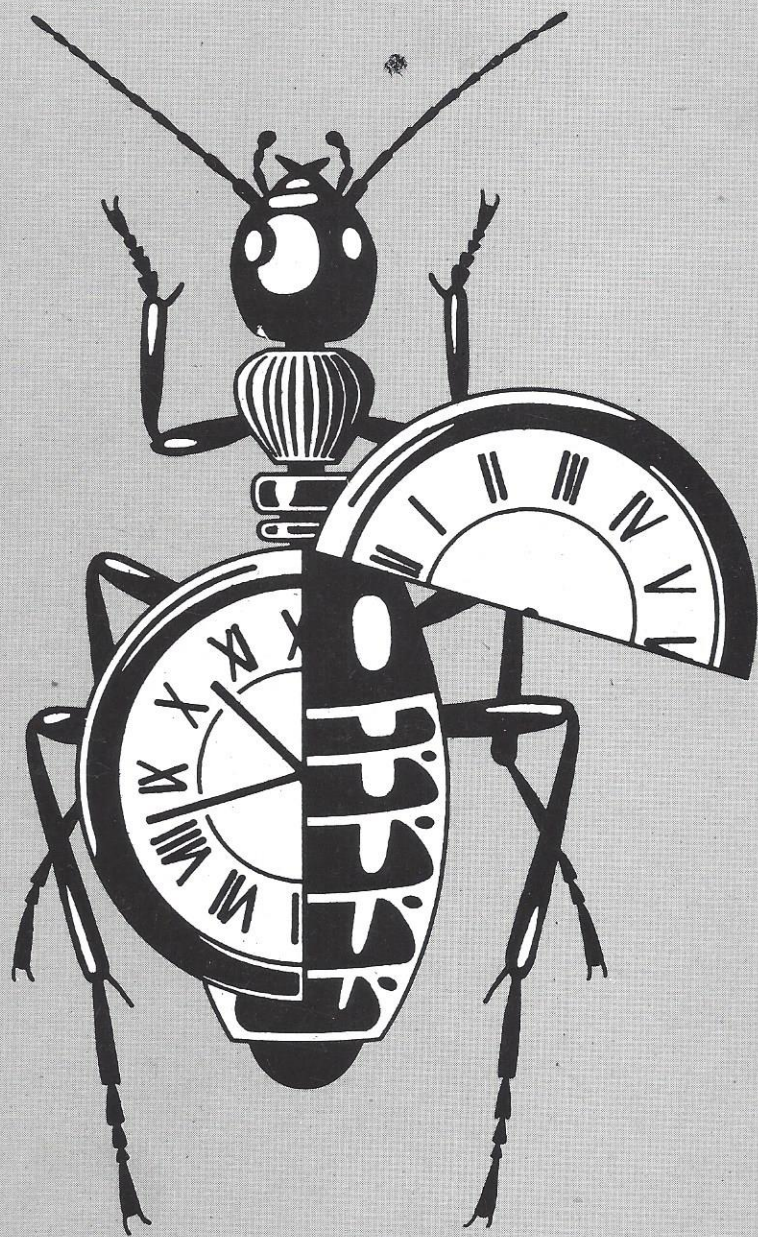


EVOLUTIONARY BIOLOGY



SECOND CONGRESS
EUROPEAN SOCIETY
FOR EVOLUTIONARY BIOLOGY
ROMA, 25/29 SEPTEMBER, 1989

ABSTRACTS

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2nd CONGRESS OF EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY

Roma, Italy, 25-29 September 1989

Roma, 1989

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2nd CONGRESS OF
EUROPEAN SOCIETY
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Congress organizer: Valerio Sbordonì
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via Orazio Raimondo, 00173 Roma, Italy

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Organizing secretariat: Studio EGA srl, viale Tiziano 19, 00196 Roma, Italy

LEGENDA

L = Plenary lecture

S = Symposium

- S1 Natural selection in the wild
Organizer: A.J.Cain (Liverpool)
- S2 The *Drosophila obscura* group: a paradigm in evolutionary genetics
Organizer: D.Sperlich (Tübingen)
- S3 Plant population biology
Organizer: P.Jacquard (Montpellier)
- S4 Molecular phylogenetics
Organizer: J.R.Powell (New Haven,CT)
- S5 Conservation biology: a population biological approach
Organizer: V.Loeschcke (Aarhus)
- S6 Reaction norms: evolutionary, ecological and general significance
Organizer: S.C.Stearns (Basel)
- S7 The biological bases of homology and their phylogenetic implications
Organizer: G.P.Wagner (Wien)
- S8 Evolutionary genetics of human populations
Organizer: G.Modiano (Roma)

W = Workshop

- W1 The evolutionary significance of hybridization in nature:
byproduct or process ?
Organizers: G.M.Hewitt (Norwich) & L.Bullini (Roma)
- W2 Paracentric inversion polymorphisms: problems of analysis
and interpretation in different taxa
Organizer: M.Coluzzi (Roma)

C = Contributed paper

- C1 Behavioural and community ecology
- C2 Population structure and mating systems in plants
- C3 Geographical variation: patterns and methods of analysis
- C4 Sexual selection
- C5 Plasticity and reaction norms
- C6 Parasites and evolution
- C7 Life history evolution
- C8 Theory in population genetics and evolution
- C9 Ecological genetics
- C10 Molecular evolution and mobile elements
- C11 Speciation and isolating mechanisms
- C12 Homology, development and systematics
- C13 Manifold approaches to taxonomy and phylogenetics

P = Poster

- P1 Cytogenetics and molecular genetics
- P2 Molecular evolution
- P3 Molecular and other approaches to systematics
- P4 Speciation and isolating mechanisms
- P5 Geographical variation
- P6 Genetic variability
- P7 Population structure and plasticity in plants
- P8 Sexual selection and mating systems
- P9 Ecological genetics
- P10 Quantitative genetics
- P11 Life history evolution
- P12 Parasites and evolution
- P13 Miscellaneous

ABSTRACTS

103-21201

Editorial note: The majority of the abstracts in this volume have not been edited by the Organizers and are presented as received. A few abstracts were retyped because they were submitted in an incorrect format.

THE RELATIONSHIP BETWEEN MORPHOLOGICAL VARIATION AND GENETIC DISTANCE IN NEREIS DIVERSICOLOR AND N. SUCCINEA (ANNELIDA, POLYCHAETA)

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Nereis diversicolor, like many other brackish water species shows a high degree of morphological variability, a characteristic which has been noted by many Authors. By using the number of paragnaths on the proboscis as a discriminating character, they have recognized significant phenotypic differences among populations.

This paper compares three N. diversicolor populations in their morphological and genetic differences by using the degree of distance between N. diversicolor and N. succinea as a reference for measurement.

The morphological characteristic chosen for observation was the distribution of buccal tube paragnaths. Roughly one hundred individuals from each population were examined by counting the number of paragnaths present in each single area of the proboscis. Data were analysed by Tukey's test to verify the significativity of the differences among the populations; these differences are summarized in a dendrogram.

Genotypes were analysed by electrophoresis. Allelic frequencies in 17 loci were studied in N. diversicolor and 21 loci in N. succinea. Using these data Nei's identity and distance indices were calculated. A dendrogram was constructed using the resulting genetic distance index values.

Comparison of the two dendrograms reveals a high degree of correspondence between the genetic and morphologic differentiation levels, indicating that the morphological parameter chosen is a highly suitable phenotypic means of expressing the degree of genetic differentiation reached by the populations.

FEMALE PREFERENCES OF LEKS AND MALES IN THE BLACK GROUSE

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The basic assumption for the evolution of lekking behaviour is that males increase their mating success by joining each other. To test this we compared simultaneously leks of different size, and in fact the average mating success of males increased markedly with the size of the lek. The distribution of males conforms to the ideal free distribution with unequal competitors, contradicting the predictions of the hotspot model. Neither is it likely that leks would evolve as assumed in the hotspot model, since also the top males gain from the presence of subdominant males. Female preference of larger leks to facilitate mate choice is likely to be the most important factor for the appearance of leks in this species. Females use several days in sampling the males within a lek, and prefer to mate with the males that are most successful in male-male interactions. The top males are the ones that can, through active fighting, keep other males furthest away while females visit their territories. The continuous fighting may well work as a test of the viability of the male. The modest tail ornament has a slight positive correlation to the male mating success, and a negative correlation to the load of intestinal parasites.

THE INFLUENCE OF MALE PLUMAGE COLOUR ON FEMALE MATE CHOICE IN THE PIED FLYCATCHER FICEDULA HYPOLEUCA

Rauno V. Alatalo and Arne Lundberg

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Dept. of Zoology, Uppsala University, Sweden

The importance of female choice for the evolution of male secondary sexual characteristics is controversial. We performed two field and one laboratory experiment, using the pied flycatcher Ficedula hypoleuca, to test the female choice aspect of sexual selection. Observational data suggest a slight preference for dark males by females but in field experiments when we presented males with territories at random sites (no choice of a territory) or altered male colour of concurrently arriving males, we found no preference for darker ones. Similarly, estradiol-treated females did not show a preference for black or brown males in the laboratory. Thus, there is very little support for the idea that female choice has been an important mechanism in the evolution of sexual dichromatism in the pied flycatcher.

PHYLOGENY OF DOLICHOPODA CAVE CRICKETS: A COMPARISON OF scDNA HYBRIDIZATION DATA WITH ALLOZYMES AND MORPHOMETRIC DISTANCES

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Dolichopoda cave crickets are currently the object of extensive research in our laboratory aimed at elucidating patterns of adaptation, population divergence and speciation by means of several approaches. In this paper we attempt to investigate relationships between the amount of genetic divergence at nuclear genes, and the degree of morphological differentiation at different sets of characters.

Eight populations belonging to five Dolichopoda species from Central and Southern Italy have been studied. The overall genetic divergence at nuclear genes was estimated both by scDNA-DNA hybridization and allozyme frequencies at 21 loci. Euclidean distances have been obtained for two multivariate sets of morphometric variables used as descriptors of body and appendage morphology and the male epiphallus shape, respectively. Results showed a close agreement between the branching patterns of ΔT_m values from DNA hybridization and Nei's allozyme distance values. Both these variables were positively related to the available data on postzygotic isolation estimated by the frequency of viable progenies from hybridization tests in the lab. On the other hand, patterns of morphological divergence showed independent trends, and of the two character sets considered only the epiphallus morphology matched at some extent with the phylogenies inferred from molecular data.

Implications of these findings on the geographic speciation theory and the calibration of molecular clocks are discussed.

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The three different approaches to the estimation of the role of selection and overdominance in maintaining allozyme polymorphism are considered:

1. The analysis of the stationary distribution of allelic frequencies;
2. The comparison of the genotypic distributions at early and late developmental stages in subsequent generations of the same population;
3. The analysis of the joint variability of monogenetic and polygenic traits.

The arguments are presented in favour of an important role of balancing selection in maintaining biochemical polymorphisms in natural populations. The adaptive advantage of heterozygotes can be discovered only in suboptimal environment.

It is concluded that allozyme polymorphism is not a transient phase of molecular evolution (as it follows from the neutral theory) but is the universal adaptive strategy of nature providing for stability and integrity of native populations.

The hypothesis of historically formed optimal level of heterozygosity as a measure of maximum population fitness is grounded.

The mechanisms of maintaining this optimum are:

- a) selective mating and other types of adaptive behavior;
- b) subdivision of the total population to semiisolated groups;
- c) limitation of random genetic segregation;
- d) different types of balancing or cyclic selection;
- e) population physiological homeostasis.

W1

TWO HYBRID ZONES BETWEEN ORCHIS MORIO AND ORCHIS LONGICORNU: PATTERN AND DIFFERENCES

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Hybrids between *Orchis morio* and *O. longicornu*, named *O. x cortesii*, were detected in southern Corsica and Sicily. A genetic analysis of these two areas was carried out by means of 4 enzyme loci found diagnostic between allopatric populations of *O. morio* (from continental Italy) and *O. longicornu* (from Sardinia). In southern Corsica and Sicily both *O. morio* and *O. longicornu* specimens were found, together with F_1 hybrids and various recombinant and introgressed genotypes, estimated by genetic index scores. This indicates a complete interfertility between the two taxa. The hybrid zone in southern Corsica appears geographically quite restricted, with *O. longicornu* confined at the extreme southern edge, while *O. morio* is widespread throughout the rest of the island. The center of the hybrid zone apparently coincides with the border between the miocene calcarean Bonifacio plateau (formerly connected with Sardinia) and the surrounding granitic substrate. Along this border the genotype distribution changes significantly over a distance of 100m. In Sicily, hybridization and introgression is much more extensive. No pure populations of either *O. morio* or *O. longicornu* were detected, the proportion of recombinant genotypes always being of at least 50%. The highest levels of hybridization were found in samples from the Etna and Nebrodi mountains, apparently an area of secondary contact between *O. morio*, that would have spread from Calabria, and *O. longicornu*. The wider hybrid zone in Sicily than in Corsica might reflect a more prolonged contact between the two species in the former island. It also seems to be related to the higher habitat alteration by man and volcanic activities in Sicily. Differences were found between loci in the extent of penetration of one species' alleles into the other's genome, possibly due to different selective pressures.

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Up to the present only a few studies based on morphological characters have dealt with the evolution of Eurasian frogs.

In the present study an electrophoretic and cytogenetic survey was carried out on Iberian brown frogs in order to assess the amount of genetic differentiation among them, as well as their phylogenetic relationships. For this purpose, several populations were sampled: 4 corresponding to *Rana temporaria*, 3 to *R. iberica* and 1 to *R. dalmatina*.

The electrophoresis results show that the northwest populations of *R. temporaria* have achieved the highest degree of polymorphism, while *R. iberica* and *R. dalmatina* show very little variation. The cytogenetic analysis, based on C-banding and fluorescent banding techniques, has shown an interpopulational differentiation between northwest and northeast populations of *R. temporaria*. This result is congruent with the results of the allozyme analysis.

Finally, based on both data sets, the evolutionary relationships among these populations are discussed at an inter and intraspecific level.

P8

SEXUAL SIZE DIMORPHISM IN THE GREAT TIT (*Parus major*) WITHOUT CONGENERS.

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The magnitude of sexual size dimorphism is dependent on the number of coexisting congeners, being more pronounced in places with few competitors (Ebenman 1986, *Oikos* 47: 355-359). Therefore, we would expect in places without congeners an increase in sexual size dimorphism. In the orange plantations of Sagunto (Valencia, Spain) close to the Mediterranean shore-line the Great Tit is the sole species of the genus *Parus*. In these groves we have measured the same morphological characters in similar samples of both males and females as in Ebenman's study: wing length, tarsus length, bill length, bill width and bill depth. Both males and females of the Sagunto Great Tit show a smaller wing length in comparison with the Swedish populations, the bill length is similar and the other characters show a greater dimensions in the Sagunto population. Furthermore, although sexual size dimorphism of wing length is maintained the remaining four characters show no differences between the sexes, and do not fit Ebenman's hypothesis.

C3

THE USE OF SPATIAL AUTOCORRELATION IN ANALYZING GENE FREQUENCY DATA

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Spatial autocorrelation analysis is a widely used technique to analyze spatial patterns in geography. For some time, the method has also been used in population genetics on gene frequency data with the aim of drawing inferences about processes acting on populations. In such studies, the main purpose of applying spatial autocorrelation statistics is to find non-random patterns which should point to gene flow, selection effects or historical occurrences.

Simulation studies with selection, mutation and gene flow acting in sub-populations show that the variation is high between alleles which have undergone the same processes. Therefore, spatial autocorrelation statistics on the gene frequency data does not allow the estimation of the amount of gene flow in the simulation. These findings restrict the application of the spatial autocorrelation technique in population genetics to a limited range of problems.

C1

DO PLANTS PLAY DEFENSE GAMES?

Magnus Augner, Torbjörn Fagerström, Juha Tuomi

A game theoretical model on the coexistence of defended and undefended plants, i.e. anti-herbivore defense, is constructed. The model consists of a two-strategy game, played between relatives, where inclusive fitness is included. A mixed ESS, in the form of an evolutionarily stable polymorphic state for the population, is possible, even when the players are unrelated. This mixed ESS corresponds to a coexistence of defended and undefended plants. As relatedness increases the possibility for such a coexistence increases. The cause for this is kin selection. Thus, environmentally mediated interactions between plants may be dynamically important in the evolution of plant defense strategies.

C3

Genetic Differentiation in the Ground Beetles *Carabus punctatoauratus* GERMAR and *Carabus auronitens* FABRICIUS

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In 31 populations and demes, respectively, of the sisterspecies *Carabus punctatoauratus* and *Carabus auronitens* the genetic variation of three multiallelic loci has been studied by a standard method of polyacrylamide gel electrophoresis. In *C. punctatoauratus*, which is distributed from the eastern to the middle part of the Pyrenees, 6 allozymes of the glutamate-oxalacetate-transaminase-1, 11 allozymes of the glucosephosphate isomerase and 12 allozymes of an esterase could be identified. In this species significant variations in allele frequencies were found on the macrogeographic scale. The populations are partly characterized by private alleles (in the sense of NEEL, 1973). Some populations show the effects of bottlenecks (reduced heterozygosity, lack of rare alleles, shifts of allele frequencies). On the microgeographic scale, too, quantitative differences have been found between samples collected in a distance of a few kilometers inside a homogeneous habitat.

C. auronitens is widely distributed from the Montagne Noire and the Cevennes Mountains (France) to the middle and eastern Europe. In the southern populations of *C. auronitens* there is some genetic variation in the studied genloci, which is smaller than in most of the studied *C. punctatoauratus* populations. In the northern populations of *C. auronitens* nearly no variation is detectable in the three loci (and in 12 more loci mean while studied; the mean heterozygosity H varies between 0 and 0.03). The reduction of the genetic variation seems to be a consequence of the postglacial recolonization.

C7

THE IMPORTANCE OF NEGATIVE DATA: AN EXAMPLE IN *DROSOPHILA* REPRODUCTIVE EFFORT

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The reproductive effort in *Drosophila subobscura*, *D. simulans* and *D. phalerata* was investigated under semi-natural conditions. Couples of F1 individuals (obtained from wild-caught parents) were kept in separate tubes with axenic medium, placed in an outdoor shelter. The daily fecundity and mean daily egg volume per female were measured as well as female longevity and thorax length. In each species, samples were formed in different seasons in order to cover the whole year.

Two possible trade-offs between life-history traits were investigated: between fecundity and longevity, and between egg volume and egg number. There was only a slight tendency for more fecund females to be shorter lived, either within each sample or when different species were compared. Similarly, there was no obvious inverse relationship between the daily number of eggs and their mean volume, nor between mean egg volume per female and female lifetime fecundity. An inverse relationship between egg volume and fecundity was only apparent across seasons, with fewer but larger eggs in winter. Bigger females tended to be more fecund and to lay larger eggs within each species. Reproductive effort (mean female fecundity times mean female egg volume divided by female thorax volume) did not vary predictably with age. The differences between seasons were strong and consistent, suggesting an influence of temperature on both fecundity and egg volume.

Overall, different demographic parameters varied relatively independently of each other, without clear trade-offs. Thus, without denying the heuristic value of Life-History Theory, in particular with respect to potential trade-offs between parameters, it seems that the relationships are complex and dependent on a vast array of factors (temperature, genetic structure, and probably others).

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A variety of tests have shown that molecular evolution does not behave like a stochastic clock as predicted by the neutrality theory: the variance in evolutionary rates is much too large. There is currently no validated theory that predicts the properties of the molecular clock, which properties must therefore be explored empirically. The most important issue is the confidence with which one can extrapolate from well-timed recent events to the remote past, or vice versa, and from well-dated lineages to other lineages. Few data sets exist for carrying out meaningful tests. One concerns cytochrome *c*, which has an acceptable clockwise behavior. Another set involves the copper-zinc superoxide dismutase (SOD), which behaves like a very erratic clock. Part of the erratic behavior of SOD is due to an apparent acceleration of evolutionary rates over evolutionary time. The apparent rate of amino acid replacements (corrected for superimposed and back replacements) is five times greater among the mammals than when comparisons are made between animals, plants, and fungi. Models that assume different rates of evolution for different parts of the molecule can account for this type of variation, although they are ad hoc. More difficult to explain with a molecular clock is the disparate behavior of different lineages. For example, the rate of amino acid replacements is four times slower in some plant than in some animal lineages, and there also are systematic variations within the plant kingdom.

S2

TAXONOMY AND GEOGRAPHIC DISTRIBUTION OF THE DROSOPHILA OBSCURA GROUP SPECIES

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At present 35 species are included on the *Drosophila obscura* species group. In general the flies are brown to black and have a body length of 2 - 4 mm. Males show two tarsal sex combs on the foreleg and red testes. Females are characterized by the shape of the ovicape and the contrasting whitish ventral side of the abdomen.

The analysis of the systematic position of the species within the group has reached a model standard by use of cytological and biochemical methods as well as by behavioral studies.

15 species are found in the Palearctic and 15 in the Nearctic region. The Nearctic species *D. pseudoobscura*, however, reaches the uplands of Colombia and 5 species are distributed in the mountains of Kenya and Zaïre. With some exceptions the species are faunistic elements of the temperate woodlands and the distribution pattern is considered to be connected with the ecological properties of these woodlands. By human action 3 species have been introduced in regions outside of the original distribution area, where they have obviously found suitable living conditions.

P7

GENETIC STRUCTURE OF A *FAGUS SYLVATICA* POPULATION IN THE NORTHERN APENNINES (ITALY).

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Preliminary results of a study on the genetic structure of a *Fagus sylvatica* population from the northern Apennines (Riserva orientata "Guadine-Pradaccio", Parma, Italy) are presented. This study is part of a research project on the effects of atmospheric pollution on the genetic structure of forest populations. The results of gel electrophoretic analysis on 95 trees from four different altitudes (1100, 1300, 1450 and 1650 m) are presented. Twenty enzyme systems were studied in buds collected from January to April and maintained at 4°C.

Maintaining the material at 4°C does not seem to alter the observed zymograms.

The following two enzymes show no activity: GDH, GLDH; APH, FDH, GAPDH, LAP, LDH, ME, MDH, MPI, 6PGD, PGM and SORDH show low activity or variability; ACPH, ADH, EST, GOT, GPI, ICD and SKDH are polymorphic in our population. Enzymatic variability is evaluated in relation to trees' altitudinal location and morphological characteristics.

S2

Molecular studies on chromosome evolution in the *Drosophila obscura* group

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From cytological localizations of enzyme loci and from in situ hybridizations of single copy DNA on the polytene chromosomes of the various species of the *D. obscura* group it became evident that unique sequences do not change from one chromosome element to another, non-homologous element in evolution but middle repetitive DNA does. This can be demonstrated from in situ hybridizations of probes containing the histone gene cluster or a copy of a gene of the actin gene family respectively. The general pattern of middle repetitive DNA on the chromosome seems to be organized in a way that frequent transposition events in chromosome evolution must be assumed. However, the most striking differences between the species of the *D. obscura* group have been found for the composition of highly repetitive DNAs. CsCl density centrifugation of genomic DNAs and differential staining of the mitotic chromosomes reveals that base pair compositions of satellite DNAs can be very different even between closely related species. Sequence data from cloned satellite repeats from the various species can be used for comparisons and as a basis to discuss the possible significance of satellite DNA in species formation and cladogenesis.

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Constant numbers of equivalent parts play a central role in plant taxonomy. Their constancy is primarily due to developmental canalization, which buffers the number of organs against variation in the size of the meristem that produces them. Phyllaries (involucral bracts) and achenes (fruits) on ripe composite capitula provide a model system with sufficient phenotypic variability to permit genetic analysis. Two factors contribute to numerical canalization: (1) The spiral phyllotactic arrangement of organs causes nearest neighbors in space to be a Fibonacci number (1,2,3,5,8,13,21...) apart in temporal sequence of development, (2) There are radial determination gradients causing concentric rings of organs with equal differentiation. As a consequence, variation in the size of the capitulum is accompanied by a logarithmic stepwise response in the number of organs, of which any small section may be realized in the natural phenotype. Phenotypic variance will thus strongly depend on the phenotypic mean, and the response to selection for a particular number, given sufficient genetic variance, will depend on the number in question (a constant number of 7 parts is virtually impossible to achieve). If there is a genetically determined difference in capitulum size between two plants, a heritable difference in the number of organs may be a consequence of the size difference or it may also include genetic differences in the determination of organ numbers itself. This greatly influences the taxonomic and evolutionary interpretation of natural phenotypic variation and the predicted outcome of selection. We shall illustrate this with selected examples and show how single genes affecting the number of meristic characters can be demonstrated. Developmental canalization adds to the effect of plasticity in dissociating phenotypic from genotypic variation and thereby softens the impact of selection on a large part the genome.

P3

THE PHYLOGENY OF THE *Drosophila affinis* SUBGROUP
(*D. obscura* GROUP) BASED ON MITOCHONDRIAL DNA.

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Mitochondrial DNA from several populations species belonging to the *D. affinis* subgroup, and representatives from Palaearctic and Nearctic members of the *D. obscura* subgroup have been analysed.

The experimental procedure consisted of simple and double digestions with ten restriction endonucleases, and hybridization with mitochondrial DNA probes from *D. yakuba* (1) to obtain restriction maps.

Two types of data analyses have been carried out:
i) cladistic analyses (Wagner method, etc.) and,
ii) estimates of nucleotide substitution rates.
D. yakuba, of which mitochondrial DNA sequence (1) and restriction maps (2) are available, was used as a valid outgroup to locate the hypothetical ancestor of the *D. obscura* group in the phylogenetic tree.

Our results agree with others, previously reported (3, 4), in the sense that *D. obscura* group should be classified according to three subgroups: *obscura*, *affinis*, and *pseudoobscura*.

One striking result is the apparent low mitochondrial DNA divergence within and between species of the *D. affinis* subgroup. Moreover, the average distance with respect to the hypothetical ancestor of the group is several times smaller than the average distances of the *D. obscura* and *D. pseudoobscura* subgroups.

This results will be discussed on considering the particular mitochondrial DNA evolution of *Drosophila*.

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(2) SOLIGNAC, M. et al. (1986) J. Mol. Evol. 23: 31-40.

(3) LAKOVAARA, S. and KERANEN, L. (1980) Genetika 12:157-172.

(4) LATORRE, A. et al. (1988) Mol. Biol. Evol. 5(6):717-728.

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Current methods of gene-frequency patterns analysis (correlation of genetic and geographic distances, spatial autocorrelation, variogram) assume stationarity of gene frequencies in space, i.e. the differences between populations depend on their geographic distance, and are statistically constant at a given distance. Recent studies on the effects of gene flow point out it is possible to infer the presence of physical and behavioural factors isolating populations, if genetic differences are large in small areas.

One can envisage the geographical distributions of gene frequencies as a set of 3-dimensional surfaces, whose elevation represents the frequency of the allele of interest. Geometrically, the regions of abrupt genetic change are zones of high slope in the pooled surfaces. Developing an idea put forward by Womble in 1951, we propose a method for detecting such zones on the basis of gene-frequency data: 1. Construction of continuous surfaces from discrete data by interpolation; 2. Computation of the first derivative of each surface at various locations; 3. Averaging of the derivatives across surfaces; 4. Plotting of a map evidentiating the areas where the average derivative exceeds an arbitrary threshold. Examples of application of this method to natural populations are given.

C7

POSSIBLE BENEFITS OF EGG CANNIBALISM IN THE LAND SNAIL
ARIANTA ARBUSTORUM

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Hatchlings of the land snail *Arianta arbustorum* (L.) were used to test whether the ingestion of conspecific eggs confers nutritional advantages to a cannibal in form of increased growth rate and survival. In the field, hatchlings of this herbivorous species consume unhatched sibling eggs as well as eggs from neighbouring batches. In a laboratory experiment each of 10 newly hatched siblings from 24 egg batches were fed either on conspecific eggs or on lettuce for 10 days. The snails' growth during this period was recorded, as well as their subsequent growth and survival until maturity. During this latter period the animals of both groups were kept under identical conditions and fed on lettuce. Hatchlings fed a cannibalistic diet during their first 10 days of life experienced an increase in wet weight 2.6 times as high as those fed on lettuce. Different diets did not affect hatchling survival, but they influenced the snails' future survival: 66.6% of the individuals initially fed on eggs attained adulthood compared to 38.0% of those fed on lettuce. Snails fed different diets during the hatchling stage differed neither in time to complete shell growth nor in adult size. However, the latter findings may be influenced by the greater proportion of cannibalistic snails surviving until maturity. Considering in both treatments the same number of individuals completing shell growth, snails initially fed on eggs became mature earlier than those fed on lettuce. Thus, a cannibalistic diet during the hatchling stage provides accelerated growth and higher survival to the cannibal.

C13

MORPHOLOGICAL AND GENETIC DIFFERENCES IN ECOLOGICALLY DISTINCT POPULATIONS OF PETROSIA (PORIFERA, DEMOSPONGIAE).

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Variations in morphological (growth-form, structure of the aquiferous system, spicular size and rates among spicular types) and genetic features (by electrophoresis of gene/enzyme systems) have been comparatively studied in sponges of the genus Petrosia in order to elucidate also its intricate taxonomic status.

The populations of Petrosia inhabiting the rocky cliffs of the Ligurian Sea, usually identified as P. ficiformis, show different morphological characters linked to particular environmental features. Mushroom - shaped specimens are present on exposed cliffs, from the surface to 50 m depth. In sheltered zones, subjected to low intensities of light and water movement (crevices, roofs, caves) the specimens are cylindrical with anastomoses, forming a creeping network, or spherical with a single apical oscule. These last two forms differ in spicular sizes and composition, skeletal morphology and aquiferous system organization. Spherical and cylindrical forms, are also separated by a genetic distances of 0.55 resulting from an electrophoretic analysis based on 9 loci (Pgi, Hk, Es, 6Pgd, Mpi, Mdh, Tr, Got and Ak). The two forms were found fixed for alternative alleles at two loci (6Pgd and Ak). These data probably indicate reproductive isolation between the two forms which could therefore be considered as separated biological species. Part of mushroom forms (16 %) have spicules similar to those of the cylindrical forms whereas the rest (84 %) are more similar to the spherical specimens.

A possible hypothesis explicating also this last point is that the examined populations of Petrosia are formed by two sympatric species which, for the external morphology, are indistinguishable in exposed sites but distinct in sheltered ones.

L

The genetics of evolution and the evolution of genetics

Bengt O. Bengtsson

The lecture will cover two topics: 1) The amount of genetic details needed to understand evolutionary processes, and 2) the evolution of these details. Particular attention will be given to the Mendelian segregation ratio 1:1.

C9

WHAT CAN PROMOTE THE INTERACTION OF ECOLOGICAL, GENETICAL AND MOLECULAR APPROCHES TO THE STUDY OF EVOLUTION.

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Abstract

Evolutionary questions require the use of techniques from different disciplines. Using molecular tools along with ecological and genetical analysis, allows a more complete understanding of organism evolutionary ecology. Thus, we have tried to answer two questions. First, why are both female and hermaphrodite individuals maintained in natural populations of some species (e.g the shrub Thymus vulgaris L.)? Second, what are the level of introgression of some molecular markers across the hybrid zone of two divergent subspecies (e.g. two grasshoppers Chorthippus parallelus parallelus and Chorthippus parallelus erythropus)? We attempt to show the interrelationship of these discipline in the study of these two different questions.

C5

STAYING AHEAD IN THE PLANKTON: THE EVOLUTION OF CYCLOMORPHOSIS IN AUSTRALIAN DAPHNIA

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Some microcrustacean zooplankton develop morphological defenses in response to the seasonal presence of predators. This seasonal change in morphology (cyclomorphosis) in the cladoceran Daphnia carinata in Australia results from the growth of a large dorsocephalic crest that prevents predators from handling their prey effectively. Another species that is most common during summer when predators are abundant, D. cephalata, is permanently crested. The fact that the developmental response of D. carinata is induced by water borne factors released by its principal predators, and the dominance of D. cephalata in predator rich environments suggest a close coevolution between predators and prey. But why have the predators not evolved mechanisms to deal with crests? - or do they need to? Can both predators and prey be winning in the plankton down under?

