of the cuttlefish *Sepia officinalis* collected around the Iberian peninsula from Galicia to Cataluña. Clinal allele frequency changes found at 4 loci between the Atlantic and Mediterranean ends of the sample range suggest secondary contact and introgression between previously isolated and divergent populations. Estimates of genetic divergence (Fst) between samples all around the Iberian peninsula are consistent with an isolation by distance model of genetic exchange. Distinct "step" changes in allele frequencies at all loci and overall estimates of divergence between samples spanning the area of the Almería-Oran oceanographic front suggest a distinct isolating effect of this feature.

We suggest that present patterns of genetic variation in *Sepia officinalis* are a product of limited gene flow on a local geographic scale (consistent with the life history parameters of the species), with the additional isolating factor of the Almería-Oran front, superimposed on the relict gene frequency distributions of previously isolated Mediterranean and Atlantic populations. We also suggest that microsatellite markers have provided a more detailed and informative picture than previous allozyme studies.

## Evolutionary implications of population structure in Lake Malawi pelagic cichlids

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The extensive and rapid radiation of cichlid fishes within Lake Malawi is well documented. However, the mechanisms responsible are still a subject of considerable debate. Traditionally, allopatric modes of speciation were proposed to account for the complete species flock. More recently, it has been suggested that sympatric divergence may contribute to, if not drive, the rapid radiation of these fishes. A necessary prerequisite for the demonstration of allopatric speciation processes is evidence that subdivision of the gene pool of a species has occurred, or at least that life histories and present levels of population structuring suggest that it might have occurred in the past under suitable environmental conditions. These circumstances have been clearly demonstrated in the rocky shore 'mbuna' cichlids: populations are highly structured due to the presence of relatively small habitat barriers, and some populations show clear evidence of divergence in traits which are associated with reproductive isolation among sympatric species.

Here we present data from large samples of three species of pelagic cichlids, screened at 6 microsatellite DNA loci, that suggest that these species currently comprise single, largely panmictic populations across the whole of their known range within Lake Malawi. Data from microsatellites and mitochondrial DNA also suggest that population sizes of these species may have been very large and stable for many generations. These results will be discussed with reference to possibilities for allopatric and / or sympatric speciation.

### Spontaneous mutation in Arabidopsis - morphology and fitness

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For a study of spontaneous mutation in *Arabidopsis thaliana*, 120 lines were initiated from a single inbred Columbia founder and advanced 17 generations by single-seed descent. Sublines for generations 0, 8 and 17 were then established simultaneously. We have assayed reproductive and morphological traits in plants representing all three generations grown contemporaneously. For each of three reproductive traits, mean number of seeds per fruit, number of fruits, and dry mass of the infructescence, the mean differed only slightly and not significantly among generations. Nevertheless, by generation 17, significant divergence among lines was detected for each trait. For three morphological traits measured at flowering, only leaf length changed in a consistent direction over generations. For all traits, standardized measures of mutational variance accord with those obtained for other organisms. Together, these findings suggest that the distribution of mutational effects may be approximately symmetric, even for components of fitness, in contrast to the usual assumption that mutations have almost exclusively deleterious effects on traits directly related to fitness. The finding of a near-symmetric distribution of mutational effects. An alternative approach will be outlined and simulation results presented.

Digging for phylogenetic gold in the genomic junkyard: historical retropositional dynamics of sines and the evolution of salmonid fishes in the genus *prosopium*.

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Short interspersed repetitive elements, or SINEs, are retroposons found throughout eukaryotic genomes and can be present in well over 10<sup>4</sup> total copies per individual. The enormous volume of independent, irreversible SINE insertions per organism makes them important evolutionary agents for shaping the diversity of genomes and offers a potential treasure trove of systematic information for diagnosing common ancestry among host taxa. The most extensive characterization of non-mammalian SINEs has been completed for salmonid fishes by Okada and colleagues over the past decade. In particular, the SINE families SMA I, Hpa I and Fok I have been used as a model to illustrate the use of SINEs for phylogenetic inference in this group of commercially important vertebrates. Previous characterization of the historical insertion dynamics of Hpa I subfamilies has suggested that the MP subfamily specific to the genus *Prosopium* should provide excellent phylogenetic information for resolving species relationships in this poorly known genus of coregonine fishes that present a Pleistocene species complex. Results are presented from PCR detection of SINE insertions within *Prosopium* species for previously isolated Sma I and Hpa I loci as well as from newly characterized MP loci. Implications of these historical patterns of SINE retroposition for understanding the general evolutionary mode of SINE elements are also discussed.

## Genetic Diversity in isolated Negev desert populations of Acacia raddiana

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Acacia raddiana, A. tortilis and A. pachyceras (formerly known as A. gerrardii ssp. negevenis) are major trees in the Negev desert of Israel and constitute a major ecological feature. Acacia trees are important in the desert environment because they provide shade and vital forage to animals during summer. The native Bedouins use Acacia leaves and pods for firewood, fodder and resin as a source of medication.

There is widespread concern over mortality of Acacia trees in the Negev desert, Israel. Mortality varies widely, and may reach as high as 61% in populations of adult trees. The threat of extinction is becoming evident in these *Acacia* spp. because of high mortality and rare recruitment of seedlings. It is hypothesized that diminished genetic diversity has resulted from population decline. The present study focused on *Acacia raddiana* because it is the most widespread species of the native Acacias. We selected the four sites with the highest mortality and four sites with the lowest mortality out of 75 sites surveyed. It is hypothesized that *Acacia* populations with high mortality and low recruitment have reduced polymorphism. Random Amplified Polymorphic DNA (RAPD) markers are used to assess the relationship among those populations and genetic diversity among those populations will be discussed.

## **Reconstructing Ribozyme Phylogeny: Who Begat Whom?**

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The selfsplicing Group I intron has been used in the laboratory of Dr. Gerald Joyce for directed evolution experiments. At each generation of evolution, the selected population was sampled and the sequences were recorded. This dataset represents an exploitable record for phylogenetic reconstruction that includes internal node sequences. With the exception of some experimental bacteriophage T7 data, this dataset represents a unique perspective of molecular evolution.

We report the phylogenetic reconstruction of a Group I intron lineage evolved through 63 generations to cleave a DNA substrate over the wild type RNA substrate. Assessment of various phylogenetic approaches, statistical sampling concerns, and structural components of the evolution of the molecules will be addressed. The role of phylogenetic reconstruction and ribozyme evolution will b discussed in the context of an RNA world.

## IPower to detect QTL in a free-living polygynous population

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Ever since Fisher's Fundamental Theorem of Natural Selection (1930) evolutionary geneticists have been interested in the heritability of fitness. Whether major genes for fitness and fitness components segregate in the wild is still unclear. A major obstacle to detecting quantitative trait loci (QTL) in natural populations is a lack of statistical power due to insufficient sample size and/or necessary pedigree information. Using a real pedigree from the intensively studied red deer (*Cervus elaphus*) population on the Isle of Rum, Inner Hebrides, we have compared the power to detect QTL of the widely used half-sib design with that of a more complex pedigree using computer simulation. The complex pedigree has dramatically greater power than the half-sib design, although power is still low. For example, the power to detect a QTL of 1.0 phenotypic standard deviation was 0.67 for the complex pedigree and only 0.21 for the half-sib design.

# The evolution of specific pollinator acquisition in the sexual deceptive orchid genus Ophrys

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The orchid genus *Ophrys* consists of various lineages and most of them differ only slightly in floral morphology. More than 140 species have been named so far, often based on minute floral morphological differences and species are often connected with transitions. The taxonomic value of those species remains debatable. Nonetheless the lineage richness suggests that the genus underwent an adaptive radiation. A major cause for the adaptive radiation may be the acquisition of specific pollinators which generates an ethological isolation among *Ophrys* taxa. Therefore we investigated the evolution of pollinator acquisition among members of the sexual deceptive orchid genus *Ophrys*. We first established phylogenetic relationships among *Ophrys* species based on nrDNA and cpDNA sequences and then mapped pollinator identity onto the cladogram to study the evolution of pollinator acquisition.

# Expression of the heat-shock protein HSP70 in Drosophila buzzatii lines selected for thermal resistance.

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The level of HSP70 expression induced by a non-lethal high temperature was examined in lines selected for increased thermal resistance and in corresponding control lines of *Drosophila buzzatii*. The lines used were subjected to two types of selection. In adult selection lines, hard selection was implemented every second generation after mild heat hardening and in larval selection lines, larvae were exposed each generation to laboratory "natural" selection. In all lines induced HSP70 levels were measured in adults twice, twenty generations apart, and in the late generation experiment also in third instar larvae. In comparisons within generations, lines selected as adults showed a higher HSP70 expression than controls, both in third instar larvae and in adults. Comparisons between generations showed negative or near zero estimated values of response to selection over the last 20 generations for almost all lines (adult selection, larval selection and controls). A strong negative response to selection of HSP70 expression was found in all larval selection lines that were selected at cycling temperatures suggesting that the different methods of selection applied affect HSP70 expression differently.

## Dominance theory of Haldanels rule and speciation

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Haldane's rule states that "when in the F, offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous [heterogametic] sex" (Haldane, 1922). In the past fifteen years much theoretical and experimental work has been devoted to understand the genetical basis of this rule (see Orr, 1997). The "dominance theory" is the explicative hypothesis that is gaining favour in the most recent literature (especially for the case of heterogametic hybrid inviability). This hypothesis (*e.g.* Orr and Turelli, 1996) attributes a key role to (completely or partially) recessive alleles that cause, in a hemizygous condition, inviability or sterility in the heterogametic hybrid.

The aim. of the present theoretical work was to investigate the role in speciation of unisexual hybrid inviability or sterility, assuming the genetic architecture envisaged by the dominance theory of Haldane's rule. In particular, the focus was on conditions under which this type of postzygotic isolation can persist in spite of gene flow. It turned out these conditions are much more restrictive than in the case of some other postzygotic isolating mechanisms (e.g. underdominant genes). These results point out some theoretical difficulties that induce to be cautious in attributing to this mechanism a primary role in (not stríctly allopatric) speciation processes.

## Genetic Structure related to Social Behavior in Panthera leo

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Given the social system of the lion several predictions about how a lion population should be genetically structured can be made. When new prides form they always settle next to their "mother" pride. Clustering of prides with shared ancestry should then result, since some neighboring prides will be closely related, while others are not at all related or only very remotely related. For females the degree of relatedness should therefore decrease with increasing distance.

This pattern will be attenuated more or less by the dispersing males. The strength of this effect will wary with dispersal distances. The ratio of pride forming events to male dispersal events is even more important. If new prides form very seldom, and males disperse relatively often, the population should show few tendencies of clustering.

In this study of a free-ranging lion population some of the above predictions failed. I have used samples from about 100 individuals in over 10 prides from Selous Game Reserve, Tanzania. The population structure was inferred from microsatellites. Prides were found to be composed of related females, as confirmed by demographic and behavioral data. However, the degree of relatedness between prides did not decrease with distance, but increased. Pairwise comparisons showed the same significant pattern for all prides. Stong selection for inbreeding avoidance in males is one likely explanation.

## Lamarckian Evolution of Antibody Variable Genes

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Available evidence relevent to the mechanism of somatic hypermutation of rearranged antibody or immunoglobulin (Ig) and T cell receptor (TCR) variable region genes (V[D]J)\* in mouse and human B or T lymphocytes is consistent with a molecular mechanism involving error-generating reverse transcription (RT), utilizing as a template pre-mRNA or mRNA of the rearranged V[D]J region. The cDNA derived from the two error-prone processes of transcription and reverse transcription would then homologously recombine into the chromosomal DNA. In mouse VH and Vk loci the J-C intronic Enhancer-Nuclear Matrix Attachment Region (Ei/MAR) is proposed to contain unique sequence motifs or secondary structures which ensure that only V[D]J sequences mutate whilst other functional regions of the genome are not mutated. We also outline all the current molecular evidence which supports the conclusion that the signature of somatic hypermutation coupled with antigen-mediated selection of successful V mutants appears to be written into the germline (unrearranged) IgV segment repertoire ie. somatically generated IgV sequences from B lymphocytes have been fed back to germline DNA over evolutionary time. (For recent review see Blanden RV et al 1998 *Immunological Reviews* 162 : 117-132) \*Generic symbol for a somatically rearranged V gene.

#### Inheritance of fitness defects from parthenogens to sexuals: flatworm indication for mutation accumulation

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Genetic material in the germ line of organisms is perpetually subject to mutation and hence deterioration. According to the mutational theory for the maintenance of sex, the counteracting force, natural selection, is more efficient with sexual than asexual reproduction. As a result mean fitness of asexual populations should decrease with time.

In previous work we found that embryo mortality is increased in obligate parthenogenetic forms of the freshwater planarian *Schmidtea polychroa*, relative to their obligate sexual conspecifics which occur at the same sample sites. To find support for our conjecture that deleterious mutations are responsible for this defect, we investigated the inheritance of the fitness trait embryo mortality. This is possible, because *S. polychroa* are hermaphrodites, and parthenogens produce sperm capable of fertilising sexual eggs. The sexual offspring inherits half of its genes, and with them the supposed mutations, from the parthenogenetic father. We performed a crossing experiment in which parthenogens acted as mothers and as fathers simultaneously, and recorded embryo mortality in both the clonal egg-offspring and the sexual sperm-offspring of these parthenogens. Both measures were found to be correlated, suggesting that these developmental problems may be caused by the sort of mutations envisioned in the context of mutation theory.

These results will be evaluated in the light of the evolutionary relationships between sexuals and different parthenogenetic lineages that occur at our sample site. The use of nuclear and mitochondrial genetic markers will yield information about extent and direction of gene flow between the subpopulations in this lake and may therefore shed some light on the evolution of parthenogenesis and the relative age of different parthenogenetic lineages in this species.

#### Evolutionary genomics of insect resistance in arabidopsis.

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We seek to elucidate the evolutionary and ecological factors maintaining levels of quantitative genetic variation in populations. By combining QTL mapping with information on candidate genes and genomic DNA sequence, it is possible to identify the actual loci responsible for insect resistance in *Arabidopsis* and wild *Arabis*.

To identify candidate genes for resistance to insect herbivores, we used differential display RT-PCR to analyze gene expression in response to diamondback moth (*Plutella xylostella*) herbivory. Of 49 putative herbivory-induced genes, at least 15 appear to be regulated by insect feeding. Furthermore, we are studying molecular evolution of such resistance genes in nine different *Arabis* species.

To identify additional candidate defense genes, we are studying mutants with altered insect resistance. 11,000 EMS-mutagenized plants have been screened for altered herbivory by diamondback moth, and these putative mutants are being verified by several generations of progeny testing. These approaches will yield candidate genes that may correspond to QTLs influencing insect resistance in natural plant populations.

#### Selfish genetic elements and sex ratios in parasitoid wasps.

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Parasitoid wasps have been used as model organisms both to initiate much of the current sex ratio theory and to test many of the the different sex ratio models. Most of the sex ratio theory deals with optimal sex ratios for nuclear genes located on autosomes, and cannot be used to explain the often bizarre sex ratios found in different parasitoid wasps. The sex ratios are often caused by sex ratio distorting factors with a non-mendelian inheritance. Such sex ratio distorters appear to be very common and many several species are known that harbor several different sex ratio distorters. While most known sex ratio distorters in parasitoid wasps are cytoplasmically inherited and cause an over-abundance of female progeny, two cases have now been found of parasitic B-chromosomes that cause males carrying these chromosomes to father exclusively male progeny again carriers of this chromosome. I will discuss in detail the interactions in a system consisting of the parasitoid wasp *Trichogramma kaykai*, a cytoplasmically inherited bacterium (*Wolbachia*) causing the infected mothers to produce exclusively female progeny- both from fertilized and unfertilized eggs- and a parasitic B-chromosome leading to all male progeny from fertilized eggs. In this system we expect several nuclear adaptations (suppressors) to the presence of these sex ratio distorters. I will discuss our efforts to find such supressor genes.

## Intra- and Interspecific DNA sequence variation at Myrosinase loci in Arabis and Arabidopsis species

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Myrosinase (B-thioglucoside glucohydrolase) comprises a group of enzymes that hydrolyze glucosinolates within Brassicaceous species. These compounds are known to be functionally important in interactions between the plants and other organisms.

Sequence variation at myrosinase loci was analyzed for *Arabidopsis thaliana* and multiple species of *Arabis*. We reconstruct the evolutionary history of myrosinase alleles in the *Arabis* genus. In addition, we compare phylogenetic relationships based on myrosinase sequence data to those inferred from other loci, i.e. chalcone synthase (chs), chitinase and alcohol dehydrogenase (Adh).