MALE LIMITATION OF FEMALE REPRODUCTIVE SUCCESS IN A PIPEFISH: EFFECTS OF BODY SIZE DIFFERENCES

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In the pipefish *Syngnathus typhle*, a species with exclusive male parental care, males limit female reproductive success as a result of their limited brood pouch space and long pregnancy. Sexual size dimorphism is absent in one year old animals, but increases with age so that older females are larger than similar-aged males. As fecundity is related to size in both sexes, this will increase female fecundity more, relative to male fecundity, as the fish get older. Older/larger males can therefore be predicted to limit the reproductive success of similar-aged females more than do younger/smaller males.

To measure a female's maximal reproductive rate, she was provided with an excess of males (i.e., three), and the result was that small, one year old females produced as many eggs, or produced eggs at the same rate, as a male of similar size could care for. Such females filled on average 1.06 males within the time span of one male pregnancy, and actually produced on average 10 eggs fewer than needed to fill a similarly sized male. Large, two year old females, on the contrary filled 2.7 similarly sized males within the course of one pregnancy, and produced on average a surplus of 149 eggs. The difference between females of the two size classes was highly significant. In field samples larger females also contained more left-over eggs by the end of the reproductive season compared to small females. As natural sex ratios were equal, older females in nature are probably more constrained by male availability than are small females. Even small females may be limited by males in nature, however, as they begin reproducing later than large females, that is, when mate supply is dwindling.

In mate choice experiments a preference for larger partners was demonstrated in both males and females of large and small body size at the beginning of the reproductive season. In large females choosiness decreased significantly towards the end of the reproductive season, contrasting to the pattern in small females, large males and small males. As might be expected, larger females were extremely eager to spawn towards the close of the breeding season.

Reasons for the observed sexual growth dimorphism may be higher male reproductive costs, resulting in decreased growth in males, and a stronger directional selection for large female body size in older individuals.

P8

MATING SUCCESS IN RELATION TO BODY SIZE IN *DROSOPHILA* *MELANOGASTER*

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The adult component of selection is a relatively important part of the total selection during the life cycle of *D. melanogaster*. Particularly factors concerning the mating process, such as mating preference and mating success, are of significance. The mating success of flies does not only depend on their genetic composition but is also affected by constitutional and environmental factors. We have studied the effect of differences in body size, brought about by different levels of crowding during the pre-adult stage. The results showed that larger males are significantly more successful than smaller ones. On the other hand males seem to have no preference for females of a particular size. Furthermore, a mass-choice experiment revealed no assortative mating for size, although large flies tend to mate faster than small ones. The possible consequences of these results are discussed in relation to the fecundity of females.

P12

ALLOZYME MONOMORPHISM AND GENETIC HOMOGENEITY AMONG ITALIAN POPULATIONS OF *VARROA JACOBSONI* OUD. (ACARI: VARROIDAE).

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Varroa jacobsoni is an ectoparasitic mite of honey bees. Its original host was *Apis cerana* in eastern countries. Recently the mite was transmitted to the European honey bee *A. mellifera* and spread over most beekeeping areas of the world with serious economic consequences.

On morphometric bases, the honey bee mite is usually considered as a single species, although lately some objections have been made. The electrophoretic approach has been considered useful for obtaining taxonomic information on the genetic basis.

The analyzed mite samples came from regions of Northern, Central and Southern Italy. By means of starch gel electrophoresis, they were surveyed for 17 enzyme loci.

Results show complete monomorphism at all loci with the same allele occurring in all the samples.

Haplodiploidy and repeated population bottlenecks may account for the uncommonly low level of genetic variability observed. The genetic homogeneity between the samples supports the idea of a single origin of the Italian population.

P4

BREEDING ECOLOGY AND REPRODUCTIVE ISOLATION OF A WIDESPREAD STICKLEBACK FISH (*GASTEROSTEIDAE*) IN NOVA SCOTIA, CANADA.

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A stickleback with brilliant white dorsal breeding colors is widely distributed in northeastern Nova Scotia, Canada, where it often breeds sympatrically with the threespine stickleback, *Gasterosteus aculeatus*. Breeding males are highly conspicuous and visible at distances of 20m or more whereas sympatric *G. aculeatus* are cryptic and difficult to detect even at 2m. The white stickleback nests only above the substrate in filamentous algae, whereas *G. aculeatus* nests only on the substrate. The white stickleback is smaller in size and more terete than *G. aculeatus*, but it is morphologically similar in having a complete row of lateral plates and similar lateral plate and gill raker numbers. The white stickleback occurs only in environments where there are filamentous algae (which appears to be an obligatory nesting substrate) and where the water is clear, saline, and relatively still. Female choice tests in the laboratory show that the white stickleback is reproductively isolated from *G. aculeatus*, and field observations on natural spawning support this conclusion. We suggest that the bright breeding coloration may have evolved through sexual selection and/or to advertise unprofitability to predators.

S4

GENE PHYLOGENIES AND SPECIES PHYLOGENIES: RETICULATION AND MOSAICISM
IN THE GENUS *Mus*

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One of the best known Mammalian models, the House mouse has drawn attention of workers in many fields among which evolutionary biology is no exception. As to molecular phylogenies, there is a fair amount of data available, ranging from electrophoretic, immunological, amino-acid sequence variation in proteins to DNA data such as sonDNA hybridisation, sequence comparisons and RFLP data for various gene loci including mtDNA, repetitive sequences and structural genes located on various chromosomes... Consensus trees summarizing available information show that the genus *Mus* has undergone at least three successive adaptive radiations, each of them occurring in relatively short time spans (i.e. multifurcations) and represented in present day taxa at the subspecific, specific or even subgeneric level. The aim of this presentation is to situate the various phylogenetic images obtained using the above data sets within this framework. In fact, following the fate of individual genes shows that their history is not always superimposable that of the species as illustrated by mtDNA and Y chromosome evolution which give discrepant resolutions of these multifurcations. The mechanisms responsible for these discrepancies are relevant to the population and species levels at which retention of ancestral polymorphism (e.g. for the MHC class I and II genes) and secondary exchanges (e.g. for the t-haplotypes) have been evidenced. Thus, reticulation and mosaicism could be a general feature of gene transmission in widespread genera with large geographical ranges such as *Mus*. It is therefore very important that no definite phylogenetic image should be deduced from a single marker.

C7

SEASONAL VARIATIONS AND BALANCED POLYMORPHISMS IN
VARIOUS TRAITS OF THE REPRODUCTIVE POTENTIAL IN
TEMPERATE *DROSOPHILA MELANOGASTER* POPULATIONS.

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Various traits involved in the reproductive potential of temperate populations of *D.melanogaster* are subject to cyclical seasonal variations. These variations concern at least three morphological, physiological or behavioral genetically determined characteristics : viz. number of ovarioles, initial retention in virgin females and oviposition blocking capacity. They were observed, for several successive years, on flies from the first generation of isofemale lines founded by wild flies collected in Spring, Summer and Autumn in two French populations.

The variations consist of an increase in frequency of genotypes controlling large number of ovarioles, long preovulation period in virgin females and strong oviposition blocking control in Spring and Autumn samples. The opposite genotypes i.e. low number of ovarioles, short initial retention and weaker oviposition blocking capacity, resembling the ancestral afrotropical phenotypes, are favoured in Summer generations.

This balancing selection, induced by environmental temperature variations, modifies temporarily the genetic equilibrium of the population. This enhances the frequency of better adapted genotypes when conditions becomes less favourable and maintains the wide genetic variability of each trait.

P6

Heterozygote deficiency in a marine lagoon bivalve:
the paloude *Ruditapes decussatus* L.

Philippe BORSA*, Michel AMANIEU, Bernard DELAY**

Heterozygote deficiencies relative to Hardy-Weinberg expectations are a common feature among marine bivalves. They characterize mostly juveniles: the deficiency tends to disappear in samples of older individuals, because of a (commonly observed) survival / heterozygosity positive relationship.

The paloude does not fit to this classical scheme: the genotypic structure of juveniles (spat) is consistent with H.W. model, whereas stronger heterozygote deficiencies are exhibited by samples of adults. Since the latter are constituted of several cohorts, one possible hypothesis is the existence of genetic differences between cohorts. This explanation is considered and discussed, with other alternative hypotheses: selective and/or according to the breeding structure.

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W1

INTROGRESSION PATTERNS OF DIPLOID AND HAPLOID MARKERS
ACROSS A HYBRID ZONE.

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The genetic transition between *M. m. domesticus* and *M. m. musculus* across their hybrid zone occurs through 30-40 km. wide, concordant allele frequency clines for the 7-10 autosomal markers studied, both in Bulgaria and Denmark. The mitochondrial DNA (mtDNA) cline is of the same order of width but its position is shifted into the *domesticus* territory in Bulgaria. In Denmark, the *musculus* populations are fixed for a mtDNA variant of *domesticus* origin which is not found in the *domesticus* territory in this region. The transition across the hybrid zone is a cline concordant with the autosomal clines. The transition from one Y chromosome type to the other occurs in 3-4 km. only in the center of the autosomal clines, indicating that selection is preventing the introgression of this haploid nonrecombining chromosome and that migration rates must be very low in the hybrid zone, of the same order as the width of this Y cline. If migration rates are so low and if, as is thought, the secondary contact between the two subspecies is very recent, we cannot exclude that the autosomal and mitochondrial clines are due to neutral diffusion. It is possible that hybrid breakdown is due in this case to only a few genes (with at least one of them on the Y). None of these genes however has yet been identified.

C7

GENETIC AND PHENOTYPIC SOURCES OF VARIATION IN THE ADAPTATION OF CRICKET LIFE HISTORIES TO A SEASONAL ENVIRONMENT

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The adaptation of insect life cycles to a seasonal environment permits the critical testing of life history models that are based on readily identifiable selection pressures.

For the cricket *Allonemobius fasciatus* the number of generations produced per year (voltinism) varies along a latitudinal cline of season length. Optimization modelling predicts that development time should match season length, and should be halved when the switch from a univoltine phenology to a bivoltine one occurs.

I tested this model by rearing *A. fasciatus* collected from across the cline of voltinism in a number of environments which simulated the seasonal cycles of the sampling locations. Development time was not different between populations of the two phenologies in any of the environments; I am therefore unable to confirm this prediction of the life history model. Large genetic differences were, however, found in the norms of reaction for the production of overwintering diapause eggs.

Thus for *A. fasciatus*, traits such as diapause expression, for which an inappropriate response may result in a drastic reduction in fitness, a combination of phenotypic plasticity and genetic differentiation produces the observed life history variation. For other traits, which may be regarded as 'fine tuning', selection has not (yet) resulted in a close fit to the optimization model.

L

COEVOLUTIONARY INTERACTIONS OF THE MONARCH BUTTERFLY, *Danaus plexippus*, WITH AVIAN PREDATORS AND THE NORTH AMERICAN MILKWEED (*Asclepias*) FLORA.

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The monarch butterfly is unique among 157 species of the tropical Nymphalid subfamily Danainae in having successfully invaded the temperate zone by a bird-like migration. Following massive population increase over the summer through 4 generations of breeding on the diverse North American milkweed resource, the monarchs enter reproductive diapause in September and migrate for up to 2000 miles to the Sierra Transvolcanica in central Mexico. Here they overwinter on a few mountain ranges in clusters of 10 million butterflies per hectare. This dense clustering is possible because monarch larvae sequester and store vertebrate heart poisons (cardenolides) from milkweeds that protect the adults. In late March, the monarchs fly back into the southern USA and oviposit on very toxic milkweeds that chemically protect the new spring generation which then recolonizes the entire breeding range in eastern North America. My colleagues and I found that monarchs have dynamically exploited the milkweed-derived defense, but that some bird and mice species have breached the defense in ways suggestive of a coevolutionary arms-race.

S1

SELECTION 'WEBS' AND INDUSTRIAL MELANISM: PAST AND FUTURE APPROACHES

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The strengths and weaknesses of traditional approaches to investigating the processes involved in the evolution of industrial melanism will be outlined. Present-day declines in melanic frequency and the development of ideas about measuring the crypsis and survival of living insects in nature provide opportunities for a more realistic and experimental approach to studies of natural selection. There has also been some advance in the understanding of the regulation of melanization in insects and a realization of the importance of interactions between the effects of major genes controlling melanism on the visual colour pattern and those on various non-visual aspects of the phenotype. Some early results of a study of such interactions in a laboratory system will be described. It is stressed that any hypothesis to explain industrial melanism in a particular species will need to take fuller account of such interactions and of the multiple influences of natural selection.

C10

THE VARIABILITY OF SUBSTITUTION RATES - HOW BLIND IS THE CLOCKMAKER?

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An improved method will be presented for testing uniformity of substitution rates (constancy of the molecular clock) and for estimating substitution rates with their standard errors within lineages. Some results on synonymous rates in different orders of mammals will be discussed.

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Recently, mainly due to its hereditary characteristics and technical facilities, mtDNA polymorphism has become a powerful tool in evolutionary studies. We have used this molecule in the analysis of the population structure and geographic differentiation of *D. subobscura* and its phylogenetic relationships with other related species of the *Obscura* group. 61.2% of the total mtDNA variation found in the Palearctic populations of *D. subobscura* is due to differences among regions. The high differentiation of the Canary Islands with respect to the rest is striking, the more frequent nucleomorphs in Canaries being absent in other regions. Maximum nucleomorph distance and the abundance of endemic forms on the Canaries suggest that this molecular differentiation is most probably due to the very old age of the Canary Islands populations rather than to drift and founder effects. Only 0.25% of the total diversity is due to differentiation between localities within regions, though the relatively small sample sizes could explain this result, the distribution of nucleomorphs among samples makes us suspect that a fine scale differentiation is realistic. Temporal fluctuation is stronger in Northern than in Southern populations. Only the two wide spread nucleomorphs out of 26 detected for the species in the Palearctic have been found in the New World, confirming the recent colonization of South and North America by this species. The phylogenetic relationship of *D. subobscura* with the two closest species *D. guanche* and *D. madeirensis*, clearly supports the pair *subobscura-madeirensis* as the most related one.

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Recent studies in our laboratory (as well as others) have indicated that insect genomes are highly heterogeneous in their rates of change in DNA sequences. This intragenomic variation is much greater than previously documented in other groups of organisms. Whether the fast-evolving fraction of the genome is due to a high rate of accumulation of nucleotide substitutions or insertions/deletions of larger pieces of DNA remains unclear. However, attempts to clone and sequence the fast and slow evolving parts of the genome indicate that at least part of the fast-evolving portion of the genome is due to accumulations of point mutations. This phenomenon in insects makes some forms of DNA data unsuitable for phylogenetic studies. We have been exploring alternative methods of measuring the differences in the relatively slowly-evolving fraction of the genome for phylogeny reconstruction which will allow phylogeny reconstruction over greater distances. In particular we are studying the relative rate of evolution of total single-copy DNA (scDNA) versus DNA coding for protein sequences (cDNA).

P11

CONTRASTING AGE STRUCTURES IN CAVE CRICKET POPULATIONS:
PATTERNS AND SIGNIFICANCE.

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Adaptation to cave habitat as a seasonally constant environment is expected to affect several life history traits. In this paper we investigate the age structure and phenology of 27 *Dolichopoda* cave cricket populations from artificial and natural cave habitats subjected to different environmental regimes and trophic resource stability conditions. Field recorded morphometric data clearly revealed the occurrence of different age structures and phenology, basically indicating two contrasting patterns.

In artificial caves, which have been colonized by *Dolichopoda* only in historical times and where food resources and climate are chiefly dependent upon surface environment, a seasonal age structure was observed. On the contrary in most natural caves, where cricket colonization appears to be much older and stability of both climatic parameters and trophic resources is higher, a constantly heterogeneous age structure was revealed. However a seasonal-like age structure also occurs in natural caves characterized by either recent origin (i.e., travertine caves) or low temperature regime. This suggests that age structure phenology in *Dolichopoda* is influenced by historical factors, stability of trophic resources and environmental stress as well.

In seasonal crickets, synchronization of life cycle is expected to depend largely upon the expression of embryonic and/or nymphal diapause. Variation of this trait appears to be at premium in natural caves, allowing for a reduced competition among crickets of different age and size. Further experimental work is now planned to investigate the role of genetic variation and phenotypic plasticity in the evolution of this trait.

P11

MIXIS INDUCTION IN THE ROTIFER *Brachionus*
plicatilis AS A RESPONSE TO MEDIUM
PRECONDITIONED TO POPULATION DENSITY.

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The factor most consistently implicated as an inducer of sexuality in the rotifers of genera *Brachionus* is crowding or high population density, both in laboratory cultures and in natural populations. The basis for the crowding effects in *Brachionus* is not understood. The density effect in short-term cultures has been attributed to the accumulation of a substance released into the medium by the rotifers themselves.

To determine the existence of chemical-mediated induction we have conducted several experiments in the species *Brachionus plicatilis* to investigate if conditioned medium has the same inducing properties as lived females. We have obtained positive results. Additional experiments have been made in order to test the specificity of the density effect.

C6

GENETIC STRUCTURE OF HOST *DROSOPHILA* LARVAL POPULATIONS IN RELATION TO INFESTATION BEHAVIOR OF PARASITIC WASPS

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Parasitic wasps of *Drosophila* larvae have different searching behaviors: ovipositor searching behavior involves a random probing of the ovipositor into the substrate while vibrotaxis searching behavior allows the wasp to detect a host due to its movements.

These different wasp behaviors can influence the genetic structure of the host population.

The locomotory behavior of *Drosophila* larvae varies greatly. The "sitter" phenotype or shallow forager has reduced locomotion characterized by short-distance movements. The "rover" phenotype or deep forager has increased locomotion characterized by long-distance movements. These phenotypes have an autosomal genetic basis.

We demonstrate that susceptibility to parasitization is a product of larval-locomotory and wasp-searching behaviors. Because of the alternate and species-specific wasp behaviors, the selective pressure on larvae varies depending on which wasp species is present. Therefore, a *Drosophila* population can be genetically modified in different ways by different parasitic wasps. Evidence is given that rover/sitter genotypes frequency varies from one location to another in relation to local parasites.

P5

MULTIVARIATE MORPHOMETRICS AND GEOGRAPHICAL VARIATION OF *DOLICHOPODA* CAVE CRICKET POPULATIONS.

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Several morphological and ecological descriptors of the *laetitiae-geniculata* complex within the cave cricket genus *Dolichopoda* have been studied over a wide number of locations in Central and Southern Italy. Data have been treated with a number of multivariate and space analysis techniques including Kriging for identification of spatial trends both of single descriptors and/or their combinations.

Unlike other morphological variables, the male epiphallus shape revealed significant differences between species, and a discontinuous trend in geographic variation. On the other hand, body and appendage morphometric descriptors did not allow to discriminate among species, but showed a clinal variation across cave biotopes characterized by different climate vegetation types (from "mediterranean" areas to mountain areas). The spatial trend was well related not only to geographical structure of the sampling design but also to the spatial configuration of ecological descriptors. Average cave temperature stands as the most important ecological factor associated with external morphometric variation.

Results from this study, compared with previously recorded data on allozyme variation, enlighten on the different roles of phenotypic plasticity, selection, gene flow and genetic drift in shaping the variation and evolution of the various character sets.

C4

TIMING OF BREEDING AND FITNESS CONSEQUENCES IN THE COOT (*FULICA ATRA*).

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As in many other bird species, in the coot old birds nest early in the season and have a high reproductive output. At that time, however, conditions for raising chicks are less favourable than later in the season. In fact, the early-nesting old pairs devote more time in feeding young than the late-nesting young pairs. As the survival rate of the early-fledged young is higher, this higher parental effort seems justified.

Young pairs are presumably prevented to nest early by competition with old birds for suitable territories. This competition is mainly between the males, since it is found that territorial quality is related to the age of the male, and age and number of the neighbouring males.

Females mated to old males (having better territories) are able to lay early. Such females are generally old. Due to this early laying, and by spending more effort in raising chicks, the members of an old pair increase their fitness.

W1

A HYBRID ZONE BETWEEN THE PLETHODONTID SALAMANDERS *HYDROMANTES ITALICUS* AND *H. AMBROSII*

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The plethodontid salamanders *Hydromantes italicus* and *H. ambrosii* are differentiated at the isoenzyme level, with four diagnostic loci (*Ldh-1*, *Ldh-2*, *Ck*, *Pt-2*), and four highly differentiated loci (*α-Gpdh*, *Me-2*, *Idh-2*, *NADHdh*), out of the 27 analyzed.

The subspecies *H. italicus gormani*, described from the Apuan Alps, has proved to include recombinant and introgressed genotypes, with different combinations of *italicus* and *ambrosii* alleles. In this area a narrow hybrid zone has been detected, about 5 km wide; neither *F₁* hybrids nor parental specimens have been observed. Heterozygote deficiency has been found at some differentiated loci (e.g. *α-Gpdh*, *Me-2*). Alleles of two diagnostic loci (*Ck* and *Pt-2*) do not cross beyond the hybrid zone, indicating a low fitness of recombinant genotypes at these loci. Other loci show a differential spread in the alien species (e.g., the *ambrosii* alleles *Pt-2* 92, *NADHdh* 85 and *α-Gpdh* 95 penetrate respectively about 6, 20, and 75 km in the *italicus* range). Introgression is asymmetric, with a much wider spread of *ambrosii* alleles in the *italicus* genome than viceversa.

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The molecular analysis of the chloroplast genome (cpDNA) has proceeded rapidly, owing to both a small genome size and a relatively conservative rate of sequence evolution. Several chloroplast-encoded genes have now been sequenced in a number of plant taxa. These include the ribosomal protein genes *rpl2*, *rpl23*, and *rps19*; the chloroplast coupling factor genes *atpBE*; and the gene encoding the large subunit of ribulose-1,5-bisphosphate carboxylase (*rbcL*). The genes *rbcL* and *atpBE* appear to evolve at a regular rate, and are therefore especially well suited for phylogenetic inference. In contrast, the genes encoding the *rpl2* and *rpl23* loci exhibit anomalous patterns of evolution in some plant taxa.

The use of complete DNA sequence data to infer phylogenetic relationships will be illustrated. Most emphasis will be placed on the relatively extensive data set accumulated for the gene *rbcL*. In addition, relative rates of evolution for different cpDNA-encoded genes will be analyzed and differences in evolutionary rates among annual plant species and long-lived species will be discussed.

C1

MODELS OF RANDOM REPRODUCTIVE SUCCESS; COEXISTENCE AND MEAN-VARIANCE TRADEOFF.

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Models are constructed for population dynamics when reproductive success of different species or of genotypes within a species varies between individuals, locations, and generations. It is shown that in large well mixed populations, the long term representation of a particular type depends only on the mean individual fitness, and is independent of the individual variance. There is a mean-variance tradeoff when fitness varies between generations, or when there is limited localised dispersal. Variance increases the probability of extinction of small finite populations as during colonisation, or of rare favourable mutants. In this case, there is a mean-variance tradeoff in the long term future representation of different types. The conditions for coexistence of different types are defined.

GENETIC STRUCTURE AND DIVERGENCE OF HYPOGEAN AND EPIGEAN CYPRINID FISH

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Cyprinid fish are good candidates for adaptation to cave life and actually seven genera are known to live in caves and groundwaters from East Asia to East and Central Africa. Two Somali species, *Phreatichthys andruzzii* and *Barbopsis devechii*, are of particular interest representing two different steps of adaptation to cave life as indicated by several morphological features including eye regression. *Phreatichthys* is completely anophthalmic while *Barbopsis* shows a highly variable microphthalmia. These two species occur allopatrically in the phreatic layer of limestone and evaporitic formations of Lower to Middle Eocene.

Population samples for each species have been studied electrophoretically at 32 enzyme loci in order to compare their genetic structure and to infer their evolutionary relationships. Three samples of epigeal species belonging to genus *Barbus* were also analysed as representative of epigeal taxa and as outgroups for systematic analysis.

Results showed a close relationship between *Barbopsis* and *Phreatichthys* suggesting their origin from a common epigeal ancestor. Population structure of the two species differs and levels of gene flow are much higher between *Barbopsis* populations than between *Phreatichthys* ones. Two possible scenarios leading to the present situation are hypothesized. Heterozygosity values were higher in the cave specialist *Phreatichthys* than either *Barbopsis* or *Barbus*, supporting our previous findings from other cave dwelling organisms.

P4

Geographical isolation, local adaptation in four *Asellus aquaticus* populations, freshwater crustacean isopod.

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A species distributed along a cline shows diverse inter-population patterns of life cycle due to diverse pressure acting upon individuals of different habitats (Baur and Raboud 1988). Hybridations were made in order to evaluate the different degree of reproductive isolation (r.i.) between four population of *Asellus aquaticus*, species colonizing almost all Europe and undergoing to a true evolution for some physiological characters (Vitagliano et al. 1988).

Individuals collected from Sarno river (Napoli= N), Tevere river (Roma= R), dutch channels (Utrecht= U) and scottish channels (St.Andrews= S), fed on leached detritus were breed at 16°C and L/D 16/8. Surely fertile animals were used for the interpopulation crosses.

The results show that in all the crosses a high r.i. exists; high hybrid sterility was also found.

In conclusion from our results we hypothesize that r. i. may be due to different local adaptation, even though we cannot exclude the presence of certain amount of gene flow.

W1

COMPARATIVE PHENETICS AND GENETIC COMPATIBILITY IN TWO SEPARATE HYBRID ZONES BETWEEN THE SILKMOTHS *Hyalophora gloveri* and *H. euryalus*.

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The hybrid zone between *Hyalophora gloveri* and *H. euryalus* in the California Sierra Nevada is characterized by great phenotypic variability beyond that seen in lab hybrids. Wild hybrid females are fertile but non-reciprocal incompatibility may occur when parental phenotypes collected near the hybrid zone are crossed. Extensive introgression occurs in one direction away from the hybrid zone. Preliminary evidence from a study of a second hybrid zone in the Bitterroot Mts. of Idaho and Montana shows much less variability. Adults resemble primary hybrids but no parental phenotypes occur in mid hybrid zone. Larvae possess unique, non-parental phenotypes. An abrupt change to the *gloveri* phenotype occurs to the east, probably due to low population density resulting from rain shadow effects on host plant occurrence. Hybridization reveals fertility barriers with allopatric *gloveri* but not with *euryalus*.

S1

ADAPTIVE CHROMOSOMAL VARIATION IN THE *ANOPHELES GAMBIAE* COMPLEX

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Malaria vector studies in the Afrotropical region have involved in recent years routine cytotaxonomy of the sibling species of the *Anopheles gambiae* complex. More than 65,000 field collected specimens from some 1,000 different localities were scored for polytene chromosome analysis in our laboratory. This parasitologically-based activity has provided also data of evolutionary interest mostly in relation to the patterns of spatial and seasonal distributions of polymorphic paracentric inversions which are shown to be important selection units in these mosquitoes. Relevant cases of "adaptive" chromosomal variations were mainly evidenced throughout the comparative study of populations of the most anthropophilic member of the complex, namely *Anopheles gambiae* s.s. This taxon is closely associated to man all over its range of distribution which includes most of Africa south of the Sahara and extends from tropical rain forest up to pre-desertic areas. Forest populations are monomorphic (or nearly so) for the standard chromosome-2 arrangement while savanna populations are differentiated by various inverted arrangements generally intergrading with the standard. Assuming a forest origin for the taxon, its adaptation to drier areas appears as a process of polygenic reorganization for which paracentric inversions constitute the basic evolutionary mechanism. Highly significant correlations are shown between inversion frequencies and variations in climatic parameters along different transects from forest to dry savanna. The frequencies of arrangements 2Rb and 2La, possibly acquired through introgressive hybridization with *Anopheles arabiensis*, show the most striking correlation with the degree of aridity at the sampling sites.

P10

ADULT LOCOMOTOR ACTIVITY IN *DROSOPHILA MELANOGASTER*: A GENETIC ANALYSIS OF A "FICKLE" BEHAVIOUR

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A genetic analysis of adult locomotor activity in *D. melanogaster* was performed by using a wild type stock and 13 morphological markers of chromosomes 3 and X. Locomotor activity was measured as the total stretch covered in 90" in a horizontal ring of 10 cm diameter (3 mm internal diameter). An approach suggested by Jayakar et al. (1977) was adopted and the results obtained suggested the presence of several genes influencing locomotion on both chromosomes 3 and X (Costa et al., 1989). The present work takes into consideration another aspect of locomotor activity, defined as "fickle" behaviour, which is described in terms of number of inversions of direction recorded in the course of the 90" of observation. As far as chromosome 3 is concerned, a great heterogeneity has been observed among stocks and between sexes. In fact, while males and females of the wild stock show a very similar behaviour, in all marker stocks the difference between sexes is statistically highly significant, the males showing greater fickleness. Highly significant differences are observed also among stocks. The linkage analysis performed with backcross families indicates the presence of some genes influencing fickleness along the chromosome, particularly in the region of *st* and *red* loci. The comparison of these results with those previously obtained for locomotion suggests a different genetic determination of the two aspects of adult spontaneous activity.

Costa R. et al., 1989. Heredity (in press).

Jayakar S.D. et al., 1977. Proc. Int. Conf. Quantitative Genetics, Iowa Univ. Press, pp. 161-175.

P12

EVOLUTIONARY BIOLOGY OF HOST-PARASITE ASSOCIATIONS: DIFFERENTIAL PARASITE SUSCEPTIBILITY IN HOST HYBRID ZONE.

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In this study, we give genetic evidence for naturally occurring hybrids between *Mytilus edulis* and *M. galloprovincialis* on French Atlantic coasts. In order to analyse the susceptibility of the *M. edulis* - *M. galloprovincialis* complex to larval stage of *Prosorhynchus squamatus* (Trematoda), three samples of typical *M. edulis*, typical *M. galloprovincialis* and hybrid mussels were exposed to infection during one year in a floating suspended culture.

Parasitologic and genetic observations disclosed a strong specificity of this Trematode to *M. edulis*. In addition, the parasitized individuals of the hybrid mussels sample were *M. edulis* like.

Since *P. squamatus* leads to total castration of mussels, our results suggest that this parasite is an agent of differential selection in the host hybrid zone.

C2

MALE-STERILITY IN HIGHER PLANTS: THE RESULT OF A MULTI-LEVEL SELECTION.

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Presence of females (or male-steriles) among hermaphrodites is a common trait in Angiosperms (10% of species). Measures of life-time fecundities of females and hermaphrodites, their frequency in populations and results of crosses lead to the conclusion that most often genetic determinism of male-sterility is nucleo-cytoplasmic (i.e. both nuclear and cytoplasmic genes are involved). However restricted polymorphism within a population can lead this determinism to become nuclear (if only one cytoplasm is present) or cytoplasmic and frequency of females will vary widely depending on the mode of inheritance. In the case of cytoplasmic determinism (i.e. maternal inheritance) a slight advantage of females (in terms of life-time fecundity) is sufficient for females to invade a population, whereas in the case of nuclear determinism females must be at least two times more fertile than hermaphrodites (over their life-time) to be present in a population. Founder effects, which restrict polymorphism within a population, can thus lead to very different dynamics of male-sterility among populations. As a result frequency of male-sterility within a set of populations should depend (aside relative performances of females and hermaphrodites) on population structure in terms of frequency and magnitude of founder effects. Moreover, cytoplasmic polymorphism can be maintained if populations that produce more propagules contribute more to founders of new populations. Observations in Thymus vulgaris will document such processes.

C10

POLYMORPHISM AND STRUCTURAL ORGANIZATION OF THE AMY LOCUS IN DROSOPHILA ANANASSAE AND ITS RELATIVES

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The small amylase gene family has been extensively studied in Drosophila melanogaster. Amylase electrophoretic polymorphism of D. ananassae, another worldwide distributed species, is surveyed here. This species appears to be highly polymorphic (13 isoamylases recorded) while related species have weak activity and much more limited variation. A striking geographical pattern is observed within D. ananassae with significant differences in phenotype frequencies between populations, the African ones being the most polymorphic.

Multibanded electrophoretic patterns indicate more than two copies of the Amy gene. This is confirmed by crossing experiments, in situ hybridization to the salivary gland chromosomes and southern blot analysis using a D. melanogaster Amy probe. A genomic library constructed in λ EMBL3 allows to produce a restriction map of the Amy region in D. ananassae.

C2

MATING SYSTEM VARIATION IN POPULATIONS OF ARRHENATHERUM ELATIUS

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An investigation of mating-system variation is made on Arrhenatherum elatius individuals originating from normal and toxic habitats. The estimation of mating-system characteristics is made for each individual by the comparison of seed set produced in self-pollination and in crossing.

Self-fertility is higher for individuals originating from toxic habitats, whatever the population density. Polymorphism for selfing is revealed with individuals with high and low levels of self-fertility. The higher heterozygote deficit previously observed in natural dense populations probably has for origin a gene flow limited to neighbours which enhances the inbreeding already produced by selfing.

Selfing ability of individuals is stable from one year to the next and is partially transmitted to the progeny which suggests the existence of a genetic component in this aptitude.

The comparison of viability and fertility in open-pollination between selfed and open-pollinated offspring did not reveal consistently any clear inbreeding depression.

The mating-system polymorphism observed in individuals from toxic habitats joined to the lack of inbreeding depression lead us to ask the question: does Arrhenatherum elatius become autogamous in toxic environments?

C2

EVOLUTIONARY POTENTIAL IN SPHAGNUM

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Bryophytes have long been considered as having little evolutionary potential because they are restricted by a number of basic organisational constraints (eg lack of a vascular system) and the predominant stage of the life cycle is haploid. A high level of morphological plasticity has been noted in many species of Sphagnum and this has led to a certain amount of taxonomic confusion. These two observations, allied to the apparent rarity of new individuals derived from spores, suggests that single individuals may cover large areas. Those plants best adapted, or arriving at the appropriate time, may have given rise to extensive clones whose separate ramets may have adapted differently to local micro-environmental conditions. Recent studies have indicated that isozyme variation may be considerable in some mosses, including Sphagnum. How significant are these variations, and how is the balance between plasticity and potential for the creation of new genotypes weighted?

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Transposable elements from different *Drosophila* species have been extensively described. Until now the best characterized elements have come from *D. melanogaster* in which approximately 25 to 30 different families have been detected. In order to better understand the evolutionary history of these elements we have studied the distribution of different *D. melanogaster* families of mobile elements among 15 species of the *obscura* group by Southern blot analysis at three different levels of stringency. Strong differences among the various elements were found. While very little evidence for elements that induce hybrid dysgenesis (P, hobo and I) was found in any of these species, the presence of some retroposon-like (D, G, F and jockey) and some copia-like (copia, gypsy, 412, 297, mdg3 and 3S48) elements was established. A strong heterogeneity among elements was observed among the latter two types of families. While hybridization to F and G element probes was observed in all the species at high stringency, hybridization to D was weak and occurred only at low stringency and no hybridization to the jockey probe was observed under any conditions. Very little homogeneity among species was observed with respect to the retroposon-like families. In contrast, large differences among species and element probes were observed in the copia-like families. Strong hybridization to the gypsy probe was observed in *D. subobscura* and to the 412 in *D. pseudoobscura*, but hybridization was weaker in the other species examined.

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C8

POPULATION GENETICS OF FITNESS-RELATED
QUANTITATIVE CHARACTERS

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Most models on the evolution of life-history traits are models of phenotypic evolution, in which physiological constraints define the set of possibilities among which the selected strategy in a given environment can be calculated. Alternatively, quantitative geneticists assume that components of fitness, which are quantitative characters, are determined by a high number of loci having small individual effects on the phenotype. This allows to estimate the components of phenotypic variance, and other parameters such as the heritability and genetic correlations between characters. These parameters, defined for one state of one population in its environment (or at most in a few environments in order to determine the variance of GxE interaction), begin to be used by evolutionists who are interested in having a fixed value for the 'heritability of one character'.

Here we used a simple genetic model with three loci to simulate the phenotypes for quantitative characters such as the number and the weight of seeds, the number of pollen grains, etc. One locus determines the individual acquisition of resource as a function of the environment, and two other loci determine the allocation of this resource between different fitness-correlated functions, in a pleiotropic manner. Although no hypothesis of normality is made anywhere in the model, computer simulations of an experimental design with micro-environmental variation allow us to obtain a normal distribution of phenotypes, corresponding to what is usually observed by plant breeders on most quantitative characters on a set of individuals.

This model was then used to simulate an evolving population, where we studied the influence of temporal and spatial environmental variability, and of genetic drift on the maintenance of polymorphism for resource allocation to survival and reproduction through male and female functions. Quantitative genetics parameters and their evolution were calculated from this evolving population. On the other side, starting from random samples of this population, we simulated crossing designs aimed at estimating the same parameters by the methods of quantitative genetics. We could then compare the estimations and their evolution with the calculated values. We also tested the robustness of calculated parameters such as heritabilities and genetic correlations to gene frequencies and linkage disequilibrium of the initial pool of gametes.

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The genetic form of phenotypic plasticity can be described as a norm of reaction. Genetic variation in phenotypic plasticity can in the case of crossing reaction norms be described by a genotype by environment interaction. If the contributions of all loci to the norms of reaction for two characters show genotype by environment interaction, the additive genetic covariance between the character will in general change sign. Over part of the environmental range the sign of the additive genetic covariance will be different from the sign in another part of the environmental range, for populations that are identical in genotypic composition. The exception, no sign change possible, is of biological interest, as it indicates a functional and developmental integration between the characters. The possibility of a sign change in the additive genetic covariance with environmental change, with otherwise identical populations, has profound implications for the interpretation of the additive genetic covariances in life history theory.

W2

EXPERIMENTAL INTROGRESSION OF PARACENTRIC INVERSIONS
BETWEEN *ANOPHELES ARABIENSIS* AND *ANOPHELES GAMBIAE*
S.S.

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Chromosomal changes due to paracentric inversions are an important genetic mechanism for biological differentiation and speciation in the *Anopheles gambiae* complex (Coluzzi, 1982). Polymorphic inversions are particularly common in *An. gambiae* s.s. and *An. arabiensis*, the two most anthropophilic and widespread members of the complex in tropical Africa. Most of these inversions occur on chromosome-2 and some of them show very similar break-points in the two taxa determining parallel polymorphisms (*sensu* Carson, 1969). At least three parallel inversions appear to have exactly coincident break-points: these are inversions 2Rb, 2Rc and 2La. The hypothesis presented by Coluzzi et al. (1979) about transfer of these rearrangements from one species to the other by introgressive hybridization via fertile hybrid females has been experimentally tested. *An. arabiensis* Xbcd, 2Rab, 2La, 3Ra/+, 3L was crossed with *An. gambiae* s.s. Xag, 2R, 2L, 3R, 3L. The F1 hybrid females were backcrossed with males of either parental strain and subsequent generations were scored for female polytene karyotypes. Each type of progeny showed a tendency to stabilize the chromosomal constitution of the parent used for the backcross. The heterospecific X chromosomes were lost very rapidly, being practically absent from the sample already at F3. The heterospecific autosomal arrangements were decreasing in frequency up to values lower than 10% at F6, eventually disappearing in subsequent generations. The only exception refers to the 2La arrangement in the backcross with *An. gambiae* s.s. This produced a strain showing the same polytene sequence of the parental *An. gambiae* s.s. but with a stable 2La inversion polymorphism (2La=50%) acquired from *An. arabiensis*.

RAMET SURVIVAL IN CLONAL FRAGMENTS OF A PHALANX PLANT SPECIES (*Drosera intermedia* Hayne).

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One of the possible adaptive values of clonal propagation is the reduction of genet mortality risks as new ramets are being produced. This benefit can only occur if the fate of one ramet is independent of the fate of other ramets of the same genet. Demographical data of two *Drosera intermedia* populations, a perennial herbaceous species with a conspicuous phalanx growth form, were used to test for independence of ramet survival within clonal fragments. Over a three year period, the number of clonal fragments of which all the ramets showed the same behaviour (i.e. they all survived or died) deviated significantly from the expected number calculated under the hypothesis of statistical independence, in only one winter period in one population. This suggests that in a plant species with a phalanx growth form, in which the ramets of a clone remain close to each other, these ramets can suffer independent mortality. *D. intermedia* is, however, probably not a typical phalanx species because, although they remain close to each other, the ramets become morphologically separated early in their lives. The question remains if independent mortality and physiological integration are compatible. If not, then the benefits of integration outweigh those of risk spreading in phalanx species.

INTRASPECIFIC MOLECULAR PHYLOGENIES OF MITOCHONDRIAL DNA REVEAL PATTERNS OF COLONIZATION OF SOUTH-WEST EUROPE BY *MUS SPRETUS*

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DNA sequencing data of the mitochondrial DNA (mtDNA) D-Loop region of mice captured over the whole geographic range of *Mus spretus* are compared with Restriction Fragment Length Polymorphism (RFLP) analysis of total mtDNA from the same individuals. The RFLP results show a network of different variants suggesting the presence of three main morphs, one dispersed over south-Europe and north-Africa, and two typical of north-Africa. There are rarer variants that are easily linked to the main morph of their geographic region. However, the sequence data obtained by direct single-strand sequencing after Polymerase Chain Reaction (PCR) show that the variations within the three main RFLP morphs are not the same depending on their geographic origin. The higher variations in Morocco suggests this is the diversification area for this species. These results support the hypothesis that *Mus spretus* colonized South-Europe from North-Africa and the sequence data allows us to measure the decrease of polymorphism due to the founder effect that accompanied this colonization.

This study also shows that the D-Loop is evolving faster than the whole mtDNA and that it contains a small region of 150 nucleotides which is hypervariable. The observed mutations are essentially substitutions with a bias toward transitions. Only a few insertion or deletion events occurred.

P12

MITOCHONDRIAL PHYLOGENY OF SCHISTOSOMES

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Schistosomes are tropical endoparasites that infest man and several other vertebrates. Although different species have been described on morphological and epidemiological criteria, experimental hybrids are easily obtained. This raises the question of the real taxonomic status of these so called species.

The mitochondrial molecule is particularly convenient for phylogenetic studies because of its clonal evolution (maternal transmission).

We have already characterized by RFLP the mitochondrial DNA of two species: *S. mansoni* and *S. rodhaini*. Their restriction patterns differ for at least two enzymes. But the scarcity of the material does not allow us to apply RFLP to natural populations.

More sophisticated molecular tools, as specific labelled probes, and PCR (Polymerisation Chain Reaction), will allow us to study the genetical variability of schistosome mtDNA at an individual level, and to quantify the divergence between different species or, at an intraspecific level, between geographically distant populations.

S8

RAPID EARLY EXPANSION OF THE HUMAN POPULATION DETECTED BY MITOCHONDRIAL DNA ANALYSIS

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By sequencing a hypervariable part of the mtDNA in more than 200 individuals, we were able to examine the pattern of branching in the genealogical tree and thus to estimate rates of population expansion at various stages in human evolution. The growth rate increased enormously, reaching a peak roughly half way between the root and the twigs and then declined dramatically. Most of the mtDNA types show a high degree of regionalism, only a minority of the cases of identical types are shared by individuals from different populations. The observed distributions of times to common ancestry in these populations are significantly different from expectations based on inbreeding theory applied to neutral alleles indicating that the probability of mtDNA lineage survival has not been steady through time. It is well known that population expansion strongly influences mtDNA lineage survivorship and the mean sequence difference within a population is proportional to the time when the expansion occurred. Therefore, the mean sequence differences within populations are a useful tool to trace the history of the dispersal of human populations. The non random branching pattern of the phylogenetic tree and the within population sequence differences observed in Cann et al., 1987 suggest similar conclusions for the world populations and the pattern of population expansion is in good agreement with our results.

S6

Cyclomorphosis in cladocerans: the paradigmatic reaction norm

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Species in several groups of animals show cyclomorphosis: a seasonal variation in form. Cyclomorphic organisms include certain freshwater ciliates, algae, rotifers, and cladocerans, and certain intertidal snails, barnacles and bryozoans. The morphological responses are due to a mixture of seasonal succession of genotypes and to phenotypic plasticity of individual genotypes. In many cases, cyclomorphosis is an adaptation to predation. Morphological changes associated with cyclomorphosis confer some protection against predators, often specific predators. In most, perhaps all, cases the morphological defenses are induced by the actual presence of predators, via a chemical signal. The predators of cyclomorphic species are active only part of the year, cause significant mortality, and are shape and size selective. Curiously, the great majority of examples of cyclomorphosis occur in aquatic or intertidal habitats. We do not yet understand why cyclomorphosis is an uncommon predator defense, in the vast majority of organisms, including insects, arachnids, vertebrates, and higher plants.

S5

Habitat spatial structure and population extinction risk.

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not received

S1

Herbivory and the problem of co-evolution: the interdependence of vegetation and grazing animals exemplified by *Branta* geese.

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Ongoing studies of two *Branta* geese (Barnacle goose *B. leucopsis* and Brent *B. barents*) centre around the problem of how these two arctic-breeding species manage to balance their annual energy budgets. Two periods emerge as bottlenecks: 1) spring migration which brings the birds into a still inhospitable environment and thus implies bridging a nutritional gap of at least six weeks in addition to direct cost of flight 2) fall migration which follows on the heels of the annual moult. Crucial to the approach is the ability to follow the fate of individually marked birds through the years, a co-operative programme with the Wildfowl and Wetlands Trust. Case histories collected so far confirm that successful breeding in the arctic is only possible for individuals achieving adequate body condition at the spring staging grounds, and a causal explanation of how these individual differences arise will be attempted. On the second point, current work on Spitsbergen indicates that the vegetation immediately surrounding the Tundra Lakes to which the geese are restricted during the moult is the limiting factor setting the capacity of the breeding grounds. Here too, competition is intense and not all families achieve the body condition needed to reach the wintering grounds in western Europe. Recent experiments substantiate the feed-back loop between geese and the vegetation they exploit (nutrient recycling) and lead to the speculation that the birds are manipulating their food resources, albeit within limits. Quantitative models relating food choice to body mass change underline the dependence of geese on their food supply, and the question of long-term impact on the vegetation enhancing food on offer will be touched on, the crux of co-evolution.

C7

REPRODUCTIVE STRATEGY AND SENESCENCE IN TWO GENOTYPES OF DAPHNIA CUCULLATA.

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I collected life history data in the laboratory on two clone groups of Daphnia cucullata distinguished by the GPI locus ('FM' & 'MM' genotypes). FM neonates and adults aged 10 to 21 days were larger than MM animals of the same age. MM animals grew faster than FM animals from 16 to 30 days. The increase in body length and width within any age class depended on total body size and differed between groups. The brood intervals were shorter in MM. The egg ratio in animals younger than 16 days was smaller in MM clones, for older Daphnia, the egg ratio was smaller in FM clones. It is suggested that this decrease in egg ratio in the FM genotype which produces more eggs until day 16 implies a 'cost of reproduction' and can be explained by Williams' hypothesis of pleiotropic gene action on senescence.

S1

NATURAL AND SEXUAL SELECTION IN POECILIA RETICULATA: EFFECTS OF PREDATORS, VISION, AND LIGHT

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Guppies (*Poecilia reticulata*) are small Poeciliid fishes native to small rain forest streams in north-eastern South America. They live in fish communities ranging from those in which there is only one weak predator to communities in which there are many predators which are dangerous to guppies, and this results in visually-mediated gradients in natural selection along the lengths of the mountain streams. The colour patterns of guppies are used to escape predation, but also are used in sexual selection. As a result a male colour pattern cannot be too "bright" or it will result in predation, and it cannot be too "dull" or it will result in few or no matings by the male. A series of field and greenhouse experiments demonstrates the dynamic balance between sexual selection and predation on guppies.

Since most courtship takes place early and late in the day, whereas most predation takes place in the middle of the day, the ambient light conditions are very different during courtship and predation. Both the intensity and colour of light is different during sexual selection and predation, and as a result the brightness and colour contrast is different at these times, and it is different in such a way that the same colour pattern may be relatively "dull" during predation risk and relatively "bright" during courtship.

The differences in "brightness" during courtship and predation risk due to variation in ambient light colour are enhanced by the differences in colour vision between guppies and their major predators.

S3

POPULATION GENETICS AND DYNAMICS, AND WHOLE PLANT PHYSIOLOGY OF METALLOPHYTES: INTERACTIONS WITH EVOLUTIONARY BIOLOGY

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Silene vulgaris (= *S. cucubalus*) will be used as example how principles of cellular compartmentalisation and within-plant (re)translocation are the background processes for the evolution of metal resistance in plants. Whereas zinc and nickel are mainly accumulated in the vacuole, cadmium resistance is associated with the binding of Cd to phytochelatins. Copper resistance is related to changes in biomembranes and binding to metalloproteins. The consequences of the various kinds of metal resistance will be highlighted for the individual plant.

For the access of herbivorous insects to the various parts of metal resistant plants the metal concentration in leaf, stem and root tissue is obviously too high for insects, whereas the low metal concentration in capsules and seeds does not hamper the development of semivivorous insects, as long as the diameter of the capsule is not changed as response to predatory pressure.

The genetic variability of the often geographically and ecologically isolated population will be discussed in relation to the above-mentioned processes.

C1

AUTUMN FOOD SUPPLY AND POPULATION DENSITY IN THE EUROPEAN NUTHATCH - AN EXAMPLE OF PROSPECTIVE RESOURCE DEFENCE

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The European nuthatch (*Sitta europaea*) is a passerine bird that maintains territories the year round. During winter it mainly relies on seeds, i.e. a non-renewing food source.

Natural fluctuations in autumn population size of nuthatches in central Sweden were positively correlated with the size of the hazelnut (*Corylus avellana*) crop, an important winter food. To study the influence of the autumn food in more detail, two marked populations of nuthatches were closely followed during five years and three large-scale feeding experiments were performed. During each experiment, sunflower (*Helianthus annuus*) seed was liberally provided from June through November. Thus, supplementary feeding was terminated before the onset of winter, which is the season of food scarcity, and the experiments mimic autumns with good seed crops. Therefore, the effects on the populations were caused by social behaviour rather than direct competition for food and subsequent starvation.

Population density in autumn increased by about 85% when food was added, and the correlation with the hazelnut crop disappeared. At the same time, mean territory size decreased about 40%.

C5

STRATEGIES OF PHENOTYPIC VARIATION IN AN ANNUAL SELF-POLLINATING PLANT

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The wild tetraploid wheat *Triticum turgidum* var. *dicoccoides* was studied in different habitats of a native site during a five-year period. Self progenies of plants from fixed sampling points were each raised in a variety of nursery environments. Their study provided us with an insight into diverse strategies employed by this taxon to meet changes in the environment. Each of the different habitats appears to be occupied by numerous electrophoretically detectable genotypes. However plants derived from a given habitat are markedly similar in certain quantitative morphological and phenological traits. Some of these, e.g. leaf width or time of first awn appearance, are modulated by growing conditions but maintain their provenance specific position relative to phenotypes derived from other origins. Other traits, especially those dependent on availability of resources, change greatly with the ambient growing regime and lose their provenance specificity in certain environments. This is shown for the traits: tiller number, distribution of biomass over tillers, and the spike to tiller ratio. Implications for mechanisms of plasticity in a species with few heterozygous loci are discussed.

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SUMMARY

DNA hybridization techniques have recently revealed the exact nature of human mitochondrial DNA (mtDNA) polymorphism. Unfortunately, this polymorphism has only been studied on small or heterogeneous samples, not always representative of real populations. The required size of a sample is studied here as a function of the number of nucleotides effectively surveyed in molecular analyses, using the sampling theory of neutral alleles in populations at equilibrium. When reconstructing type phylogenies, sample sizes must be much larger for mtDNA than for classical genetic markers, due to a high mutation rate of the mitochondrial genome. Evolution of human mtDNA is also studied at a population level. It is found that most available samples present an artificially reduced molecular diversity. It follows that the conventional genetic distances computed from mtDNA type frequencies are not proportional to population divergence times. Thus, current data on mtDNA cannot be used to safely infer the history of human settlement.

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When selection is made in one environment, the performance assessed in another, different, environment is a correlated response. The correlated response depends on individual differences in environmental sensitivity (reaction norm), and differs according to the direction of selection. Theory predicts that the best all-round performance, the average of both environments, will be achieved by selection in an environment unfavourable to the character selected.

The theory will be outlined and published experiments will be reviewed to see how far they support the theory.

P11

Life history strategy of *PROASELLUS COXALIS* Dolf. in Tevere river (Rome).

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The key life history traits are the brood size, the age at first reproduction, the reproductive effort and the adult mortality. The general theoretical problem is to predict which combinations of traits will evolve in organisms living in specific circumstances (Lewontin 1965, Stearns 1976).

Proasellus coxalis showed a circummediterranean geographical distribution and since 1970 it is spreading towards the North (Fano 1977, Herhaus 1977).

We studied the biological characteristics of a Tevere population of *Asellus aquaticus* sympatric with the prevailing competitor *P. coxalis*, in order to explain the numerical supremacy in this biotope of *P. coxalis* on *A. aquaticus*.

The results show that *P. coxalis* has:

- a greater clutch size than *A. aquaticus*
- a smaller age at the first reproduction
- a smaller reproductive effort (shorter time of development from eggs to larvae in the maternal brood pouch)
- a survival curve of II type (Slobodkin 1962)

These data explain the numerical supremacy of *P. coxalis* on *A. aquaticus* in Tevere river and according to the hypothesis of Mertz (1973) also its geographical expansion.

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C11

LOCAL AND CLINAL GENETIC VARIATION BETWEEN HOST RACES OF *RHAGOLETIS POMONELLA* (TEPHRITIDAE:DIPTERA)

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It has been proposed that speciation in host specific parasites may be initiated in sympatry when populations shift to new hosts. The recent shift of the apple maggot fly, *Rhagoletis pomonella* from its native host hawthorn (*Crataegus spp.*) to introduced, domestic apple (*Malus pumila*), provides a direct test of the "sympatric speciation" hypothesis by indicating whether partially reproductively isolated host races can evolve in the absence of geographic isolation. We report finding significant allele frequency differences for six allozymes between paired apple and hawthorn infesting populations of *R. pomonella* from across eastern North America. Latitudinal allele frequency clines exist among both apple and hawthorn populations, however, for a majority of loci displaying racial differences. Inter-host genetic differentiation is therefore superimposed on clinal patterns of variation within races such that the magnitude of host associated divergence is a function of latitude. The results indicate that host associated races can form in sympatry and implicate differences in host plant recognition and developmental timing related to ambient temperature as key factors restricting gene flow between apple and hawthorn populations. Some of the same processes differentiating apple and hawthorn populations at sympatric sites also appear to be occurring within the two host races across their respective ranges. *Rhagoletis pomonella* populations are therefore diverging with respect to both their host plant affiliations and local environmental conditions.

STUDIES ON THE FERTILIZATION OF SWEET CHESTNUT (*Castanea sativa* Mill.) AND THE POSSIBILITIES OF NON-RANDOM POLLINATION.

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In sweet Chestnut (*Castanea sativa* Mill.) the offspring from six controlled crosses were analyzed by means of starch gel electrophoresis. Zymograms were observed at gene loci for which the female parent was homozygous and the male parent heterozygous, so that the male gametic contribution is identifiable in each seed. This procedure was necessary to analyze the possibility of non-random mating due to incompatibilities or competition between different pollen types. Results show four cases of non-random pollination. This can be explained with some kind of competition between genotypically different male gametes. Other controlled crosses were carried out to compare the effectiveness of the same pollination on two different female parent trees having the same genotype for the loci AP-A and PGI-B but different flowering habits. The first one was chosen among a sample of grafted trees characterized by a complete male sterility; the second one with normal production of female and male flowers. The male sterility of the grafted trees of the cultivated variety "marroni" is well known, although its biological causes and significance have not yet been explained. In this study both parent trees were pollinated with the same pollen collected from different individuals and used separately as well as in a mixture. Results show that no difference in seed production from the grafted and the wild female parent tree can be detected with this kind of pollination at the two analyzed gene loci.

P8

EFFECTS OF PREDATION RISK ON FEMALE MATE CHOICE IN THE SAND GOBY, *POMATOSCHISTUS MINUTUS*.

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Males of the sand goby, *Pomatoschistus minutus*, build nests under mussel shells on shallow marine bottoms. They attract females to spawn in their nest and then guard the fertilized eggs until hatching. An experimental study was carried out in order to look at female mate choice in situations with and without a predator present. Gravid females were allowed to choose between two males with artificial nests in one-way mirror aquaria. High predation risk was simulated by putting a cod in an aquarium next to the female compartment. Females were found to prefer larger males over smaller ones. But when a predator was present no significant preference was found. The choice of individual females are thus plastic and show variability depending on the circumstances. Conflicting demands and stress situations force the females to make trade-offs between different behaviours. High predation pressures could put constraints on mate choice in the wild.

FOUNDER EFFECTS IN COLONIZING POPULATIONS: THE CASE OF *DROSOPHILA BUZZATII*

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Founder effects have been considered as indication of the speciation potential of a colonizer. Some cosmopolitan species, like *Drosophila buzzatii*, have been qualified as colonizers that do not fulfill the necessary requisites leading to significant speciation changes. However, there has never been a thorough approach to study the founder effects in these species. This work is intended to analyze some of the genetic changes that have accompanied *D. buzzatii* colonization from its South American original localities to its new territories in the Mediterranean area. These studies comprise the chromosomal and the allozyme polymorphisms, and the assessment of the fitness components. Chromosomal and allozyme polymorphisms have changed during colonization, but in a different way. Overall, the former has not diminished, except in some marginal colonized populations. In fact, some rearrangements have substantially increased their frequency and contributed to a higher colonizing polymorphism. On the other hand, the latter shows less gene diversity in colonized areas, but mostly due to the loss of rare alleles. Fitness components have experimented a reweighting in their pattern of endocyclic selection. Some components, such as fecundity, seem to operate in a similar way in original and colonized populations, but other components, e.g. viability, have changed their way of action. Many of these changes can be explained by founder effects, although adaptive changes may also be involved. Since there is no ground to think of any speciation process in *D. buzzatii* colonization, these results cast serious doubts about the sufficiency of founder effects to promote speciation by colonization.

P2

Biochemical characterization of an enzymatic system implied in insect resistance to organophosphates: the glutathion-S-transferases.

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Insect resistance to organophosphate insecticides often results from increased detoxication by several enzymatic systems. For example, in *Musca domestica*, resistance due to an increase in glutathion transferase activity is well established. We present here the biochemical characterization of this system which is not well understood in invertebrates, despite its importance in the molecular genetic analysis of resistance.

In Diptera (housefly, *drosophila*) these enzymes are usually homodimeric and can be subdivided into at least two families according to their molecular weight and their isoelectric point: this insect enzymatic system seems as complex as the mammalian one. Antibodies raised against the isoenzymes allowed us to try to find the molecular forms involved in resistance. With the probes obtained we expect to see differences between susceptible and resistant strains.

Furthermore, the fact that these enzymes can be found from bacteria to man with almost no sequence homology but with a high function conservation raises interesting questions about the evolution of this genic superfamily.

TAXONOMIC DIVERSITY: A SEARCH FOR PROCESSES BEHIND THE PATTERN.

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Several authors (e.g. Willis, 1922; Dehalu & Leclercq, 1951; Walters, 1961, 1986; Clayton, 1974; Dial & Marzluff, 1989) have studied the size distributions of subtaxa within higher taxa. These distributions are generally interpreted as a mixture of (a) actual diversity patterns mostly dependent on speciation and extinction rates and (b) arbitrary classification schemes, i.e. tradition and practical requirements.

We have studied the frequency distributions of genus size (as species number) for 104 taxa of different rank and size. For all taxa, data strongly suggest a power law $N(x) = ax^{-b}$ where $N(x)$ is the number of genera with x species. The parameter a , acting as a scaling factor, predicts the number of monotypic genera; the parameter b accounts for the steepness of the curve; the values determined for different taxa are very close each other (mammals: $b = 1.6$; birds: $b = 1.5$; tapeworms: $b = 1.4$).

Unlike previous analyses on taxonomic diversity, we find that our distributions are strongly characterized by the relative abundances of the genera with 1, 2, 3, ... 10 species each, i.e. by the frequency distribution of the smallest and most isolated clusters of species, thus possibly suggesting taxon-specific evolutionary parameters as frequency of adaptive shifts, and/or speciation.

C11

MATING EXPERIMENTS BETWEEN DROSOPHILA PSEUDOOBSCURA FLUSH-CRASH POPULATIONS OF DIFFERENT BOTTLENECK SIZES

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Some results are reported on multiple-choice mating experiments carried out over a set of flush-crash *Drosophila pseudoobscura* populations. The flush-crash protocol has been developed through more than 4 years and 8 cycles. There are populations with 1, 3, 5, 7, and 9 pairs of flies as founders at the beginning of each flush-crash cycle. Besides that, control ancestral populations have been maintained under usual laboratory conditions.

Sexual selection indexes have been applied to the data. There are several cases of significative assortative mating. They correspond almost exclusively to mating experiments implying derived populations, not between derived and ancestral populations. A few populations show a relatively high proportion of such assortative matings. They all are populations of small bottleneck sizes, say 1 and 3 pairs.

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THE RELATIONSHIP BETWEEN REACTION NORMS AND ENVIRONMENTAL TOLERANCE

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The optimal breadth of adaptation can be predicted from within-generation and between-generation variability and from spatial heterogeneity of the environment by assuming that the tolerance curve of each individual is determined by two complex quantitative characters: its optimum on the environmental scale and its width. If an organism is, in addition, able to direct partially the expression of the genotype during development by recognizing some environmental cues, its environmental tolerance can be enhanced by exploiting a reaction norm. The selective advantage of evolving such reaction norms is calculated depending on the environmental conditions. If the variability of the environment between generations is larger than the expected variation within a generation, there is a strong selection pressure to evolve a reaction norm for the setting of the optimum of a tolerance curve.

P10

QUANTITATIVE GENETICS OF EXERCISE PHYSIOLOGY IN *Mus musculus*

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Physiological ecologists often study adaptation, but the genetic basis of most physiological traits is poorly known. Hence, we have initiated quantitative genetic analyses of selected whole-animal physiological traits and some suborganismal determinants in a randombred line of *Mus musculus* (ICR/HDS). We are studying elements of locomotor performance and activity metabolism because of their ecological relevance. We will estimate narrow-sense heritabilities (h^2) of body mass, maximal sprint running speed, swimming endurance, basal and maximal rates of oxygen consumption, and several underlying characters (e.g., hemoglobin levels, heart mass, gastrocnemius muscle mass), using a combined parent-offspring, full-sib/half-sib breeding design, with crossfostering.

Our second goal is to estimate genetic correlations (the result of pleiotropic gene action) and relate these to hypotheses concerning the evolution of metabolism and performance. These hypotheses involve the concepts of "trade-offs" and "constraints." Significant genetic correlations indicate that selection on one trait will necessarily result in correlated responses in others. We will test whether there is a negative genetic correlation between capacities for speed and stamina (suggesting an evolutionary trade-off) a positive genetic correlation between $\dot{V}O_{2\max}$ and BMR ("aerobic capacity model" for the evolution of endothermy), and whether locomotor capacities correlate with body mass (is bigger better?).

C13

DUPLICATIONS AT THE *Adh* LOCUS AS A TOOL FOR TRACING EVOLUTIONARY RELATIONSHIPS WITHIN THE TRY-PETINAE (DIPTERA TEPHRTIDAE)

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The number of loci controlling the alcohol dehydrogenase enzyme (*ADH*) can be used as a distinctive synapomorphic character of the Trypetinae subfamily. Alcohol degradation is controlled by a single gene in *Dacus oleae* (subfamily Dacinae, Tephritidae) and in the protorhagoletis *Rhagoletis striatella* (subfamily Trypetinae). In contrast two loci control the *ADH* function in 22 other *Rhagoletis* species, in *Ceratitis capitata*, *Trirhithrum coffeae*, *Ceratitis rosa*, *Capparimyia savastanoi* and in the *Anastrepha fraterculus* complex. In *Anastrepha obliqua* three loci are involved. In *C. capitata* the two loci are regulated in a very clear tissue specific manner. However in *T. coffeae*, *C. rosa* and *C. savastanoi* this tissue-specific regulation is somewhat "looser". The enzymes coded at the two *Adh* loci do not form heteropolymers in these four species, indicating advanced biochemical divergence between the two gene products, which suggests a long evolutionary history of independent functions of the duplicated loci. We stress however that the only direct genetic evidence for duplication at *Adh* locus comes from *C. capitata* where it has been clearly shown that the two loci are very tightly linked (0.49 cM).

P3

ECOLOGICAL AND MOLECULAR DATA ON THE SPECIES PROBLEM IN THE *EUPLOTES CRASSUS-VANNUS-MINUTA* GROUP (CILIOPHORA, HYPOTRICHIDA).

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The problem of the systematic relationships among the 3 "classical" marine morpho-species of this group is still unsettled. The smaller *E. minuta* is now almost unanimously regarded as a good separate taxon, but only some authors consider *E. vannus* and *E. crassus* as 2 distinct biological species, while for others they form a complex of 5 sibling (i.e. morphologically indistinguishable) species.