## Lake level fluctuations, population structures and speciation in Lake Tanganyika rock cichlids

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Patterns of genetic divergence among populations of rock-dwelling cichlid fishes suggest synchronization of the onset of spatial and genetic isolation by external factors such as lake level fluctuations. Any rapid rise of the lake level will inevitably shift the coastline and thus change the location and distribution of a variety of habitats. Populations situated at shallow and moderately sloping sections of a lake were repeatedly split into numerous founder populations by a rise of the lake when shallow bays are re-fludded. Since these populations are formed almost at the same time, they must exhibit the same levels of genetic divergence to each other. Future ecomorphological diversification and speciation will depend on local circumstances and will thus happen non-synchronously, even if species have the same genetic distances to each other. This mode of speciation was found in several rock-dewlling species having a limited ability of dispersal over non-suitable habitats of the genera *Tropheus* and *Neolamprologus*.

## Reassessing fitness: a differential geometry approach

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Geometrical approaches to the understanding of fitness have been present in the evolutionary literature since Wright's adaptive landscape formulation. In the contemporaneous literature the Price equation has been regarded as the most general formulation of evolutionary change. In my work the Price Equation is used to lay down the basis of a geometrical formulation of evolutionary change. The abstract formulation outlined is exemplified constructing the first and second fundamental forms of the evolutionary space in the case of two correlated evolving traits. The gauss curvature of the space arises as an integrating measure of selection. My work underlies the insight gained in the fitness understanding through an analytic formulation, in contrast to numerical solutions. As an attempt to incorporate dynamical concepts of the evolutionary process, the adaptive dynamics framework define fitness as the long term growth rate of a phenotype in a given environment. Accordingly, the Lyapunov

Exponent of the population projection matrix is used in this framework as the key measure of success of an invading mutant. Here I show the equivalence of the Lyapunov Exponents to the Gauss curvature of the space defined by the frequencies' change of the resident population and the mutant.

Through a simple geometrical measure, the gaussian curvature of a surface, I suggest a link among the so called "static" and "dynamical" approaches to the study of fitness theory.

#### Facultative sex ratio biasing and male-female conflicts in ants

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Empirical studies have shown that workers in several species of ants are able to manipulate sex allocation ratios in their favour. In particular, workers in single queen colonies were shown to alter colony sex ratios in accordance with queen mating frequency, such that colonies headed by single-mated queens specialize on female production and those headed by multiple-mated queens specialize on male production. These findings have resulted in further theoretical developments concerning the opposing interests of colony queens and their male mates. As a result of the haplodiploid sex determining system males never father sons, hence a male that ends up co-siring a colony faces zero fitness, if, as predicted by theory, the workers rear an all-male sexual brood. Males may, however, have evolved various mechanisms to mitigate such worker manipulation, such that also colonies with multiple-mated queens produce at least some females. One way to accomplish this is by sperm clumping, where sperm from each of two fathers is used in alternating bouts through time. Another way is by male continence where a second male transfers a small amount of sperm. In both cases a high enough relatedness asymmetry may ensue to cause the production of female-only brood, in accordance with male preferences. In this paper we will present data on year-to-year variance in paternity shares and sex allocation in *Formica truncorum*, an ant with long-lived perennial colonies. Furthermore we will analyze the effect of mating order on the proportion of offspring fathered, to evaluate the male continence hypothesis.

#### Experimental Excursions on Adaptive Landscapes: Density-dependent Selection on Egg Size

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Theories of density-dependent natural selection suggest that intraspecific competition will favor juveniles of high competitive ability. Empirical evidence has been provided from laboratory selection experiments, but field studies are lacking due to the logistical difficul-ties in testing this idea. Here, we present data from an experimental field study of lizards that overcomes these difficulties. Removing older juvenile competitors from some areas not only increased the overall survival of later progeny but also intensified the strength of selection on egg size; analysis of selection gradients revealed that late-hatched juveniles from larger eggs survived disproportionally well in the experimental areas, whereas those from small eggs had lower survival than in the control areas. These findings refute a classi-cal idea in evolutionary ecology, namely that offspring size increases during the season as an adaptive response to competition between early and late young. We suggest that the rela-tive importance of within- and between-cohort competition as well as the interaction between density- and frequency-dependent selection pressures needs to be taken into account to understand the evolution of offspring size. We emphasize the utility of combining both experimental manipulations of individual phenotypic traits (e. g. egg size) and manipula-tions of the selective environment (e. g. density or frequency of competitors) to reveal both the target as well as the agent of selection. The fact that we were able to change selection pressures in the wild by manipulating the intensity of competition illustrates the ecological lability of fitness surfaces in nature and has some implications for the classical debate between R. A. Fisher and Sewall Wright over the utilitity of "the adaptive landscape".

## Emergence of arginine and tryptophan after the major microbial diversification

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The classical explanation for the unity of the genetic code is that life went through a bottleneck from which all subsequent life has descended. Implicit in this hypothesis, which is knows as the "frozen accident", is that once the genetic code was fixed it was inherently resistant to drift or to selected change. As an alternative explanation, I have proposed that the uniform genetic code was directly selected because of the occurrence of horizontal gene transfer (1). If horizontal gene transfer were a sufficiently powerful force in the evolution of modern life, it follows that any life that could not read foreign genes would be at an evolutionary disadvantage. Since this scenario does not assume inherent rigidity in the genetic code, it opens the possibility that the code could have continued to evolve after the diversification of life into its major kingdoms.. The present talk will present an analysis from whole genomic comparisons that supports the hypothesis that the introduction of the amino acids arginine and tryptophan in protein synthesis occurred after the diversification of the three kingdoms - the archaea, the eukarya and the bacteria, and even after divergence of some major bacterial divisions. The evidence for this involves a comparison of gene sequences for a number of different metabolic pathways found in common in archaea, eukarya and bacteria. These unusual conclusions have been reached from an analysis of genes unique for tryptophan biosynthesis and for the synthesis of arginine from ornithine. Distance trees for these genes have unusually short internal branches that fail to discriminate major clades. I will introduce a graphical whole-matrix rate test that shows that these genes are young compared to the age of the underlying species clades. The whole-matrix rate test supports the hypothesis that the more ancient genes diverge by a time-dependent stochastic process.

1. M. Syvanen (1984) Cross-species gene transfer; implications for a new theory of evolution. J. Theoret Biology 112:333-343.

#### Life history trade-offs in broodcare of mouthbrooding cichlids

#### Barbara Taborsky

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The decision of how much time and energy to invest in broodcare is an important component of *the* two major life history trade-offs, i.e. between (i) current and future reproduction, and (ii) number and quality of offspring. Three mutually non-exclusive hypotheses may explain the duration of broodcare of mouthbrooding cichlid fish in relation to the mentioned major life history trade-offs. Prolonged broodcare (1) may be used to compensate for a small initial size of eggs, (2) it may increase the survival of young, or (3) it may be critically constrained by the volume of the buccal cavity of the caring parent.

The following expectations can be derived from these hypotheses; (1) young should be released to independence in a similar developmental stage, even when eggs size varies; (2) broodcare should be extendend in risky environments; (3) large clutch volumes relative to female size should be brooded for shorter periods than small ones.

In the African cichlid *Ctenochromis horei*, females carry the brood in their mouths for three to four weeks without taking up food, and guard the young for up to a week thereafter. Testing the second prediction in lab experiments, I found that broodcare took significantly longer when a potential predator of young was present, as compared to a control situation with the same female, but without predator. There was no support for the two other expectations. Moreover, although egg size correlated positively with female body condition, the duration of broodcare was not condition-dependent. I shall discuss whether this can be explained either by low energetic costs of broodcare or by the higher value of broods towards the end of the breeding cycle, which may make high investment beneficial even at considerable costs in future reproduction.

The importance of ecology for the evolution of reproductive and social behaviour: Case studies from Lake Tanganyika

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The cichlids of the great East African lakes are a pivotal paradigm for explosive speciation. The Lamprologini of Lake Tanganyika are a particularly interesting group with regard to the evolution of reproductive and social behaviour. In contrast to mouthbrooding cichlids which dominate the other great lakes, these substrate breeders exhibit a very wide range of brood care, mating and social patterns. Some species of this tribe show the most highly advanced social systems known among fish. Populations of particular species or of very closely related species are distributed along the entire coastline of the lake, which extends over more than 1300 km and varies considerably with regard to ecological conditions, both on a small and large geographical scale. Behavioural variation accross different populations may be caused by phenotypic plasticity and by local adaptations due to a very low gene flow between populations, as planctonic stages are lacking. The importance of particular ecological conditions on reproductive and social patterns may be illustrated by a comparison between the ecology and behaviour of different populations.

The cooperatively breeding *Neolamprologus pulcher/brichardi* shows important variation in social patterns between northern and southern populations. Apparently, this is mainly due to differences in predation pressure, which influence relatedness patterns within families and alternative life history trajectories of helpers. *Lamprologus callipterus* is a snail brooding species exhibiting three distinctly different, alternative male reproductive tactics. Here, variation in the abundance of suitable breeding substrate appears to cause significant differences between the reproductive patterns of different populations. With these examples I discuss the great potential influence of single ecological factors on the variation in behaviour and reproduction of Lake Tanganyika cichlids. This may indicate that factors other than food and sexually selected traits may be important as well for evolutionary patterns and speciation of African cichlids.

# Phylogenetic relationships and incomplete lineage sorting among cichlid fishes in Lake Tanganyika - An approach from insertion patterns of retroposons

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The process of adaptive radiation of cichlid fishes in Lake Tanganyika in East Africa has long been of interest to evolutionary biologists. Nevertheless, information about their phylogenetic framework still remains limited in spite of application of several molecular phylogenetic analyses using either mitochondrial or nuclear DNA markers. In recent years, short interspersed elements (SINEs), which are members of retroposons, have been shown to be excellent markers of molecular phylogeny since their integration at a particular position in the genomes can simply be considered to be a synapomorphic character. In this study, we isolated the AFC family, which is a SINE family distributed mainly in African cichlids. From our investigations of patterns of insertion of members of this family at orthologous loci, we identified several monophyletic lineages among the major groups (tribes) of cichlids in Lake Tanganyika. These relationships, each of which was supported by several independent loci, showed good agreements with the previously reported phylogenies using molecular markers. However, some of the other loci showed inconsistencies of insertion patterns of a SINE with each other, suggesting that the phylogeny of each of these loci itself does not necessarily reflect the species phylogeny of the cichlids. We postulated that such discrepancy has been caused by incomplete lineage sorting of the loci due to extraordinarily rapid speciations of these fishes at some stages of their evolutionary history.

## Constraints on determination of adult size in a moth

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Optimality models in the theory of life-history evolution aim at explaining and predicting values of life-history traits. Explanatory framework of the traditional models is a purely demographic one, possible constraints are often ignored, or incorporated in an abstract, phenomenological way. Demography-based explanations appear, however, to be clearly insufficient for some life-history traits. A clear deviation of the observed value from the predictions of demographic optimality models could be considered indicative of constraints.

I was not able to propose a demographic explanation for observed values of adult body size in a moth species (Ecological Entomology 23: 80-89). Because fecundity increases linearly with body size, and no costs of large adult size are known, one should expect female larvae to grow larger to increase their individual fitness. No realistic mortality schedule could explain why a larva should not prolong its growth period to attain larger size. It should therefore be proposed that constraints preclude evolution in that direction. It seems plausible that the constraint is formed by fixed number of larval instars, combined with non-plastic growth trajectories within each instar. It can thus be proposed that further evolutionary increase in body size in this species is possible only after either of these constraints is relaxed. A comparative method could be used to test for this hypothesis.

## A Corynebacterium plasmid composed of elements from throughout the eubacteria kingdom

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The 51409-bp DNA sequence of the multiresistance plasmid pTP10 from the gram-positive human pathogen *Corynebacterium striatum* M82B has been determined. Fully automated genome interpretation led to the identification of 47 open reading frames. Analysis of the genetic organization of pTP10 suggests that the plasmid is composed of eight DNA segments the boundaries of which are represented by transposons and insertion sequences. The DNA segments of pTP10 turned out to be highly similar to (i) a plasmid-encoded erythromycin resistance region from the human pathogen *Corynebacterium diphtheriae*, (ii) a chromosomal DNA region from *Mycobacterium tuberculosis*, (iii) a plasmid-encoded chloramphenicol resistance region from the soil bacterium *Corynebacterium glutamicum*, (iv) transposable elements from gram-negative phytopathogenic *Pseudomonas*, *Xanthomonas* and *Erwinia* species, and (v) to a plasmid-encoded aminoglycoside resistance region from the gram-negative fish pathogen *Pasteurella piscicida*. The complete DNA sequence of pTP10 provides genetic information about the resistance mechanisms to 16 antimicrobial agents of six structural classes. In addition, the DNA mosaic structure of pTP10 represents an evolutionary consolidation of antimicrobial resistances from microorganisms of different habitats into a single plasmid molecule via mobile elements, resulting in the generation of a multiresistant bacterium causing human infections.

#### Sympatric speciation - molecular evidence and ecological mechanisms

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There is mounting evidence that speciation occurs frequently under sympatric conditions. However, the actual mechanisms leading to speciation in sympatry under natural conditions have still to be understood. We present two datasets from our laboratory pertinent to this question. One concerns a recent (less than 13000 years) radiation of cichlids in a small lake in Cameroon (Lake Ejagham). All forms in the lake were analysed by D-loop sequencing and microsatellite analysis and one pair of forms was studied ecologically in detail. This pair is characterised by a unique breeding coloration and differs only in size and age at reproduction, but not in overall morphology. We find that the breeding and habitat ranges for this pair are broadly overlapping both in time and space, but that their gene pools have nonetheless started to separate. The separation can be linked to a life history parameter, namely age at reproduction, which leads to size differences that allow the exploitation of two different habitats, and to assortative mating with consequent genetic separation. As the pair of forms studied here is clearly monophyletic, this proves that different life history strategies can lead to speciation under fully sympatric conditions. Another dataset concerns a molecular study on populations of Salamanders in europe, whose distribution pattern suggests that postglacial recolonizations have started from distinct source populations. Intriguingly, it appears that different, albeit very closely related, source populations have been successful in different interglacial periods, indicating that the distinctness of these populations is actively maintained. Thus, assortative mating, territory defense and/or ecological competition appears to be an important component of the earliest stages of speciation in land animals.

## The population structure and mating pattern of Formica rufa (Hymenoptera: Formicidae)

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Eusocial Hymenoptera (i.e., ants, bees and wasps) are of special interest in the study of social evolution because they exhibit group living behaviour which subjects them to selection pressures at the individual, group and population levels. Understanding their population genetic structures therefore should consider the spatial structure of their habitats, and knowledge on the types of genetic relationships shared between individuals from different colonies, as well as the mating patterns of the sexuals and the number of reproductives present within colonies is required. Our study organism is *Formica rufa*, a red wood ant species with long-lived colonies. In a continuous habitat such as on the main land, individual colonies may contain either single or multiple queens, both of which have been known to occupy the same habitat. Contrary to this, the population structure and mating pattern of *F*. *rufa* on fragmented habitats are not well understood. In this study, *F*. *rufa* worker and male samples were collected from 70 colonies on the archipelago of south-western Finland. Using data obtained from both allozyme and microsatellite markers as well as taking into consideration the fragmented archipelago habitats, we analysed these samples to infer the population genetic structure. Further more, the dispersal and mating patterns of males and females and levels of inbreeding in both polygynous and monogynous colonies will be presented. The interplay between the genetic population structure and the social structure of this perennial ant species will be discussed.

## The genetics and natural history of the sex ratio polymorphism in Silene latifolia, a dioecious plant.

## Douglas R. Taylor

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Genetic elements that distort Mendelian segregation to enhance their own transmission (so-called "selfish" genetic elements) have long been recognized as a potent evolutionary force. The most extensively documented examples of these elements are those that cause a sex ratio bias (e.g. sex chromosome meiotic drive). Our classical genetic studies have implicated selfish elements as the cause of a widely studied example of sex ratio bias in plants. This system bears a remarkable resemblance to the classical examples of sex ratio meiotic drive in animals (e.g. *Drosophila*). The sex ratio bias is severe, the genes involved appear to abort male gametes, and the resulting male-fertility reduction is likely to influence the transmission of these elements in nature. Recent work has focused on extending our genetic studies into natural populations. Specificially, we have found small scale spatial structure in the sex ratio genetics that accounts for most of the sex ratio variation in nature.