In the present report we discuss data on morphologically characterized strains, obtained using different approaches: autoecological characterization (salinity and temperature tolerances); rDNA restriction enzyme mapping; isoenzyme electrophoretic pattern analysis (only *E. crassus* strains).

The 3 morphospecies were proved to display quite distinct salinity and temperature tolerances as well as different rDNA maps, supporting the idea they really constitute 3 separate taxonomic units. All the strains belonging to the same morphospecies showed homogeneity in these characteristics with one exception: 2 sets of *E. crassus* strains behaved differently in low salinity tolerance tests. These 2 sets proved to be intrafertile and intersterile, and to show differences in 3 out of 5 isoenzyme patterns analyzed. Hence, our results suggest the existence of effective reproductive barriers within at least one of the 3 morphospecies.

C5

INHERITANCE OF REACTION NORMS FOR LIFE HISTORY TRAITS IN *DROSOPHILA*.

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6 stocks of *Drosophila melanogaster*, derived from a natural population and made completely homozygous with chromosomal balancers, were crossed in all 36 possible ways. Developmental time and dry weight at eclosion were measured in nine environments (22, 25, 28 °C; 0.5, 1, 4 % yeast concentration). The slopes and intercepts of the reaction norms along the environmental gradients were measured using linear regression on the double log transformed data. Genetic and environmental variance components were estimated for the traits within environments and for the regression parameters. Heritabilities were generally low (< 10 %) for both traits. The relative magnitudes of the variance components were affected by the environmental variables and could be predicted based on the genetic variances of the regression parameters. This is taken as evidence that a heritability of reaction norms can be defined as the additive genetic proportion of the variance of slopes. This measure could be used in models of the evolution of phenotypic plasticity.

S5

POPULATION VIABILITY ANALYSIS: THE PROBLEM OF THE META-POPULATION

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Population viability analysis (PVA) leads to a prediction of the probability of extinction of a population by the end of a set period of time, typically 100 years. Shaffer's early analysis emphasized genetics, environmental and demographic stochasticity, and catastrophes. Spatial fragmentation, yielding a metapopulation structure, impacts and confound all of these, and such spatial structure can often be of overriding importance. We review several examples.

S5

THEORY AND PRACTICE OF EXTINCTION RISK EVALUATION

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Reasonably well developed methodologies exist for assessing the risk of extinction for a single biological population. But most species do not exist as single populations in nature. Usually there are several populations that are either isolated from each other or that exchange a limited number of individuals. Understanding the link between population extinction and species extinction has obvious practical implications for predicting the fate of species under anthropogenic impact. Factors that affect population extinction are the population's size and age structure, life history parameters, demographic and environmental stochasticity that cause variation in these parameters, and the correlations among life history parameters within populations. Species extinction risk depends on all these, plus other factors that describe interactions among the populations, including how many populations there are, the correlations of environmental conditions they experience, and the migration that leads to recolonization of locally extinct populations.

Having multiple independent populations lowers the risk for the ensemble, but having low abundances at each site increases the risks of extinction for each of the populations. Geographical proximity allows migration and potentially recolonization, but it can also result, because of similarity in environmental patterns experienced by the populations, in their behaving as one population with respect to stochastic environmental changes and thus increase the risk that all will be lost. These trade-offs and other complexities in the relation between population and species extinction probabilities, prevent our making unconditional generalizations about whether a particular management strategy will increase or lower overall extinction risks.

W1

SCATTERED CLINES IN A HYBRID ZONE: A STUDY OF ACOUSTIC AND BIOCHEMICAL VARIATION IN THE *Geocrinia laevis* COMPLEX

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The two Australian frog species, *Geocrinia laevis* and *G. victoriana*, are very similar in morphology and ecology. Despite having distinct advertisement calls, and experimentally demonstrated female preferences for conspecific calls, they form narrow hybrid zones in two separate contact areas of their ranges. Analysis of allozymic variation across the northern part of the longer contact zone showed that stepped clines at two marker loci coincide roughly with the transition determined by acoustic studies, while clines at two other marker loci are displaced to opposite sides of the hybrid zone. This pattern of scattered clines suggests that different components of the genome respond independently to selection pressures along an environmental gradient. Possible consequences of the differentiation in the acoustic communication system for the genetic dynamics of the hybrid zone are discussed.

C8

THE EVOLUTION OF PHENOTYPIC PLASTICITY IN A TWO-LOCUS, TWO-ALLELE MODEL IN ALTERNATING ENVIRONMENTS

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A two-locus, two-allele model of natural selection in a temporally varying environment is analyzed to study the evolution of phenotypic plasticity. One locus controls the mean expression of the phenotype while the second locus controls the environmental sensitivity of an individual. The conditions which are most favorable to the evolution of phenotypic plasticity are when the optimum phenotypes are more extreme than those present in the population. When the optimum phenotypes are within the range of phenotypic expression of the population, evolution is more complicated. The final equilibrium phenotype and the plasticity of the population may depend on: linkage, initial conditions and the strength of selection. Natural selection does not always move the population towards the optimum phenotype. In fact, it is possible for evolution to cause the population to move away from the optimum phenotype.

C1

BEHAVIORAL FLEXIBILITY AND THE FORAGING ECOLOGY OF SEED-EATING ANTS

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In an ant colony, behavioral flexibility occurs at several levels of organization. Within a colony, individual workers change tasks when environmental fluctuations cause changes in the colony's need for nest maintenance work, patrolling, or foraging. Groups of workers engaged in one task modulate their own activity depending on events affecting other task groups. At the colony level, decisions about where to forage depend on interactions with neighboring colonies, and on the abundance and variability of food sources. Flexibility also occurs at several timescales. From one hour to the next, worker groups respond to experimental perturbations. From one day to the next, interactions between neighboring colonies may develop into long-term conflict, depending on food availability. From one year to the next, both the internal dynamics of colony behavior, and the status of relations between neighboring colonies, change as colonies grow older. Compared to younger (2 yrs old) colonies, older (5 to 15 yrs old) colonies react to disturbance more homeostatically, and are more likely to avoid conflict with neighboring colonies.

Colonies vary in their behavioral flexibility, which affects their foraging success and thus their capacity to reproduce. What role does variation among colonies in behavioral flexibility play in the evolution of their social organization?

GENETIC DIFFERENTIATION IN INTERSPECIFIC HYBRIDS BETWEEN *D.mauritiana* AND *D.simulans* SIBLING SPECIES.

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The rare fertile interspecific hybrid Masi-2 (Goulielmos and Alahiotis, Genome 32(1):146-154, 1989) obtained from a *q.mauritiana* x *simulans* ♂ cross was examined for various fitness components, several generations after its construction. Each species and the hybrid was found to exhibit characteristic values for fecundity, fertility, viability, developmental time and oviposition rhythm while the sex ratio in the hybrid deviated from the normal ratio. Enrichment of Masi-2 genome with genome from *simulans* or *mauritiana*, showed gradual genetic differentiation in terms of the percentage successful matings with either parent, while the coadaptation rhythm was found to be depended on the species genome added. Analogous situation is also true when we take into consideration the generations passed after the construction of Masi-2. Parallel experiments using *Sima* (♀ *simulans* x *mauritiana* ♂) hybrids enriched by genome from each parent, under various environmental regimes, show species-specific and temperature-dependent coadaptation rhythms. The observed genetic differentiations and the gradual evolution based on population dynamic implies that macroevolutionary changes can be controlled by mechanisms responsible for microevolutionary ones, while the multifactorial mode of reproductive isolation is also supported.

RIBOSOMAL RNA SEQUENCES SUPPORT THE DIVISION OF ALL LIFE FORMS IN THREE PRIMARY LINEAGES

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Determining the number of existing primary lineages of life is a fundamental issue for understanding the early steps of evolution. This question has been investigated using molecular phylogeny techniques applied to the highly conserved ribosomal RNAs. Two opposite views have been expressed. From analysis of the small subunit (SSU) rRNA, Woese and co-workers proposed that there are three primary lines of descent: eubacteria, archaebacteria, and eukaryotes. Later, sequencing by Leffers et al. of the large subunit (LSU) rRNAs from three archaebacteria (an extreme thermophile, an halophile, a methanogen) was interpreted as supporting the same universal phylogeny. A conflicting view has been proposed by Lake, initially from reasons rooted in differences between thermophile and halophile ribosomes in three dimensional structure, and recently after a molecular phylogeny analysis of SSU rRNA using the evolutionary parsimony (EP) method. Lake proposes to define two groups: a proto-eukaryotic group made of eukaryotes and thermophiles, and an essentially prokaryotic group containing eubacteria, halophiles, and methanogens. We sought to solve this controversy by evaluating the efficiency of tree-making methods for recovering early divergences. We report that rRNAs strongly support the division of life forms in three primary groups. All three methods employed (pairwise distance, maximum parsimony, EP method with either the LSU or the combined SSU+LSU rRNAs) support this view. By simulating the divergence of sequences according to an evolutionary process similar to that found with SSU rRNA, we have shown that the EP method is much less efficient than the distance method in recovering the true tree. The conflicting results of the EP method between SSU and LSU rRNAs probably derive from this method being highly sensitive to unequal rates of transversion substitutions.

GENETIC RESOURCES: NEUTRAL VERSUS SELECTED POLYMORPHISMS

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Evolutionary genetics on one side and Plant and animal breeding on the other, have shown, around the years 70 a remarkable convergence. Evolutionists have tried to explain how could natural processes have increased the diversity of living forms (within and among species) over evolutionary times while applied geneticists were looking for systems which would allow them to maintain the diversity of their populations under selection.

Remarkably, these two questions have in general not been linked. As a result, plant and animal breeders have defined their problem as the problem of maintaining a preexisting variability; the idea that a new one could arise from a good population management does not seem to have been considered.

This paper tries to show (1) that a common reflexion about the problems of evolution in the wild and in cultivated populations could be very useful and (2) that it is already possible to say that the problem of maintaining diversity in artificial populations cannot be treated simply by thinking in terms of neutral polymorphisms. The rules maximizing the amount of variability are certainly not the same on these two types of polymorphism and thus, instead of pretending to solve all problems by treating neutral polymorphisms, it could be more efficient to try to distinguish the different types of polymorphism and treat them separately.

Gene conservation and the preservation of adaptability

Hans-Rolf Gregorius

Preservation of the adaptability of a resource population is emphasized as an indispensable objective of gene conservation. Therefore, methods of dynamic conservation deserve priority. Adaptability requires the existence of genetic variation that is either adaptively inferior or neutral under the respectively prevailing environmental conditions. On this basis, the significance of genetic load and environmental heterogeneity for the maintenance of genetic variation in gene resource populations is discussed, and some elementary principles to be considered in gene conservation are pointed out. It is suggested that criteria for the determination of resource population sizes be oriented at the loss of genetic variation that can be tolerated over a specified number of generations as a consequence of random genetic drift. A model taking account of this aspect is presented, and the population sizes resulting for different systems of reproduction are computed.

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In Scots pine there is evident clinal differentiation in adaptively important quantitative characters such as bud-set phenology of seedlings during their first growing season (Mikola 1982). Scots pine is wind pollinated and pollen can be transported over long distances. As the result of considerable pollen migration, there is little variation in allelic frequencies between populations in adaptively neutral characters. Using isozyme loci, the degree of genetic differentiation between populations has been found to be low. G_{ST} values are from 0.017 to 0.029, which means that less than 3 % of overall variation is between the populations (Muona & Harju 1989). We have studied the level of pollen migration in the seed crops of Scots pine seed orchards. The orchards studied are of northern origin and are situated in Central Finland. Sarvas (1970) stated that Scots pine of northern origin flower earlier in Central Finland than the local trees which should prevent pollen immigration to the seed orchards. In contrast to this expectation 30-60 % of germinating seeds were fertilised by pollen from outside the seed orchards. We studied how the timing of female strobilus receptivity of single trees relative to the maximum pollen production in the area affects the proportion of seeds fertilised by immigrant pollen grains.

C12

ESTIMATION OF HOMOLGY: IMPLICATIONS FOR THE METHODOLOGIES OF CLASSIFICATION

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Estimation of homology is a prerequisite for any kind of phylogenetic analysis. Any inference of homology (or analogy) and apomorphy (or plesiomorphy) leads to a phylogenetic statement with a certain degree of likelihood. Accordingly, the final phylogram is a probabilistic approximation of the historic process in phylogeny. Moreover, "evolutionary gaps" correspond with high degrees of probability of the respective stem lineages. Because the phylogram (and not phylogeny) is translated into a classification, these differences in likelihood should be reflected.

The recently proposed clado-evolutionary method of classification combines the advantages of the evolutionary (flexibility) and of the cladistic method (unequivocal retransformation into the phylogram). Taxa and their categories are based on the different degrees of probability in the basic phylogram. This is done by the use of specially marked, so-called *orthophyletic* taxa, paraphyletic groups from which only one descending line is excluded. Otherwise the method follows largely Wiley's conventions.

This classification method enables the incorporation of both aspects, clado- and anagenesis, allows equal treatment of recent and extinct groups, and expresses ancestor--relationships unequivocally. Indeed, there is full congruence of character-weighting, of the phylogram and of the classification, which are all based on the same principle. Thus, the clado-evolutionary method is proposed as a synthesis of the formerly opposing methodologies.

EMPIRICAL COMPARISON OF QUALITATIVE AND QUANTITATIVE APPROACHES IN THE EVALUATION OF PROTEIN ELECTROPHORETIC DATA

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Empirical data sets of Artiodactyla (Antilocapridae, Bovidae, Cervidae, Suidae), Carnivora (Mustelidae) and Rodentia (Sciuridae, Cricetidae, Arvicolidae, Muridae), obtained by horizontal starch gel electrophoresis of 15-34 isoenzyme systems, were used to calculate genetic distances and to construct phylogenetic trees by the following methods: Nei's D (corrected for small sample sizes) - UPGMA; FITCH, KITSCH (out of Felsenstein's PHYLIP-package), Rogers-distance - distance-Wagner tree, maximum-likelihood approach (Cavalli-Sforza - Edwards), maximum-parsimony method (Wagner), Hennigian cladogram. The results were reexamined using the statistical methods of jackknife and bootstrap.

The following problems became apparent and were studied in more detail: inconstancy of molecular evolutionary rate among taxa, inconstancy of evolutionary rate among isoenzymes, possible convergence of alloenzymes, different evolutionary histories of taxa (radiations/bottlenecks), methodological influences (sample sizes/rare alleles, compatibility of data sets).

The results show, that many branches of the various phylogenetic trees are fairly constant. The ambiguous position of the remaining OTU's is due to insufficient evidence in the primary data rather than to the properties of cluster algorithms. However, since these problematic cases are also uncertain in phylogenies based on morphological characters and palaeontological results, even an increased data set may not lead to a clear decision. Molecular evolutionary rate among taxa seems to be accelerated in some cases, possibly due to random fixation of different alleles during bottlenecks, when a highly polymorphic ancestral form underwent a series of rapid adaptive radiations. Isoenzymes can be divided into groups with different evolutionary rates. Thus, data sets are only comparable with respect to genetic variability and differentiation, when they contain a similar amount of representatives of each of these categories.

P7

GENOTYPE X ENVIRONMENT INTERACTIONS FOR COMPONENTS OF FITNESS: A COMPARATIVE STUDY OF ANNUAL AND PERENNIAL GENOTYPES OF *Medicago lupulina*

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We test the hypothesis that the plasticity of annual genotypes is greater than those of perennial genotypes. Here we define the plasticity as adaptation to different environments, and we measure it by the homeostasis of fitness relatively to the maximum in each environment.

Twenty different full-sib families of *Medicago lupulina* (ten annuals and ten perennials) were cultivated in Montpellier. The families were placed in three different artificial environments (one with a cut at flowering, one with interspecific competition (barley), and a control) with two replicates of five plants each per family per environment. The vegetative yield components (growth and dry matter) and the reproductive yield components (flowering date, podding date, length of the flowering and fruiting period, seed set and seed viability) were measured.

Different analysis of genotype x environment interactions will be presented, including genetic correlations between characters within and across environments.

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This is a preliminary account of a thesis-project for the cand. scient. degree (masters), describing the use of shell structures (ultrastructures) in systematics of Archaeogastropoda (Mollusca).

Shell structures are useful in this context because they show good coincidence with established taxa on the family/subfamily level and because variation is sufficient to allow easy identification.

The present study only includes recent material, but it will provide the basis for future studies on fossils. The main reason for using shell structures is that they are present in all recent specimens and in many fossils, providing one of the few character-complexes available in living as well as extinct families. Consequently, it may be possible to get a better description of the phylogeny of all archaeogastropods and, possibly, the more ancient molluscs - the origin of all modern species.

It should be noted that the technique is fairly simple - the main technical requirements being access to SEM and x-ray powder diffraction.

Various types of shell structures will be presented, including all types observed within one family

JOSEPH HELLER

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M. tuberculata ranges from far-eastern Asia into Africa.

Throughout much of its distribution area it reproduces parthenogenetically. In Israel however, males have been found.

Males (easily distinguished from females by their red gonad) have narrower shells than females. Shell size frequencies suggest that males and females have similar life spans. It is as yet unclear why some populations should have males while others lack them.

To investigate whether sex ratios of M. tuberculata are related to environmental factors (frequency of trematode infections, water chemistry or faunal diversity), 34 populations were sampled. Seven of these contained no males, fifteen contained less than 10%, ten had 10-36%, one had 46% and one had 66% males. Male frequency is not related to the infection frequency of trematode parasites. These results do not support the view that sex is favoured by selection resulting from host-parasite interactions. Male frequency is not related to habitat diversity, as expressed by the number of mollusc genera found at a site. Male frequency is negatively related to concentrations of Magnesium, Potassium and Chloride in the water. Very sparse populations lack males.

The two highest male frequencies are found in highly unstable habitats (water bodies that were dry in the last two years). The most stable, predictable habitats have lower-than-average frequencies. These results support the view that sex is related to instability of the environment.

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Heritabilities of fledgling weight and tarsus length of nestlings were measured in a single population during the last three years. Cross-fostering experiments were performed to separate genetic and environmental factors. In contrast to earlier years, food became scarce during the second half of the 1988 breeding season. This influenced fledgling weight and survivorship of nestlings profoundly. Heritability of fledgling weight was moderate under good conditions but zero under food deficiency. At the same time effects due to care-taking of the (unrelated) fosterparents were dominant under food limitation. This pattern did not apply for tarsus length which was still heritable under bad conditions.

Fledgling weight was not neutral, it correlated with local recruitment rates. It is suggested that the evolutionary impact of severe selection may be diminished in traits exhibiting less additive genetic variance under these conditions.

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The accepted dogma, with respect to the effect of bottlenecks on genetic variability, is that as the number of individuals contributing to the next generation diminishes, genetic variability is farther reduced.

In our laboratory, we are keeping a long term experiment, the "flush-crash" protocol. With this procedure we are reproducing population dynamics where the number of individuals increases for several generations after which populations are subject to strong competition and a bottleneck. This cycle is been repeated regularly.

We have kept several Drosophila pseudoobscura lines with this protocol for the past 4 years, and we have used five different bottlenecks sizes (1, 3, 5, 7 and 9 couples). Besides, we have kept the ancestor strains with normal laboratory maintenance conditions.

Several quantitative traits, most of them morphometric and abdominal bristle numbers, are been scored both in the "flush-crash" lines and in the ancestral ones. Parents and their offspring (two sons and two daughters) have been measured under controlled density conditions in order to estimate genetic components of the variance.

Preliminary results of these experiments are presented and discussed.

P3

PHYLOGENETIC INFERENCE IN *Triturus* (Amphibia:Urodela) BY C-BANDING PATTERNS ANALYSIS.

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C-banding patterns of nine species and two subspecies of *Triturus* were used to determine phylogenetic relationships by means of maximum parsimony methods.

This analysis suggests that: i) the established subgenera (*Mesotriton*, *Paleotriton* and *Neotriton*) form a monophyletic group, ii) from the common *Paleotriton* trunk *Neotriton* arised earlier than *Mesotriton*, iii) *Triturus boscai* may be included within *Paleotriton* group and *T. vittatus* within *Neotriton* group, iv) *riturus italicus* is the oldest species of the genus and v) some particular chromosomes regions seem to have suffered higher rates of C-banding changes, the centromeres being the more stable areas.

W1

POSTGLACIAL INTROGRESSION BETWEEN SPECIES OF GRASSHOPPER IN THE PYRENEES

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Many hybrid zones must have formed near their present positions after the last ice age, during which poor climatic conditions had forced the species nearer to the tropics. The several ice age advances and retreats will have produced cycles of range contraction and expansion that were probably the major factor influencing genetic divergence.

The grasshopper *Chorthippus parallelus* has two distinct subspecies, *Cp. parallelus* in France and *Cp. erythropus* in Spain, that form such a zone along the Pyrenees. They have diverged considerably for morphological, chromosomal, allozymic and song characters, so that F hybrid males are sterile. These traits have introgressed to form climes of different width, and dispersal measures suggest that some are wider than expected.

The interplay between selection, dispersal, density and history in producing this situation will be discussed. Particular attention will be paid to Nucleolar organising regions, stridulatory pegs and mating preferences. Possible scenarios will be preferred in order to examine how these may be tested.

C10

THE EVOLUTION OF CYTOPLASMIC GENE TRANSFER TO THE NUCLEUS

Rolf F. Hoekstra

There is solid evidence, that in the course of evolution there has been a trend to transfer genes from cytoplasmic organelles to the nucleus. As a result, these organelles possess very small genomes compared to the nucleus. Moreover, the nucleus seems to control many activities in the organelles.

I have considered the problem of identifying systematic selective forces giving rise to such a process. Using a theoretical population genetic approach, various possible scenarios have been studied, such as competition between organellar genomes for segregation advantage, and differential sensitivity for segregation distortion between nuclear and cytoplasmic genomes.

C2

MOSES WITH CONTRASTING BREEDING SYSTEMS : POPULATION STRUCTURE, OUTCROSSING RATES AND EVOLUTIONARY CONSEQUENCES.

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Mosses posses abundant mechanisms for asexual propagation. The question is whether this leads to a strongly clustered population structure, or whether there is sufficient sexual reproduction to prevent this.

In four congeneric moss species the spatial distribution of different genotypes (based on 21 enzyme loci) will be compared.

Estimates of outcrossing rate in monoecious populations are made by the electrophoretic analysis of maternal gametophytes (n) and their accessory sporophytes (2n). Estimates of effective population size will be discussed.

P3

PHYLOGENETIC RELATIONSHIPS WITHIN THE MOSS GENUS PLAGIOTHECIUM BASED ON ALLOZYME VARIATION, MORPHOLOGY AND CYTOLOGY.

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The systematic status of some Plagiothecium species is still uncertain and is difficult to determine with conventional systematical methods alone. Most diagnostic morphological characters used so far, differ only quantitatively and show too much overlap to be decisive criteria for distinction between some pairs of taxa.

An electrophoretic comparison (21 enzyme loci), combined with a biometric analysis (a.o. principal component analysis) and cytological data, may help to solve these systematic problems. Therefore these methods were applied together to investigate the phylogenetic relationships between several populations of ten different taxa of the genus Plagiothecium. The different data sets were used alone and combined to construct phylogenetic trees (PAUP, Phylip, Tresearch). To enable outgroup comparisons the closely related Herzogiella seligeri was included in this study.

S3

EVOLUTION OF MIXED SELFING AND RANDOM MATING: NEW SOLUTIONS FOR AN OLD PUZZLE?

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Relative amounts of selfing and random outcrossing vary widely within and between species in many plant genera. The genetic and environmental components of this variation are seldom fully explored but for more than four decades, several evolutionary models have puzzled us as to why breeding systems evolve and how their genetic regulation might be understood. More recently, several new models which include parameters of inbreeding depression, gene flow in subdivided population, both uni- and bi-parental inbreeding, and selection have focussed on the following query: Is mixed mating system stable in terms of some sort of evolved property as an equilibrial and adaptive mode or simply transient as most species would move to nearly complete selfing versus outcrossing system? We present a brief review of these models in order to emphasize their assumptions and comparative features. Then we survey a few examples of mixed mating system in a search for the estimates of various parameters in the models. Clearly, most examples offer only partial information but one could argue that variation in outcrossing mechanisms and numerous correlated features of resource allocation, flowering, pollinator attraction, etc. on one hand and of genetic recombination, fate of progeny under varying environments, gene flow, etc. on the other might allow many species to maintain a stable mixed mating system.

P3

GENETIC DIVERGENCE AMONG BIVALVIA POPULATIONS FROM CENTRAL AND EASTERN PACIFIC.

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The pearl oyster Pinctada mazatlanica (Bivalvia, Pteridae) is found along the oriental coast of the Pacific Ocean, from the Gulf of California to Panama. P. margaritifera is largely spread from the Red Sea and the Indian Ocean to Hawaii and French Polynesian islands in the Central Pacific.

P. mazatlanica and P. margaritifera that are separated by a 5000-6000 km land free ocean which is thought to act as a good barrier to gene flow, have been considered as conspecific. Ranson (1961) assigned to P. mazatlanica a specific status on the basis of new diagnostic criteria, such as morphology of the anal process.

In this study (1) anal processes were examined in both Pinctada samples and this criterion was not found diagnostic; (2) the genetic divergence between samples of P. margaritifera from Polynesia and Mauritius island and the presumptive P. mazatlanica from Baja California, was estimated through allozymic variation at 18 loci.

According to this analysis, P. margaritifera and P. mazatlanica were shown to share a large amount of genetic community (mean gene identity = 0.846) and none locus proved to be diagnostic between these species.

Opportunity for larval migration through the Pacific barrier able to support gene flow cannot be excluded. Moreover P. mazatlanica and P. margaritifera are thought to be separated recently.

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C1

EVOLUTIONARY STABLE DISPERSAL IN A FLUCTUATING ENVIRONMENT - A WATERSTRIDER AS AN EXAMPLE

Arja Kaitala, Veijo Kaitala and Wayne Getz

Evolutionary stable dispersal strategies of a waterstrider were studied in a system consisting of two different habitats, sea bays and rock pools. Both habitats fluctuate unpredictably. We relate strategies to the idea of risk spreading. In a simple model for dispersal between the two different habitats the evolutionary stable strategy (ESS) is the one in which the offspring of a female always distribute between the two habitats despite of the magnitude of fluctuations. A more detailed multiple rock pool habitat model was used to combine life history of the species to the concept of ESS by studying a model in which females may lay all eggs in one site and histolyze their flight muscles or they may maintain flight ability and lay fewer eggs over many sites. Density dependent flight muscle histolysis is an ESS compared to strategies where females either always histolyze their flight muscles or they always maintain their flight ability. The problem of using ESS theory in stochastic situations as well as the use of ESS in studying life history strategies is discussed.

C2

IS THE POLYMORPHISM FOR CYANOGENESIS IN TRIFOLIUM AN ACCIDENT OF ITS DESCENT?

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Trifolium repens and *T. nigrescens* are the only cyanogenic species reported in the genus. Several studies indicate that *T. repens* is an allotetraploid ($2n = 32$). The putative parent species are *T. nigrescens*, a diploid ($2n = 16$) annual species, and *T. occidentale*, also treated as a diploid variety of *T. repens* ($2n = 16$).

I studied cyanogenesis in *T. repens*, *T. nigrescens* and their F_1 hybrid. The properties of the enzyme linamarase that hydrolyses the cyanogenic glucosides are so much alike in the two species and in the F_1 that they are virtually indistinguishable. The enzyme characteristics studied include: Molecular weight, iso-electric point and enzyme-substrate kinetics. Linamarase of the F_1 hybrid is recognized by an antilinarase raised against purified linamarase isolated from *T. repens*. As the *T. repens* parent of the F_1 lacked linamarase, the linamarase in the F_1 must have been coded by *T. nigrescens*.

In view of the fact that *T. occidentale* lacks linamarase the conclusion seems warranted that *T. nigrescens* is the donor of the linamarase gene in *T. repens*. Genetical and cytogenetical studies show that the two genomes in *T. repens* show absolute preferential pairing. That means that segregation does not normally occur. To explain the polymorphism in *T. repens* we have to assume that either a mutation or an illegitimate cross-over took place in the lineage of the species. The latter is far more probable. The result of a crossover between homeologous chromosomes would be a chromosome pair, with limited pairing and recombination. The existence of such a mechanism would explain the association of Li with other, unrelated characters, observed by several authors. Indeed the location of Li in a gene complex has been proposed by Daday, one of the first students of the cyanogenic polymorphism, more than twenty years ago.

P7

Poster: A RAPID AND SENSITIVE METHOD TO DETECT CYANOGENESIS USING MICROTITERPLATES

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The poster describes a method to study cyanogenesis in plants, using very small samples. In *Trifolium repens* a piece of a leaf of 2 mg is enough to distinguish cyanogenic and acyanogenic plants. The method is a semi-quantitative one and can be applied to samples of individuals in population studies as well as to samples of different organs or tissues of one plant in physiological studies.

In species polymorphic for cyanogenesis, like *Trifolium repens* and *Lotus corniculatus* the method can also be used to determine if acyanogenic plants are deficient in cyanogenic glucosides, in the hydrolyzing enzyme or in both. The tests are performed in batches of max. 96 samples (24 samples if enzyme and substrate are tested separately) and can be completed within one day.

P9

FITNESS EFFECTS AND INVERSION FREQUENCY CHANGES IN DROSOPHILA MELANOGASTER

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The clinal distribution of inversion (2L)t in *Drosophila melanogaster* has been explained by different responses of the karyotypes to environmental factors (e.g. temperature).

Temperature dependent traits, such as survival, developmental rate, weight and longevity were measured for these karyotypes. Artificial populations were set up under different environmental conditions.

The changes in inversion frequency are in agreement with the large fitness differences found between the karyotypes. The high inversion frequency at high temperatures is mainly caused by a higher heterozygote fitness in relation to the homozygous karyotypes.

P7

MATING SYSTEM PATTERNS IN A NORTHERN MARGINAL POPULATION OF PINUS SYLVESTRIS

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In wind pollinated Scots pine populations, gene flow is so efficient that effective population sizes are relatively large, there is considerable genetic variation within populations, and hardly any differentiation between populations in neutral characters. Inbreeding occurs at low frequency. However, in the northernmost populations, mating patterns of Scots pine may differ from central populations. We compared the mating systems of a northern timber line population from Lapland with a more central population. We measured the rate of inbreeding from allozyme loci, and inbreeding seems to be slightly more common in the northern population. Possible causes for that are reduced effective population size due to variation in flowering, or genetically based differences in self-fertility. For this reason, we also studied variation in reproductive effort in the northern population. The variation is extensive between individuals and years: the coefficient of variation of pollen production between trees was 1.24 and 1.39 in the years 1987 and 1988, respectively. This suggests a considerable reduction in effective population sizes, which may account for some of the increased inbreeding which we found. Studies on the possible differences in self-fertility between southern and northern populations are underway.

C6

Testing the pathogen hypotheses for the maintenance of sexual reproduction.

Dr. Steven E. Kelley, Wolfson College & Institute of Virology, Oxford, U.K. and Dept. of Botany and Program in Genetics & Cell Biology, Washington State Univ., U.S.

Pathogens have been frequently invoked as a driving force for the evolution and maintenance of sexual reproduction. Sex has been posited to reduce the incidence and/or consequences of pathogen infection when pathogens are transmitted from 1) parent to offspring or 2) offspring to offspring. These hypotheses have been tested using *Anthoxanthum odoratum* and 3 naturally-occurring viruses which infect it. The experiments were conducted using sexual and asexual progeny which had been inoculated with known viruses or mock inoculated with water and then planted directly into the field from which the parents had been sampled. The data show: 1) that viruses can accumulate quite rapidly among previously uninfected sexual and asexual sibships grown in the field, 2) that viruses have significant fitness effects, 3) that there is genetic variation for resistance to virus infection in natural populations, but 4) that no advantage for sex could be clearly linked to the presence of the specific viruses studied in these experiments. The results suggest that the relationship between viruses and their wild plant hosts is likely to be complex, but that this relationship can be elucidated using manipulative field experiments.

C9

ECOLOGICAL GENETICS OF BARK BEETLE CLONES

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European populations of *Ips acuminatus* (Coleoptera: Scolytidae) are mixtures of sexual females and males plus triploid, sperm-dependent parthenogenetic (pseudogamous) females. Extensive electrophoretic investigations of Norwegian, Swedish, Finnish, West German, and Bulgarian populations have revealed that each has several to many pseudogamous clones, but that clonal composition varies markedly among populations.

This talk will report preliminary results of laboratory breeding now being carried out now to investigate clonal niche breadth: why are different populations dominated by different clones, despite the fact that populations are apparently not genetically isolated? Are clones locally adapted, or are they ecologically similar and selectively neutral with respect to one another? An overview of the *I. acuminatus* population genetics research to date will be presented, including a comparison of (laboratory) reproductive success for sexual and pseudogamous females and comparisons among three different dominant clones from eastern Norwegian populations.

S8

NUCLEAR DNA POLYMORPHISMS IN HUMAN POPULATIONS

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In a collaborative project with Prof. Cavalli-Sforza our two labs, at Yale and Stanford, have now studied over 100 DNA markers in five populations and a substantial subset of those in several other populations. The 107 DNA markers studied to date represent 69 genes or chromosomal regions; 42 are known genes and 27 are anonymous DNA segments. Lymphoblastoid cell lines have been established for all the populations under study. Those with at least two dozen loci typed include Mbuti pygmies from the Ituri forest in N.E. Zaire, Biaka pygmies from the Central African Republic, Nasioi Melanesians from Bougainville in the Solomon Islands, Chinese born in mainland China (primarily the south), Japanese, Caucasoids of northern or central European origin, the Surui and Karitiana from western Amazonia, and Mayans from the Yucatan. The majority of the RFLPs are polymorphic in all populations, suggesting that they predate the diversification of modern *Homo sapiens*. The variation between populations (measured by F_{ST}) is highly significant. Known genes and random segments have no significant difference in the F_{ST} values, (about .15), or in the average heterozygosity (28%). The F_{ST} distance between all populations considered in pairs, and averaged over all loci, favours a primary split between Eurasia and Africa. Preliminary comparisons with levels of DNA polymorphism being found in baboons suggest heterozygosity at the DNA level is considerably lower in humans than in wild yellow baboons.

Most of the nearly 2,000 RFLP loci currently cataloged were defined and described on Caucasians. There are now several specific examples of variants being detected in non-Caucasian populations that have not been seen in large samples of Caucasians. In addition, at some loci, alleles that are infrequent in Caucasians are common in most other populations. These data document the self evident: Caucasians represent only a subset of the normal, common genetic variation in the species.

We have recently begun to use PCR methods to compare alleles in humans with alleles at the homologous loci in other higher primates. In the case of an allele (found so far only in African pygmies and at a frequency of about 20% in that population) that differs from the common allele by the insertion of 100bp, we have shown that all other higher primates have the shorter allele, indicating that the longer allele in the pygmies is a recent insertion event.

Work supported by NSF grant BNS-8619703 and NIH grant GM020467. The many individuals who helped us collect these samples and the several members of the labs at Stanford and Yale who collected the RFLP data are too numerous to acknowledge individually but have had critical roles in this multifaceted project.

P11

Autogenous Density Fluctuations Can Favour Iteroparity: Murphy's Model Reanalysed

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A.Bogmér (Computer Center of Eötvös University)
M.Jankovich (student)

Murphy's (1968) simulation study is one of the most frequently cited one on the question of semelparous - iteroparous decision in a fluctuating environment. He used a quite simple one locus - two alleles selection model: fertility does not vary with age but it is higher for the semelparous type. The iteroparous genotype lives exactly two years without any mortality between ages of 1 and 2. Juvenile survival of both variant is determined by a kind of intraspecific "contest" competition: there is a certain number of resource fragments (e.g. refuges): every iteroparous adult has a fragment and as many juveniles can survive as many fragments remain free. Changes in the environment cause random fluctuations in juvenile survival which lead to fixation of the iteroparous type. However, Murphy's restricted simulations didn't reveal the complicated dynamics of the environmentally undisturbed population: he believed that it is always the more fertile semelparous genotype which spreads in the population in a stable environment. "Contest" competition let juveniles get varying number of free resource fragment, which leads to fluctuation in juvenile survival emerging autogenously (without any environmental effect). We used the haploid analogue of Murphy's model to investigate the impact of autogenous fluctuations on the outcome of selection between the semelparous and iteroparous variants. Numerical simulations discovered that from a certain domain of starting points the iteroparous type becomes fixed in the undisturbed population due to the autogenous fluctuations. The effect of autogenous fluctuations therefore contributes to that of random environmental ones in Murphy's simulation. The existence of autogenous fluctuations however is strongly dependent on the assumption that iteroparous adults survive until a certain age with probability 1 when all of them dye.

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Plantago coronopus is a gynodioecious species, which implies the occurrence of male sterile plants (= females) together with hermaphrodites. The hermaphrodites are capable of selfing, while outcrossing rates for individual plants differ considerably (.20 to .98).

Selfing is often thought to be important for the maintenance of male steriles in natural populations, because male steriles produce only outcrossed seeds, which gives them an advantage compared with hermaphrodites provided that inbreeding depression is considerable. However, until now the difference in performance between male steriles and hermaphrodites as observed in our study is of such an order of magnitude, that inbreeding depression cannot be the only factor involved in maintaining male steriles.

Recently much more attention has been given to the importance of the "mode of inheritance" for the dynamics of the gynodioecious breeding system. For several species it has turned out that there were not only nuclear genes involved in the determination of male sterility, but also cytoplasmic genes. These cytoplasmic genes are located in the mitochondria and can, in contrast to nuclear genes, only be transmitted to the next generation by means of ovules, and not by pollen. This asymmetry in the transmission of nuclear and cytoplasmic genes is thought to be primarily responsible for the maintenance of male steriles in natural populations. In this paper preliminary data on both factors will be presented with respect to Plantago coronopus.

S2

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The use of chromosome gene arrangements in assessing phylogenies in the Drosophila obscura species group.

Nine species belonging to the obscura group of the genus Drosophila: D. obscura, D. ambigua, D. tristis, D. guanche, D. madeirensis, D. subobscura, D. subsilvestris, D. microlabis, D. kitumensis, have been investigated; the homology among segments of their respective giant chromosomes was established, as inferred by banding pattern similarities. Data have been gathered for elements B, D and E. From these data phylogenetic relationships are derived by a computer program estimating the minimum number of inversions between two gene arrangements. This program also searches for ancestor gene arrangements common to two or more transition pathways. Thus it permits the construction of the most parsimonious possible tree. Simulations have shown that trees constructed this way are totally parsimonious when hot break points are absent. The comparison among trees, derived from different chromosomes, confirm that they are rather congruent. The species studied fall in four clusters, each one composed of closely related members; first the obscura cluster [including also ambigua and tristis], second the guanche cluster [including also madeirensis and subobscura], third the African [with microlabis and kitumensis], finally a one member group, that of subsilvestris. These clusters ultimately derive from a common ancestor, closely related to D. obscura. While the other clusters derive from this ancestor directly the, guanche cluster and D. subsilvestris share a common ancestor, which is directly related to the common ancestor of all clusters.

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The two species of sorrels, Rumex acetosa and R. acetosella (Polygonaceae), are dioecious perennials in which vegetative reproduction (apomixis) also is commonly observed. In the present study, I examine sex ratios, life history variation and microhabitat differentiation of males and females in Finnish Rumex populations. Additionally, I explore the genetic structure related to habitat variation and life histories. Potentially, genetic differentiation could be reduced due to phenotypic plasticity and asexual reproduction, which are specially strong features in R. acetosella. Chemical characteristics of soils on study sites were analyzed and found to differ significantly between habitats.

The sex ratios of ramets and genets (genetic individuals) were revealed to be quite similar and were female-biased in all populations of R. acetosa and in most populations of R. acetosella, in which more extensive sex ratio variation between populations was expressed. The sex ratios based on dry weight were even more strongly female-biased than ramet and genet sex ratios. No density effect on the sex ratios was observed. The possibility of spatial segregation of sexes was investigated and was found to occur in several populations. This could only partly be attributed to the effects of vegetative reproduction. Sex-linked niche differentiation may reduce intraspecific competition and be a selective force in the evolution of dioecy in plants. In the examination of genetic variation, the degree of isozyme differentiation between populations appeared considerably more extensive in the hexaploid R. acetosella than in the diploid R. acetosa. This may be due to the genetic and life history characteristics of R. acetosella.

P11

REPRODUCTIVE EFFORT IN RELATION TO FOOD SUPPLY AND DAY LENGTH IN THE COMMON TREECREEPER, Certhia familiaris.

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Effects of food supply and day length and seasonal changes in these on reproductive success were studied comparatively and experimentally in the Common Treecreeper. The seasonal reproductive pattern is based on an initial increase in clutch size with time, eventually followed by a decrease. This is thought to be consequence upon a parallel change in resources. The food supply was found to follow a similar seasonal trend, and to consist mainly of spiders, which Treecreepers use as food for their nestling food. The parents were actively feeding their nestlings for 89% of the time between sunrise and sunset, there being a clear correlation between feeding rate and nestling age. The hourly feeding rate did not correlate with brood size, although the daily feeding rate did. These results suggest that the adult birds cannot increase their hourly feeding rate but can increase their daily feeding rate as the days lengthen, and in this way feed a larger brood. Experiments were conducted by preventing feeding of nestlings for three hours in each day over a period of six days. These nestlings developed significantly more slowly and showed a higher mortality than those in the control nests. The results support the idea that day length is of some importance in determining the feeding capacity of Treecreepers, but the major factor is food supply.

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The behaviour of the *Drosophila obscura* group species is not well known, even though at least 17 species of the group have been under study. The best known species are the American *D. pseudoobscura* and the European *D. subobscura*. The main objects of interest in the behaviour of the *D. obscura* group flies have been the courtship and mating behaviour, response to light and gravity and orientation. Genetics of behaviour of the *D. obscura* group flies is very poorly known. Only some hints about the inheritance of phototactic and geotactic behaviour are available.

Most of the behavioural studies in the *D. obscura* group have been carried out in the laboratories. There are some modes of behaviour, however, which cannot be found or which are extremely difficult to study in the laboratory. One of these is territorial behaviour and related phenomena. This type of behaviour is very distinct and typical for the *D. obscura* group flies. It can be supposed that most of the species in the group express this type of behaviour, but it can be clearly found in the wild only.

For the behavioural studies in the wild a video camera with remote control system and tape recorder is the best equipment. A series of pictures, which can be repeated hundreds of times tells always more about the behaviour of small-sized flies than the observations made by human eye.

Behaviour is very important isolating mechanism in the *D. obscura* group.

P13

EVIDENCE OF CHEMICAL SIGNALLING IN *TIGRIOPUS FULVUS*
(COPEPODA, HARPACTICOIDA).

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In *Tigriopus fulvus* it has been ascertained that females release a chemical compound promoting sexual attraction in males, in the culture medium; this chemical signal is species-specific. The males, on the contrary, wouldn't release any signal. In addition, the results of another series of experiments indicate that ovigerous females physically eliminate non-related first-stage nauplii. Assuming that ovigerous females can only recognize their own offspring, a mathematical model has been developed which allows to calculate the number of survivors in relation to females crowding.

P12

GENETIC STRUCTURE AND EVOLUTIONARY IMPLICATIONS IN *TRICHINELLA* Railliet, 1895 (NEMATODA, TRICHINELLIDAE)

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Allozymic studies on *Trichinella* parasites showed a genetic pattern more heterogeneous than expected. Pozio *et al.* (1988) and La Rosa *et al.* (1988) analysed the allelic composition of 120 worldwide isolates through the Factorial Analysis of Correspondences and they found the presence of seven distinct gene pools (T1-T7). Four of them were formed by isolates previously regarded as *I. spiralis* (T1), *I. nativa* (T2), *I. pseudospiralis* (T4) and *I. nelsoni* (T7). The other three pools, previously undetected, were formed by: Euroasian isolates (T3) previously considered *I. nelsoni*, two N. American (T5) and four N. American (T6) isolates before supposed *I. nativa*. Assuming that levels of genetic differentiation found in *Trichinella* gene pools are correlated with their time of separation from the last common ancestor, it is possible to infer some evolutionary considerations. The earlier diverging gene pools were T1 and T4. They are highly differentiated from each other and from other groups. *I. pseudospiralis* (T4) was usually considered the most ancient species because it can infect bird hosts, unlike pig-infecting *I. spiralis* (T1). T7 is also genetically distinct and clusters with T2 and T6; its independent evolution could be due to its isolation in the Ethiopian Region. T2, T6 cluster is genetically distinct from T3, T5 cluster. Both T5 and T6 N. American isolates were previously considered *I. nativa* (T2), but only T6 is related to T2. On the contrary N. American T5 pool appears to be much closer to T3 Euroasian isolates than to *I. nelsoni* (T7) as previously thought. This relationship suggests a recent dispersion of T5 in N. America.

S3

The evolution of the breeding system in flowering plants: *Armeria maritima* as a study case.

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In the specific complex *Armeria maritima* (Mill.) Willd. (Plumbaginaceae) the dimorphic self-incompatible populations from Western Europe, the homozygous "papillate stigma - finely reticulate pollen" morph appears to allocate less in the male function in having smaller pollen grain than the heterozygous "cob stigma - coarsely reticulate pollen" morph, the number of pollen grains per ovule (P/O ratio) remaining constant for the two morphs. In heavy metal tolerant populations the self-incompatibility system undergoes alterations leading to the occurrence of partially self-fertile individuals, the papillate morph appearing as a better selfer than the cob morph. This trend toward selfing is counter-balanced by inbreeding depression in the selfed seeds which show a low germinating ability. Nevertheless complete selfing is reached in Arctic monomorphic self-compatible populations where all the individuals have the compatible "papillate stigma - coarsely reticulate pollen" combination. In such individuals the P/O ratio and the expenditure in sepals, petals and stamens are 3 times as low as in the dimorphic populations while the seed weight remains unchanged. The autogamous arctic populations are the most likely direct ancestors of californian populations where allogamy is recovered through gynodioecy. In these populations allocation to male function is restored to a higher level in hermaphrodites as well as allocation to pollinator attraction. These changes in the relative allocations to male and female functions, accompanying the variation of the breeding system of the species, illustrate the evolutionary importance of the quantitative trade-off between male and female allocations.

P5

Variation in chromosome number and type in
Hydrotaea irritans and H. meridionalis

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In H. irritans the number of chromosomes ranges from 11 to 15 with an average number of about 13 (slightly above in a Dutch population sample and slightly below in 2 Danish population samples each containing more than 50 individuals). The chromosomes that vary in number were acrocentric and highly heterochromatic, and at least two different common types were identified. Preliminary results indicate that no male specific karyotype could be identified in at least the Danish samples which points to an autosomal sex-determination. However, only a few adult males gave successful preparations.

In H. meridionalis the chromosome number was found to vary between 11 and 13. Apart from the 5 common pairs, three different chromosome types were identified. A rather common large acrocentric and heterochromatic chromosome, a smaller heterochromatic acrocentric chromosome, and a small heterochromatic submetacentric chromosome. The large acrocentric chromosome was found in 128 out of 129 individuals (larvae) and in above 70% as a pair with none of the other two types present. All four adult females that gave successful preparations carried only the large acrocentric chromosome while the only adult male had a pair of those together with the small submetacentric one. This could indicate a X-Y sex determining mechanism which also was supported by the segregation pattern in three out of four mother-offspring combinations. However, one of the combinations with 15 offsprings showed only a pair of acrocentric chromosomes in all offsprings.

P2

EVOLUTIONARY RATES AND CHARACTERS IN DACTYLIS GLOMERATA L.
(GRAMINAE)

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Paleontologists and evolutionary biologists working on the same taxa often obtain contradictory evolutionary schemes. One reason could be that they measure different characters which do not evolve necessarily at the same rate. Two examples of such situations are examined in Dactylis. In one, the divergence occurred in the Far-East at the end of the Tertiary period and is due to a geographical barrier. In the other, the situation concerns climatic modifications, several ten thousand years ago, in the Near-East.

In both situations, the evolutionary rate is observed to be high for morphological characters relating to vegetative growth (e.g. plant and leave size) but much lower for the morphological characters which concern reproduction. The rate is also high for molecular characters determined mainly by regulatory genes (e.g. flavonoid compounds) but much lower for molecules specified by structural genes (e.g. enzymes of primary metabolism) and for chloroplast DNA. It is clear from these results that information about the differential evolutionary rates of characters have to be considered when results from multidisciplinary studies are compared.

P8

BENEFITS FROM MULTIPLE MATINGS IN FEMALES; A
MECHANISM IN SMALL AND ISOLATED POPULATIONS.

JON LOMAN, THOMAS MADSEN AND THOMAS HAKANSSON

We present a model demonstrating that female multiple mating, that results in several males sharing paternity in the female's brood, can result in increased female fitness. The model is applicable to species where the males' contribution to his offspring is restricted to his genes and to females in small and isolated populations. The model is based on the ideas that (1) the offspring may compete with each other for representation in future generations and that (2) the quality of the offspring may differ depending on their father. An obvious example is cases where certain male - female combinations are incompatible. In such situations it is better for a female to have some "good" and some "bad" offspring each year, rather than all "good" in one and all "bad" in another year.

Ref: (1) Loman, J., T. Madsen and T. Håkansson. Increased fitness from multiple matings, and genetic heterogeneity: a model of a possible mechanism. *Oikos* 52:69-72. (2) Arnqvist, G. On multiple mating and female fitness: comments on Loman et al. (1988). *Oikos* 54:24-8-250. (3) Loman, J., T. Madsen and Thomas Håkansson. A better title: "Female benefits from multiple matings - a model". *Oikos* 54:250-251.

P13

Evolution and stability in a specific pollination system.

J. MADSEN, Aarhus, Denmark

not received

P13

PATTERNS OF ALTRUISM: AN EVOLUTIONARY GAME-THEORY APPROACH TO THE STUDY OF PRIMATE GROOMING BEHAVIOUR.

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Theoretical models predict that an animal should behave cooperatively towards a partner in relation to the estimated probability to meet it again, and to its actual reciprocal responses. In this study we tested the predictions of the game-theory Prisoner's Dilemma on grooming behaviour of long-tailed macaques (*Macaca fascicularis*). Familiarity with an individual was supposed to be used by monkeys as an index of whether an encounter (i.e., a game) is likely to be repeated. We tested whether the monkeys cooperated or defected in terms of their willingness to groom a familiar or an unfamiliar cage-mate. Monkeys in the familiar pairs exchanged more grooming and had a higher probability to accept grooming invitations than those in the unfamiliar pairs, but they resisted the possible attempts of the partner to be the recipient of two consecutive grooming bouts. Grooming between unfamiliar monkeys was scarce; however, unfamiliar monkeys that were particularly afraid of their partner groomed it regardless of reciprocation.

C13

GENETIC VARIABILITY AND PHYLOGENY IN THE TRYPETINAE (DIPTERA TEPHRITIDAE)

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Electrophoretic data at twenty seven orthologous loci were scored for several fruitflies species of the Trypetinae subfamily. Genetic variation within and between species was considered in order to understand:

- the differential geographic dispersal patterns observed among species of *Ceratitis* and *Trirhithrum* genera;
- the gene flow in the sympatric populations of *Ceratitis* and *Trirhithrum* species;
- the phylogenetic relationships among the species as inferred from genetic similarity in comparison with traditional taxonomy.

The same species were analyzed for the interspecific variation in nuclear DNA content. The genome size data are considered with respect to the measures of genetic variability and to the phylogenetic position deduced by the electrophoretic data.

C4

NEST GUARDING IN RELATION TO INVESTMENTS MADE AND TO FUTURE REPRODUCTIVE POSSIBILITIES IN THE COMMON GOBY, *POMATOSCHISTUS MICRIPS*.

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The common goby, *Pomatoschistus microps*, has paternal care, with males building nests and guarding the fertilized eggs until hatching. A field experiment was carried out in order to look at the response of males to predation risk in relation to maturation of the eggs. Artificial nest substrates were placed in a shallow soft-bottom bay. When nests were built and eggs laid in the nests, the male *P. microps* were presented to a presumptive predator, the eelpout, *Zoarces viviparus*, in a glass jar 10 cm from the nest. The male was chased away from the nest, and the flight distance and time of return was measured. This was repeated once a day during the brooding period. Both flight distance and time away from the nest decreased with time. Another male *P. microps* was also presented to the nest guarding males in a similar manner, simulating competition for the nest. The same decrease in return time was found, but the fish always returned faster than when presented to a predator. Factors influencing the risks taken by nest guarding male *P. microps*, such as investments already put into the offspring and the prospect of future reproduction, is discussed.

P2

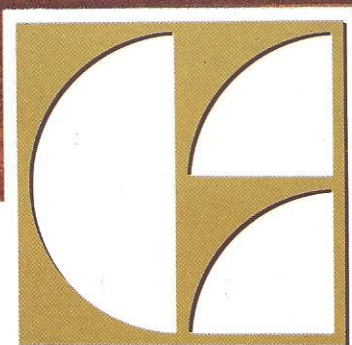
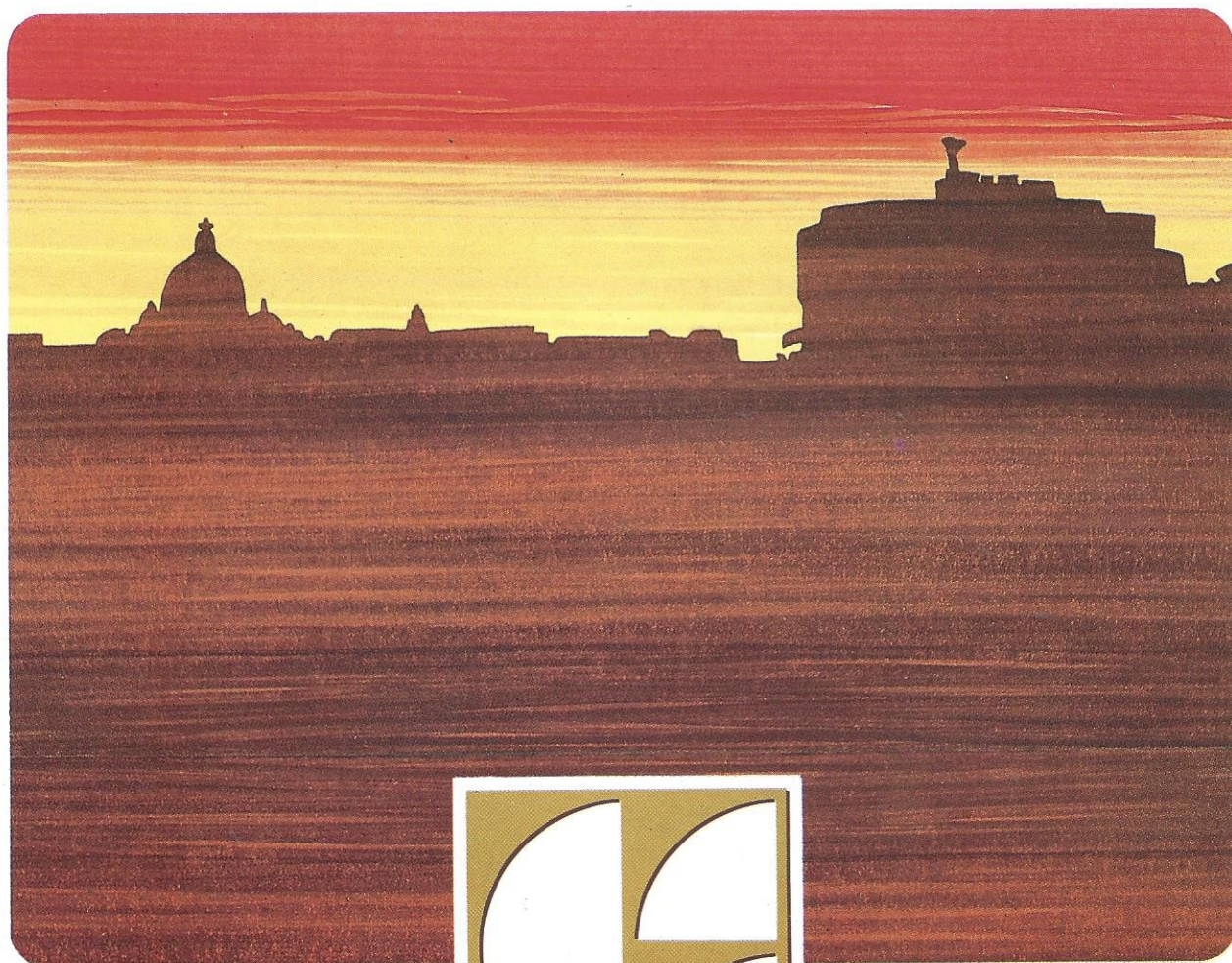
CHROMATIN COMPARTMENTS AND APE CYTOTAXONOMY M.G. Manfredi Romanini, C. Pellicciari

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The genome in nuclear chromatin can be divided into different compartments, depending upon the biochemical, cytological or functional parameters chosen for their definition; in fact, these compartments have distinct biological meanings, although being defined on a strictly methodological basis. In this work, we attempted to quantify by cytochemical methods the amount of DNA corresponding to constitutive heterochromatin (C-heterochromatin) in several species belonging to the primate superfamily Hominoidea. The genome fraction corresponding to C-heterochromatin is defined by us as the DNA resisting to the C-banding pretreatments (which essentially consist of DNA denaturation-depurination, renaturation and hot-salt-extraction procedures).

From the cytotaxonomical point of view, it was found that the amount of C-heterochromatic-DNA can account for the differences in total DNA amount between the species of Hominoidea so far studied, thus demonstrating, for the first time on a quantitative basis, a strict relationship between variations in genome size and different amounts of constitutive heterochromatin.

Human lymphocytes were also studied after different times of mitogenic stimulation with phytohemagglutinin: it was observed that the amount of DNA resisting to the C-banding pretreatments decreases during the passage from G₀ to G₁ phase of the cell cycle. This finding suggests that the different resistance of chromatin DNA to the procedures used to detect C-heterochromatin on metaphase chromosomes, can be also used as a parameter of nuclear functionality in interphase.



CASSA DI RISPARMIO DI ROMA

La tua amica Banca.

ENERGIA & AMBIENTE

A long-exposure photograph of a waterfall, creating a silky, flowing texture for the water. A vibrant rainbow arches across the upper middle of the frame, its colors clearly visible against the dark background. The scene is dramatically lit, with bright highlights on the water's surface and deep shadows in the surrounding areas.

A.C.E.A.

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L'ENEL è l'azienda italiana che maggiormente si è impegnata alla realizzazione di estese e sistematiche indagini sulle coste e sui principali corsi d'acqua italiani. Inoltre, per ridurre il depauperamento del mare e dei fiumi sono stati realizzati allevamenti ittici che utilizzano il calore residuo delle centrali termoelettriche. Con il **Progetto Ambiente 1989**, l'ENEL promuoverà su scala industriale lo sviluppo di tali allevamenti per la produzione di pesce di mare e d'acqua dolce per l'alimentazione dell'uomo. Il Progetto prevede, inoltre, con la collaborazione del Ministero della Marina Mercantile, la riproduzione di pesce per il ripopolamento delle acque.

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LA VITA.

C13

PHYLOGENY OF THE GENUS BACILLUS (INSECTA PHASMATODEA):
ALLOZYME EVIDENCE OF B. GRANDII AND B. ATTICUS
CONTRIBUTIONS TO SICILIAN HYBRID TAXA.

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Two instances of interspecific natural thelytokous hybrids have been described in southern Sicily, namely the diploid B. whitei and the triploid B. lynceorum. Very recently another diploid thelytokous hybrid taxon has been discovered in northern Sicily: B. rossius-grandii benazzii.

From body and egg morphology, karyology, and allozyme analysis B. whitei turned out to derive from the cross B. rossius x B. grandii and B. lynceorum appeared to be a backcross of B. whitei to B. grandii (see Bullini and Nascetti in 1st Int. Symp. Stick Insects: Phylogeny and reproduction, 1987, Centrooffset Siena). More recently, however, the high genetic heterogeneity of B. lynceorum has been explained through the contribution of B. atticus (a thelytokous grandii-like taxon), so that B. lynceorum would represent a double allotriploid (Scali and Mantovani, 1989, Boll. zool. 56).

Gene-enzyme analysis shows that B. rossius-grandii benazzii derives one set of alleles from monomorphic strains of B. rossius and the other one from rather polymorphic bisexual B. grandii benazzii, the three taxa being actually syntopic. The hybrid constitution of this taxon is well supported even at morphological and karyological levels.

Reproductive biology data clearly indicate that B. whitei and B. lynceorum reproduce only by parthenogenesis, while for B. rossius-grandii benazzii also hybridogenesis seems to occur.

P3

CHROMOSOMAL EVOLUTION IN TREEHOLE BREEDING
ANOPHELES (DIPTERA: CULICIDAE)

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The Coelodiazesis group of Anopheles mosquitoes include 6 nearctic and 2 Old World species. These species breed in treeholes and artificial containers with similar water composition. The group is morphologically and biologically distinct from other container breeding anophelines and in general from species of the Anopheles subgenus. Of the 3 species considered here, An. plumbeus is the only palaearctic representative of the group. The North American An. barberi and An. judithae are closely related and quite removed morphologically from the other species of the group. An. barberi is distributed throughout eastern U.S.A., An. judithae is present in southwestern U.S.A. and northern Mexico. The chromosome complement of the 3 species consists of 2 pairs of autosomes and 2 heteromorphic sex chromosomes. The X and Y chromosomes differ among the 3 species in size and heterochromatin content. The sex chromosomes of An. barberi are most distinct from the other species, having a dot like Y and a small subtelocentric X. In An. plumbeus and An. judithae the sex chromosomes are both submetacentric with the Y slightly shorter than the X. The C-banding pattern of An. barberi is also distinct from the other 2 species. C-positive heterochromatin is localized at the telomeres of the autosome pairs while is centromeric in the other species. Clear differences are also present in the banding pattern of the sex chromosomes. An. barberi is considered the most modern species of the group. Its karyotype has probably evolved towards a reduction of heterochromatin material and heterochromatin repatterning while the other 2 species retained a more ancestral karyotype.

P11

Evolution of the monogeny in Asellus aquaticus populations

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Charnov & Bull (1977) and Bulmer & Bull (1982) hypothesized that in species with weak genetical sex determination (GSD) the environmental sex determination (ESD) prevailed in order to favour the sex whose fitness is environmentally influenced. Many crustacea show ESD (Legrand et al. 1987). In Asellus aquaticus L. (A.a.) and Gammarus duebeni, Migliore et al. (1983) and Naylor et al. (1983) identify ESD with photoperiod. A.a. has no heterochromosomes and has monogenic (sons or daughter biased) families (Vitagliano et al. 1958). Larvae from the same mother, kept half at 14/10 and half at 18/6 light hours are GSD (Valentino et al. 1988). We will demonstrate that Dutch, French and Italian A.a. at 16°C, summer photoperiod, standard food, show a sex ratio of respectively 200:10, 10:10, 10:200. Excluding ESD and differential deaths we statistically evaluated the sex ratio of single pairs. Dutch, French and Italian populations produce respectively 32%, 12%, 4% of daughter biased and 4%, 8%, 36% of son biased offsprings. We conclude that evolution toward daughter biased mothers gives evolutionary advantage where diapause exists; sons biased mothers are in advantage where in summer the environment imposes a reduction of the newborns. This last hypothesis has already been expressed (Vitagliano, 1976).

C13

THE KARYOTYPES OF BACILLUS GRANDII BENAZZII AND ITS
NATURAL HYBRID WITH B. ROSSII (INSECTA PHASMATODEA)
FROM SICILY.

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In 1988 two new taxa have been discovered in north-western Sicily, namely: B. grandii benazzii and a new interspecific hybrid taxon which, owing to its derivation and reproductive mode, has been named B. rossius-g. benazzii (Scali, this congress).

North-western representatives of B. grandii share the same karyotype of south-eastern Sicilian demes with: o, 2n=34, XX; o, 2n=33, XO and a basically similar structure. Differentiating features are: the number, size and localization of satellites, which in C-banded slides appear heterochromatic; the constant AgNO₃-detected NORs; the chiasma frequency and position in male meiosis. Therefore, cytological characteristics appear to support a subspecific differentiation.