# Are demersal, sand-dwelling cichlid species from Lake Malawi as poor dispersers as the rock-dwelling mbuna?

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Lake Malawi boasts a spectacular cichlid fish fauna, probably exceeding 1000 species. These species have evolved at an unparalleled rate: evidence from geological and molecular studies suggest the entire haplochromine cichlid flock has probably evolved from a single ancestor in under 1 million years. Recent studies have demonstrated that habitat discontinuities such as areas of deep water or stretches of sand can prevent gene flow between adjacent communities of rock dwelling mbuna. Whilst the mbuna appear to have evolved in an allopatric manner with the presence of physical barriers to reproduction, there are many hundreds of sand-dwelling demersal cichlid species that live in an area apparently devoid of such barriers. Microsatellite markers and mtDNA d loops will be used to investigate whether demersal species are divided into reproductively isolated sub-populations. Levels of gene flow will be calculated and the approximate geographic distance required to prevent or substantially reduce gene flow estimated. The effects of geographic features such as river estuaries, areas of very deep water and underwater reefs will also be considered in the analyses.

## Mutator, Sex, and the Adaptation of Bacterial Populations.

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Bacterial mutation rates can increase and produce genetic novelty, as shown by in vitro1 or in silico2 experiments. Despite the cost due to a heavy deleterious mutation load, mutator alleles, increasing the mutation rate, can spread in asexual populations during adaptation because they remain associated with the favourable mutations they generate. This indirect selection for a genetic system generating diversity (second-order selection) is expected to be highly sensitive to changes in the dynamics of adaptation. We show by a simulation approach that large population size, large number of favourable alleles, and high selective values of these favourable alleles helps mutator to become fixed. We also show that rare genetic exchanges, such as bacterial conjugation, can dramatically reduce the selection of mutators. This is partly because recombination dissociates beneficial mutations from the mutator background, but more importantly because sex speeds up adaptation by associating favourable mutations appearing in different individuals. The latter effect reveals how competition between adaptative strategies can affect second order selection, leading to sub-optimal genetic systems. Experiments of *in vitro* evolution of *Escherichia coli* populations confronted to various stresses are in process.

#### Natural genetic transformation of plants by Agrobacterium rhizogenes

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*Agrobacterium rhizogenes* transfers root-inducing DNA (T-DNA) to the host plant genome during infection of a wound. The transformed roots induced at the wound site have an altered phenotype, and they regenerate abnormal shoots, showing increased branching, altered flowering, and leaf wrinkling. Certain aspects of this transformed phenotype have possible adaptive significance. Key genes carried by Ri T-DNA probably function by changing polyanúne pools and thus increasing developmental plasticity. The possible evolutionary significance of the Ri T-DNA will be discussed, including the hypothesis that plant genes provide a genetic resource for soil bacteria and the speculation that rhizosphere microorganisms serve as genetic bridges among plant species.

#### Combining protein structure with protein evolution

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The relationship between phenotype and survival of the genotype is central to both genetics and evolution. We have been studying this relationship at the molecular level. The idea is that protein sequences are almost genotype and protein structures are a fundamental unit of phenotype. Our work is motivated by the fact that protein structures change more slowly over time than do protein sequences. We are exploring the constraints on protein sequence evolution that serve to maintain protein structure. Our model-based approaches and their applications to the study of evolution will be discussed.

# Phenological adaptation of a generalist spring-feeding moth, *Operophtera brumata*, to leaf flush of its host plants

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In deciduous forests, phenological matching to the leaf flush of host plants is critical for spring-feeding insect herbivores. Quercus robur L. is the main host of the generalist moth, Operophtera brumata L. (Lepidoptera, Geometridae) in the temperate zone, while Prunus padus L. is commonly used in the southern boreal zone. These two plant species represent the two extremes of timing of leaf flush in spring. We studied phenological adaptation of O. brumata to leaf flush of its hosts in different vegetation zones of Fennoscandia. During springs of 1998 and 1999, eggs of 3 populations (eastern Finland, south-western Finland, Denmark; 18-25 broods per population) were reared in laboratory at constant and at ambient temperature. Outdoor rearings were done at two locations, in eastern Finland and in southern Sweden. The hatching of larvae and the leafing of host plants, in relation to the cumulative temperature sum, were recorded. The larvae of the eastern Finnish population hatched in synchrony with the leaf flush of P. padus, which was significantly earlier than the larvae of two other populations. The larvae of the south-western Finnish population and the Danish population hatched in synchrony with the leaf flush of Q. robur. The results of the different experiments were in agreement with each other. We also found significant differences in the among brood variance of the studied populations, but not in within brood variance. Our results show that in different vegetation zones of Fennoscandia O. brumata is well adapted to the leaf flush of its main hosts; in the southern boreal zone to the leafing phenology of P. padus and in the temperate and hemiboreal zones to Q. robur. We suggest that, although hatching phenology is critical life history trait of O. brumata, there is genetic variance enough in this trait which allows perfect adaptation to the leaf flush of different host plants.

Reproductive system and pop'ulation structure of an endangered alpine plant (Eryngium alpinum L.): assessment of AFLP markers.

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Informations on the reproductive system and population structure are fimdamental for our understanding of the general functionning of a species. This requires studies on the breeding system, gene flow and the structuration of neutral markers distribution. For endangered species, this information will help, propose management practices, but has to, be obtained very rapidly. This raises the problem of what kind of markers should be used. We briefly review the, advantages and flaws of the different markers currently used (Le. isozymes, RFLP, RAPD, microsatellites) and compare them to, recently developed markers, AFLPs.

We have used AFLP markers to study the population structure of *Eryngium alpinum* L., an endangered alpine plant restricted to, 30-40 sites in the French Alps. Field studies on the breeding and pollination systems indicate that the species has a mixed mating system with restricted pollen flow. We therefore expect a strong genetic structure.

## The impact of within-host genetic diversity on virulence

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The evolution of virulence (the reduction in host fitness caused by parasitic infection) has stimulated lots of interest in evolutionary biology. Several theoretical models have been proposed that attempt to shed light on how different virulence schedules arise. Many of these focus on between-host competition, and the most popular of these is the adaptive trade-off model. In this model, virulence is assumed to be an unavoidable side-effect of within host replication, which is favoured by selection. However, replication rate cannot increase indefinitely because, above a certain threshold, it will kill the host and so reduce the parasite's own transmission. This trade-off between prudent exploitation and rapid reproduction determines the optimal level of virulence.

These between-host competition models can be extended to within-host competition. What happens to virulence when genetically distinct, conspecific parasites infect the same host? It is expected that "prudent" parasites which slowly exploit host resources will be outcompeted by "ruthless" ones, resulting in higher optimal levels of virulence. This assumption can be tested by infecting a host with two parasites that differ in their individual levels of virulence. Such an experiment is described which was carried out using a rodent malaria (*Plasmodium chabaudi*).

## Costs and benefits of early pairing in the Harlequin duck

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To investigate costs and benefits of early pairing in the Harlequin Duck, *Histrionicus histrionicus*, we compared time budgets and frequency of agonistic, courtship, and mate guarding interactions of paired and unpaired males and females. Overall, the proportion of feeding time in 401 half-hour focal-animal sampling sessions did not differ between paired and unpaired males and females. However, females spent more time feeding than males throughout the winter. While diving, paired males spent less time underwater than unpaired males, 22.89±6.61 s vs. 23.87±8.34 s, respectively. No difference in time underwater of paired and unpaired females was found. Paired males performed a greater frequency of interactions than unpaired males (2.05 vs. 0.59, respectively). Pairing status did not affect the overall frequency of interactions received by females, however, interactions received by paired females decreased from 1.68, in late October, to 0.42 by early May, while interactions received by unpaired females increased from 0.33 to 1.44, for the same period of time. Thus, early pairing may be costly for males: paired males spent less time underwater (presumably feeding) and more time in interactions. Benefits of early pairing for females are not clear. Paired females showed a decrease in the frequency of interactions received, however, pairing status did not affect the time females spent a decrease in the frequency of interactions.

#### Variation of evolutionary rate and the universal tree of life

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Phylogenetic analyses of gene and protein sequences have led to two major competing views of the universal phylogeny, the evolutionary tree relating the three kinds of living organisms, Bacteria, Archaea, and Eukarya. In the first scheme, called "the archaebacterial tree", organisms of the same type are clustered together. In the second scenario, called "the eocyte tree", the archaeal phylum of Crenarchaeota is more closely related to eukaryotes than are other Archaea. A major property of the evolution of functional ribosomal and protein-encoding genes is that the rate of nucleotide and amino acid substitution varies across sequence sites. Here, we show using distance-based and maximum-likelihood methods that universal phylogenies of ribosomal RNAs and RNA polymerases built by ignoring this variation are biased towards the archaebacterial tree because of attraction between long branches. By contrast, taking among-site rate variability into account gives support for the eocyte tree.

### Ecological interactions during adaptive radiation

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Adaptive radiations have played a pivotal role in the evolution of biological diversity, but the underlying causes of adaptive radiation have been difficult to disentangle. Using the common aerobic bacterium *Pseudomonas fluorescens*, we have examined the effects of environmental heterogeneity on the origin and maintenance of diversity. When provided with ecological opportunity, as spatial structure, identical populations diversify morphologically. After three days of growth in microcosms containing 6 ml medium, a single isogeneic ancestor gives rise to extensive morphological diversification. The majority of morphological variants are one of three types: the ancestral smooth (SM), wrinkly-spreader (WS), or fuzzy spreader (FS) morphotype. The ancestral SM morph grows primarily in the broth phase, while WS and FS morphs proliferate at the air-broth interface and microcosm bottom, respectively. Under appropriate conditions, the evolution of variant morphs is highly repeatable and competition between morphs is responsible for the maintenance of the newly evolved niche-specialists. But in the absence of ecological opportunity, no such diversification is observed.

## Three different lineages of South African barbs (Barbus, Cyprinidae) revealed by mitochondrial DNA and karyological data

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Cyprinids constitute a major component (about 500 species) of the African freshwater ichthyofauna. The genus Barbus is one of the most species-rich genera on the continent and includes species for which the only common morphological character is often limited to the possession of barbels. Moreover, the genus includes species that show three ploïdy levels-: diploid, tetraploid and hexaploid.

This difference in the species ploïdy level imposes a statistical problem in inferring phylogenies using nuclear markers (like allozymes or microsatellites), because of the different number of variables between the taxa. In order to overcome this difficulty, wWe used complete sequences of the mitochondrial cytochrome b gene in order to infer phylogenetic relationships between diploid, tetraploid and hexaploid species found in South Africa). Our results indicate that the South African tetraploids probably originated from African diploids and belong to a monophyletic group distinct from that found in the Mediterranean region. The small-sized diploid species, seem to be paraphyletic, while the hexaploids (also called 'large-sized barbs') are of recent origin and form a monophyletic group. Based on this data we discuss the taxonomic implications and the evolution of polyploidy in the group, as well as colonisation patterns on the African

The present study includes species that belong to the principal African biogeographical groups (North of the Sahara and East, West and South Africa). All ploïdy levels were treated.

The hexaploïd species (often called 'big barbs') appear to form a monophyletic group while the diploïds are paraphyletic,

The tetraploïd species seem to fit in two independent lineages :one spread in North and the other in South Africa continent.

## North American ciscoes (Pisces : Salmonidae) : a long history of introgressive hybridization and flawed taxonomy

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Contacts between diverged lineages is a creative evolutionary pathway that can lead to adaptive phenotypic variation, and introgressive hybridization has now proven to be part of the evolutionary history of several adaptive radiations. While introgression and hybridization has long been suspected among coregonid fishes, the extensive ecomorphological polymorphisms of North American ciscoes (genus Coregonus) has generally been studied in the rigid context of divergent evolution. This study investigates the phylogenetic relationships among NA ciscoes using a wide geographic survey and complete taxonomic coverage. Polymorphisms at 10 microsatellite loci and in the mitochondrial genome (ca. 700 pb) were determined for 1200 fish from 35 locations including all recognized extant ciscoes taxa and most reported ecomorphotypes. Phylogenetic relationships revealed by traditional and nested-clade analyses clearly identified C. sardinella and C.laurettae as divergent lineages. Unexpectedly, C. autumnalis, a taxon mostly recognized on the basis of geographic and life-history criteria, proved to belong to the 'C. artedi species complex' clade. Both mtDNA and microsatellites data indicate that C. autumnalis is a Beringian race that has colonized inland lakes via an Hudsonian dispersal route. The zone of introgression is remarkably wide and extends over most of the 'C. artedi species complex' range (Mkm<sup>2</sup>). Three currently recognized taxon failed to represent distinct lineages, and lakes with sympatric taxon or eco-morphotypes were caracterized by a mixture of both races, suggesting that the increased genetic variance resulting from introgression may have favoured the repeated evolution of a mozaic of a variety of eco/morpho-types.

#### Prisoner's dilemma in an RNA virus

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The evolution of competitive interactions among viruses was studied in the RNA phage f6 at high and low multiplicities of infection (that is, at high and low ratios of infecting phage to host cells). At high multiplicities, many phage infect and reproduce in the same host cell, whereas at low multiplicities the viruses reproduce mainly as clones. An unexpected result of this study was that phage grown at high rates of coinfection increased in fitness initially, but then evolved lowered fitness. Here we show that the fitness of the high-multiplicity phage relative to their ancestors generates a pay-off matrix conforming to the prisoner's dilemma strategy of game theory. In this strategy, defection (selfishness) evolves, despite the greater fitness pay-off that would result if all players were to cooperate. Viral cooperation and defection can be defined as, respectively, the manufacturing and sequestering of diffusible (shared) intracellular products. Because the low-multiplicity phage did not evolve lowered fitness, we attribute the evolution of selfishness to the lack of clonal structure and the mixing of unrelated genotypes at high multiplicity.

#### Diversity of satellite profiles and low rate of satellite DNA sequence change

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Satellite DNA sequences have been characterized in species of the genus Palorus (Coleoptera): PRAT in P. ratzeburgii, PSUB in P. subdepressus, PGEN in P. genalis and PFIC in P. ficicola. All of them are pericentromerically located, A+T rich, have lengths close to 150 bp either in the form of monomer or creating higher order repeat unit and comprise a considerable portion of the genome (20-40%). Despite insignificant sequence homology, all the satellites exhibit sequence induced curvature of DNA helix axis. Using PCR assay, it has been shown that all the sequences are present in each of the tested Palorus species: one of them is amplified into a high copy number or a major satellite, while the others are in the form of low-copy-number repeats. Each of the satellites is interspecifically highly conserved concerning the sequence despite the fact that according to the analysis of 3' end of mitochondrial Cytochrome Oxidase I gene of tested Palorus species the last speciation event occurred at least 7 My ago. These results explain satellite DNA evolution confirming the hypothesis that related species share a "library" of satellite sequences, some of which could be amplified into a major satellite. Quantitative changes in satellite DNAs, induced by occasional amplification of satellite repeat from the "library" could possibly occur in the course of the speciation process, thus forming a species-specific profile of satellite DNAs. Due to the evolutionary dynamics of satellite DNAs, the content of the "library" is variable: the elimination of some sequences parallels the creation of the new ones. Interspecific conservation of satellite sequences points to the very low substitution rate, which is in contrast with a high rate of sequence change proposed for noncoding DNA. Low rate of satellite sequence change might be related to their heterochromatic location, or due to selective pressure necessary to conserve some feature of functional significance.

# Population genetic structure of three avian species in fragmented habitats of Fennoscandia

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The mitochondrial control region was sequenced from three avian species in Fennoscandia: the Siberian jay (Perisoreus infaustus), the Siberian tit (Parus cinctus) and the grey partridge (Perdix perdix) in order to study the effect of habitat fragmentation upon genetic variation of the species. The Siberian jay and the Siberian tit are both birds of old growth, coniferous forests. The grey partridge is a bird of open arable lands. The Fennoscandian populations of these species have decreased in numbers during the 20th century. The main causes of the declines are attributed to habitat loss and fragmentation. There were weak geographical substructuring in the Siberian jay,  $\phi = 0.1$ . The nucleotide diversity was lower in the region that probably has been isolated already for decades. The estimated time to the most recent common ancestor for the Fennoscandian population coincides with the beginning of the Weichselian ice age (95 000 years). Distant lineages from the Taimyrian Peninsula and middle Yenisei valley differed from Fennoscandian lineage by 17 nucleotide substitutions and almost as much from each other. No geographic substructuring was found in the Fennoscandian Siberian tit population and all the genetic variation was between individuals in the Siberian tit. The most recent ancestor for the Fennoscandian Siberian tit population was estimated to be about 100 000 years ago. Despite of the recent shrinking of the populations of the Siberian jay and the Siberian tit, sequencing results suggest signs of expanding populations. The grey partridge population in the northernmost part of its distribution area is differentiated from the populations of the Southern Finland by one point mutation in the control region 1. French grey partridge lineage has coalesced from the Finnish lineage about 500 000 years ago. Probably the declines of the populations of these species are due to ecological factors. The study of these species shows that fragmentation of habitats can affect on species population genetic structure even in short timescale.