The unisexual B. rossius-g. benazzii clearly derives its uneven diploid set (2n=35) from syntopic thelytokous B. rossius and B. g. benazzii; the hybrid karyotype actually reflects parental sets in details, including the satellites and the constant NORs. This karyological feature is in line with the likely way of reproduction by hybridogenesis (Mantovani et al., this congress). On the other hand the structural uniformity of this northern hybrid sharply differs from the chromosomal condition found in the "parallel" southern hybrid B. whitei (= B. rossius x B. g. grandii), which shows several structural rearrangements (Scali and Marescalchi, 1987, in "Evolutionary biology of orthopteroid insects", B. Baccetti Ed., 541-549).

W2

INVERSION POLYMORPHISM IN CHIRONOMIDAE

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Polymorphic paracentric inversions have been investigated in a number of groups in the Chironomidae, mainly in the subfamily Chironomini. The major problem that arises is one of nomenclature, with several systems being used by different workers. The pros and cons of some of these systems will be discussed.

Another problem concerns the accurate identification of inversion breakpoints, particularly where these occur in groups of very similar bands. In phylogenetic studies this creates the problem of deciding whether apparently similar sequences in species which are not closely related are actually identical and, further, whether the sequences occur due to homology by descent or as a result of separate occurrence. Molecular genetics may offer some assistance in solving this problem in some instances.

An example will be given of the use of inversion polymorphisms to recognize the existence of essentially homosequential sibling taxa in the genus *Chironomus*.

P1

MULTIPLE SEX DETERMINER SITES IN *Chironomus oppositus* - POLYMORPHISM OR CRYPTIC SPECIES?

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Sex determination in the genus *Chironomus* is male heterogametic. Whether an individual is to be male or female is determined by a single gene or group of genes (MD). The MD may occur at a number of locations in the genome, that is at sites within six of the seven chromosome arms.

The southern Australian species *Ch. oppositus* comprises a number of cytologically-recognised taxa whose specific status is not yet certain. The location of MD differs between some of these taxa, but in form *whitei* four different MD locations have been identified. Karyotypic and allozymic analysis of this form has been used to determine the status of the multiple sites, which if they are polymorphic must, from theoretical considerations, constitute an unstable polymorphism. Alternatively they may indicate the existence of cryptic taxa. Future work will attempt to further clarify this situation.

P11

POSITIVE GENETIC CORRELATIONS BETWEEN LIFE HISTORY TRAITS IN A MARINE OLIGOCHAETE

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Antagonistic pleiotropy may allow the maintenance of the substantial additive genetic variance for life history traits that have been observed in the wild. Pleiotropic alleles with opposite effects on characters subjected to directional selection will remain at intermediate frequencies generating protected life history polymorphisms. Antagonistic pleiotropy should also result in negative genetic correlations between life history traits. In a laboratory study I found that there were differences for age specific reproductive rate and longevity among clones of the marine oligochaete *Paranais litoralis* from a population at Flax Pond, New York, USA. The study also showed positive genetic correlations between reproductive rate early in life with both reproductive rate late in life and longevity.

Recently, several authors have reported positive genetic correlations between life history traits and pointed out factors that might change the sign of the correlations and, thus, overpower antagonistic pleiotropy. Among those factors, genotype-environment interactions might play an important role. The experimental design of the present study did not allow for clone-environment interactions, whose effects on genetic correlations will be investigated in future studies.

P5

Drosophila subobscura MITOCHONDRIAL DNA GENE FLOW IN THE PALEARCTIC AREA OF DISTRIBUTION.

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A total of 156 isolines belonging to the palearctic area of distribution of *D. subobscura* has been studied using mitochondrial DNA (mtDNA) restriction analysis. Ten restriction enzymes, recognizing six and four base pairs yielded a total of 13 distinct composite patterns or morphs. The restriction map showed the existence of a total of 32 sites, 12 of which are polymorphic. Most of the polymorphic sites are concentrated on protein genes, mainly on distinct subunits of the NADH dehydrogenase complex.

The 13 morphs can be connected in an unrooted phylogenetic tree that minimizes the total number of mutational steps. In this tree the two most frequent morphs (I and II) occupy a central position.

The mtDNA distribution pattern throughout Europe does not agree with any kind of clinal distribution. Populations are substructured according to the two most frequent morphs as well as to local morphs. The low rate of mtDNA flow and the recent appearance of local morphs, all together, could account for such relative level of population substructure.

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At present, the "thermodynamics of accumulation processes"/TAP/ and the "thermodynamics of irreversible processes" /TIP/ are two branches of non-equilibrium thermodynamics. TAP deals with phenomena /processes and effects/ associated with the introduction, transformation and accumulation of mass or energy or both in affected systems /open or closed systems/ i.e., phenomena due to positive work done upon the systems by exogenous impacts /influences/ during a measurable impact time. An "universal evolution criterion" has been proposed in TIP; it demands a minimum entropy production $d_i S$ in the evolutionary system: $d_i S/dt \leq 0$, /t is the time/, but that inequality contradicts to basic TIP-principles: $d_i S$ cannot be < 0 ; a form: $d_i S/dt = 0$ corresponds to reversible processes - they can be accepted as evolutionary ones in no wise. A new evolution criterion has been accepted in TAP, based on the definition: "Each new evolution development degree of a non-isolated system is manifested and proved by acceleration of the total impact exercised by that system upon other systems or environment in general". The TAP-criterion is expressed by:

$$\sum_{k=1}^n d^2 W_k / dt^2 > 0, \text{ where } W_k$$

is the work of energy kind "k" done by the system; the total number n should be sufficient for the characterization of the whole impact as exemplified in the paper.

C1

Competition and Optimization

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If the competing populations are limited only by a single resource, fitness optimization is equivalent to the optimal exploitation of this resource. The population with the highest resource exploitation will win the competition regardless of the initial conditions. The populations must be characterized not only by their tolerance to the shortage of the limiting factor (that is their tolerance to the high density) but by their exploitation of this resource, as well.

If the populations are limited by more than one resources, more than one population can coexist. There is no general optimization or other type principle that determine which populations can coexist and which ones extinct, because this result of the competition depends on the initial conditions. Otherwise, the optimal resource exploitation principle can be applied separately for every coexisting population in a well-defined sense. An advantageous mutant that only slightly different from its ancestor can replace or coexist with its ancestor but never replaces its ancestor's competitor. Populations limited in more than one season can be discussed in the same way (niche-segregation in time).

C13

Phylogeny and Evolution of the Mediterranean "Brown-Frogs" (*Rana temporaria* complex)

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 C. Giacomini, E. Balletto

The phylogenetic relationships among the Mediterranean "brown-frogs" (*Rana temporaria*, *R. iberica*, *R. dalmatina*, *R. graeca*, *R. latastei*, *R. camerani*, *R. macracnemys*, *R. holtzi*) were studied mostly by enzyme electrophoresis, cladistics of osteological characters and biometric analysis. Evidence from other sources (karyology etc.) was also evaluated.

P1

PATERNAL MITOCHONDRIAL DNA
 IN THE EGG OF THE HONEY BEE
 (*Apis mellifera* L.)

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Mitochondrial (mt) DNA is believed to be inherited exclusively maternally since paternal mtDNA has never been found in offspring. Polyspermic fertilization and complete sperm penetration in the honey bee favours an influx of cytoplasmic paternal DNA into the oocyte of the honey bee. In this work we study the fate of the paternal mtDNA in the first stages of egg development with the use of molecular analytical methods as restriction fragment length polymorphism and probe hybridisation.

THE INFLUENCE OF LOCAL EXTINCTIONS ON THE
PROBABILITY OF FIXATION OF CHROMOSOMAL
REARRANGEMENTS IN A SUBDIVIDED POPULATION.

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Many closely related species differ by a small number of chromosomal inversions or translocations. Those chromosomal differences are reported to provoke negative heterotic effects, thus rendering the character underdominant.

At an underdominant locus, there exists an unstable equilibrium. Therefore when an allele is at a frequency lower than its equilibrium frequency it is selected against, and vice versa. When the equilibrium frequency of a given allele is low, the range of frequencies leading to its final fixation is greater. Thus any evolutionary force tending to diminish the equilibrium frequency of an allele in an underdominant system will facilitate its eventual fixation.

When a chromosomal rearrangement first arises, it is at a frequency below its equilibrium one, and therefore it is selected against. The ultimate fixation of such rearrangements (like the fixation of centric fusions in mice), demands an elucidation of the possible mechanisms allowing such rearrangements to become frequent and finally fixed.

Previous studies have shown that genetic drift and meiotic drive in favor of the rearrangement could explain such fixations. Particularly, in a subdivided population the probability of fixation as well as the time to fixation are a monotonically decreasing function of the interdeme migration rate.

In the present study we examine the role of local extinctions on the probability of fixation and on the time to fixation of an initially rare allele (5%) in a subdivided population. We consider the interaction of underdominance (with an heterozygotes disadvantage of 2%) and meiotic drive in favor of the initially rare allele alone (segregation distortion=1%).

Among other results, we find interesting interactions between the migration and the extinction rates. In particular the probability of fixation as a function of the interdeme migration rate follows a humped curve. We show that there is a genetic load associated to underdominance.

Local extinctions increase genetic drift in each deme since during the few generations following an eventual recolonization the effective deme size is reduced. Thus the rare allele may become frequent in one deme by chance. Once it became fixed or almost in one deme it can migrate in the homozygous state (which presents no disadvantage). On the other hand local extinctions reduce global population's size and increase gene flow, accelerating in this way the whole process of fixation.

DEVELOPMENTAL PATHWAYS, HOMOLGY AND HOMONOMY
IN METAMERIC ANIMALS

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1. Two processes, or structures, can be regarded as homologous in so far as they share in a common informational background. Owing to the complex, mostly interactive network of informations (both genetic and epigenetic) existing behind all biological processes and structures, we must be prepared to recognize different degrees of homology, instead of a clear-cut distinction between homology and non-homology.

2. Within a single individual, a common informational background certainly relates repetitive structures, as metameres, antimeres, but also lesser units such as scales, or bristles (Van Valen, 1982). Therefore, it seems to be justified to regard homonomy as (a special case of) homology.

3. Body segmentation is achieved through different pathways in different phyla, therefore 'segments' are not homologous throughout the animal kingdom. Care must also be paid in homologizing 'segments' of different developmental stages of the same animal.

4. Sometimes, segmentation stops at an early stage of expression in some sections of the body, while further progressing in others, therefore 'segmental' units are not necessarily homologous (-homonomous) throughout the body length.

C12

PECTORAL FIN RAY HOOKS AS A MODEL FOR AN
EVOLUTIONARY NOVELTY

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In Blennies and many other groups of benthic fish the pectoral fin possesses a peculiar morphological differentiation as an adaptation to ground dwelling: the ventral part shows fin hooks consisting of an asymmetric regression of the fin web, a mesodermal condensation on one of the hemisegments, and a cuticle, an epidermal differentiation. In the Blenniini these three subcharacters appear only in the ventral part of the fin, though defining the fin hook, while in other groups of the suborder Blennioidei the subcharacters are not restricted to the ventral field in the fin. In the Labrisomidae, which is the most primitive extant family of blennies, the mesodermal condensation is found on all fin rays, regardless whether there is a fin web regression or not. In addition two symmetrical mesodermal condensations appear on each bony fin ray. A differentiation of the epidermis is always correlated with the condensation. In more advanced groups e.g. the Salariini, the condensation appears only on one hemisegment. Furthermore the size of the condensation decreases toward the dorsal part of the fin. The situation in the Blenniini could thus be a consequence of a trend towards a correlated expression of the subcharacters, resulting in a developmentally constrained system.

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C6

PARASITES AND SEXUAL ORNAMENTS: TEST OF
THREE ASSUMPTIONS OF THE HAMILTON AND ZUK
HYPOTHESIS

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Parasites may play an important role in mate choice, because of the indirect benefits of choosing a mate that signals resistance to parasites through the quality of its plumage or displays (Hamilton & Zuk 1982). This hypothesis is based on three assumptions; (1) that parasites negatively affect fitness; (2) that resistance to parasitism is partly heritable; and (3) that parasites directly affect the expression of plumage or display ornaments.

I tested these assumptions by manipulating loads of the haematophagous mite *Ornithonyssus bursa* in the nests of its swallow *Hirundo rustica* host. Reproductive success of the swallows was affected by experimental manipulations of mite loads of their nests. Swallows were shown to have heritable resistance to the mite in a partial cross-fostering experiment. Resistance was strongly positively related to the size of tail ornaments. The change in size of the tail ornament from one year to another was significantly affected by the mite load of the individual and its nest during the previous breeding season. The experiments thus could not refute the assumptions of the Hamilton and Zuk hypothesis.

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The chromosomal location of the Heat Shock Proteins (hsps) Genes have been established in three Drosophila species of the Obscura group by in situ hybridization: D. subobscura, D. madeirensis and D. guanche. In order to obtain this data polytene chromosomes of these species were hybridized with the radiolabeled probes 301.1, 122.1, pPW227, 88.5 and 88.6 which contain D. melanogaster DNA segments coding for hsp83, hsp70, hsp68, hsp28-23 and hsp26-22 respectively.

The same hybridization patterns appear in the three species of the Obscura group: hsp83 hybridizes to the 18C locus; hsp70 and hsp68 hybridize to 89A and 94A loci; hsp28-23 and hsp26-22 hybridize to the 27A locus. Moreover the hsp genes of these species and those of D. melanogaster show strong similarities at a cytological level. In all species hsp loci are located in the same chromosome elements: 3R, 3L in D. melanogaster and O, J in species of the Obscura group. This agrees with the idea that chromosome elements from different Drosophila species retain their essential identity.

On the other hand, the results indicate that the degree of homology between hsp70 and hsp68 genes is higher in Obscura group species than in D. melanogaster.

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The "eclipse of darwinism" lasted in Italy until the fourth decade of this century. In the years 1937-1939 some young biologists brought to the attention of the students the work of the geneticists which was opening the way to the foundation of the "synthetic theory". Soon after the war the first chairs of genetics were established in the university of Naples (1944), Pavia (1948) and Milan (1948). The research on evolutionary problems was implemented in the three centers, and soon developed also in other universities and research centers of the National Research Council. It was directed mainly into two fields: animal genetics and human genetics with the main purpose to recognize the action of natural selection as a cause of adaptation to environmental conditions leading to racial differentiation and eventually to speciation. A considerable work was made along these lines. Attention was paid also to historical and philosophical aspects of darwinism.

INTEGRATING DEVELOPMENTAL AND POPULATION GENETICS: THRESHOLD EPISTASIS

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Recent developmental-genetic studies emphasize that the development of characters is controlled by teams of functionally related loci involved in specific interactions. I present a general model of genetic architecture based on information that this approach has yielded. Specifically, this model incorporates the fact that functionally related loci can act as penetrance modifiers of each other. Changes at one or more of these loci can increase the penetrance of semidominant or recessive alleles at other loci in the team. If this genetic behavior is of population importance, it is expected to result in a substantial increase in expressed genetic variance. I examined this idea by comparing the genetic variance resulting from the same set of wild third chromosomes, tested in wild type and mutant backgrounds in Drosophila melanogaster. The mutant background consisted of a mutation affecting the character studied, on an X-chromosome otherwise isogenic with the wild type X. To test for the generality of this model, the character chosen was sternopleural bristle number, a typical quantitative character with little expressed epistatic variance. A twofold increase in genetic variance was observed in the mutant background. It resulted from strong interaction of some chromosomes with the mutant background. A technique imported from developmental genetics is used to test the idea that these chromosomes carry polygenes that are functionally related to the mutation used as the mutant background. The implications of these results are discussed with respect to founder event evolution and population bottlenecks.

MATING SYSTEM AND INBREEDING IN A NARROW-RANGED SPECIES, PINUS LEUCODERMIS ANT.

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Analysis of megagametophytic and embryonic genotypes in open-pollinated seeds from adult trees of two Italian populations of Pinus leucodermis Ant. allowed the estimation of mating system parameters t , outcrossing rate and p , pollen allele frequency. Four isoenzymatic loci were analyzed through horizontal starch gel electrophoresis. Results indicated that a mixed mating system model, with a minimum variance mean outcrossing rate of 74 and 84 % respectively, described the mating system of the two populations. These estimates are relevantly lower than those observed in Conifer species, which are usually above 90 %.

There is a significant variability in the mating system of this species, as it is attested by the difference in the estimate of the outcrossing rate in the two populations: this could be due either to genetic factors or to ecological factors, such as stand density or substructuring.

Comparison of progeny (embryos) and parental genotypic distributions indicated that a major genetic shift between the two life-cycle phases occurred in both populations: there was a significant reduction of homozygosity in the adult trees, which could be caused by selection against homozygotes derived from inbreeding.

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With the use of nuclear and mitochondrial (mt)DNA markers it is possible to reveal effects of sexual selection in natural populations. MtDNA is inherited maternally whereas nuclear DNA is transferred by both sexes. In honeybees mtDNA markers can be used to study the impact of swarming on natural selection. Both an analytical and a simulation approach show that the fitness of the male sex has significant impact on mtDNA equilibrium frequencies (f_{mt}). There is a negative correlation between f_{mt} and the fitness of the males which are initially produced by queens carrying the corresponding mtDNA. Empirical data from Africanized honeybees in Venezuela show that these honeybees carried the European mitotype. This is in line with observations of an increased fitness of Africanized drones. It is unlikely that mtDNA can be used as a diagnostic tool for the identification of Africanized honeybees. However, mtDNA is useful for the study of the selection dynamics in hybrid zones.

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This paper presents a comparative analysis of the early skeletal development in crocodilians and birds. Both the carpus and the tarsus of crocodilians are highly derived in terms of their reduced number of skeletal elements - a trend further enhanced in birds. Traditional explanations of these phylogenetic element reductions rest on recapitulatory concepts that assume large numbers of secondary fusions and deletions. In contrast, the present study emphasizes the truncation of skeletogenic processes at various developmental levels. This ontogenetic information is used to present a hypothesis of progressive paedomorphosis underlying the evolution of archosaur limbs. Several invariant patterns of skeletogenesis provide a basis to re-address the issue of homology from a mechanistic ontogenetic point of view.

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Fertility and viability are both important components of fitness. However, especially the male component of fitness has been poorly studied until recently. It is difficult to get measures of actual reproductive success, even if ways to measure reproductive effort exist. We measured male reproductive effort and reproductive success in two experimental orchards of *Pinus sylvestris* in Finland (Viitaselkä and Vilhelminmäki). The Viitaselkä orchard consisted of 25 genotypes, which have been vegetatively reproduced on the average to 25 ramets, to produce an orchard with about 500 even-aged trees. The Vilhelminmäki orchard consisted of 28 genotypes, about 1000 trees. We counted male strobili on sample branches to obtain the total pollen production of the tree, which we used as an estimate of male reproductive effort. There was extensive variation in pollen production between the genotypes, with coefficients of variation of 0.41 and 1.08 in Viitaselkä and Vilhelminmäki, respectively. Reproductive success was estimated by studying the gametic contributions of different genotypes in the fertilizing pollen pool of the seed crop corresponding to the studied pollination season. Paternity analysis was made using 13 polymorphic enzyme loci, which allowed us to assign unique pollen parents to about 10-15 % of the seeds. There was a significant linear regression between pollen production and gametic contributions, but the regressions accounted for only a fourth of the variation in reproductive success.

Abstract

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On the effects of spatial variation in food availability and temperature on breeding parameters in Great Tits (*Parus major*).

In population biology hypotheses about mechanisms acting on the individual are nearly always tested on yearly mean values of large groups. In principle, the same mechanisms could also explain part of the variation within groups. Can the within year environmental variation in breeding parameters be explained from detailed spatial information about the environment?

From prior to the onset of laying until fledging of first broods, daily minimum and maximum temperatures and weekly samples of available food were collected for several groups of three nestboxes differing in altitude of over 400 m during the breeding seasons of 1988 and 1989. As a first step, laying date, clutch size, egg size and nestling growth rate are related to the local environmental conditions.

C12

COVARIATIONAL PATTERNS IN AVIAN SKELETON - AN HEURISTIC APPROACH TO FUNCTIONAL INTERPRETATIONS DERIVED FROM MORPHOMETRICS.

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As an alternative and extension to the traditional concept of functional analyses in morphology a morphometric approach is outlined by the example of avian skeletons.

Contrary to the traditional concept (i.e. detailed investigations of structures and physical circumstances in few species only) the morphometric concept is based on a trendfinding procedure within monophyletic groups (each including numerous species) by means of multivariate statistics. At first the skeletal measurements are logarithmically scaled for allometric reasons. In using principal component analyses (PCA) the data are represented in the space of the factor score coefficients and covariational subsets of characters are extracted as the next. Bearing in mind that organisms are optimized systems these covariational subsets are interpreted finally as cofunctional (selectively tolerated) units with regard to arguments from biology (e.g. ecology, chorology and ethology).

This approach is demonstrated within two monophyletic groups differing by phylogenetic age and systematic level (Finches - family of Carduelidae: n = 208, 44 species and 44 measurements; pigeons and doves - order of Columbiformes: n = 237, 36 species and 85 measurements).

C5

THE NON-HEREDITARY PHYLOGENETIC CHANGES AND THEIR MEANING IN EVOLUTION

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It was often claimed that only hereditary changes (mutations) do concern evolution and natural selection. There is, however, a lot of evidence against this conclusion. The properties of any given organism are determined by both its hereditary constitution (genotype) as well as by its external and internal environment. Changes in of phenotype may be thus caused either by mutations or by changes in internal or external medium. The internal changes determine the ontogenetic development, the external ones the range (=norm) of reaction.

The time of duration of the environmentally induced phenotypic change depends on the duration of the inducing external factor. Long-time environmental changes like those due to the continental drift (c.f. the plate tectonics) result in longtime phenotypic changes. For these the term non-hereditary phylogenetic changes has been suggested (c.f. Novák 1981, 1984, 1988). They may affect natural selection and thus also evolution.

The possibility of fixation of non-hereditary changes has been shown by Schmalgauzen (1969) on the basis of his conception of the stabilization selection. In this way the range of reaction of a new modification may be narrowed and thus it becomes separated from the original broad range form. In this way adaptive hereditary changes may appear in a long series of generations. It means that a strict difference between hereditary and non-hereditary changes does not exist and they both are important in evolution.

C11

CYTOPLASMIC INCOMPATIBILITY IN TRANSPLASMIC LINES OF DROSOPHILA SIMULANS.

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Cytoplasmic incompatibility has been observed in natural populations of *Drosophila simulans*. When a female of an "incompatible" line is crossed to a male of a "compatible" one, the cross is either sterile or produces few adult progeny.

The involvement of a microorganism is the most favoured explanation for this phenomenon but the mechanism is not yet understood. Electron microscope examination showed in fact intracellular procaryotes in the "compatible" strain but not in the "incompatible" one. These procaryotes were seen to be very similar to rickettsia *Wolbachia pipientis* already described in mosquitoes.

The cytoplasm of one of the "compatible" strains has been injected into the posterior pole of the egg of another "compatible" strain. As the two "compatible" strains carry two different types of mitochondrial DNA, the integration of the cytoplasm of the donor has been analyzed looking for mitochondrial heterogeneity in different sublines. The results of the crosses performed after the injection showed that the females of the original line had become "incompatible" to the males of the same line injected with a foreign cytoplasm.

These results seem to suggest the existence of a great variability of the factors responsible of this phenomenon either due to the involvement of different bacteria or to extrachromosomal factors.

P9

FITNESS OF ALLOZYME GENOTYPES IN WILD DROSOPHILA MELANOGASTER

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We have studied in *Drosophila melanogaster* wild females the effect of enzyme variation of four loci (Adh, -Gpdh, Est-C and Pgm), on several fitness components. Three fitness components (female fecundity, rate oviposition and egg to adult viability) are studied under two environmental conditions: optimal or marginal temperature (22°C and 28°C). Two other fitness components (rate of development and female productivity) are studied under four environmental conditions: optimal or marginal temperature, and optimal or competitive density. Statistically significant differences exist for four of the five components of fitness. No single genotype is best for all fitness components rather the relative fitnesses of genotypes are reversed when different parameters are considered or when they are studied in different environmental conditions. The data are discussed according to several forms of selection that may account for these enzyme polymorphisms in nature.

HIGH RATE OF MULTIPLE INSEMINATION IN A NATURAL POPULATION OF *DROSOPHILA MELANOGASTER*

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Captured wild fly females were permitted to lay eggs individually in standard food vials, during five consecutive days. Then genotyped at two loci on the second chromosome (Adh and Gpdh) and two loci on the third chromosome (Est-C and Pgm). The progenies (a sample) of homozygous females for the second or/and third chromosome, were examined electrophoretically for the same loci that their mothers. Those containing more than two different genotypes were considered to stem from more than one father, there being no crossing over in the males. The observed frequency of multiple mating represent only a part of the true frequency. Using the appropriate statistical probabilities, the actual frequency can be inferred. Our data demonstrate that multiple paternity is present in more than 30 % of the cases. The results are discussed in relation with fitness and sexual selection in females of *Drosophila melanogaster*.

EVOLUTION OF DISPERSAL IN A METAPOPULATION MODEL

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Most theoretical models on the evolutionary genetics of subdivided populations consider that traits such as the migration rate between the local populations, the age-specific fecundities and survival rates, and the reproductive system are fixed entities that do not evolve themselves. In fact, colonization/extinction events, as well as the processes of ecological succession, have important consequences on the evolution of those traits.

We present a theoretical metapopulation of an asexual, iteroparous species, without mutation or drift, under density-dependant regulation of juvenile and adult survival. Computer simulations are used to find the evolutionarily stable strategy of the between populations migration rate. We study the influence of landscape parameters (local extinction rates as a function of the age of the local population, and duration of ecological succession) and genotypic parameters (age-specific fecundities and survival rates) on this ESS for dispersal.

The model allows us to distinguish the optimal strategy (which maximizes the overall metapopulation equilibrium density, or carrying-capacity) from the evolutionarily stable strategy for the migration rate. In particular, in some, but not all, cases, phenotypic plasticity allows the ESS to be closer to the optimum of the metapopulation.

Finally, we argue that the observation of the growth-rate of local populations does not necessarily imply anything about the possibility of maintaining a species in a given landscape. Depending on the probabilities of local extinctions and the speed of ecological succession, it might be possible that he species can maintain itself locally, but not at the level of the landscape. The opposite might be true as well. This could have consequences for managing biological reserves.

Our model provides a framework to study other traits of the genetic system which are likely to experience different selection patterns between the foundation and the extinction of each local population. For instance, for certain sets of parameters, a disruptive selection for life-history traits was found.

CONSERVATION GENETICS OF PLANT POPULATIONS: PHENOTYPIC VARIATION IN *Salvia pratensis* AND *Scabiosa colum- baria* POPULATIONS OF VARYING SIZE.

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Conservation biological theory predicts a relation between (effective) populationsize and intrapopulation level of genetic variation. As a consequence of loss of genetic variation small populations might exhibit a general decrease in viability.

We tested this hypothesis on the plant species *Salvia pratensis* and *Scabiosa columbaria*. Both species are insect-pollinated perennials and predominantly outcrossing. Variation in morphological, and for *Scabiosa* also reproductive, characters in 5 *Salvia* and 7 *Scabiosa* populations was studied in a greenhouse, using offspring of 6 - 7 motherplants.

The total phenotypic variation within populations showed a clear relation with populationsize in both species, the smallest population having the lesser variation. Significant between-family variation was observed for several characters, indicating the existence of a genetic component. As most effects are observed in the characters of seedling or juvenile stages, a maternal component might be present.

Differences between populations were investigated using discriminant analysis. The *Salvia* populations differed on a "growth rate" axis, the larger populations growing faster than the small ones. For *Scabiosa* the differences between populations were mainly on a "reproductive effort" axis. These differences showed no relation with populationsize, however.

The results are in agreement with the expected relation between populationsize and genetic variation. Loss of variation does not necessarily lead to loss of viability, however.

ASPECTS OF THE REPRODUCTIVE-CYCLE IN PROASELLUS COXALIS (CRUSTACEA ISOPODA): VARIABILITY WITHIN AND AMONG POPULATIONS

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Proasellus coxalis, freshwater isopod, is a polytypic species widely distributed in the mediterranean area.

We have examined three populations of different geografic origin, already described as subspecies: the first from river Ciane near Siracusa (*Proasellus coxalis wolffi*, Dudich 1925), the second from river Tevere, Roma (*Proasellus coxalis italicus*, Dudich 1925), the third from Zippori, Israele (*Proasellus coxalis coxalis*, Dolfus 1892).

The analysis of variance was used to study the variability of some reproductive characters among the three populations. The factor analysis was carried out using the significant variables: the plotting of each individual on the first and the second factor, indicates that the variability is well explained by this trasformation. The distribution of the clouds is not completely confirmed by the reproductive compatibility observed in the hybrid-cross among the populations. The variables employed are: the number of deliveries, the total number of borns, the number of borns for each delivery, the period of embryonic development, the number of prolific femals against the crossed ones.

P13

ANTI-HUMAN ANTIBODIES RECOGNIZE FIBRONECTIN-LIKE MOLECULES IN PLANARIAN ECM

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Planarians provide an excellent embryonic model for studying regulatory mechanism of morphogenetic events because of their peculiar organization. Cell migrations are at the basis of both somatic cell renewal and development of the regenerative blastema.

Recently studies have clarified the molecular nature of the cell substrate interactions involved in promoting cell migration and cell differentiation.

In this study fibronectin(FN)-like molecules were detected by immunoelectron microscopy, using anti-human monoclonal antibodies, during planarian blastema cell migration. Immunolabeling with anti-FN antibodies was observed in the ECM used as substrate for the migration of blastema-forming cells. It is of interest that the labeled clusters were detected at cell-matrix contacts where actin was also present (Pascolini et al., Tissue and Cell, 20:157,1988). These data indicate that FN has high evolutionary constancy. In planarians it may be involved in promoting cell migration and in modulating cell differentiation.

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C12

DIVERSITY IN ARTHROPOD CIRCULATORY ORGANS: WHAT ARE THE EVOLUTIONARY CONSTRAINTS?

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A comparative study of the circulatory organs supplying the antennae of arthropods revealed an unexpected diversity in structure and function. In Crustacea (Malacostraca) and Myriapoda, antennal vessels exist which originate from the dorsal vessel as lateral arteries caudal to the brain. Insects in general have separate antennal vessels with basal ampullae, which communicate with the haemolymph sinus in front of the brain. The connection to the dorsal vessel is considered a plesiomorphic state, which apparently was lost early in insect phylogeny. Space constraints due to constructional changes in the cephalic capsule are discussed as a possible reason for this loss. In a number of ancestral insect groups the ampullae are not pulsatile. In most orders, however, the ampullae are pulsatile as a result of associated muscles. These muscles diverge in their attachments and act either as dilators or compressors of the ampullae; a derivation from pharynx dilators is strongly indicated.

C7

On the ecological and evolutionary classifications of life-history strategies

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In the last three decades several ecological classifications of life-history strategies were created (e.g. Pianka, 1970; Grime, 1974; Southwood 1977; Sibly and Calow 1984; Begon 1984). All these classifications consider life-history traits as adaptations and they are based on postulated adaptive "correlations between the life-history traits and features of the environments in which the life-histories are found". The analysis of these classifications reveals that the key features of the adaptational circumstances explaining life-history variations are:

- the amount and age-specificity of unavoidable mortality;
- the age-specificity and severity of competition;
- the age-specific fluctuations in unavoidable mortality and competition and
- the trade-off structure.

The adaptational circumstances can be defined in different ways, that is one of the reasons why the classifications differ from each other. Finally, it will be shown that in a few cases adaptation to the ecological circumstances makes species walk into an evolutionary trap.

C9

PGI GENOTYPES IN Gammarus insensibilis: DIFFERENTIAL RESPONSES TO ENVIRONMENTAL VARIATION

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In the field of evolutionary biology, the problems of genetic adaptation to the environment is still largely unsolved. The mechanisms by which enzyme polymorphism is involved in the adaptive process could be more easily detected through the consideration of loci with metabolic relevance. Studies concerning the dynamics of gene and genotype frequencies of PGI locus were carried out, during a period of about ten years, on a Venetian population of the brackish water Amphipod Gammarus insensibilis. The differential survival and the enzyme activity of the three most frequent genotypes at the PGI locus (i.e., C/D, C/C and D/D) were carried out in relation to temperature. Survivorship experiments were conducted at 27°C for 36 hours, and enzyme activities were estimated at 4°, 20° and 37°C. The results show a high constancy of gene and genotype frequencies during the study period. Considering the survivorship results jointly with the enzyme activity, the highest fitness was exhibited by C/D as indicated by its lower mortality and higher PGI activity. The opposite situation was found in homozygote D/D, which showed the highest mortality and the lowest activity. Intermediate values for both parameters were exhibited by C/C. Such a situation can account for the maintenance of this polymorphism in nature reflecting a mechanism of "balancing selection".

C12

DEVELOPMENTAL CONSTRAINTS ON PECTORAL FIN HOOK NUMBER IN BLENNIES

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In Blennies and many other groups of benthic fish the pectoral fin possesses a peculiar morphological differentiation as an adaptation to ground dwelling: the ventral part shows fin hooks consisting of a cuticular differentiation, a mesenchymal condensation and an asymmetric regression of the fin web (see MISOF & WAGNER). The dorsal part of the fin shows none of these characters. Morphological variation of the fin hooks concerns mainly the shape of the fin web and the number of fully differentiated hooks (Type 1 hooks) per fin. A comparison between five species of Blennies with different habitats from deeper sublittoral to supralittoral reveals that habitat correlates with the number of Type 1 hooks but not with the total number of hooks, which remains constant. A model of fin hook development is proposed which predicts that the number of fin rays capable of hook differentiation is determined by the shape of the fin, and tested with morphometric data from larval and adult individuals. These data reveal that fin hooks can develop only ventrally to the longest fin ray. Fin web regression between two fin rays only occurs if the ventral ray is shorter than the dorsal one by at least 5%. It appears that the position of the longest fin ray remains constant during evolution, determining the number of hooks, while adaptation to habitat only concerns the degree of hook differentiation.

Supported by the Austrian FWF, projekt Nr.
P 7311

P1

PRELIMINARY DATA ON THE PRESENCE OF THE EVOLUTIONARILY CONSERVED GATA REPEATS IN THE ASELLUS AQUATICUS GENOME.

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Caryological studies had been previously carried out by us on some species of Asellidae for a better understanding of their genome and phylogenetic collocation.

We are now extending the cytogenetic analysis at the molecular level to study the genomic organization of both males and females of two populations of *Asellus (Asellus) aquaticus* (L.) Racovitza by investigating in their total DNA the presence and eventually the amount of a Bkm-related sequence and by analyzing its restriction pattern. *A. aquaticus* is a sexually dimorphic isopod crustacean that has no morphologically distinguishable sex chromosome pair. Bkm (banded krait minor) is a DNA fraction that was isolated as a minor satellite from the DNA of the females of the elapid snake *Bungarus fasciatus*. This extra satellite band is absent from the male DNA. Bkm has been shown to be present in a great variety of eukaryotic species both vertebrates and invertebrates. In some species this sequence appears to be arranged in a sex specific pattern and to be more abundant in the heterogametic sex. The Bkm satellite includes several types of no cross-hybridizing sequences. The probe used by us, is a Bkm-positive fragment of *Drosophila* clone CS319 that contains 37 copies of the tetranucleotide GATA.

P2

HORDEIN VARIATION IN WILD AND CULTIVATED BARLEY

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Five different monoclonal antibodies, raised against hordeins from the barley cultivar 'Bomi' (*Hordeum vulgare* ssp. *vulgare*) (Ullrich et al. 1986) were tested in immunoblot assays against hordeins extracted from the following barley species: *H. vulgare* ssp. *spontaneum*, *H. murinum*, *H. pusillum*, *H. bulbosum* and *H. brevisubulatum*. In future studies the antibodies will be used to investigate the genetic organization of the hordein coding genes in *Hordeum* species with different breeding patterns.

Many of the investigated species had hordeins with identical antigenic sites. This indicates that there are conserved structural homologies between the molecules. Antibodies that reacted against many hordein polypeptides in Bomi also reacted against hordeins from many other species. This correlation is probably due to the position of the recognized epitope, so that common epitopes are presumably situated in the well conserved parts of the polypeptide, while rare epitopes are located in the more changeable regions of the molecule.

A wide difference in reaction pattern shows that there is a high rate of evolution among the hordeins. From the band patterns can also be seen that the hordeins must have undergone concerted evolution. This is evident from the electrophoretic mobility difference between homologous molecules in different species.

Reference:

Ullrich, S.E., Rasmussen, U., Høyer-Hansen, G. and Brandt, A. 1986. Monoclonal antibodies to hordein polypeptides. -Carlsberg Res. Commun. 51:381-399.

C10

EVOLUTIONARY SIGNIFICANCE OF MOBILE ELEMENTS ON THE DIFFERENTIATION OF DROSOPHILA POPULATIONS.

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P, hobo and pogo are families of mobile elements in *Drosophila melanogaster*, presenting structural similarities. Complete elements of each family are about 2-3 kb length, with short inverted terminal repeats.

At the population level, a survey of current strains examined over The States, Europe and Asia, has revealed the presence of full-sized elements and of specific deleted-derivative elements. A major geographical differentiation has been observed for the P system, which appears to be stable over the last decade. No geographical differentiation was observed for the others systems.

Temporal analyses indicate that the majority of strains derived from natural populations in the Americas and in Europe before the mid 1950's harbor no or few P and hobo sequences. In contrast, all recently derived and present day populations tested carry numerous P and hobo elements. No such a temporal distribution was found for pogo.

An evolutionary process occurring in the *D. melanogaster* species may be proposed, as the result of a modification of the genetic structure of American populations in the first half of this century. This modification is plausibly related to environmental changes affecting this species, commensal with man. In response to these changes, a genetic reshuffle may have occurred, enabling the recombination - reactivation of transposable elements, and the genomic integration of one (or more ?) of such elements introduced by horizontal transfert, before their spread into the global species.

C5

ADAPTABILITY OF STORAGE ALLOCATION IN *DAPHNIA MAGNA* STRAUS

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Natural populations of Cladocerans experience large fluctuations of resource availability. To cope with such variations, *Daphnia* stores reserves during periods of food abundance, and uses them to survive periods of food shortage.

There are however some costs to storage, because stored energy could be invested otherwise into reproduction, or into body structures to enhance further acquisition. Storage allocation therefore is expected to be optimized, the optimal strategy depending on the temporal patterns of resource abundance.

Under our standard laboratory conditions, adults *D. magna* store enough energy to survive 7-10 days, to moult once, and to produce 0-3 eggs without any food. But, when refed after a starvation period of 4-6 days, *D. magna* increases its storage to a supernormal level, thus enabling 10-13 days survival, 1-2 moults, and the production of 5-10 eggs without any food.

These results not only confirm the dependence of the optimal storage strategy on the temporal patterns of resource abundance, but also show that *Daphnia* can learn from environment, and adapt its allocation strategy to local conditions.

C12

HOMOLOGY PROBLEMS IN MILLIPEDE SEGMENTS

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The trunk of a millipede (Diplopoda) consists of unusual segmental units: a collum, 3 'segments' with one pair of legs and many 'diplosegments' with 2 pairs of legs each. Conventional arguments from comparative anatomy (sclerites, muscles and their nerves supply) and developmental biology (teratology, patterns of exuviation) have led to contrasting interpretations of (a) homologies (-homonomies) of the units within a single animal, and (b) homologies between these units and those of insects. I try to re-examine them in the light of the current understanding of arthropod segmentation, as seen in *Drosophila* (e.g. Nüsslein-Volhard & Wieschaus, 1980; Martinez-Arias & Lawrence, 1985; Meinhardt, 1986) and tentatively generalized to the other tracheate arthropods (Minelli & Bortoletto, 1988). As far as segmentation is actually achieved, in millipedes too, in such an early and hierarchical way, under the control of specific segmentation genes, we must recognize segmental units of 1st, 2nd, 3rd... order, and a diplosegment is to be regarded as a 'chimaera', dorsally of order n and ventrally of order $n+1$. That is indirectly supported by the existence (in *Drosophila*) of a genetically flexible control of dorso-ventrality.

P1

NEW VARIANT RESTRICTION FRAGMENTS ON HUMAN Y CHROMOSOME

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J. Wolfe**

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Y chromosome derived cosmid clones were isolated from a cosmid library constructed from a somatic cell hybrid (3E7) which has only the human Y chromosome in a mouse background. For each individual a total of 2027 nucleotides were examined (a grand total of 42567 considering that an average of 21 individuals have been examined for each probe for each enzyme).

Out of this study we have found only three variant phenotypes. We have compared our results with the analogous, much larger study of Donis-Keller et al (1986) with autosomal probes. Their data could be used to predict how many RFLPs we should have found if the Y chromosome showed the same degree of polymorphism as the remainder of the genome. According to this data we expected to find a number of polymorphic restriction sites variable from 0.35 to 1.46 in the 12 enzymes used. On the other hand, our results agree on the whole with the distribution of RFLPs per chromosome given by Kidd et al (1988), where only 6 RFLPs out of 158 probes tested on Y chromosome are reported. In conclusion, it is highly probable that less DNA polymorphism is present on Y chromosome than in the remainder of the genome, possibly due to the absence of recombination in the Y specific segment.

Donis-Keller et al (1986), Cold Spring Harbour Symposia 51: 317-324.

Kidd et al (1988), HGM 9.5 Cytogenetics and Cell Genetics 49 n°1-3: 132-135

P13

A NEW APPROACH TO INSULAR "EQUILIBRIUM".

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The authors give population data for terrestrial molluscs and oribatid mites and the main historical, geographic, floristic and ecological characteristics of the single islands of the Tuscan and Aeolian Archipelagos and then perform an analysis of the mollusc and mite populations using physical methods for complex systems instead of the classical method of McArthur & Wilson. The new approach takes the essence of the Island Equilibrium Theory (i.e. the continuous interaction between immigration and extinction) and develops its assumptions, eliminating the more restrictive hypotheses (i.e. the imposition of stationary state).

The function P , indicated as the colonization potential, expressed in terms of the main variables of the island systems in question, provides a synthesis of these variables and allows the impact of each on the system to be evaluated. Once P has been determined for an archipelago, it is possible to predict the number of species of a given zoological group, if its saturation value has first been calculated by the method of finite fluctuations.

The validity of the method seems confirmed by substantial agreement between the theoretical and experimental data, especially for terrestrial molluscs.

A. Piazza

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The latest biological evidence, mostly genetic but with some contribution from palaeontology, strongly indicate a single, and discrete African origin for *Homo sapiens sapiens* at a date much closer to the present than former views would have imagined, perhaps only 200,000 years ago or so, with all non-African diversity perhaps no more than 100,000 years old.

Three major and interely independent sources of evidence might be used to reconstruct our history: (1) direct but limited data from fossil bones and artifacts by palaeontology and archaeology; (2) indirect but copious data on the degrees of genetic relationships among living people; (3) relative similarities and differences among languages: We might attempt to correlate these separate sources, searching for similarities in pattern.

By using the principle that the greater the genetic difference between two living ethnic groups, the older is likely to be their separation, in a recent work in collaboration with Cavalli-Sforza (PNAS, 85: 6002-6006, 1988), we were able to recognize many branches in the human family tree and a considerable parallelism between genetic evolution and linguistic change.

One might have anticipated very little correlation between language and the tree of human ancestry. Conquerors can impose their languages as well as their will. Tongues interpenetrate and merge with an explosive rate not granted to genes. Yet the mapping of linguistic phyle upon our genetic tree is remarkable in its degree of overlap, both at the world (42 ethnic groups tested with 120 genetic markers) and at the micromapping levels (Italy, France and Sardinia). This high correspondence, also at a microgeographic level, can only mean that a great deal of human diversity achieves a remarkably simple explanation in history itself: if one knows when a group split off and where it spread, he has the basic outline of its relationships with others. The primary signature of time and history is not effaced by relatively recent episodes of conquest and amalgamation. We propose that the romanization of Italy and Europe, obviously of the greatest importance for many other aspects of our history, is not likely to have changed the genetic individuality of the conquered populations in a substantial way.

Even if history covers her paths by erasing so much evidence from her records, yet biology and linguistics can recover what history might have hidden in its later changes: the genetic and linguistic structure of contemporary populations reflect the history of our distant past as if it had lain frozen for centuries.

C9

CADMIUM EXCRETION AND CADMIUM-INDUCED GROWTH REDUCTION IN POPULATIONS OF *ORCHESSELLA CINCTA* (L.) (COLLEMBOLA) WITH DIFFERENT HISTORIES OF EXPOSURE

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Heavy metals tend to accumulate in the organic layers of soil profiles. If metal concentrations reach toxic levels, locally adapted populations of soil inhabiting species may develop by a process of selection. The results of this process can be studied by comparing populations with different histories of heavy metal contamination.

The springtail *Orchesella cincta* was chosen as a test animal. The characteristics "cadmium excretion-efficiency" (EE) and "cadmium-induced growth reduction" were determined in laboratory F1 individuals. Both characteristics bear a close relationship with the functioning of animals at contaminated sites.

Animals were collected at a reference site (Ro), at two industrial sites (Bu and St) and at a mining site (Pl).

To determine the EE, laboratory first generation animals were exposed to cadmium during a single intermoult interval. Following each moult, the midgut is regenerated and the old midgut, containing waste products, is excreted. The EE is calculated as the ratio of the amount of Cd present in the pellet and the amount assimilated. Analysis of variance revealed significant differences between the frequency distributions of the EE: the mean EE in Bu was 34.9%, in Ro 38.8%, in St 42.9% and in Pl 47.2%.

To determine the growth response to cadmium, laboratory first generation animals were exposed to either a low or a high concentration of cadmium in the food. The weight gains before and during exposure were determined for each individual. An index of growth reduction was developed to describe the individual change in weight gain following exposure. Statistical analysis revealed a significant interaction between exposure level and population. The growth response of an individual depended on both exposure level and site of origin. Animals from Ro and Bu showed a significant growth reduction at the high exposure level, whereas the other populations showed comparable responses at both exposure levels.

Both experiments show the presence of population differentiation in this species with respect to heavy metal tolerance. Populations at highly contaminated sites have the highest Cd excretion efficiency and are also more tolerant to Cd in terms of body-growth. Since differences were observed in the F1 generation, they probably have a genetic component.

P7

RESPONSE TO WATER STRESS AT POPULATION LEVEL IN *Ornithogalum montanum* (Liliaceae)

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Differential selection results in genetic divergence of populations. One of the limiting factors in *Ornithogalum montanum* diffusion is water availability.

In this study, genetic replicates of 6 different populations have been grown at different water dosages.

Several parameters (e.g. leaf growth rate, emergence, number of flower branches) were measured during the vegetative cycle.

After ANOVA, two populations seem to be characterized by extreme responses for all but one parameters so far examined. Those two populations come from the lowest and highest elevation respectively. The remaining demes are arranged between the previous ones both in responses and in elevations.

The lowest water dosage represents an evident stress condition; as a matter of fact, many parameters vary as far as water amount does. Those parameters that are not influenced by treatment should be mostly characterized by their genetic components.

The authors are going to compare the results coming from the study of phenetic differentiation with those from a previous population genetics and cytogenetics analysis, which are so far available.

S4

MOLECULAR PHYLOGENETICS: INTRODUCTORY REMARKS AND COMMENTS

Jeffrey R. Powell, Yale University, New Haven, CT, USA

As an introduction to this symposium, I will comment on the principles and theory underpinning the use of molecular data to reconstruct phylogenies. Several points will be stressed: (1) Molecular data present relatively objective information in a simple, linear form; (2) The phylogenetic distance over which molecular data can be used is greater than for other forms of data; (3) Technically, it is becoming easier to obtain molecular data; (4) Theoretical studies of phylogeny reconstruction using molecular data are increasing; (5) The information content of molecules is enormous. After emphasizing these virtues, cautionary comments will also be stressed. Of most importance is the fact that as biologists (rather than chemists) we must not lose sight of the primary reason for interest in phylogenies: the history of the origin of diversity of life forms. Molecular phylogenies only have life in the light of the biological properties of the organisms being studied.

W2

Molecular studies on paracentric inversions

J.R. Powell (New Heaven, CT.)

NOT RECEIVED

P3

THE USE OF PROTEIN ELECTROPHORESIS TO DERIVE PHYLOGENETIC RELATIONSHIPS IN BIRDS.

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Phylogenetic relationships among several bird species belonging to 3 orders (Galliformes, Strigiformes, Falconiformes), were studied with protein electrophoresis. Data were coded as discrete character states and as genetic distance matrices. Dendrograms were derived using different algorithms.

The resulting phylogenies are discussed to check the power and the limits of protein electrophoresis, as well as of the different methods used to obtain dendrograms. Rates of protein changes are evaluated and compared with rates of molecular evolution at the DNA level.

C3

ALLOZYME ANALYSIS AND GENETIC POPULATION STRUCTURE OF GREAT TIT (*PARUS MAJOR*) POPULATIONS

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The ecology, behaviour, demography, and geographic distribution of the great tit, *Parus major*, are probably better known than that of any other bird species.

Although this species offers a unique opportunity for testing predictions made from population genetic theories this has hitherto not been done.

By means of electrophoretic analysis of protein polymorphisms in five great tit populations of southern Germany we studied:

- The degree of geographic variation in allelic and genotypic frequencies;
- The genetic population structure by comparing the allele and genotypic frequency distributions within groups;
- The role of evolutionary forces (selection, gene flow, non-random mating) in the formation of population-specific distribution patterns of alleles.

These points are discussed in view of the knowledge about the demographic parameters for these populations gained through field ornithological methods.

C11

Evolutionary significance of
cytoplasmic incompatibility: example of the
mosquito *Culex pipiens*.

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The sterility phenomenon referred as cytoplasmic incompatibility was first described in the mosquito *Culex pipiens*, and is now known in other insects. This sterility is characterized by a drastic decrease of female fertility: in *Culex pipiens*, a female mated with an "incompatible" male produces a normal number of fertilized eggs, but no or very few larvae hatch. Former authors found that these sterility are maternally inherited and independent of nuclear genes, hence they were referred as "cytoplasmic incompatibilities". But their evolution was not understood, which explain why their use for biological control failed.

We present an evolutionary explanation of these incompatibilities, which lead us to pinpoint a major theoretical and experimental weakness not seen by all former authors.

P11

EVOLUTION OF PHOTOPERIODIC DIAPAUSE IN *DROSOPHILA VIRILIS* GROUP

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To study the evolution of seasonal traits in general and diapause in particular is not an easy task. However, the *virilis* group of *Drosophila* appears to offer a chance for this kind of study.

There are eleven species in the *virilis* species group and it is divided into two phylads: *montana* and *virilis*. This study concerns the species of the *virilis* phylad.

D. virilis is a domestic species which is distributed all over the world. It has no photoperiodic diapause and is therefore incapable of overwintering out of doors in temperate climates. The three North American species *D. americana americana*, *D. a. texana* and *D. novamexicana* do not diapause either. Only *D. lummei* has a northern distribution and a photo-periodically induced diapause accordingly. Two major genetic factors control the diapause-non-diapause reaction in these species: the ability to diapause inside the double inversion on the X chromosome shared by *D. lummei* and the North American species, and the locus controlling the critical daylength for diapause located on the 5th chromosome.

C7

ENVIRONMENTAL INFLUENCE ON *Macrotrachela quadricornifera* (ROTIFERA; BDELLIOIDEA): EVIDENCE FROM LIFE HISTORY AND ISOZYMES DATA OF SOME STRAINS.

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Bdelloid rotifers are widespread poikilothermic parthenogens commonly dwelling in both water bodies (ponds, rivers, etc.) and terrestrial mosses. Different strains of the same species (*Macrotrachela quadricornifera*), collected from both water and moss environments geographically coupled, are cultured under laboratory conditions in order to study their life table under different temperatures. The response to temperature, measured as variation of R_0 (net reproductive rate) and r (intrinsic rate of natural increase), conforms to the conditions of the source habitat of the aquatic strains but seems to be random when strains from terrestrial moss are concerned. Life-table parameters, such as embryological time, age at first reproduction, reproductive effort, mean lifespan, R_0 and r are calculated. On these parameters, standardized and normalized, a single link cluster analysis is performed. The same strains are processed for isoenzymatic analysis: six enzymes (APK, PGI, EST and ME and LAP) are considered and the banding patterns indicate genetic differences among strains. A single link cluster analysis is performed on a matrix of banding patterns constructed from the relative mobility of the staining bands for each strain. Both cluster analysis indicate that moss and aquatic strains respectively are closely related, regardless to their geographical origin.

S7

HOMOLOGY AND THE PATTERN OF MORPHOLOGICAL VARIATION

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Within the general aspects the path of explanation is differentiated from the path of discovery and the path of composition (evolution or development), since they have been confused both in taxonomic literature and in comparative anatomy. Further the precondition of what we expect of a causal explanation is discussed. The explanatory principle adopted has to do with functional burdens of the inner organisation leading to constraints and acting against environmental adaptation.

The principles of preserved patterns are sorted in four types:

1) The morphology of standards can be explained by three effects. Standardized parts are conservative as soon as they are numerous, low in position in the system and have many functions. 2) The morphology of interdependency lets us expect a feed-back system of information. 3) The morphology of hierarchical patterns shows a correlation between the amount of conservativity and the number of dependent functions. 4) The morphology of traditive patterns lets us expect the conservation of old genetic information in the modern genom.

C10

PHYLOGENY OF PHYLUM PLATYHELMINTHES BY 18S rRNA SEQUENCES

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We have analyzed partial sequences of 18S rRNA from several species belonging to the Phylum Platyhelminthes, including parasite groups and free living forms. The free-living forms from Cl. Turbellaria, included two orders, O. Rhabdocoelidae and O. Tricladidae. Tricladidae were represented by three families: F. Dugesiidae, F. Planariidae and F. Dendrocoelidae. Sequence data were compared to a large number of animal and protist sequences using an evolutionary distance method.

The intra-group analysis supports the following conclusions:

(1) Sequences analyzed fell into two independent groups, one comprising the O. Tricladidae and O. Rhabdocoela and the other including the trematodes (Fasciola) alone. This grouping does not support the hypothesis of the possible origin of the trematodes from a rhabdocoel form.

(2) Within the O. Tricladidae a close relationship was observed between the three dugesiids as compared to the other species (belonging to two other families). F. Planariidae and F. Dendrocoelidae appear to form a sister group to F. Dugesiidae.

The comparison of platyhelminth to other sequences supports the following conclusions:

(1) Platyhelminthes is a monophyletic group, since all the species clearly branch together.

(2) Flatworms are an old group which branched very early from the rest of metazoans, and consequently can not be a simplified form derived from any of them. Phylum Platyhelminthes contains great diversity: evolutionary similarities between its deeper branches are in the same range as that found between species of different phyla (e.g. nematode and mollusc; annelid and coelenterate).

(3) Preliminary data suggest that Platyhelminthes are a true sister group to the coelomate animals, whereas other non-coelomate animals, such as Nematoda and Nemertines, actually are derived from the coelomate radiation. This supports a flatworm-like ancestral form for bilateral animals.

P2

ALIGNMENT OF TRYPTIC PEPTIDES OF A GLOBIN OF THE EUROPEAN EEL

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17 complete sequences of teleost fish globins are known. All of these sequences concern the infradivision Euteleostei, while the other three infradivisions have been ignored so far. The European eel, *Anguilla anguilla* (L.), belongs to the infradivision Elopomorpha: this is the phylogenetic reason for sequencing its globins. Another reason is given by the unusual functional and structural features of the hemoglobins of this species. Usually the teleosts which have hemoglobins with different functional properties, have some sensitive to the concentration of hydrogen ions and organic phosphates, while others are insensitive to both of them. Instead, in the eel the two effects are separated on different hemoglobins, namely the acidic ones are sensitive to hydrogen ions, whilst the basic ones are sensitive to phosphates. From the structural point of view the most strange feature is the low molecular weight of the β polypeptide of the basic hemoglobin: 138 residues instead of 146-7. This is the polypeptide we are sequencing according to Chang's method. (The alignment is based on the usual residue number; L means Leu or Ile).

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1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
V E W S A H F S          G L Y D H R   A
D D L G A E A L S R          V
Y F S H P P D L G P G R S L L T G F P
L P P G K          M N D L V G A L H A L H D
L H R          F S E R          L D P
G S F G R          V L F A A L G D A
L G K          D V L D A G H K          A V
G L H R

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C5

INTERACTION BETWEEN NORMS OF REACTION AND ANTAGONISTIC PLEIOTROPY IN THE SAND CRICKET, *GRYLLUS FIRMUS*.

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Two phenomena thought to be important in the evolution of life history traits are antagonistic pleiotropy and norms of reaction. The former refers to the genetic basis of the frequently observed tradeoffs between life history characters. Though the phenotypic basis of such tradeoffs is well established there are few cases in which these correlations have been demonstrated to be genetically based and hence examples of antagonistic pleiotropy. In wing dimorphic insects the advantages of migration accruing to the macropterous (flight capable) morph are offset by a delay in the age at first reproduction and a reduced fecundity relative to the micropterous (flight incapable) morph.

By selecting for an increased and decreased frequency of the macropterous form I demonstrate that the observed phenotypic tradeoff in the sand cricket, *Gryllus firmus* reflects a genetic correlation, and hence the evolution of wing dimorphism and the age schedule of reproduction in this cricket will be constrained by the antagonistic pleiotropy between the traits.

The incidence of macroptery, development time and the age schedule of reproduction are subject to environmental influence. I show that the norms of reaction are such that the relative fitnesses of the two morphs are modulated by environmental conditions and that under suitable conditions antagonistic pleiotropy between traits may have no impact on the course of evolution.

P11

DEMOGRAPHIC STRATEGIES IN *DROSOPHILA* UNDER SEMI-NATURAL CONDITIONS

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Drosophila species enable us to study easily several demographic parameters. It is important to realize such studies in conditions close to the natural ones, eg with outside temperatures, in several seasons and using the F1 generation. Studies of this nature have been carried out since 1982 in *Drosophila simulans*, *D. subobscura* and *D. phalerata*, whose population fluctuations were already known in the wild. Couples of F1 individuals were kept in separate tubes (containing axenic medium) in an outdoor shelter. The sexual immaturity time, longevity and daily female fecundity could be measured. From 1985 on, egg volume was measured periodically for each female. Additionally, percentage egg eclosion and larval-adult mortality were determined in *D. subobscura*. Samples were kept in several seasons for each species.

There were marked differences between species and between different seasons in the same species. *D. simulans* has higher fecundity and shorter sexual immaturity time in Summer, and *D. subobscura* in Spring; the pattern is less clear for *D. phalerata*. Longevity in all species is higher in Winter. In general, *D. subobscura* is the least variable species between seasons but the most variable within seasons. Egg volume for all species is highest in Winter and lowest in Summer, with *D. simulans* having the largest and *D. subobscura* the smallest eggs. A plateau of high percentage of egg eclosion in *D. subobscura* is longest in Winter and shortest in Summer. Larval-adult mortalities are more similar between seasons, though with higher pupal mortality in Winter.

Thus in each species different demographic parameters have the optimum values in different seasons. From this we deduce the importance of studying several parameters during various seasons in order to understand the demographic strategy of a species. Overall, *D. simulans* is more "r" in Summer and more "K" in Winter. The situation is less clear-cut for the other two species, perhaps due to *D. phalerata* (a fungal specialist) being under a disadvantage under laboratory conditions, and, in the case of *D. subobscura*, to its great genetic variability.

P9

ENVIRONMENTAL CUES AND HATCHING STRATEGY FOR RESTING EGGS IN ELECTROPHORETIC CLONES OF *HETEROCYPRIS INCONGRUENS* (CRUSTACEA, OSRACODA).

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The effect of temperature on survivorship and population size of different electrophoretic clones of *Heterocypris incongruens* has been studied in the field and in the laboratory.

Differences exist among electrophoretic clones in the proportion of resting eggs produced at different temperatures. Hatching after dessication and maintenance in different conditions seems to depend on temperature for the *H. incongruens* clone dominant in winter in the field.

Other environmental cues seem important for the post dessication hatching and deposition of resting eggs in the clone dominant in the field during summer.

The *H. incongruens* clone found in the field in small numbers, all year around, shows low resting egg production and post dessication hatching patterns that are fairly constant in different environmental conditions.

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Homology as a topic has to do with what is conserved in evolution. The problem of systematics (e.g. Patterson 1982, 1988)--to find homologues, and in so doing, to identify taxa--is distinct from the problem of identifying what kinds of features tend to be conserved, how, and why (e.g. Van Valen 1982; Roth 1982, 1988). The two sets of issues intersect (and are fundamentally interdependent) at the point that (a) one identifies the characters one wishes to study, or at the point that (b) the systematist decides what constitutes a single character. Interesting difficulties (apparent paradoxes) arise because taxic, transformational, and genetical notions of homology are not entirely congruent.

Homology is a manifestation of continuity of information (Van Valen 1982). The complexity of development defies simplistic attempts to locate that information within the genome. The problem of understanding why some features, rather than others, are conserved in evolution becomes one of identifying and understanding what have been called developmental constraints (Wagner in press). An understanding of iterative homologues, as natural experiments within a single genetic individual, becomes illuminating.

I will review some specific problems concerning the conjunction test (of taxic homology), homology of genetic material, and homology in morphometric data.

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P7

Genetic variation for recombination in Barley

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Ten different two-row spring type barley lines, representing the genetic variation present in North Europe, were investigated with respect to their amount of recombination. Recombination was studied using four different methods; 1) by the sterility in inversion heterozygotes, 2) by a cytological investigation of inversion heterozygotes, 3) by three linked morphological markers, and 4) by two electrophoretic markers in the hordein loci. The first three methods revealed genetic variation for recombination over a region in the short arm of chromosome 1. Consistent results were obtained when the first two methods were used over two growing seasons. The results showed that the modern variety Alva had less recombination than the other lines including two of its parents, Gull and Hanna.

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Although the fate of genetic information depends as much on the physiological processes involved in the phenotype x environment interaction as on the reproductive and genetic systems, the contribution of physiology to plant population biology is limited. The strength and weakness of various contributions are analyzed as well as the prospect of current approaches.

Intraspecific diversity of plant physiology has been demonstrated for most physiological functions. The relative range of inter-species, inter-populations and inter-genotypes physiological diversity is briefly illustrated. Space and time scales of ecotypic differentiation are mentioned and the relationship between plasticity and genetic differentiation is addressed.

The establishment of covariations between physiological characteristics and genetic markers (enzyme polymorphism, DNA sequence, DNA quantity) has been used as a means to integrate physiology and genetics. This approach is illustrated and its limitations are discussed.

The knowledge of the impact of variations in physiological traits on the fitness of the individual is a major goal to achieve. Advantages and limitations of both the correlative and mechanistic approaches are discussed. The prospect of whole plant functioning studies and models to increase the relevance of physiology to population biology is developed.

P4

GENETIC DIFFERENTIATION AND INTROGRESSION IN THE *OCHTHEBIUS QUADRICOLLIS* COMPLEX (COLEOPTERA, HYDRAENIDAE)

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The taxonomic status of *Ochthebius quadricollis* was so far investigated only at the morphological level. Two subspecies were described: *O.q. quadricollis*, distributed along the Thyrrhenian coast, and *O.q. steinbuhleri*, along the Adriatic coast.

Multilocus electrophoresis showed that two main population groups exist within *O.q. quadricollis*, provisionally indicated as A and B. They have an average Nei's genetic distance of 0.60, with distinct alleles at four loci. *O. quadricollis* A is widespread in Corsica, Sardinia, Sicilia, minor Thyrrhenian islands and a number of localities along the Italian Thyrrhenian coast. *O. quadricollis* B is found on Thyrrhenian and Ionian coasts. Several sympatric sites between *O. quadricollis* A and B were detected in Campania and Calabria. In these localities no F_1 hybrids were found, while a number of introgressed individuals, both of A and B, were detected on the basis of the diagnostic loci *Mdh-1*, *6Pgdh*, *Pgm*, and *Gpi*. Introgression is higher for the first two loci (e.g. at *6Pgdh* the alleles of *O. quadricollis* B spread on average into 16% of individuals of *O. quadricollis* A, while the latter's alleles are found in about 3% of individuals of *O. quadricollis* B). At *Pgm* and *Gpi* the proportion of introgressed specimens is much lower, generally below 2%.

The Adriatic *O.q. steinbuhleri* is more related to *O. quadricollis* B ($D = 0.26$) than to *O. quadricollis* A ($D = 0.57$). No overlap between the ranges of these taxa was found, nor introgressive phenomena. Rare F_1 hybrids were detected in laboratory crosses between *O. quadricollis* B and *O.q. steinbuhleri* (3-5%), showing low vitality. This would indicate that *steinbuhleri* is a good species, reproductively isolated from *O. quadricollis* B.