## Effects of environmental changes on natural selection active on human quantitative traits.

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In recent times many industrialized countries have achieved such an improvement in living conditions that a change in natural selection acting on human populations has likely occurred. Such a change may be succesfully assessed by studying quantitative polygenic traits, which are in general strongly affected by environmental factors. The environmental changes can produce a relevant decrease in the environmental component of the phenotypic variance in a quite short time, resulting in a more homogeneous phenotypic expression of the trait. The trait would then be less prone to selection. In humans perinatal mortality as a function of birth weight is one of the clearest examples of stabilizing selection. In fact, perinatal mortality preferentially eliminates babies whose weights greatly deviate from the mean and reaches its minimum in subjects close to the mean. We described in previous papers the relaxation of this kind of selection for several populations living in industrialized countries. In the present study we analysed the changes over time in the efficiency of stabilizing selection (measured by the reduction of birth weight variance between all births -i.e.still plus livebirths- and livebirths) and in the room available for selection (birth weight variance of the cohort exposed to stabilizing selection -i.e. all births). The considered period starts soon after the World War II and corresponds to about three generations of births. In such a relatively short time, socio-economic level and general sanitation have highly improved in Italy. In this new scenario, we found that the "classic" rules of selection are not at work any longer. New evolutive theories, more culturally focused, seem to be in order in the near future.

#### Effects of Wolbachia infections in three species of spider mites of the genus Tetranychus

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*Wolbachia* are maternally transmitted cytoplasmic bacteria that occur in nematodes, mites, isopods and are widespread in insects. These symbionts manipulate host reproduction in ways that promote their increase in frequency in a host population. Phenotypes induced by *Wolbachia* symbionts include: cytoplasmic incompatibility (CI), parthenogenesis, male killing and feminization. With the exception of CI, these mechanisms directly promote the increase in frequency of infected females. CI is the phenomenon where *Wolbachia* infected males become reproductively incompatible with uninfected females (or females harboring a different *Wolbachia* variant), thus reducing the fecundity of females that do not transmit the bacteria.

The genus *Tetranychus* comprises phytophagous arrhenotokous spider mite species that occur on a broad variety of host plants. Uni and bi-directional reproductive incompatibilities between different populations of the same species are commonly reported. These include: reduction in hybrid (female) offspring numbers resulting in male biased sex ratios, sterility among hybrids, or reduced viability of their haploid F2. The latter phenomenon, termed hybrid breakdown, usually predominates.

Here we report on the effects of *Wolbachia* infections in three species of the *Tetranychus* genus: *T. kanzawaii*, *T. turkestani*, and *T. urticae*. We investigated the effects of the infection in isofemale lines of the three species and looked for phenotypic variation within and between species. A cost for harboring the bacteria was generally observed. Infected females produce fewer adult offspring than uninfected females. Effects of *Wolbachia* in reproductive incompatibility can be expressed in F1 (CI) or F2 (hybrid breakdown) generations, but may also be absent. Interestingly, changes in sex allocation, i.e. increased female production, by infected females were also observed. This may aid in spreading the infection through an uninfected host population.

## Sex roles, parental effort and offspring desertion in the Curlew

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The reasons for female desertion and the evolution of predominant male care among monogamous bird species are not clearly understood. We studied parental effort during incubation and chick rearing period in the Curlew *Numenius arquata* in western Finland. Males and females contributed equally to incubation. There was also no difference between the sexes in the intensity of mobbing behaviour towards a potential nest predator (stuffed crow) shortly after hatching, whereas males became the more aggressive parent after the chicks left the nest. Females deserted their offspring approximately halfway through the fledging period (c. 16 d after hatching), while males remained with chicks until near independence (c. 35 d). Females at late season nests deserted their offspring sooner after hatching than at broods produced earlier in the season. Curlew females deserted younger chicks in north-east Europe, where laying dates were later, breeding seasons shorter and migration distances were longer, than in western and central Europe. We suggest that the most likely reasons for offspring desertion by females may be associated with increased female survivorship and maintenance of pairbond between years.

## The evolution of dangerous liaisons

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Many ecological interactions that are called 'mutualistic' involve in fact mixtures of parasitic and mutualistic aspects. For example, nitrogen-fixing bacteria may become parasites if conditions change. In this study we analyse, using an adaptive dynamics approach, conditions for the evolution of such 'dangerous liaisons'. The model that serves as a basis has a venerable pedigree (it was proposed as early as 1934) and is based on the idea that partners have to form a complex in order to interact. In particular, we devote much attention to the problem of how to distinguish common interests from the selfish interest of interacting partners, and how this depends on density or other contextual variables.
### Postfledging movements and natal dispersal in the Great Tit Parus major.

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The decision to undertake natal dispersal, the movement of an individual from its birth place to its place or first reproduction, is most commonly assumed to be under control of the dispersing individual. However, if parents control dispersal of their offspring to solve parent-offspring conflict over limited resources, e.g. territories, and avoid competition between kin, or to increase opportunities for habitat selection, this perspective may lead to a misinterpretation of the adaptive value of dispersal. Therefore, we have studied movements of juvenile great tits in their family groups before they are able to forage independently, because literature suggests that parents control these movements. We test 1) wether postfledging movements affect the probability of natal dispersal, 2) wether there is a relation between future survival and reproductive success of the parents and postfledging movements and 4) wether postfledging movements affect the probability of inbreedeing. These results are then discussed in relation to the major hypotheses formulated to explain the function of natal dispersal, more specifically inbreeding avoidance, avoidance of competition between kin and non-kin, mate selection and habitat selection

### Quantitative genetics of fluctuating asymmetry

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Whether or not developmental instability (DI) has evolutionary potential is subject to much debate. Generally, studies fail to detect significant heritability for fluctuating asymmetry (FA), a trait assumed to reflect DI. In addition, between-trait correlations in FA are low, suggesting that DI is trait- rather than individual-specific. Among the various attempts to explain these patterns, the overall weak correlation between FA and DI at the individual level has received most attention. Presently the concept of hypothetical repeatability (R) of individual FA allows to correct for this weak relationship, transforming patterns of FA into unbiased patterns of DI. By applying R to data presented in the literature, we show that heritability of DI remains lower than predicted but between-trait correlations in DI substantially increase after transformation. We further provide evidence that DI changes from a trait- to an individual-specific property with higher values of R. As increasing hypothetical repeatability might co-occur with increased environmental or genetic stress, we discuss the potential implications of our results for the study of evolution of stress resistance. From this we conclude that there is an urgent need for studies that compare the evolutionary potential of developmental instability under a variety of stress conditions.

### The evolutionary ecology of dominance-recessivity

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An *adaptive dynamics* modelling approach to the evolution of dominance-recessivity is presented. Fitness derives from an explicit ecological scenario, and both evolutionary attractivity and invasibility of resident populations are examined. The ecology consists of a within-individual part representing a locus with regulated activity, and a between-individual part that is a two-patch soft selection model. Evolutionary freedom is allowed at a single locus. The evolutionary analysis considers directed random walks on trait space, generated by repeated invasions of mutants.

Additive genetics is evolutionarily unstable when selection and evolution maintain two alleles in the population. In such a situation, dominance interactions can become stationary and close to additive genetics or they continue to evolve at a very slow pace towards dominance-recessivity. Evolution then approaches a population state where every phenotype in the population has maximum viability in one of the two patches.

When the within-individual part is replaced by a housekeeping locus that codes for a metabolic enzyme, evolution favours a population of two alleles under the same conditions as for a regulated locus. In the case of a housekeeping gene, however, the evolutionary dynamical system approaches a population state where the heterozygote and only one homozygote phenotype are equivalent to the optimum phenotypes in the two patches.

# Microsatellite analysis of genetic diversity of African buffalo (Syncerus caffer) populations throughout Africa

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Genetic diversity was analysed with fourteen microsatellite markers in 162 African buffalo from nine populations throughout Africa to study the effects of habitat fragmentation and population bottlenecks caused by rinderpest epidemics. Genetic distances among most populations of subspecies Cape buffalo were small, with most population differentiation probably being ancient. Within population genetic diversity was very high, indicative of long-term effective population sizes of at least 2,600 which implies that rinderpest epidemics only had a limited impact. Current census sizes of many buffalo populations are smaller than this minimum estimate, which means that they will loose genetic diversity without regular immigration. There was strong population differentiation between Forest buffalo and Cape buffalo supporting their classification as distinct subspecies. An increased genetic distance was observed between Cape buffalo in Kruger (South Africa) and other Cape buffalo populations, which coincided with a lower heterozygosity. This was probably due to ancient habitat fragmentation, but rinderpest epidemics could also have had some effect. Although the small genetic distances among Cape buffalo indicated high migration rates, migration could still be restricted by geographical barriers as was observed in Kruger and between Tsavo and Amboseli (Kenya). Genetic distances of the more polymorphic markers were negatively biased which was most likely due to their high mutation rate, in agreement with predictions by theoretical studies. By comparing expected heterozygosity between different markers with varying polymorphism we were able to differentiate ancient from recent habitat fragmentation. Furthermore, negative bias of F, compared to Rho (R) was used as an indicator of ancient habitat fragmentation. However, this did not imply that absence of this bias automatically meant recent habitat fragmentation.

### Costs and limits of plasticity in the clonal plant Ranunculus reptans

### Mark van Kleunen, Markus Fischer and Bernhard Schmid

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Several costs and limits of plasticity may constrain natural selection for genotypes that perform optimal in each environment. If replicates of many genotypes are grown in different environments energetic costs of plasticity (including costs of maintenance, of production, of information acquisition and genetic costs) can be estimated from regressions of fitness components on plastic traits. Similarly, the presence of developmental instability costs and of a developmental range limit can be estimated by correlations. Clonal plants are especially suitable for such studies because genotypes can easily be replicated by vegetative reproduction. Moreover, plastic responses to the environment may be very important for several characters unique for clonal plants. Clonal plants may forage for resources through plasticity in both leaf and internode lengths, they may respond plastically by arranging ramets compact or loosely, and they may plastically adjust their allocation to sexual versus vegetative reproduction. We searched for costs and limits of plasticity in these traits in the clonal herb Ranunculus reptans. We grew vegetatively replicated offspring of 104 genotypes of *R. reptans* solely or in competition with a naturally co-occurring grass species. As fitness components we assessed the total number of rosettes per plant, the number of rooted rosettes, and the number of flowering rosettes. We detected significant energetic costs of plasticity in all studied traits. However, results depended on the fitness measure used, on the environment in which fitness was assessed, and on the regression model. For several traits variation among replicates within genotypes was significantly positively correlated with plasticity in the same trait, suggesting developmental instability costs. However, again results were not consistent for both environments. Genotypes with the least plastic ratio of flowering over rooted nodes had the most extreme mean ratios, indicating a developmental range limit. Our results indicate that plasticity in R. reptans is constrained by costs and limits.

### **Clonal integration: coincidence or adaptation?**

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Physiological integration in clonal plants may be adaptive or be a coincidental consequence of the clonal life form. In an experiment with 27 genotypes of the stoloniferous herb Ranunculus reptans we studied fitness consequences of clonal integration in a spatially heterogeneous light environment. Moreover, we examined genetic variation in maintenance of integration and in effects of integration. We grew 216 ramet pairs of the 27 genotypes with mother ramets in the light and daughter ramets in the shade. In half of the pairs we severed the stolon connection between the two ramets. During the experiment half of the pairs with originally intact connections disintegrated because of stolon decay or death of planted ramets. We detected significant variation among genotypes in this physical integration. Survival of planted ramets was higher for originally integrated pairs. In surviving plants clonal integration decreased size differences between plant parts developing from mothers and daughters, but there was no overall synergistic benefit of integration in terms of growth or reproduction. We detected significant variation among genotypes in growth and reproduction. We also found marginally significant variation among genotypes in the effect of integration on growth and reproduction. Integrated daughters had significantly longer leaves and internodes than daughters in severed pairs indicating that integration stimulated plant foraging in both the vertical and horizontal plane. Observed effects of integration on fitness components in combination with genetic variation in maintenance of integration and in effects of integration suggest that clonal integration in the study population was subjected to selection. We conclude that physiological integration in clonal plants can be adaptive rather than coincidental, and that future studies on clonal integration should use defined genetic material of more than a few clones.

### Habitat-linked variation in life-history traits in Drosophila

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The effects of climatic factors on various life-history traits are well demonstrated in latitudinal and altitudinal clines. On a much smaller scale, (micro-) climatic variation can be also considerable, for instance between primary forest and open grassland.

In our first study in the Philippines, we investigated intraspecific genetic variation in development time and starvation resistance between populations of eight *Drosophila* species from different habitats. The traits were measured in the F2 generation in a common lab environment. The results showed significant genetic variation between populations within several species. This variation is correlated across the eight species.

In our current study in Panama, the aim is to investigate the genetics and the expression of life-history traits in the field. First, we measured the expression of development time, starvation resistance and body size simultaneously in twelve *Drosophila* species in three habitats in the field. In a second experiment, we transplanted individuals of four species to the two other habitats and simultaneously measured in the original habitat to establish reaction norms of the populations from different habitats. Third, we measured the expression of these traits in a common lab environment as in our first study.

The molecular clock runs at different rates among allelic lineages at the rabbit *IGKC1* locus: Evidence from sequence comparisons and population studies.

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In rabbit (Oryctolagus cuniculus, L.) the constant region of the light chain of the major immunoglobulin fraction is encoded by the IGKC1 gene. The rabbit IGKC1 locus is unique among known vertebrate protein loci in that its products show allelic variation at more than 50% of the 104-107 amino acid (aa.) composing the IGKC1 domain This unusual degree of gene diversity raises a variety of evolutionary questions, notably those concerning the rate of change and the nature of the selection pressure maintaining this variation. Previous studies have provided strong evidence for diversity enhancement selection at this particular locus. Here we present different, converging lines of evidence indicating that evolutionary rates can differ markedly among allelic lineages. Indeed, (1) Felsenstein's test of likelihood ratio's, when applied to allelic sequences, indicates significant differences in substitution rates among lineages; (2) comparisons of homologous and allelic sequences (between and within species), show that some of the less apomorphic allelic lineages have evolved at rates that are similar to the slowest rates inferred for mammalian IGKC genes; (3) patterns of synonymous substitutions are directional among alleles and correspond to a relaxation of codon preference of the more apomorphic lineages; (4) cytonuclear correlations in the populations of the aboriginal species range suggest that turnover rates of plesomorphic lineages are slower than that of lineages of more apomorphic lineages. Because genes belonging to latter lineages, when compared with plesomorphic lineages, (1) are more used in the heterozygous individual, and (2) occur consistently at higher frequencies in populations, we suggest that these differential evolutionary patterns have to do with asymmetries in the marginal fitness matrices of the different genotypic combinations.

Effect of population bottlenecks on the gene diversity at IG loci in wild rabbits (Oryctolagus cuniculus L.) of the islands of Porto Santo (Madeira) and Flores (Azores).

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Previous genetic studies have documented a severe reduction in population diversity in the wild rabbits of the Atlantic Islands of Porto Santo (Madeira) and Flores (Azores). The hypothesis that this is due to very small sizes of founder populations (i. e. a single pregnant female for Porto Santo) was corroborated by the reduced frequency variances among alleles at the remaining polymorphic loci. These studies did concern protein and mitochondrial polymorphism's that are probably selectively neutral. Here we study the effect of population bottlenecks on the gene diversity at loci known to be exposed to diversity enhancement selection. These loci are the preferentially expressed variable region gene of antibody heavy chain *IGHV1*, and the *IGKC1* gene, which encodes the constant domain of the light chain of the major antibody fraction (*previously:* the *a*- and the *b*-locus allotypes, respectively). Our observations on number of alleles and their frequency variances are not in contradiction with the hypothesis of a rabbit "Eve" of Porto Santo, nor with a colonisation of Flores by its descendants. At the same time, it appears that the founders were polymorphic at both loci, with at least two alleles at the *IGHV1* locus and three alleles at the *IGKC1* locus, and that these polymorphism's have been transmitted, apparently undiminished.

### Host race formation in the anther smut fungus Microbotryum violaceum

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Plant parasites can often employ more than one host species, and show intra-specific variation in host use. A central question in evolutionary biology is how such variation originates and is maintained, and under which conditions it may lead to host-race formation and speciation. In phytopathogenic fungi, host specialization is well documented, but the underlying mechanisms are still poorly understood. To study such mechanisms more explicitly we use as a model system the anther smut fungus, *Microbotryum violaceum*, in sympatric populations of two of its host species, *Silene latifolia* and *S. dioica*, common roadside weeds. The most striking symptom of an infection with this fungus is the overriding of the genetically determined sex expression in dioecious host species. In diseased female plants ovaries are aborted and both male and female plants develop flowers with stamens filled with diploid teliospores instead of pollen. Teliospores are dispersed among flowers by insects, serving the dual role of pollinators of the plant and vectors of the disease. Another interesting feature of this model system is provided by hybrids of both host species, which may facilitate host shifting.-

We study the mechanisms that could contribute to reproductive isolation of host specific strains in sympatric populations of hosts, e.g. host selection behavior of vectors and assortative mating of pathogen strains. Preliminary results show that strains in allopatry are genetically differentiated and, when competing with strains originating from the other host, are slightly favored on the host of origin.

Genetic diversity and structure in declining populations of *Primula vulgaris* in relation to population size and habitat fragmentation

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*Primula vulgaris* (= *P. acaulis*, Primulaceae) is a rare, declining plant species in Belgium. It shows a distribution range restricted to a few areas in Flanders, consisting of about 30 populations, mostly of small size and fragmented in small patches. It occurs in moist woodlands, hedgerows and wet ditches alongside pastures; these habitats in Flanders are highly fragmented and threatened by the intensification of the agricultural practices.

We investigated for all the populations still existing in Flanders, genetic diversity and structure using allozyme markers in relation to habitat fragmentation, population size, density and shape. The aims of this study are to assess (1) if genetic erosion can be detected in small and/or fragmented populations, (2) the isolation degree of the patches, and (3) if the small, linear elements of the landscape can function as corridors between populations. The acquisition of these data will contribute to set up priorities for conservation and management of the remnant populations.

### Elasticities link demographic and evolutionary dynamics

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Ecologists interested in demography often use matrix projection models to determine the impact of different phases in the life cycle on the population growth rate ( $\lambda$ ). Management plans for endangered species can then be targeted at those phases that increase  $\lambda$  most. Evolutionary ecologists want to find the targets of natural selection, and the mechanisms behind fitness differences among individuals. But since the population growth rate is also the mean fitness of individuals (at equilibrium at least) the approaches are related. However, the parameters differ: elasticities or sensitivities in the demographic setting, vs. selection gradients or differentials in the evolutionary setting. This is confusing, and may hamper integration of the two fields.

There is a lot to say for using elasticities in both cases. An elasticity quantifies a trait's impact on  $\lambda$  on a proportional scale. An elasticity of 0.3 indicates that a one percent increase in trait mean increases  $\lambda$  by 0.3 per cent. Furthermore, matrix projections and selection analysis can be combined to yield "elasticity path diagrams" from which key factors in the demography as well as selective forces and selection responses can be evaluated. First, a transition matrix is constructed, given the life cycle of the organism. Elasticities for components of fitness can be derived from the properties of the projection matrix. Next, relationships between phenotypic traits and fitness components are added, using statistical methods (multiple regression or path analysis). Finally, elasticities are genetic variances of traits that are expressed on a proportional scale (i.e., standardized by dividing by the mean). (Comparative) analysis of selection on life history traits, evaluation of the genetic potential for evolutionary change, and studies on the impact of traits on the demographic properties of a population would all benefit from the

use of elasticities

### Intrapopulational genetic polymorphism in relation to temporally varying environments

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Like most *Daphnia* species, *D. magna* is a cyclical parthenogen. When conditions are favourable, it reproduces clonally, but when a risk of extinction is involved, it reproduces sexually with the formation of resting eggs. Due to the short generation time during clonal reproduction, populations may quickly expand, enabling the succession of genetically distinct groups of animals within one growing season. The presence of diapausing stages may strongly facilitate the occurrence of intrapopulational genetic polymorphism associated with temporally varying environments. Especially in the case of temporal habitat selection, where genotypes show differences in time of emerging from resting stages and of entering diapause, genetic specialisation to a restricted period of the growing season may occur. In a life-table experiment, a set of *D. magna* clones that hatched under 'summer' conditions in previous laboratory experiments ('spring' and 'summer' clones were derived from the same populations), were both cultured under spring and summer conditions, to see whether differences in relative fitness among clones were associated with the conditions under which they hatched. If such an association is observed, it provides a strong indication for the occurrence of temporal habitat selection in natural populations of *Daphnia*.

### Flowering and fructification studies in quercus suber and quercus ilex in Portugal

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Mixed stands of Quercus suber (cork oak) and *Quercus ilex* (Holm oak) are a common situation for the settlement of the two species in Portugal. Hybridisation among the two species is known to be possible, but Portuguese studies are virtually absent.

With the aim to characterise the absolute and comparative reproductive behaviour of the two species, flowering and fructification are being appraised through quantitative observation on a permanent plot of 39 cork oak trees and 25 holm oak trees from a mixed natural stand in Évora.

Since synchronised temporal occurrence of flowering of the two species is a basic requirement for the occurrence of interspecific crosses phenological phases of flowering of the two species has been observed and registered.

The two species are widely known as having desynchronised flowering, holm oak roughly flowering 3 to 4 weeks before cork oak. This trend has been confirmed on the observation on the permanent plot where this study is taking place.

Data from 1998 show that on the 64 trees of the plot, (39 of cork oak and 25 of holm oak) overlapping of flowering only occurred during a short period among one tree of each species.

Estimation of relative male reproductive success by paternity analysis in the androdioecious Phillyrea angustifolia L.

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Androdioecy - presence of both males and hermaphrodites within a population- has been described as a rare and unlikely breeding system, intermediate in the evolution of reproduction in plants and thus of great interest. For androdioecy to be maintained by selection, males must have a twofold increase in male fertility as compared with their hermaphrodite counterparts. In the Mediterranean wind-pollinated shrub *Phillyrea angustifolia* L, controlled, single-donor pollinations have shown that hermaphrodites are male-fertile and self-incompatible, and that male pollination results in twice as many fruits as hermaphrodite pollination. Part of this male reproductive success difference was due to incompatibility among hermaphrodites. To confirm this first indication of a functional androdioecy, paternity analysis were performed on more than a thousand seeds collected on 12 hermaphrodites in a isolated, natural open-pollinated population of 50 individuals, using microsatellite markers. Male reproductive success was evaluated for both sexual phenotypes. The results will be discussed in light of hermaphrodite self-incompatibility and the maintenance of the androdioecious breeding system.

### QTL Analysis: A Highway or a Dead End?

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Over the past several years, great progress has been made in detecting and mapping genes of major effect for several phenotypes, such as diseases and spontaneous mutations in various organisms. Now, due to innovations in quantitative and molecular genetics, it is becoming possible to study the genetic basis of polygenic traits; to identify, map, and measure the effects of quantitative trait loci (QTLs). The impact of QTL studies on evolutionary genetics is only now being realized and is opening new research avenues into persistent problems in genetics and evolution. We have used these new genetic and statistical techniques to investigate the genetic architecture of a number of polygenic traits such as body size and mandibular morphology. Genetic architecture plays a critical role in determining phenotypic evolution through its effects on patterns of genetic variation. By genetic architecture we are referring to the number of loci potentially affecting the trait, the distribution of gene effects, and the underlying patterns of gene action, including additivity, dominance, sex-specificity, epistasis and pleiotropy. These investigations have allowed us to address three important evolutionary topics: (1) the evolution of additive genetic variation, (2) the evolution of dominance variation, and (3) the evolution of pleiotropy versus genetic correlations. Here we summarize these results and demonstrate the utility of QTL studies in furthering our understanding of the underlying genetics of quantitative traits rather than relying on untested and previously untestable assumptions concerning the nature of allelic effects on quantitative characters.

# A new method for detecting balancing selection from DNA sequences: application to the *b1* mating type gene of the fungus *Coprinus cinereus*

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Balancing selection, an evolutionary process occurring in self-recognition systems such as homomorphic self-incompatibility in plants and mating factors in higher fungi, leads to the maintenance in populations of a large number of functionally distinct alleles for extended periods of time. Until now, evidence for balancing selection and extended residence times has almost exclusively depended upon identification of transspecific polymorphisms; polymorphisms retained in populations through speciation events. We develop a new method for detecting balancing selection from DNA sequences of putatively selected loci, based on the recognition that two genealogical processes with markedly different time scales occur at these loci: (1) functionally distinct alleles are evolving over extended periods of time, producing genealogies with a topology like that of neutral alleles but rescaled in time, with a scaling factor, fs, proportional to selection intensity; (2) allele copies within a functional allelic class are evolving neutrally because they encode the same compatibility type, but on a much shorter time scale determined by the frequency of the corresponding allelic class. We show that the effect of balancing selection can be detected by contrasting the levels of variation maintained by neutral evolution, i.e. considering variation among allele copies within allelic classes, with that maintained under selection, i.e. considering variation among distinct allelic classes. The method will be illustrated with results from numerical simulations as well as with molecular data obtained from the b1 specificity gene of the A mating type factor of the basidiomycete Coprinus cinereus, where both functionally distinct alleles and replicate alleles of the same type were isolated and sequenced.

### Geographical parthenogenesis and mixed sexual - asexual dandelion populations

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Geographical parthenogenesis, i.e. related sexual and asexual forms having different geographic distributions, is an intriguing phenomenon and may help to explain the maintenance of sexual reproduction. The common dandelion, *Taraxacum officinale*, is a clear example: diploid sexuals having a restricted central European distribution, whereas triploid apomicts are found all over Europe. A number of hypotheses have been put forward to explain geographic parthenogenesis, e.g. a lower pathogen pressure in asexual ranges, superior colonization capacity of sexuals, the occurrence of general purpose asexual genotypes.

Sexual diploid dandelions reach their northern distribution limit in the Netherlands. Marginal sexual populations (mixed with asexuals) are found on thermophylic sites, such as south facing slopes of river dunes and summer dikes. This suggests that physiological constraints and habitat preferences may also play a role in the geographic distribution of sexuals. In the present study, the occurrence and performance of sexuals and asexuals and their reproductive interactions are investigated with respect to adjacent North- and South facing slopes of a summer dike along the river Rhine. Detailed investigations of mixed populations in a heterogeneous environment may provide a better insight in the factors that cause geographic parthenogenesis.

A molecular phylogeny of the African Muridae and patterns of nucleotide change in mitochondrial cytochrome b and two ribosomal RNA genes

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DNA sequences from parts of cytochrome b, 16S rRNA and 12S rRNA mitochondrial genes, which totalled 1089 aligned basepairs, were used to infer the relationships among 30 African murid species that represent 30 genera and 7 subfamilies. The obtained mtDNA phylogeny supports a sistergroup relationship between the Dendromurinae, the Cricetomyinae and the Nesomyinae. This clade contains seven genera that contain taxa that are seemingly not united by morphological features. The exclusion of *Acomys, Lophuromys* and *Uranomys* of the Murinae is confirmed as well as the inclusion of the Otomyinae in the Murinae. Sistergroup relationships are suggested between *Acomys, Lophuromys* and *Deomys* - a genus that is traditionally allocated to the Dendromurinae - and between *Uranomys* and the Gerbillinae. Within the African Murinae, two African clades are distinguished: a well supported *Malacomys-Hylomyscus-Praomys-Mastomys-Colomys*-clade and a tentative *Hybomys-Arvicanthis-Lemniscomys-Grammomys-Dasymys-Stochomys*-clade (that includes *Otomys*). In addition there are a *Mus-Nannomys*-clade. The molecular phylogeny suggests that dental characters - the morphological features are considered to be of 'murine' or 'cricetine' descent - are not reliable for phylogenetic inferences and that other morphological as well as molecular features are needed to obtain a reliable phylogeny based taxonomy.

### Genetic basis and fitness consequences of differences in relative growth rate in Hordeum spontaneum: a QTL approach

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The relative growth rate (RGR) of plants, a quantitative trait that is associated with a suite of physiological, morphological and biochemical characters, is often correlated with habitat characteristics. To explore the role that RGR and its underlying components play in adaptation to local environments, we will perform selection analyses on genotypes of *Hordeum spontaneum* (wild barley), a selfing annual that occurs in a wide range of natural habitats in the eastern Mediterranean basin and in western Asiatic countries. Both in the natural environment and in the greenhouse, we plan to measure fitness parameters in plants from different natural populations, and in AFLP-genotyped and phenotypically characterized progeny of a cross between plants from two barley populations of contrasting habitats. By relating phenotypic selection directly to the presence of specific (combinations of) RGR-related loci, we can analyse in detail which of the growth-related parameters are under selection, and how this selection differs between habitats. Moreover, these experiments can yield evidence for co-adapted gene complexes, i.e. do natural genotypes in their original habitat outperform recombinant lines with alternative allele combinations? If pleiotropic genes are found within the RGR complex, the experiments can provide insight in the question whether pleiotropic genes affect all associated RGR-traits in the same direction, or whether maximisation of fitness is constrained by antagonistic effects on individual traits.

# The use of L1 (LINE-1) retrotransposons for resolving and dating phylogenetic events in Rattus sensu lato and stricto (Rodentia : Muridae)

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Understanding the evolution of extant organisms depends on accurate phylogenies that reflect the genealogy of the studied taxa. Phylogenetic trees, whether based on morphological, biochemical, or molecular characters, can be erroneous or indeterminate for various reasons. For example, incorrect branching patterns can be produced by homoplasic characters (i. e., non inherited ancestral characters shared by at least two unrelated species). Furthermore, correct rooting of the tree depends on knowing the ancestral state of the characters which in many cases is difficult to determine. In addition, characters may not have changed sufficiently to resolve the very short internodal segments resulting from rapid speciation events. And finally, tree building algorithms often incorporate simplifying assumptions that may be biologically unrealistic, and may be unusable when the number of examined taxa increase exceed certain limits.

Here we used subfamilies of repeated DNA generated by L1 retrotransposons as phylogenetic characters. We identified these subfamilies by sequencing a region of 240 Rattus L1 elements cloned from various rat taxa. We then determined the distribution (presence or absence) of the subfamilies in 22 species of Rattus sensu lato and stricto. Building trees with this character is independent of the number of taxa. By assuming that the absence of an L1 subfamily is the ancestral state of the character, we obtained only a single robust tree (CI = 1) that was free of homoplasies and which significantly extended our knowledge of the phylogeny of these lineages. In addition, we estimated the age of each L1 subfamily from the extent of sequence divergence between its members and showed that Rattus sensu stricto arose 5-6 Mya and subsequently underwent two episodes of speciation. An intense one occurred  $\sim$ 3 Mya and produced at least five lineages in less than 0.3 My, and a second one  $\sim$ 1 Mya that generated numerous extant Rattus species. We conclude that L1 DNA subfamilies are robust, homoplasy free phylogenetic characters that can resolve and date even very intense cladogenic events.

# Genetic variation in isolated populations of the drumming wolf spider Hygrolycosa rubrofasciata.

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The wolf spider H. rubrofasciata is very suitable species for studying phenotypic and genetic differences between populations. It has patchy distribution on suitable habitats that are bogs, meadows and abandoned fields. These patches are more or less isolated from each others by forest habitats and the dispersal between them is very limited. We have observed great differences between populations in body mass even between populations located very near (few hundred meters) each others. Generally spiders originated from wet bog habitats are ca. 30 % larger in size than spiders from meadow or field habitats. Because size is one of the most essential fitness related character in invertebrates, we tested whether these observed differences are genetical or plastic responses to different environmental conditions (e.g. food availability). We manipulated growing conditions of spiders from different origin both in the laboratory and in the field. In the laboratory spiders from 7 different populations were raised to adults in two different food levels: scarce or medium. In the field spiders from three different origin (bog and two meadow habitats) were raised either in bog habitat or meadow habitat in large enclosures. There were significant interactions between growing conditions and origin of spiders both in the laboratory and in the field. In the bog enclosure spiderlings originated from the bog habitat grew significantly better than spiders from the meadow habitat. In the meadow enclosure there were no significant differences in size between spiders originating from bog and meadows. Our results suggest that observed differences in size between populations are at least partly genetical and might be adaptive responses to different food conditions .

### Nuclear DNA variation in the genera Antirrhinum and Misopates.

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In plants, little is known about the level of nuclear sequence variability and how it is affected by the breeding system of the populations. Therefore, we have been determining the level of nuclear DNA polymorphism in several populations with different breeding systems in the genera Antirrhinum and Misopates. Two kinds of genes were studied, cycloidea (*cyc*) and *fil1*. Both were found to be present as small gene families. All the nuclear genes studied so far (*cyc1A*, *cyc1B*, *cyc2*, *cyc4*, *fil1A*, *fil1B*, and *fil1C*) show no, or very little, variability. In addition, a low level of divergence is observed when species of these genera are compared with *Digitalis purpurea*, whose most recent common ancestor with Antirrhinum / Misopates was approximately 5 Mya. In this work, we discuss the technical difficulties in establishing the presence of recently duplicated loci, as well as several theoretical scenarios that could account for the data.

### DNA polymorphism studies on the fused gene of Drosophila virilis.

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The *fused* gene of Drosophila is a segment-polarity gene which encodes a putative serine-threonine kinase, and which is implicated in the *hedgehog* signalling pathway. In the present work, we have surveyed the level of nucleotide variation in a 2.4 kb region of the *D. virilis fused* gene, which includes a small region of the 5' non-coding flanking sequence, the four introns of this gene and most of the coding sequence. In this species, there is a common replacement polymorphism, present in approximately 50% of the sequences analysed, where a negatively charged aspartic aminoacid is replaced by the non-charged aminoacid proline that is located within the serine-threonine kinase domain of the *fused* gene. Significant linkage disequilibrium is observed between the replacement polymorphism site and 4 other nucleotide sites, the furthest one being 82 bp away, what is unusual given that this gene is located in a region of the *D. virilis* X chromosome that experiences normal levels of recombination. Significant deviations from the expected neutral pattern were observed when three different statistical tests were used, suggesting that the *D. virilis fused* gene is under some sort of balancing selection.

### Analysing a hybrid zone of Castanea sativa (Mill.) in Turkey using genetic and morphologic data on seeds

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Turkey represents an area of particular biogeographical value because of its complex history and geology. Three main phytogeographic regions have been recognised: Euro-Siberian, Mediterranean, Irano-Turanic areas (Davis, 1965).

Turkish populations of the sweet chestnut showed a very high variability in genetic, morphologic and physiological parameters (Villani et al., 1992). A recent study based on allozyme data, highlighted and discussed the occurrence of a hybrid zone in Bithynia, which derived from a secondary contact between two differentiated groups of populations in the north-eastern and south-western regions of Turkey (Villani et al., 1999).

In order to investigate relationship between genetic structure and morphology, seeds deriving from open pollination (half-sib families) were sampled from 7 populations representative of the two geographically vicariant and genetically distinct groups and the hybrid zone itself. Seed samples were individually analysed by means of 11 allozyme loci and 13 morphometric variables.

Genetic data were used to estimate outcrossing rate and gene flow between populations. In addition, the role of selection in the hybrid zone was highlighted by comparing the genotypic composition of seeds and trees from the same localities.

### Mating system evolution in fungus-growing ants

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Fungus-growing ants have obligate mutualistic interactions with fungi. The phylogeny of the attine tribe is known and it has recently been documented that lower attines are still able to domesticate new free-living fungi, whereas the higher attines are characterised by a long history of vertical propagation of clonal fungal strains. Queens of leafcutter ants (*Atta* and *Acromyrmex*) exhibit the highest known mating frequencies (up to 10 mates per queen documented) among ants. Multiple queen-mating may have been selected to increase genetic diversity among nestmate workers, which is hypothesised to be critical in social systems with a single queen per large, long-lived colony under pressure of pathogens. Advanced fungus-growing (leafcutter) ants have large (10<sup>4</sup>-10<sup>6</sup> workers) and long-lived colonies, whereas basal genera in the attine tribe have small (< 200 workers) colonies with probably substantially shorter lifespans. We have therefore investigated whether the basal attine genera have lower queen-mating frequencies, similar to those found in most other ants.

We have analysed queen mating frequency and colony kin structure in three basal attine genera (*Myrmicocrypta*, *Apterostigma* and *Cyphomyrmex*) and the genus *Trachymyrmex* and compared them with existing data for *Atta* and *Acromyrmex*. We have used newly developed, highly informative, microsatellite markers to document that queens of basal species are single mated. Fungus growing *per se* has therefore not selected for multiple queen mating. Instead, the advanced and productive social structure of the higher attine ants, which is fully dependent on the rearing of an ancient, tightly co-evolved, clonal fungus, may have necessitated high genetic diversity among nestmate workers.

### Effect of ecosystem dynamies on long-term evolutionary patterns.

### Dita B. Vizoso

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The pattems observed in macroevolutionary dynamics have been explained classically as consequence of external events. The insertion of selPorganization models in evolutionary biology gave a new insight on the possible mechanisms explaining those pattems. Extinction and speciation occur in long-time (evolutionary) scales, while the processes determining the dynamics of the populations oecur at short-time (ecological) scales. This difference in the timescale of the dynamic units and the pattems emerging from their interactions is one of the factors that characterize selPorganized systems and is also present in the evolution of communities. Individuals are subject to natural selection, and those with traits that optimize their fitness will spread their genes in the population. Likew; se, species that are better competitors may lead other species to extinction. Even though this is not always the case, as suggested in the recent studies on coexistence, the presence of competitors is a key factor shaping the evolutionary outcome. In this study 1 analyze the macroevolutionary pattems emerging from the interspecific competition for a general set of resources. I discuss the importance of population dynamics for coexistence of competing species, the interaction between mass extinctions and diversity explosions, and the general significance of interspecific competition for macroevolutionary processes.

### Seed morphology of some species of the Alsinoideae (Caryophyllaceae) and its significance for systematics.

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Taxonomic position of the monotypic Eastern-Asiatic genus Fimbripetalum (Turcz.) Ikonn. is discussed. The seed surface of F. radians (L.) Ikonn. has been studied for the first time with the help of scanning electron microscope. Genera, sections and species can be identified by their seed characters (seed-shape, sculpture and structure). The seed surface of F. radians seems to have unique characteristics in the fam. Caryophyllaceae (sculpture is pitted, as tubercles are concave). The separation of the sect. Fimbripetalum from g. Stellaria into the independent genus is confirmed to be correct. The evolutionary trends of individual characters and their complexes within Alsinoideae are disscussed.

## Linkage mapping of loci controlling important traits in less studied species

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In model species, precise and dense maps of informative marker loci allow mapping of qualitative and quantitative trait loci with high precision. Inbred lines are available that allow for easy mapping in a backcross or linecross F2. This allows for computationally simple inference of location and effect of loci controlling important traits. For many evolutionarily important species, however, only partially informative (often dominant) markers with unknown grandparental phases may be available. Instead of line-crosses only full-sib families of unrelated parents are usually available. Segregation ratios of marker loci may be distorted. Selection of phenotypically extreme individuals for scoring of markers (selective genotyping) may introduce further complications. In principle, all of these complications can be addressed with a unified theoretical approach using Bayesian inference and Markov-chain Monte-Carlo (MCMC) techniques. With MCMC, position and effect of quantitative trait loci and other important loci can be inferred concurrently with the marker linkage map, the phases of marker loci, and segregation distorting loci in selectively genotyped offspring of a full-sib family. I will present recent developments towards this goal.

# Gene flow in a postglacial aquatic coloniser (bullhead, Teleostei) in western Europe

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Many habitats in northern Eurasia became colonised by temperate organisms after melting of the ice cap some 10,000 year ago. Although various hypotheses on the importance of refugia as source populations have been proposed, our study focuses on the micro-evolution of a single source population (clade) of freshwater fish. This permits rather accurate dating of micro-evolution, a complex problem in evolutionary biology. We chose the genetically diverse bullhead (*Cottus gobio* L.; Teleostei) to evaluate small-scale spatial structure in the Meuse and Scheldt watersheds in comparison to neighboring watersheds. Bullhead prefers well-oxygenated upland rivers and commonly shares its habitat with brown trout. Samples, obtained in the watersheds of Meuse (5 samples), Scheldt (7 samples), Rhine (3 samples), Vilaine (1 sample) and Rye (1 sample) were studied for mtDNA RFLP patterns at two adjacent fragments of 2.4 and 2.1 kb covering the *ND5/6*, *cytb* and *D-loop* respectively. Haplotypes were mostly homogenous within each sample. Genetic differences between river sites were significant and became even more pronounced at the watershed level. The recolonisation of Western European upland rivers seems to have its origin from the (mostly dry) North Sea basin some 10,000 year ago. Current gene flow between river seems to be limited; dispersal rate within a river system is estimated to be at most only tens of kilometers. Strong territoriality favors speciation in bullhead.

# Differential selection in marine versus estuarine populations of the sand goby, Pomatoschistus minutus

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Coastal communities are highly dynamic while the relatively high fecundity and mortality of marine fish implicates strong selection pressures. Nevertheless, local communities seem stable. We analysed small-scale temporal and spatial genetic structure of *Pomatoschistus minutus* (Teleostei, Gobiidae) in the well-mixed Southern Bight of the North Sea in order to understand their ecological genetics. Sand gobies are an important component of the food web as predators of small invertebrates and prey for larger fish. Samples of *P. minutus* were taken on an offshore - inshore gradient in various seasons. Allozyme polymorphisms on cellulose acetate gel electrophoresis at 16 loci were assessed. In general, spatial differentiation among samples is small and suggests the presence of a single population. This is confirmed by sequence analysis of the control region of mtDNA. However, at certain allozyme loci differences exists between the estuarine and offshore populations. We suggest that differential selection mechanisms in the estuarine and open-sea environment are responsible for the observed allozymatic differences.

### Exploring the tree space with PUZZLE

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The PUZZLE program is a widely used program to infer sequence based phylogenies. we will briefly outline the basic idea behind the puzzle step and then will move forward to illustrate how the program can be used to compute a whole set of plausible trees. thus instead of using the consensus option we analyse all intermediate trees that are generated by the algorithm. we discuss the dependencies of the number of different trees and the length of the sequences as well as the number of species. it can be shown that as sequence length increases puzzle effectively reduces the large search space of plausible trees.

# Genetic differentiation of sympatric ecotypes of whitefish Coregonus lavaretus in lake Femund, Norway

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Lake Femund, Norway, contains several ecotypes of whitefish, Coregonus lavaretus. Deepwater whitefish, river whitefish, and shallow water whitefish can be easily assorted by spawning habitat and gill raker number. We analysed variation in morphological and ecological characters and allozyme loci from 11 different spawning sites to contrast the ecological polymorphism with possible genetic substructuring of whitefish in Lake Femund. Of the individual morphological and ecological characters, gill raker number best assorted the spawning populations. In a hierarchical cluster analysis based on gill raker number, body length and age of fish, four deepwater sites grouped together as well as three samples from or closely related to inlet rivers. On the contrary, shallow water sites were more dispersed. In the allozyme analysis, nine of the 38 enzyme loci were polymorphic at the 0.99 level. The amount of genetic variation was quite similar among localities with H = 0.052 - 0.073. Allele frequencies differed significantly among localities at all polymorphic loci indicating distinct reproductive isolation between spawning sites. UPGMA clustering of pairwise genetic distances grouped samples according to spawning depth and trophic morphology rather than regional proximity. Thus deepwater spawners from both basins grouped together as well as shallow water spawners from the extreme ends of the south basin. On the other hand, adjacent samples differing by their morphology or behaviour were genetically distinct. The two groupings are somewhat different but still the association between genetic differentiation and morphological and life history variables was highly significant. Thus, the morphological differences are not due to phenotypic plasticity within single spawning population as is commonly seen in many other fish species. The possible evolutionary origins of reproductively isolated whitefish forms are discussed.

## Natural bacterial transformation as a mechanism for foreign gene acquisition

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Horizontal gene transfer can occur within and between bacterial species and is thought to foster genetic adaptation and evolution. Natural transformation is the active uptake by a cell of DNA molecules from the environment and the heritable integration of DNA into the cellular genome. Chromosomal DNA transferred by transformation between members of the same species can be integrated by homologous recombination and can lead to exchange of alleles. The necessity of homologous recombination drastically limits the integration of foreign (new) nucleotide sequences. Acquisition of foreign genes would depend on illegitimate recombination events which are rare. We have studied natural transformation in soil bacteria (*Acinetobacter spec., Pseudomonas stutzeri*) considering homologous and illegitimate recombination events. We found a surprisingly high potential for genomic incorporation of foreign gene acquisition of non-homologous stretches of thousands of nucleotides by illegitimate events. Actual foreign gene acquisition was observed. The genetic requirements and the analysis of the underlying mechanisms will be presented. The results will be discussed in the view of gene loss and gene acquisition as key processes in the evolution of bacterial gene clusters and genomes.

# On the independence against the environment uncertainty: the question of staying alive

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Some real objects show a very particular tendency: that of becoming independent with regards to the uncertainty of their surroundings. This is achieved by the exchange of three quantities: matter, energy and information. A conceptual framework, based on both Non equilibrium Thermodynamic and the Mathematical Theory of Communication is proposed in order to review the concept of change in living individuals. Three main situations are discussed in this context: *the passive independence* concerning the resistant living forms (such as seeds, spores, hibernation, ...), *the active independence* concerning the life span of a living individual (let it be an ant or an ant farm), and the *new independence* concerning the general debate of biological evolution.

## The evolution of host plant use in melitaeine butterflies: a phylogenetic analysis

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Plant chemistry is a major determinant of host plant use in phytophagous insects, often dictating the availability of possible host plants. I have investigated the evolutionary history of host plant use in melitaeine butterflies (Lepidoptera: Nymphalidae). There are four speciose genera in the melitaeines, with a total of about 250 species. Many species are mono- or oligophagous on species of plant belonging to twelve families of plants. Of these Scrophulariaceae, Plantaginaceae, Acanthaceae and Asteraceae are the most important. Eleven of the plant families utilized by melitaeines contain iridoid compounds, on which many of the butterflies apparently specialize. Plant species in Asteraceae do not contain iridoids. Using a molecular phylogeny of 80 species, I have attempted to find the ancestral host plant family of the melitaeines and then studied the patterns of host plant colonization in evolutionary time. My results show that a species of Scrophulariaceae was apparently the ancestral host plant and that Asteraceae has been colonized at least three times independently.

# RNA viruses, evolving or merely changing?

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RNA viruses and retroviruses fix substitutions approximately one million fold faster than their hosts. This diversification could represent an inevitable genetic noise, the majority of substitutions being phenotypically neutral. The alternative is to suppose that most fixed mutations are beneficial to the virus allowing it to keep ahead of the host and/or host population. These two scenarios emphasize the two sides of the molecular evolution debate: the former highlights neutrality while the latter puts a premium on positive selection. It will be shown that the relative sequence diversification of different proteins encoded by viral genomes is found to be linear. The examples encompass a wide variety of vertebrate and plant RNA viruses. The smoothness of relative divergence spans quasispeciation following clonal infection, to variation among different isolates of the same virus, to viruses from different species or those associated with different diseases, indicating that the majority of fixed mutations are neutral. This held for both mammalian and plant viruses indicating that adaptive immunity doesn't necessarily shape the relative accumulation of amino acid substitutions. When compared to their hosts RNA viruses evolution is conservative.

# Inbreeding rate at neutral loci linked to deleterious mutations in selfing and full-sib mating populations

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An analytical model based on transition matrices is used to investigate the effect of selection against partially recessive and deleterious mutations on the inbreeding process at a linked neutral locus in selfing and full-sib mating populations. Selection within lines only (type I) and selection equally within and between lines (type II) are considered. It is shown that inbreeding is always retarded by selection type I in selfing lines, the retardation being determined by the recombination fraction between the neutral and selected loci and the inbreeding depression contributed by the selected locus, irrespective of the selection coefficient and dominance coefficient of the mutant allele. For selection type II with selfing and for both selection types with full-sib mating, inbreeding is delayed by selection against mutations of small effects, due to the associative overdominance created at the neutral locus, and accelerated by selection against mutations of large effects, due to the elevated differential contributions between alternative alleles at the neutral locus within individuals and the increased variance in contribution between individuals (for selection type II). The analytical model is extended to multiple fitness loci under selection by stochastic simulations. Using empirical estimates of mutation parameters and inbreeding load in Drosophila, the inbreeding coefficient after 20 generations of full-sib mating under selection type I is predicted to be about 70-90% of the standard value without selection, in agreement with empirical estimates. For species with much larger genomes than Drosophila, linkage is not important and inbreeding is only slightly delayed by selection assuming the same inbreeding load as Drosophila.

# Variation in female morphology influences male sperm competition success in the yellow dung fly

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Female yellow dung flies, Scathophaga stercoraria, normally have three spermathecae, the sperm storage organs in which sperm from several males can be stored for weeks before being used to fertilise eggs. Sperm from different males are stored in different proportions in different spermathecae. This could allow a female to exercise cryptic female choice at egg-laying, when eggs are fertilised, as it is the female which controls the release of sperm from spermathecae. Such female choice would be in conflict to male interests, as a male would have a reduced certainly of paternity if the female released sperm from a spermatheca in which he had low representation. There are always some females in field samples which have four spermathecae. If spermathecae number is related to the degree of separation of sperm from different males, then females with more spermathecae could separate sperm more than could those with three spermathecae. Lines of females were selected for increased spermathecae number. The success of this selection shows that there is genetic variation for this morphological variation. Females with either three or four spermathecae were mated (blindly) to two males of different genotype. The success of the last male to mate, P2, was measured. P2 was similar in all small females but large females with four spermathecae showed a significantly smaller P2 than those with three spermathecae. As high P2 is in the second male's interest, this indicates that a larger number of spermathecae enabled only large females to overcome male adaptations to ensure high P2. The results show that female morphology can influence male mating success, i.e. cryptic female choice occurs in this species, and that the morphology could evolve if selection for increased cryptic choice were sufficiently strong. Why females normally only have three spermathecae will be discussed.

### Sexual conflict over female remating: the role of non-fertile sperm in butterflies

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Females of several butterfly species forage for matings to obtain nutritious male donations which increase their fecundity. Multiple matings by females creates sperm competition, so male investment mays may go to offspring sired by other males. This difference in potential costs and benefits of female remating is a potential source of sexual conflict. Apart from transferring fertilizing sperm, male butterflies also provide females with large numbers of non-fertile sperm (>90% of total sperm numbers), which function to fill the female's sperm storage organ delaying female remating. Here, using the green-veined white butterfly *Pieris napi* (Lepidoptera: Pieridae), I show that the degree of polyandry (number of matings) is also under genetic control. I examine to what extent variation in female mating frequency is related to genetic differences between females in their propensity to store non-fertile sperm. I also examine whether there is a genetic component in the liklihood that a male's non-fertile sperm are stored by females. These results are discussed in relation to female remating propensity.

# Genetic variation in three thelytokous mite species

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Thelytokous parthenogenesis has been labeled an evolutionary dead end because of the inability to produce genetic variation outside mutation. This lack of genetic variation is thought to decrease the rate of adaptive evolution and speciation and increase the rate of extinction. Most thelytokous organisms are known to have arisen from close sexual species and are thought to be short lived on an evolutionary time scale. Despite this, there are organisms where taxa higher than a species consist wholly of thelytokous parthenogens. For instance, the order Bdelloidea of rotifers and the tribe Tramini of aphids contain only parthenogens, while within the Acari there are whole families that are thelytokous.

Here we investigate clonal diversity in three thelytokous mite species (*Penthaleus major*, *Brevipalpus phoenicis*, and *Bryobia kissophila*) from different families within the Acari. All three species are phytophagous, distributed widely throughout the world with *P. major* and *B. phoenicis* being major agricultural pests. Both *Brevipalpus phoenicis* and *B. kissophila* have close sexual relatives, while none have been found for *P. major*. Clonal diversity was investigated using allozymes, RFLP's and sequence analysis of the nuclear ITS region. *Bryobia kissophila* was found to be infected with the intracellular endosymbiont *Wolbachia*. The consequences of this infection on clonal diversity within *B. kissophila* will be discussed. Clonal diversity within populations of *P. major* was high, with fitness estimates obtained from temporal sampling at two sites and manipulated field plots revealing intense natural selection acting on ecologically different clones. The maintenance of clonal diversity within populations of *P. major* will also be addressed.

# Molecular phylogeny of Wolbachia symbionts within four genera of the Tetranychidae

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*Wolbachia* are a group of intracellular vertically transmitted bacteria, which can alter host reproduction in several ways. They are widespread in insects, have been found in isopods and nematodes, and have recently been reported in several mite species. Phylogenetic studies of *Wolbachia* strains have generally used sequences from three different genes: the 16S rRNA gene, the cell-cycle *ftsZ* gene and the surface protein *wsp* gene. The 16S rRNA gene evolves at a slower rate compared to the *ftsZ* gene, which evolves slower than the *wsp* gene. Presently, *Wolbachia* strains are classified into four distinct groups labeled A, B, C and D. Groups C and D include *Wolbachia* strains found only in nematodes where host and *Wolbachia* phylogeny are concordant. The effects of the bacterium in nematodes are unknown. Within groups A and B, *Wolbachia* have been shown to cause cytoplasmic incompatibility, parthenogenesis, feminization and recently male killing strains have been found. No relationship between host phenotype and *Wolbachia* phylogeny has been found in these groups.

In spider mites (Acari, Tetranychidae) *Wolbachia* infections have already been reported in some species from three genera, *Eutetranychus*, *Oligonychus* and *Tetranychus*. Here we report on *Wolbachia* infection in two thelytokous species of the genus *Bryobia* (Acari, Tetranychidae). We have also sequenced the *ftsZ* and *wsp* genes of *Wolbachia* strains found in infected species from each of the four genera of the Tetranychidae. All *Wolbachia* strains were from the B group. Sequence variation in the *wsp* gene is greater than the *ftsZ* gene and allows greater phylogenetic resolution within the B group of *Wolbachia*. *Wolbachia* strains found in the Tetranychidae do not cluster within the B group, indicating polyphyletic origins of the infection within this family. The phenotypic effects of *Wolbachia* within *Tetranychus urticae* and *Bryobia kissophila* will be discussed.

### Predator-induced morphological shift in the pea aphid

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Aphids exhibit a polymorphism whereby individual aphids are either winged or unwinged. The winged dispersal morph is mainly responsible for the colonisation of new plants and, in many species, is produced in response to adverse environmental conditions. Aphids are attacked by a wide range of specialised predators and predation has been shown to strongly influence the growth and persistence of aphid colonies. In two experiments, we reared two clones of pea aphid (*Acyrthosiphon pisum*) in the presence and the absence of predatory ladybirds (*Coccinella septempunctata* or *Adalia bipunctata*). In both experiments, the presence of a predator enhanced the proportion of winged morphs among the offspring produced by the aphids. The aphid clones differed in their reaction to the presence of a ladybird, suggesting the presence of genetic variation for this trait. A treatment that simulated disturbance caused by predators did not enhance winged offspring production. The experiments indicate that aphids respond to the presence of a predator by producing the dispersal morph which can escape by flight to colonise other plants. In contrast to previous examples of predator-induced defence this shift in prey morphology does not lead to better protection against predator attack, but enables aphids to leave plants when mortality risks are high.

# Transmission of mitochondrial DNA variants in the mussel Mytilus trossulus from the Baltic Sea

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Doubly Uniparental Inheritance (DUI) is a rare mode of mitochondrial DNA (mtDNA) inheritance, as oposed to typical maternal inheritance with possible low paternal mtDNA leakeage in animals. Other research revealed that masculine (M) and feminine (F) genomes present in heteroplasmic specimens, which are almost exclusively males, are highly diverged. Rare examples of role reversal of those genomes have recently been reported in the blue mussel. In this study we demonstrate that genomes with low degree of divergency can also undergo the DUI. Gender associated transmission of mtDNA variants of the same size and different length variants from somatic tisues to gametes was demonstrated as a typical mechanism in the Baltic mussel species. Various mtDNA length variants were present in sperm and eggs and were also transmitted from heteroplasmic males. Therefore, various mtDNA types, including length variants are transmitted through female and male lineages. Highly diverged M genome was not found in male somatic tissues and sperm. Its role has been overtaken by variants of the F genome. However, the shortest variant (identified by PCR amplification of the putative major noncoding region) was so far observed only in males.

# Genetic differentiation of the sea trout populations from the Southern Baltic, at the microsatellite level

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Sea trout (*Salmo trutta* m. *trutta*) is an anadromous salmonid species. Its natural populations, reduced by deterioration of environment and damming of rivers in Poland, are supported by stocking activities. The main aim of this work was to study polymorphism of microatellite loci in six populations of sea trout spawning in Polish rivers. Fin clippings were collected from 40 spawners entering each river in 1996. Variation at following microstellite loci was studied: *Ssa*197, *Ssa*SL348, *Ssa*417, *Str*73, *Str*15, *Str*60 and *Ssa*171. Gel electrophoresis in a manual sequencer and silver staining was used for separation and visualization of PCR products. Significant differentiation between the sea trout populations in frequency of microsatellite alleles was observed.

### Multiple QTL control species differences in morphology between wild relatives of maize

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Investigators employing QTL mapping have demonstrate that numerous traits in crop plants are mainly controlled by a relatively small number of loci with relatively high magnitudes of effect. Morphological evolution of domesticated plants is a result of artificial selection and may not, however, provide a good model for evolution under natural selection. To test the significance of the model, we have chosen to analyze the genetic inheritance of morphological traits defining species differences in wild relatives of maize, teosinte (Zea spp.). We are here focusing on the perennial teosinte, Zea diploperennis, and the annual teosinte, Z. mays ssp. parviglumis. Both species are native to southwestern Mexico. They differ in a number of taxonomically important traits and we are here concerned with differences in the morphology of the tassel (male inflorescence). The most evident difference is that the tassels of Z. mays ssp. parviglumis branch much more abundantly and bears smaller male spiklets than those of Z. diploperennis. We used 95 genetic markers and analyzed the association between the marker loci and the traits with interval (IM) and composite interval mapping (CIM). A high number of QTLs (34 QTLs with IM and 39 QTLs with CIM) were found for tassel morphology located on nine different chromosomes. The QTLs showed small to moderate magnitudes of effect. We detected two to seven QTLs for each trait. Multiple QTLs explained about 20% to 50% of the phenotypic variance for a single trait. This study shows that the evolution of morphological differences between plant species under natural selection are controlled by multiple genes. In addition, no QTL of really large effect was found as seen under domestication.

### Junkyard genetics: transposable elements and hidden treasures in the mammalian genome

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Transposable elements that move via an RNA intermediate have the unique property of leaving behind a "molecular fossil record." Along with recently inserted elements, each genome contains older copies that record the history of the transposable element family going back millions of years. In these "fossil" elements, ancestral character states can be directly observed. Rapid evolution of transposable elements relative to other nuclear genes, the ability to directly observe ancestral characters, and the proposed correlation between bursts of transposition and speciation suggest that transposable elements will be useful phylogenetic markers across a wide taxonomic distance. Orthologous elements – elements residing at the same site in the genome as the result of a single insertion event – are also useful for phylogenetic analysis. Both the presence or absence of an insertion at a site, and accumulated chances among alleles at an orthologous site, can be used as phylogenetic characters. Retrovirus-like element are virtually identical at the time of insertion. As the element sits in the genome the LTRs accumulate change, so differences between the LTRs can be used to deduce the age of each insertion. Thus there are at least 4 levels at which transposable elements provide phylogenetic information: 1) presence or absence of a transposable element family; 2) distribution of subfamily-specific markers; 3) presence or absence of elements at orthologous sites; 4) distribution of derived changes in elements at orthologous sites.

I wish to recognize the contributions of many past and current members of my lab. This work was supported by a grant from the National Institutes of Health.

### Comparative genomics - at the crossroads of evolutionary biology and genome sequence analysis

T. Wiehe, M. Burset, + J. Abril, + S. Gebauer-Jung and R. Guigó+

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Large scale genomic sequencing projects provide us with an unprecedented amount of DNA sequence data. Of particular interest to evolutionary biologists are those data emerging from interspecific comparative sequencing, for instance in human and mouse, various species in Drosophila, bacteria and plants. During the past decade the accumulation of data has been accompanied by a rapid development of bioinformatics tools - an indispensable prerequisite for analysis and interpretation of data. Much effort is currently invested into making gene prediction more accurate. Traditionally, gene prediction techniques such as analyzing sequence composition statistics or homology searches with the help of protein or EST databases, are employed. With the launch of projects for comparative genomic sequencing a novel method for prediction of coding regions, complete gene structures and regulatory elements became available. This method utilizes gapped alignments of homologous genomic sequences. The resulting patchwork pattern of conserved and less conserved fragments — the so-called phylogenetic footprint — is the basis for the identification of potentially novel gene structures and regulatory regions. Given such a footprint, further genomic comparison can be performed at various levels: from interspecific homologous chromosomal segments of a length of several Mb down to individual exons or the intraspecific SNP's in homologous introns. In particular, the systematic comparison of splicing patterns and conservation levels of splice sites promises to add some insight into one of the fundamental problems in evolutionary biology: what are the mechanisms creating evolutionary novelty in a genome and what are their relative roles?

### Diversity of Holocene life-forms in fossil glacier ice

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Studies of biotic remains of polar ice caps have been limited to morphological identification of plant pollen and spores. Using sensitive, molecular tecImiques, we now demonstrate a much greater range of detectable organisms; from 2000- and 4000-year old ice core samples, we obtained and characterized 120 clones representing at least 57 distinct taxa, thus revealing a diversity of fungi, plants, algae, and protists. The organisms derive from distant sources as well as the local arctic environment. Our results suggest that additional taxa may be readily identified, and provide a plank for future studies of deep ice cores which doubtless will provide valuable information about ancient communities and their changes over time.

# Detailed mtDNA phylogeny of seahorses and their relatives: Inferences on the evolution of male brooding structures

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The seahorse brood pouch represents the most advanced stage of male parental care in the animal kingdom. The high diversity of brooding structures observed in the Syngnathidae (seahorses and pipefishes) ranges from a simple attachment of eggs onto the male's trunk (ie. Nerophis) to the highly derived sealed pouch observed in true seahorses (*Hippocampus*). Although this diversity has made brood pouch structure a key character in morphological-based phylogenies, a detailed understanding of the relationship between pouch morphology and systematic relationships among seahorses and their relatives remains unclear. We present data from 12S, 16S, and cytochrome b mitochondrial genes from 40 species of pipefishes and seahorses, representing the most extensive molecular study of the group to date. We map brood pouch morphology on a consensus phylogenetic tree produced from the mtDNA data to search for genetic evidence supporting the evolutionary significance of pouch structure. Molecular evidence indicates that the diversity of brooding structures observed in the Syngnathidae reflect independent lineages, suggesting that increasing structural complexity of the male brood pouch has been highly coupled with the evolution of the group.

Quantitative geneties of life history and morpliological traits in a recently established population of the Speckied Wood Butterfly *Pararge aegeria*,

### Jack J. Windig

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Two processes may influence the genetic architecture of a species when colonising a new area. (1) Colonisation may involve a bottleneck, which generally decreases additive genetic vanation, although dominance variance may be converted into additive variance. Natural selection may play an important role if the environment in the new area is different from that for the source population. The Atlantic island of Madeira was colonised by the Speckled Wood Butterfly in the second half of the seventies. Natural selection on life history traits probably has been intense after introduction, since it was the first time that the, species experienced a non-seasonal environment. In a 3-generation laboratory experiment we analysed the quantitative genefics of this Madeira population. 22 Wild caught fernales produced 19 full sib families in generation 2 and 27 full sib families in generation 3. This data set was analysed with Restricted Error Maximuni Likelihood-analyses. Traits thought to be under natural selection had low amounts of additive variance, but high amounts of dominance variance (up to 100%), while some morpliological traits had moderate amounts of additive variance.

## Density dependent competitive interactions set limits to Fisher's fundamental theorem of natural selection

### Lars Witting

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The relationship between Fisher's fundamental theorem of natural selection and the ecological environment of density regulation is examined. It is shown that the theorem holds when density regulation is caused by exploitative competition, and that the theorem fails with interference competition. In the latter case the theorem holds only at the limit of zero population density and/or at the limit where the competitively superior individuals cannot monopolise the resource. The results are discussed in relation to population dynamics and life history evolution, where evidence suggests that the level of interference competition in natural populations is so high that the fundamental theorem does not apply.

### Selection by density dependent competitive interactions explains major life history transitions

### Lars Witting

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During evolution on Earth there has been a directional change where simple self-replicators have evolved into large organisms with high metabolic rates and complex behavioural interactions. Associated with this increase there has been a transition from an asomatic, non-senescing, haploid, and asexually reproducing organism to a somatic, senescing, diploid, and sexually reproducing organism with male and female individuals. In a few special cases there has been an additional transition to eusocial communities. It is explained how selection by density dependent competitive interactions can explain all these life history transitions.

### Single-locus control of a continuous phenotype: Esterase activity1n e flour beetie Tribollum castaneum

### David Wool, Talia Agami and Lilach Front

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Quantitative measurements of esterase (EST) activity in individual flour beefles revealed considerable, continuous phenotypic variation within a single strain, suggesting polygenic: inheritance. Narrow-sense heritability estimates from offspring-parent regression were around 0.45. Family selection for high H) activity was successful and mean EST activity increased 8-fold in 5 generations, remaining stable for 3 more generations. Selection for low (L activity was unsuccessful and mean activity increased instead. Hierarchical ANOVA indicated that differences in EST activity among families were mairfly due to the male parent (dams mated to the same sire did not add significantly to offspring variance). Electrophoretic examination of individuals from the source strain and the H and L lines showed that only one of 5 EST isozymes had greatly enhanced staining intensity in H individuals, while the other isozyraes remained unchanged. This suggests that a change at only one locus controls the phenotypic variation in activity. AU individuals in the H line, now 2 years after the termination of selection, show uniformly the electrophorefically high-intensity isozyme, while the source and. L fines contain weak-staining individuals also. Two generations of family selection for carriers of the weak-staining isozyme resulted in a pure-breeding, low-activity strain. Crosses and back-crosses indicate that the low-activity allele is autosomal and there is no indication for sex-limited inheritance. We demonstrate that variation at a single locus presumably combined with non-genetic differences among individuals - can produce a continuous phenotypic distribution of enzyme activity within a population.

### PLENARY LECTURE

# The genetics of speciation: a molecular perspective

### Chung-I Wu

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We ask three questions: 1) How different are closely related species at the genic level? 2) What may be the molecular nature of these differences? 3) What forces drive the divergence of these genes? In a series of studies by chromosome-segment introgressions, we have found that the genetic differences between closely related species can be very extensive, more than 120 loci for spermatogenesis alone between sibling species of Drosophila. In the search for the Odysseus (Ods) locus of hybrid male sterility in Drosophila, we have recently identified an unusual homeobox gene at the exact expected site of Ods and named this new gene OdsH (Ting et al. 1998 Science 282: 1501-1504). Although this is the only gene of reproductive isolation cloned so far, it has provided valuable information on the nature of species divergence. In the last half a million years, the homeodomain of OdsH in Drosophila has experienced more amino acid substitutions than in the preceding 700 million years. We hypothesize that the rapid evolution may be the consequence of the acquisition of male germline functions which would then provide the opportunities for sexual selection to operate. The results are consistent with the view that genes pertaining to male reproduction often evolve rapidly, potentially contributing to the evolution of hybrid male sterility. Two new lines of observations will be discussed: i) Gene duplication leading to the formation of the OdsH locus and the subsequent functional diversification; ii) Speciation history at this locus of speciation vis-a-vis other gene regions chosen randomly from the genome. The constrast in these two type of loci is germane to the concept of species.

## A historical analysis of a human commensal yeast

### J. Xu, T. G. Mitchell and R. Vilgalys

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The diploid asexual yeast *Candida albicans* resides as a commensal in most, if not all, healthy people. It is the most common fungal pathogen of humans, particularly prevalent among immunocompromised individuals. In this study, we examined the effects of host geography, ethnicity and disease conditions on the patterns of genetic variation in *C. albicans*. Altogether, twelve geographic samples of *C. albicans* from the major human racial groups were assayed for 16 polymorphic restriction endonuclease recognition sites on nine arbitrary PCR fragments. Preliminary analyses indicated the following: (1) on average, higher genotypic diversities were observed among samples from the Old World than those from the New World; (2) there were lower levels of genetic differentiation among geographic samples originating from the New World than those from the Old World; (3) both disease condition and ethnicity of the host contributed to the overall levels of genetic variation; and (4) different patterns of allelic association were found among geographic samples. Possible mechanisms will be presented to explain the observed patterns of genetic variation within and between *C. albicans* populations.

# Genetic Diversity, Population Structures, and Phylogenetical Study of Tree Species in Tropical Forests in South East Asia

### Tsuneyuki Yamazaki

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Little information is available about the genetics of tree species in tropical forests. As the first step toward this objective, we have studied trees species in South East Asia including Dipterocarpaceae and Mangrove trees. To obtain molecular phylogeny of dipterocarp species, nucleotide sequences of the *mat*K gene, intron of *trn*L, and intergenic spacer region between *trn*L and *trn*F in chloroplast DNA were determined in 16 species throughout 10 genera. In the resultant trees, Southeast Asian dipterocarp species were divided into two clusters. One cluster consisted of *Anisoptera*, *Vatica*, *Cotylelobium*, and *Upuna*, and the basic chromosome number of this group was x=11. The other consisted of *Hopea*, *Shorea*, *Neobalanocarpus*, *Dryobalanops*, *Parashorea*, and *Dipterocarpus*, most of this group had the basic chromosome number x=7. This result was different from what was expected from classical taxonomy, suggesting that the chromosome number changed from x=11 to x=7 after *Dipterocarpus* branched in the latter cluster. The amount of genetive diversity of several species of Shorea was also estimated to be about 0.002 per site, with the selfing rate of over 50% in regions of gapC, a nuclear gene. Population structures of these inland trees are also discussed in comparison with those of a mangrove tree, Bruguiera gymnorrhaiza.

## Models of codon substitution and detecting adaptive molecular evolution

### Ziheng Yang\* and Rasmus Nielsen

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As synonymous (silent) and nonsynonymous (amino acid-altering) mutations are under quite different selective pressures, comparison of their fixation rates often provides inportant insights into the evolutionary process of the gene. For example, a higher nonsynonymous (dN) rate than the synonymous (dS) rate is a good indicator for diversifying selection. We have developed Markov models of codon substitution to examine variable dN/dS ratios among lineages, which may be due to adaptive evolution or relaxed selective constraint along certain lineages. Likelihood ratio tests are also constructed to test for variable dN/dS ratios among sites, which are useful for inferring amino acid sites under positive selection and for studying the distribution of fitness effect of new mutations.

### Parasitic castration, ant-plants and the habitat destruction hypothesis

### Yu, Douglas W., Wilson, Howard W., Pierce, Naomi E.

### Imperial College at Silwood Park, Ascot, Berks, England

There is little empirical support for the hypothesis that species can coexist solely via a competition-colonisation tradeoff. Here we describe a Neotropical ant-plant symbiosis which is ideally suited for testing spatial models of coexistence. Two genera of ants, *Allomerus* cf. *demerarae* and three species of *Azteca*, are specialized to live on a single species of ant-plant, *Cordia nodosa*, in a Western-Amazonian tropical rain forest. We parameterise a new model of species coexistence, using census data taken across widely separated localities, and show that *Allomerus* and *Azteca* can coexist via tradeoffs in their use of space. Our analysis extends the Habitat Destruction Hypothesis by showing empirically how the spatial *pattern* of habitat destruction can interact with the *amount* of destruction to produce not only non-random extinctions, but also invasions and coexistence. As *Allomerus* is a castration parasite of its host plants, this study further suggests that a spatially structured approach is essential in understanding the persistence of some mutualisms in the presence of cheats.

Molecular zoogeography of Antarctic marine organisms: from species phylogenies to intra-specific patterns of genetic variation.

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Antarctic waters represent a unique marine environment delimited by an oceanographic barrier, the Polar Front Zone, and characterized by constant subzero temperatures and presence of sea ice. The complete isolation of these waters became effective after the establishment of the Polar Front, 25-22 million years ago. The Polar front, extending to a depth of 1000 m, is considered an effective barrier to dispersal of Antarctic marine organisms that could instead be extensively dispersed within the Southern Ocean by a system of strong circumpolar currents.

Krill (Crustacea, Euphausiacea) and notothenioid fish are two key groups of the Antarctic marine environment. The first in fact represents the key resource for food in the Southern Ocean, whereas the seconds are the most important components of the fish fauna, and show a remarkable degree of endemism.

We investigated these two groups both at the inter-specific than at the intra-specific level. We produced molecular phylogenies for 11 species of krill and for 33 species of notothenioids, by sequencing mitochondrial genes. The inclusion in these phylogenies of sub-Antarctic species allowed us to understand the vicariant role of the Polar Front in the speciation process of these organisms and to understand its effectiveness as a barrier to dispersal. We also analyzed the genetic differentiation of the Antarctic krill (*Euphausia superba*), and of two nothenioids, *Pleuragramma antarcticum* and *Chionodraco spp*, by sequencing a portion of the NADH dehydrogenase gene and a portion of the control region, respectively. The pattern of fish genetic variation seems to mirror the traditional separation in two biogeographic regions (East and West Antarctic provinces), whereas the more dispersed *E. superba* shows both spatial than temporal genetic differentiation.

Krill species(Crustacea, Euphausiacea) are key resources for food in the marine food web. Krill often occupy wide distribution ranges, extending from part of oceanic basins to entire oceans; that are broadly overlapping despite the species equivalent ecological role. In subantarctic-antarctic area several species of the Euphausia genus shows slight difference in the southern limit of distribution. Here we test the hypothesis whether the present day distribution is the result of past speciation events, occurring along a North-South (climatic?) gradient. We analyzed eleven species of krill, including all the antarctic and two subantarctic Euphausia species. By sequencing and analyzing 500 base pairs of the 16S mitochondrial gene we reconstructed the phylogenetic relationship between species. Our result strongly suggest that speciation events in the Euphausia species considered

Estimating rates for sister chromatid exchange in rDNA genes of *Drosophila melanogaster* – a computer simulation approach

### B.Zangerl & Ch. Schlötterer

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Concerted evolution in rDNA sequences can be explained by two mechanisms; gene conversion and recombination. Experimental data on *Drosophila melanogaster* show almost perfect homogenisation within, but not necessarily between homologous rDNA arrays, suggesting that exchange primarily occurs between sister chromatids. We used computer simulations to infer rates of sister chromatid exchange for data on nucleotide polymorphism of the ITS 1 and ITS 2 regions of *Drosophila melanogaster*. Simulations with chromosomal exchange rates that are at least three orders of magnitude greater than those obtained from experimental data yielded homogenisation levels fitting empirical values. As these rates seem high for meiotic exchange, sister chromatid exchange may occur during meiotic and mitotic cell divisions.

# Phylogenetic relationships of cichlids based on mitochondrial and nuclear sequence data: heterogeneity of evolutionary rates among cichlid lineages

### Rafael Zardoya and Ignacio Doadrio

### Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal, 2, 28006 Madrid, Spain

The flanking regions of a (CA) microsatellite nuclear locus (TmoM27) were analyzed with maximum parsimony (MP) and neighbor-joining (NJ) to infer the phylogenetic relationships within the suborder Labroidei and, in particular, among the main lineages of cichlid fishes. The TmoM27 data suggest that (i) the Madagascan+Indian cichlids form a paraphyletic group and are basal in the monophyletic family Cichlidae; (ii) the Neotropical cichlids and the African species are monophyletic sister groups; (iii) the West African lineages are likely to be paraphyletic and basal to the presumably monophyletic East African Lineages. The nuclear evidence is in complete agreement with morphological (Stiassny 1991) and mitochondrial (Farias *et al.* 1999) evidence. The phylogenetic relationships inferred for the family Cichlidae are consistent with a Gondwanan origin of cichlids. Further analyses of the nuclear data revealed that the size and composition of the microsatellite contained in the TmoM27 locus is variable in the different groups. TmoM27 and cytochrome b data of Central American lineages suggest that evolutionary rates are quite heterogeneous among different cichlid groups. East African and Central American lineages suggest that evolutionary rates are quite heterogeneous among different cichlid groups. East African and Central American lineages suggest contained in the theorem of the minimal sequence divergence (because of rapid adaptive radiation events) whereas West African, South American and Madasgan cichlids exhibit a higher amount of genetic variation.

## Microsatellites with large repeat number: Variability and utility as molecular marker

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Microsatellite sequences have been widely used as diagnostic markers in population genetics, conservation genetics and ecological studies. Most microsatellite loci employed have a repeat number smaller than 30 units. Longer microsatellites, though not much employed in genotyping analysis, do exist in many genomes. How polymorphic are long microsatellites in population? How useful are they as molecular marker to study genetic variation? We have isolated some extremely long microsatellite sequences in two gadoid fish species, with some possessing over 150 repeat units. In this report, we will discuss some characteristics of these long simple repeat sequences.

## Eyespotsize and Development time in Bicyclus anynana: Never tear us apart?

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The tropical butterfly *Bicyclus anynana* exhibits seasonal polyphenism. In the wet season, induced by high temperatures, the butterflies are conspicious with large eyespots. In the dry season (low temperatures), they rely on camouflage and eyespotsize is reduced. Wet-seasonal animals have an environmentally induced shorter development time than dry-seasonal forms. In the laboratory, when rearing at one temperature, the same phenotypic relation between wingpattern and development time is observed. Moreover, artifical selection on the ventral hindwing eyespot reduced development time in the upwards selected lines, and increased development time in the downward selected lines. Artificially selecting on development time showed similar correlated responses. Fast and slow selected lines tended towards wet and dry season forms, respectively.

In this project, we are examining the apparent coupling between life history and development, through (ant)agonistic selection on development time and eyespot size. Selection has been applied for seven generations at an intermediate temperature. How constrained is the response to selection? Can we obtain, for example, butterflies that develop slowly, yet have large eyespots? Preliminary data for all selection lines show a larger response to selection on eyespotsize than for development time. Results will be discussed with regard to evolutionary constraints and the experimental design.

### Doubly Uniparental Inheritance of mitochondrial DNA: proximal and ultimate causes

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The transmission of mitochondrial DNA (mtDNA) in mussels is profoundly different from that in other metazooans and defy uniparental transmission of organelle DNA, which is the general rule in all eukaryotes. In mussels there exist two distinct types of mtDNA (the F and M) that have different tissue distribution routes of transmission, and rates of evolution. The F lineage behaves as the standard animal mtDNA, except that it is basically absent from the male germ line. The M type is the only or main resident in the male germ line and its presence in other tissues is negligible. It evolves much faster than the F. The term doubly uniparental inheritance (DUI) was adopted to underline the coexistence in the same species of two uniparentally transmitted mtDNA molecules. The mussel is also noticeable because of its mother-controlled sex ratio (SR), that may vary from almost zero males to 90%. DUI and female-controlled SR are, most likely, manifestations of the same phenomenon. Sperm mtDNA (i.e. the M mtDNA) enters the egg, but whether it will take residence or will be lost is determined within the first hours after fertilization. It remains unknown whether in males-to-be embryos it is the maleness of the embryo that determines the fate of the M mtDNA or it is the M's escape from elimination that induces maleness. Another feature of DUI is "masculinization", i.e. the role-reversal of the F molecule. When the M molecule becomes a minority within a male gonad (or is fully eliminated), the F assumes its role, finds itself in the sperm and behaves as M thereafter. As a result, there exist in populations mtDNA molecules whose sequences are very similar to F but whose function and transmission are those of M. Rates of substitution of old M types by newly F-derived types must play an important role in geographical differentiation, phylogeny and mtDNA evolution in mussels

# Positive Darwinian selection in Vipera ammodytes Kunitz-type inhibitor multigene family

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The venom of the long-nosed viper (*Vipera ammodytes*) contains several different non-toxic BPTI homologues. In order to study the molecular evolution of this multigene family the cDNA and genomic libraries were screened with the PCR amplified coding region of chymotrypsin inhibitor. Trypsin and chymotrypsin inhibitor cDNAs were sequenced. The length of the signal peptide was 72 bp encoding 24 amino acids. Comparison of the available signal peptides from Elapide snakes (1) tx K, BI chain of P-Btx and B2 chain of P-Btx) and *Vipera ammodytes* BPTI homologues show high conservation. The coding region of cDNAs are 195 bp long, encoding 65 amino acids long mature protein fóllowed by C-terminal extension of 12 bp encoding 4 amino acids. The 3'UTR region is 111 bp long. We isolated five different BPTI homologue genes from the *Vipera ammodytes* genomic library. Three of them. code for chymotrypsin inhibitor one codes for trypsin inhibitor and one is a pseudogene. All the genes posses the same structural organisation and are approximately of the same size. Comparison of the *Vipera ammodytes BPTI* multigene family has shown up to 93 % conservation of all introns, which is considerably more than the mature protein coding exons. The nucleotide substitution in protein coding exon occurs preferentially on the first and the second position of codons indicating positive Darwinian selection. In the last intron the truncated CR-1 LINE element was found in all genes.

# Genetic basis of body size variation in *Drosophila melanogaster*: evidence for epistasis in chromosome substitution lines.

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Body size is an important fitness related trait. As for most quantitative traits (QT), the detailed genetic basis is poorly understood. However, quantitative trait loci (QTL) found for many traits in a diverse range of species has shown that the infinitesimal model for the genetic basis of QT is incorrect. The implications of this finding has important consequences for theoretical models on the evolution of fitness and fitness traits. Moreover, the roles of additive, dominance and epistatic variation in the maintenance of genetic variation and in evolution in general are still debated. Here we report on genetic variation in Drosophila melanogaster lines selected for divergent wing area for 27 generations. Realised heritabilities over the first 13 generations were about 0.6 for females and 0.5 for males, both for lines selected for increased (L) and decreased (S) wing area. In the L line the increase in wing area is solely the result of an increase in the number of cells. In the S line, the main response in wing area is due to a reduction in cell size. In addition, a minor reduction in cell number is reported in the S line, which is significant only in males (8% reduction). Isogenic lines for the first, second and third chromosome were constructed and the means of these lines per selection treatment were identical to the means in the last generation of selection. One healthy isogenic line per treatment was picked and two sets of chromosome substitution lines (CSL) were made: chromosome one, two and three were individually placed in the isogenic control background for the L and S isogenic line. For these CSL, the wing area and cellular basis were determined. For both sets of lines, analysis indicated that nearly all the wing area differences with the control line acted additively between the chromosomes. The same applies for the cellular basis for the L lines and females of the S lines. In contrast, for the S line males, only 50% divergence between small and control isogenic lines for cell size was recovered. This was largely the result of the observation that the S chromosome three alone in the control background showed a relatively small reduction in cell size but a cell number reduction bigger than the difference between complete isogenic small and control line. This strongly implicates epistatic suppression of cell number variation on chromosome three by chromosomes one and/or two. These findings are discussed in relation to body size evolution along latitudinal clines and in laboratory populations of Drosophila melanogaster.

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