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Recent progress in analyzing developmental genes has revived interest in the relations between genes and homology. The term homology has partly different meanings to morphologists and molecular biologists. Both imply derivation from a common ancestral structure (Remane's criterion of continuity) but the former define it primarily by topological relations (criterion of position) while the latter use it to indicate a high degree of coincidence between nucleotide or amino acid sequences (criterion of specific structure). Molecular homology often is tacitly assumed to imply identical functions but a glimpse at hormon functions will reveal that this need not be so; neither need homologous body parts arise on largely identical networks of gene action. The "homebox", a highly conserved nucleotide/amino acid sequence first recognized in homeotic *Drosophila* genes is not at all restricted to these; it may be conserved because of DNA binding properties rather than a specific role in morphogenesis. Data from the fruitfly *Drosophila* will be used for defining genes that discriminate between serially homologous structures. Genes involved in generating homologous body parts in different insect species will be discussed using the scanty data available from honey bee, flour beetle and migratory locust. With the present rate of progress continuing, many long-standing questions concerning genes and homology should be answered within a few years.

P6

THE CERVETERI ETRUSCAN NECROPOLIS: HABITAT PARTITIONING AND GENETIC STRUCTURE OF A CAVE CRICKET POPULATION.

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The Etruscan necropolis "La Banditaccia" at Cerveteri, near Rome, consists of a few hundred tombs excavated in the tufa rock, varying in morphology, size, spatial organization, climate and community patterns. These tombs represent a peculiar habitat for several troglomorphic organisms and in particular the cave cricket *Dolichopoda laetitia*. Most, yet not all, tombs are inhabited by varying number of crickets, representing more or less stable subdivided units.

The opportunity to quantify several parameters such as microclimate, community patterns, and dispersion patterns among tombs, led us to investigate whether any evidence of genetic structure and/or difference in the utilization of habitat was detectable within the overall *Dolichopoda* population.

Three thousand individually labelled crickets were the basis of a year long investigation of population and "unit" sizes, dispersion patterns, age and sex structure. Genetic structure at enzyme loci was studied and Fst analysis provided evidence of a moderate degree of genetic differentiation among subpopulations.

The pattern of utilization of the necropolis was assessed both for spatial and ecological discontinuities. Based on the assumption of a potential continuous distribution, as shown by the pattern of the mark-recapture network, discontinuities were investigated comparing the utilization distribution model based on harmonic mean with a model of uniform utilization.

The relationship between genetic structure and habitat utilization is discussed.

VARIATION IN MATING CALL ACROSS THE HYBRID ZONE BETWEEN THE FIRE BELLIED TOADS *BOMBINA BOMBINA* AND *B. VARIEGATA*

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Mating calls have been measured across a transect of the hybrid zone between the toads *Bombina bombina* and *B. variegata*. Of the two components of call measured, one is diagnostic between the taxa. Toads have also been scored for 6 diagnostic enzyme loci. The diagnostic call component cline and enzyme locus clines are concordant and have similar widths suggesting that there is no strong selection on any of these characters. Comparisons between this survey and a previous survey (Szymura and Barton, 1986) where toads were collected between 1974-1981 suggest that the clines in electrophoretic markers may be wider. It seems unlikely that clines have been increasing in width at this rate since secondary contact. More likely the effect may be caused by either fewer samples in the 1987/1988 collections; or by increased disturbance of sites in the center of the zone. Strong premating isolation does not exist between the taxa since all diagnostic loci (with one exception: Gpi at Uwrocie) are in Hardy Weinberg frequencies. This suggests that no reinforcement has occurred despite the large differences in the mating systems of *Bombina bombina* and *B. variegata*. That there is no reinforcement is confirmed by looking at correlations between electrophoretic markers and the diagnostic call component. These are no stronger than would be expected if the electrophoretic loci and the genes causing mating call are neutral. This also means that there is no strong selection against intermediate mating calls.

S8

MITOCHONDRIAL DNA AND Y-CHROMOSOME SPECIFIC RFLPS IN HUMAN POPULATION GENETICS

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The analysis of mtDNA RFLPs has clearly shown the existence of genotypes peculiar to certain ethnic groups. The HpaI-3/AvaII-3 combination and a 9 bp deletion have proven to be valuable anthropological markers of Africans⁽¹⁾ and Est Asians⁽²⁾ respectively; mtDNAs with polymorphic BamHI sites were observed only in Caucasoids, but the mutation which simultaneously produces BamHI-O (loss of site at 14258) and AvaII-25 morphs was typical of Hindus⁽¹⁾.

Population studies on Y-chromosome specific RFLPs have recently started and a large variability has been detected by 49f probe on human male TaqI DNA digests⁽³⁾. These studies have already provided important anthropological markers, as type A₁C₀D₀ peculiar to Blacks, and have also enabled closely related people (Hindus from Nepal and India) to be differentiated⁽⁴⁾.

Due to the lack of recombination of both this kind of markers, the maternal inheritance of mtDNA and the strictly holoandric transmission of Y-specific RFLPs, these studies appear highly potential in determining the relationships among the extant human populations through either matriarchal or patriarchal lineages. They can be also particularly informative in clarifying the origin of some groups, and in revealing genetic admixture in detail, thus permitting to compare biological with both historical data and sociodemographic features of populations.

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GENETIC DIVERGENCE WITHIN THE ITALIAN GREEN
FROG *RANA LESSONAE*, WITH EVIDENCE
OF A HYBRID ZONE

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Multilocus electrophoresis carried out on Italian *Rana lessonae* has shown the existence of two main population groups, morphologically fairly identical, one inhabiting Sicily and southern Calabria, the second living in the rest of Italy. Their Nei's genetic distance is 0.34, with alternative alleles at four of the 24 loci tested and highly differentiated allele frequencies at a further locus. Paleogeographic data suggest that the observed genetic divergence occurred in geographic isolation during Pleistocene, when southern Calabria was separated from Italy, while being connected to Sicily by a transitory land bridge. In the late Pleistocene the two population groups came into contact, without having reached reproductive isolation, and gave origin to a wide zone of hybridization and introgression in Calabria. The geographic pattern of the hybrid zone shows a gradual transition between the two forms, with the highest level of hybrid genotypes in the Catanzaro plain. The extent of introgression is asymmetric, with a more widespread penetration of southern alleles into the northern gene pool. Alleles of the differentiated loci differ in their pattern of introgression: e.g., the southern alleles *Got-2* 80 and *Ada* 92 spread respectively 140 km and 80 km north of the hybrid zone centre, while the northern alleles *NADHdh* 100 and *Mdh-2* 100 reach respectively populations 80 km and 30 km south of it. This could be due to different selective pressures.

The Calabrian populations of the hybridogenetic *R. esculenta*, which has a *ridibunda* and a *lessonae* genome, show in the latter genome the same variation pattern found in *R. lessonae* from this area.

P4

RELATIONSHIP BETWEEN HYBRIDIZING APTITUDE AND
BIOCHEMICAL-GENETIC IDENTITY IN SOME ORCHID
SPECIES-PAIRS (FAM. ORCHIDACEAE).

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Some terrestrial orchid species present a great aptitude for forming hybrids, in contrast with some others that do not. To investigate if a correlation with allozyme identity could exist, we examined eleven species of the genus *Orchis* by means of starch gel electrophoresis of seven enzymes, for a total of nine loci. Mean expected heterozygosity for the whole group ($H_e = 0.149$) is similar to that we obtained for other orchid species, but higher than reported for other plant species ($H_e = 0.086$). Nei's identity coefficients calculated between the various populations of the same species showed a great homogeneity ($I = 0.934 \pm 0.997$). On the contrary, a certain heterogeneity (0 ± 0.767) does exist in the identity coefficients calculated between the eleven species. High values are associated chiefly with the six species-pairs of which we found hybrids. The mean I value in this group (0.571) is significantly higher than observed for the other species-pairs (0.148).

The high identity values observed between hybridizing species could be partially due to the presence of a gene flow across a hybrid bridge (introgression) among hybridizing species. These would so put in common their own genetic pool with a consequent increase of such coefficients. However our results seem to indicate a correlation between hybridizing aptitude and the degree of biochemical genetic similarity, unlike reported for animal organisms.

MEXICAN CAVE STREAMS AS NARROW HYBRID ZONES: PATTERNS OF
INTROGRESSION BETWEEN CRAYFISHES

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In tropical karst areas rapid evolution of drainage basins combined with tectonic events may alter connections of surface and cave streams, thus producing either isolation or secondary contact between biota adapted to different conditions. The Cueva de Los Camarones in Chiapas offers an excellent example of such situations. Two undescribed species of *Procambarus* crayfish inhabit the subterranean stream. They were roughly distinguishable only by comparing extreme phenotypes, ranging from dark, thick, eyed, surface dwelling-like individuals to light, elongate, microphthalmic, cave dwelling-like individuals.

Electrophoretic and morphometric analyses were performed to enlighten evolutionary relationships among individual crayfish and to explain patterns of microgeographic variation previously revealed along the cave stream. Results from multivariate morphometric analyses showed a real discontinuity between the two species mainly determined by the shape of the rostrum, chelae and telson. Moreover, these same characters exhibited clinal variation within the less cavernicolous species. The genetic structure of the two species was investigated at 23 enzyme loci, revealing unusually high levels of heterozygosity in both species. Results of analyses on individual allozymic profile corroborated morphometric results, yielding a genetic distance between the two gene pools of $D = 0.25$. Due to the occurrence of alternative alleles, we could quantify patterns of introgression revealing absence of F1 individuals and asymmetric gene flow between the two species. In the light of these data, the observed microgeographic variation in morphology within one of the two species, as well as the occurrence of aberrant phenotypes, could be interpreted as the outcome of introgression.

C13

TWO NEW PHASMIDS OF THE GENUS *BACILLUS* (INSECTA
PHASMATODEA) FROM SICILY: *B. GRANDII* BENAZZII AND ITS
HYBRID WITH *B. ROSSII*.

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In northwestern Sicily, recent collections gave four different *Bacillus* taxa: *B. rossii* (Rossi), *B. atticus* Brunner, *B. grandii* Nascetti & Bullini, and hybrids between the latter species and *B. rossii*.

B. rossii is generally represented by facultative parthenogenetic demes which, mainly on the basis of allozyme evidence, clearly belong to *B. r. redtenbacheri*. The Sicilian *B. atticus* belongs to the subspecies *B. a. caprai*. Its distributional, ecological and reproductive features have already been published (Agostini and Scali 1989, Boll. Soc. Entom. It. 121 (1): 10-12). Northern representatives of *B. grandii* feed on the lentisk and, like southern populations, show $2n = 34$, XX, female and 33, XO, male. Northern specimens have a genetic distance of 0.195 from the southern ones, suggesting a subspecific differentiation (Mantovani et al. in preparation); even body, egg and chromosome details, as well as experimental crosses, support a subspecific distinction. Therefore the names of *B. g. benazzii* for the northern taxon and of *B. g. grandii* for the southern one are here proposed. The fourth thelytokous taxon ($2n = 35$) is the hybrid between syntopic *B. rossii* and *B. g. benazzii* demes. Body and egg details differentiate it from both parents and the "parallel" southern hybrid *B. whitei* ($= B. rossii \times B. g. grandii$), which even differs at karyological level. Furthermore, while the latter is an obligate parthenogenon the northern hybrid seems to reproduce by both parthenogenesis and hybridogenesis; for this taxon the name of *B. rossii-grandii benazzii* is here suggested.

INDIVIDUAL VARIATION IN THE ORIENTATION BEHAVIOUR OF SANDHOPPERS

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Talitrid amphipods on beaches orient seaward upon encountering dry sand and landward when splashed with sea water, mainly using sun compass. This directional tendency is inherited and each population adapts its behaviour to the direction of its home-shoreline. Individuals can modify their directional tendency according to experience.

The present paper compares the orientation of individuals from different shores and with different experience, in an attempt to define the reaction-norm of this trait. Phenotypic plasticity is important in the adaptation of sandhoppers to changing shorelines, while it seems to be less important in populations from shores with a relatively constant shoreline. A certain degree of genetic variability was found in each population studied. The entity of the genetic flow along the shores is still under study. Preliminary data on the nightly migrations of marked individuals in nature are given.

THE BIOLOGICAL CLOCK IS AN ELLIPTICAL CLOCK

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We have studied the rate of substitution of bases and aminoacids in 12 α tubulins and 9 β tubulins. We reasoned that, when a protein belongs to a functional class, only a finite number of base or aminoacid substitutions is possible; when this number is exceeded, the protein loses function and is eliminated. Thus there is a maximum tolerable number of changes which is possible, and if this maximum is reached, further mutations would not alter or reduce the difference between sequences. When it is exceeded, function and protein is lost. We fitted a log-log regression to the rates of substitution on time of separation between species, and found that in tubulins the function which describes adequately the relationship between these variables is: $Y=AX^{-B}$ where Y is the rate of substitution, and X is the time in Myr. The rate of substitution appears high for short times, and low for long times of separation, and the resulting biological clock appears to be, but it is not, uniformly accelerated as the species separation approaches present time. When two species have freshly diverged, differences can accumulate proportionally to the mutation rate; when the divergence is remote, mutation rate does not result in further accumulation of differences, since more of these would result in loss of function and consequently would be eliminated by selection. Although average mutation rate might be considered constant, equivalent to the constant speed with which the hands of the clock turn on the dial, the functional constraints of protein do not consent accumulation of differences beyond the maximum. Then substitution rate appears to slow down as the split from which it is measured becomes more remote in time, in the same way as the hands of a clock which could be observed only at the rim of an elliptical dial would appear to slow down as they approach the major axis. We conclude that the molecular clock is perceived as an elliptical clock: the long axis corresponds to remote splits between species, and to low substitution rates; the short axis corresponds to recent splits and to high substitution speed.

S6

DEVELOPMENTAL ASPECTS OF REACTION NORMS

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When phenotypic reactions of organisms to environmental factors can be expressed as a continuous variable, the relationship is called a reaction norm. Because phenotypic characters are defined as all characters beyond the genetic material DNA this definition includes a large variety of phenotypic characters as for instance the abundance of a specific molecule: the level of activity of an enzyme; the size, shape, and number of cells of an organ; the intensity of metabolic activity; the growth rate and size of individual organisms and ultimately their fitness.

When we are studying a morphological character which is generated by a network of gene controlled reaction chains, each step in these chains can be affected by environmental factors. The reaction norm of the character for a specific environmental factor as the summation of the reaction norms of the separate steps which are sensitive to the environmental factor involved. Therefore, it can be expected that reaction norms of a morphological character (e.g. body size) to different environmental factors, could be quite different in shape dependent on the specific steps in the developmental pathways affected by the different environmental factors.

Nevertheless, it was shown for wing vein characters in *Drosophila* that environmental factors and genetic variability acted according to one so called Gene/Environmental Factor Mapping Function (GEPM). The shape of the mapping function of a character could be changed by mutants and by artificial selection. I will discuss the fact that such GEPMs which dominate the pattern of change of a character by environmental factors and by selection were only found when the character involved was the morphological expression of a mutant.

Further, I will demonstrate the relation between reaction norms for some characters of *Drosophila* larvae caused by different salt concentrations in the food medium. Reaction norms of two characters of the anal papillae of *Drosophila* are involved in the reaction norm of the salt concentration in the haemolymph. The last reaction norm determines reaction norms for developmental time and viability. These reaction norms determine competitive ability at different salt concentrations.

I will be concluded that understanding of the significance of reaction norms asks for an analysis in depth involving exploration of these physiological and developmental basis.

S6

Phenotypic plasticity in plants

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The plastic responses of individual traits are often considered to be an important means of adaptation to variable environments. However, because many different traits of an organism often simultaneously change in response to environmental change, there is a need for integration of traits within environments as well as coordination of the plastic responses of traits across environments. The differential plasticity of traits results in changes in the correlations among traits within environments and leads to alteration of the relationships between particular traits and fitness. Across environments, the strength of integration of plastic responses of various traits has been found to be positively related to reproductive success in multiple environments. These findings indicate that it is important to consider the plastic responses of a number of traits when assessing the consequences of phenotypic plasticity of organisms inhabiting heterogeneous environments.

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The preoccupation of population biologists with higher animals has led to the formulation of various supposedly general theories. These theories are based on the assumptions that (i) genes are mixed and packed into zygotes in a process called sexual reproduction, (ii) zygotes develop into somatic individuals whose size and reproductive value reach a maximum with age, and (iii) all cells of the soma die and genes are passed on to subsequent generations by a germline. These assumptions do not apply for those living organisms which produce most of the biomass and DNA in most of the habitats of the world: in plants and several primitive animals reproduction is most of the time not correlated with meiosis and zygote formation nor the passing through a single cell stage, but with a process called clonal growth in the widest sense. The units that are reproduced are modules which may remain connected like in a tree or become physiologically more or less independent individuals like in a rhizomatous plant. In these modular organisms the genetic "individual" or clone may grow indefinitely with age and many branches of the soma retain their ability to produce gametes.

Clonality has far-reaching ecological and evolutionary consequences beyond the demographic aspect of "vegetative reproduction". Among these are sedentary habit, growth instead of behaviour, and population strategies being expressed by single genetic individuals (within-clone plasticity, compensation, and dispersal). That these aspects may have played a major role in the evolution of clonality can be deduced from the fact that, despite claims to the contrary, genetic integrity is almost always maintained within clones. The mechanism which prevents genetic differentiation within clones, at least in plants, seems to be a primacy of form and morphogenetic patterns over potentially selfish cells during development. While much attention is presently focussed on the evolutionary forces that may favour sexuality, we should consider that the same forces may instead have led to the evolution of modular organization and clonality with only the occasional occurrence of sex in several major groups of organisms.

C6

PARASITOID FLIES (F.CONOPIIDAE) AS POTENTIAL ECOLOGICAL AND EVOLUTIONARY FACTORS FOR THEIR BUMBLEBEE HOSTS.

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Parasites may be subtle, but crucially important selective factors over ecological or evolutionary time scales. It remains, however, largely a matter of empirical studies to test whether this assertion is correct. Here, I present an overview of a system that is studied in the field. Conopid flies (F.Conopidae, Diptera) attack adult bumblebees that forage for nectar and pollen. The egg is placed inside the host abdomen and the larva lives endoparasitically until pupation when the host dies. Frequency of infestation (prevalence) is generally high, but varies according to season, study site, host species and sex (0- over 50 % in workers), (0-30 % in males). Early flying species are less affected, since the parasites do not emerge until summer. The flies cause premature death of the host and appear to be important mortality factors in field populations of bees. Adaptive shifts in reproductive timing of the host colonies in response to unavoidable parasitization have been studied further. Models predict earlier reproduction under heavy infestation which is in agreement with some observations in natural populations. Experiments, however, have produced results that are at variance with this expectation. The implications of this finding for the role of parasites and the ergonomics of social insects is discussed.

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Species of *Solidago* belong to a category of herbaceous perennials which are highly successful invaders outside their native range. To assess the phenotypic and genetic variation of an invading population of *S. altissima* in Switzerland, we grew 24 field-collected half-sib and clonal families in two environments in the experimental garden. Growth characters (shoot height, stem diameter, leaf number, leaf length, leaf width) had large heritabilities averaging c. 0.45 in sand and 0.65 in rich soil. Heritability estimates remained constant during the entire growth period, indicating that they were probably not confounded with maternal effects. Towards the end of the experiment quite different rankings of clonal families were obtained in the two environments (significant genotype x environment interactions). We conclude that this population has a considerable evolutionary potential. The unusual combination of large variation between genotypes and broad individual reaction norms may explain invading success in *S. altissima*.

P12

SUPERPARASITISM AND LARVAL COMPETITION IN CONOPID FLIES PARASITIZING BUMBLEBEES

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Data on the distribution of parasitoid brood (Conopidae, Diptera) in populations of their bumblebee hosts (*Bombus*, Apidae) have been collected in two localities of Northwestern Switzerland. Conopid flies are solitary parasitoids of aculeate hymenoptera. The larva live endoparasitically in the abdomen of adult bees and, after completing their larval development, pupate in situ. Only one progeny per host emerges, but superparasitism, i.e. more than one brood per infested host, is now being shown to occur regularly. Bees were sampled in regular intervals throughout summer 1988 and either immediately dissected to check for the presence of parasitoid brood (eggs and larva) or kept in the laboratory until the animal died naturally to check for the presence of a conopid puparium (successful pupation). On average, 1.78 brood per infested bee was observed at site Huggerwald, and 1.19 brood at site Allschwil; 32.3% of all bees contained parasitoid brood; in 28.5% of the cases a puparium was found after the natural death of the animal. The distribution of parasitoid brood among hosts is not different from Poisson. Prevalence of successful pupation usually equals prevalence of parasitoid brood in samples collected on the same occasion. At very high infestation intensities, however, prevalence of puparia drops as compared to brood prevalence. As a result, the percentage of killed hosts is close to a negative exponential function of infestation intensity, i.e. number of brood per average host. This kind of relationship is known from theory to enhance the stability of the host-parasitoid interaction.

C12

CONSEQUENCES OF DIFFERENT DEFINITIONS OF HOMOLOGY IN MORPHOLOGY AND PHYLOGENETICS.

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Which definition of homology should be preferred can only be decided with respect to the theoretical framework of the intended conclusions. There is a dilemma in biology, since many relations familiarly called "homologous" have to be excluded by definition, as long as the applied definition shall allow statements on phylogenetic relationship. This is especially true for intraorganismic relations ('homonymy') and intra-specific "homologues" (e.g. male and female copulatory organs in many species). Consequently, either a phylogenetic definition of homology ("common ancestry") or a morphological definition ("same character in different animals") can be accepted. None of these can be deduced from the general concept of "homology as caused by continuity of information".

Since there are different legitimate purposes to be served by applying the homology concept, it should be admitted to accept different definitions of homology.

C12

ON THEORIES OF MORPHOGENETIC TRANSFORMATIONS AND NATURAL SELECTION

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Many morphogenetic transformations of multicellular organisms, the higher metazoans in particular, tend to be discontinuous in their main features. These tend to be primarily specified by laws of development as manifested in different conditions of life, often through active behavioral responses to such changes. All major 19th century theorists basically agreed on such points, while perhaps differing in emphasis depending upon kinds of organisms, or stages of the morphogenetic processes. Except for Lamarck and the Geoffroy's who hardly touched the problem, these theorists also agreed on selection as playing an essential, long term controlling role, mostly after the establishment of any such transformation-- i.e. it brought in or increased "utility" as "mediator" between the laws of development and the short term effects of conditions of life. Darwin, Wallace, Naegeli and Weissmann sharply disagreed, however, on the different weights of different forms of selection within and among populations, or within individual organisms (Weissmann's "germinal selection" etc.)

Because of the general inefficiency and "shortsightedness" of natural selection on Mendelian variants, Mendelism ended up polarizing "mass" opinion into extremes such as neo-Lamarckism, macro-mutationism, "the synthesis" and a-selective forms of structuralism. Darwinian theorists opted, instead, for inter-population selection tending to play major roles in the initial phases of divergence, and stabilizing selection (sensu Schmalhausen) after.

P3

PHYLOGENY OF SOCIAL WASPS ANALYSED BY RFLPs OF MITOCHONDRIAL DNA (VESPIDAE, VESPINAE)

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The genetic relationship of social wasps (Vespidae, Vespinae) is analysed by comparison of the mtDNA restriction fragment pattern produced by 6-basepair enzymes.

The results, worked out by a method of Nei & Li, indicate a close relationship within the genera. According to that the *Dolichovespula* and *Vespula* are monophyletic groups.

A comparison of mtDNA between *Vespa crabro* and the other Vespinae indicates a closer relationship to *Dolichovespula* than to *Vespula*.

C7

EVOLUTION OF BIPARENTAL CARE IN THE HERMAPHRODITIC POLYCHAETE WORM OPHRYOTROCHA DIADEMA

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Ophryotrocha diadema is a simultaneously hermaphroditic polychaete worm with a brief protandrous phase. Mating pairs form preferentially between simultaneous hermaphrodites. Both partners of a pair regularly alternate sex roles, reciprocate egg exchange and care for eggs. Neglected eggs have a 31% probability of dying, but eggs cared for by both parents or by a single parent or even by an unrelated individual (adopter) have a 95% probability of developing. Although one parent is about as good as two in caring for brood, parents are refrained by evading parental care because sex ratio of the population is male biased. Therefore, chances of mating with another hermaphrodite are low for a deserting parent. Among pairs experimentally prevented from caring for eggs, as well as among pairs where one of the mates did not reciprocate egg exchange; intruders succeeded in substituting one of the partners significantly more frequently than in pairs allowed to care for eggs. The adaptive meaning of biparental care and of the adoption habit is discussed in the light of the life history of *O. diadema*.

ESTIMATION OF r USING AGE SCHEDULES IN CONTINUOUS ITEROPAROUS COHORTS

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The aim of this contribution is to explore the effects of different sets of assumptions on the estimation of r for continuous iteroparous populations, when stepped l_x and m_x are used. With this objective, four discrete solutions of Lotka's continuous equation --an integral equation relating l_x , m_x , x and r -- are compared. Two of them are standard solutions obtained equating the integral to a summatory, and assigning the gross fecundity ($l_x m_x$) of an interval (1) at the initial age of the interval, or (2) at the pivotal age. The other two models are developed here, and solve the integral equation assuming the constancy of fecundity between two consecutive, observed ages. One of these models (Linear Interpolation Model; LIM) assumes that l_x is linearly related to x between two consecutive, observed ages. The other model (Exponential Interpolation Model; EIM) assumes a negative exponential relationship between l_x and x ; i.e. force of mortality is constant between consecutive observations.

The rationales of these models are compared and the differences are also studied using real data from rotifer populations. The effect of both the absolute value of r on divergence between models and the frequency of observations is evaluated. These analyses suggest alternative ways of focusing the problem, and some practical rules in order to prevent major errors.

S4

MOLECULAR CLOCKS: USE AND MISUSE IN PHYLOGENETIC STUDIES

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DNA and protein sequence comparisons have added a new dimension to phylogenetic studies. This is due to the empirical observation of the "molecular clock", i.e., that base changes in any particular gene (or amino acid replacements in a protein) often appear to accumulate at steady rates. The theoretical basis of this (largely due to Kimura) is that the rate of molecular evolution reflects two factors: the underlying rate of mutation, and the subsequent constraints imposed by natural selection. If both factors remain constant, then there should be a good molecular clock.

Silent sites (3rd codon positions) in genes have been hailed as providing the ultimate molecular clock. If silent changes are truly silent (i.e., have no effect on fitness) then the "silent molecular clock" should reflect the mutation rate. Indeed, it has been suggested that this clock has the same rate in different genes, and even in highly divergent organisms.

Drawing on DNA sequence data from mammals, *Drosophila*, plants and bacteria, I will examine this "silent molecular clock". I will describe the nature (and likely origins) of variation in rate among genes and among organisms.

The conclusion is that the silent molecular clock can be useful in reconstructing and dating phylogenies - but it should not be used indiscriminately.

- Sharp et al. (1988) *Nucleic Acids Res.* 16, 8207-8211
Wolfe, Sharp & Li (1989) *Nature* 337, 283-285
Sharp & Li (1989) *J. Mol. Evol.* 28, 398-402
Wolfe, Sharp & Li (1989) *J. Mol. Evol.* 29 (in press)

SURVIVAL ANALYSIS OF THREE CLONES OF *Brachionus* *plicatilis* (ROTIFERA)

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Age-specific survival data from females of three clones of the rotifer *Brachionus plicatilis*, grown in the laboratory under different environmental conditions (3 salinities x 3 temperatures), have been recorded.

The lifespan, ranging from 3.0 to 14.8 d, showed the expected decrease with increasing temperature, but a general trend with salinity or genotype was not observed, despite important genetic differences in body size between the clones (the biggest clone was 50% larger than the smallest one, at 25°C, 12 g l⁻¹ salinity). On the other hand, lifespan shows a close linear relationship with cohort generation time, the former being nearly twice the latter. This ratio is what would be expected from King's ageing hypothesis, although other assumptions could also give similar predictions.

Polynomial regression analysis shows all survival curves are Type I curves, including the curves obtained under conditions far from optimal (r near or below zero). Three two-parameter models (linear-exponential model, Gompertz's model, and Weibull's model) were fitted to the survival data in an attempt to summarize them, and the models were tested against the exponential model (i.e. Type II curve). The fitting of these models to the data was generally poor, but Gompertz's and, to a lesser extent, Weibull's model fitted the data better than the linear-exponential model. The parameters obtained from the different survival curve analyses were compared with each other and also with other demographic parameters.

C6

Making the most of life: Egg laying strategies of solitary parasitoids.

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In solitary parasitoids, no more than one parasitoid ever emerges from a parasitised host. A number of experiments have shown that solitary parasitoids can discriminate between healthy and parasitised hosts, laying on relatively few occasions into parasitised hosts. The phenomenon of laying into an already parasitised host, a phenomenon that has been called superparasitism, does however occur.

Until recently superparasitism was viewed as a discriminatory mistake but there has been a growing number of simple optimal foraging models which suggest that much of the superparasitism observed may be adaptive. The problems to be overcome in formulating realistic optimal oviposition models such as limited egg load and changing encounter rates are closely examined.

Two complimentary optimal oviposition models are developed

- a static optimal foraging model, represented by a series of coupled ordinary differential equations, giving the optimal avoidance rate of superparasitism.
- a dynamic foraging model giving the optimal oviposition decision under a set of conditions.

The predictions of these models are compared and contrasted with the foraging behaviour of the solitary parasitoid *Venturia canescens* in the laboratory.

P2

Evolution of proteinases and proteinases inhibitors.

Y. SHUALI, D. GRAUR, Givatatim, Israel

not received

C1

THE INTERFACE BETWEEN POLLINATION, EPIDEMIOLOGY AND CHEMICAL DEFENCE.

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Due to diseases spread by pollinators, an increased allocation of resources to pollinator attractants will have an indirect cost through increased risk of infection. To avoid infection the plant can produce some sort of defence, mechanical or chemical. This production will take resources from other activities such as growth, pollen- or seed-production. By modelling this trade-off system we can study how the plant should optimize reproductive output depending on risk of infection. In a population where we have monoicous plants, a situation could occur where plants invest in defence at the cost of either sex. When infection rate is high and cost of defence is low, we could arrive at a population that is dominated by plants investing in one sex only.

S6

REACTION NORMS FOR SEX ALLOCATION:WHO'S IN CHARGE HERE?

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In studies of phenotypic plasticity, behavioral plasticity is often neglected. Yet behavioral plasticity is as important as morphological or physiological plasticity. One simple behavior, with significant consequences for fitness, is the sex ratio behavior of parasitic wasps. In these species, females have behavioral control over the sex ratio among their offspring. In the wasp *Nasonia vitripennis*, females vary the sex ratio in response to ovoposition context, as predicted by the theory of local mate competition. Analysis of different wasp genotypes reveals significant variation in reaction norms among them, with some genotypes more reactive than others. Sex ratio theory permits us to calculate the fitness consequences of such differences under simple assumptions of population structure.

P3

CYTOGENETICAL CHARACTERIZATION OF BISEXUAL/UNISEXUAL SPECIES OF *Poecilia*: PRELIMINARY DATA ON *Poecilia formosa* AND *P. mexicana* (Pisces, Poeciliidae).

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Unisexual Vertebrates pose many questions for students of evolutionary biology. Some of these relate to their origin, the way they manage to maintain themselves in nature and the possible role they play in the formation of new, bisexual polyploid species.

Among unisexual Vertebrates, the Amazon molly, *Poecilia formosa*, was the first to be described as such. Morphological, biochemical and histocompatibility studies have shown that this gynogenetic fish originated from an interspecific cross between *P. latipinna* and *P. mexicana*. *P. formosa* lives sympatrically with one or the other of its progenitor species. Sperm from the latter are necessary to trigger embryogenesis in the unisexuals. In some areas of sympatry between *P. formosa* and either of its progenitor species, there are breeding complexes in which diploid and triploid unisexuals coexist along with their sexual relatives. Obviously in some cases the mechanism of sperm exclusions break down, thus allowing incorporation of new genetic material into animals with otherwise closed gene pools.

Karyotypes and DNA contents are already known for these fish; but the aim of a new series of cytogenetical studies on bisexual and unisexual species of *Poecilia* is to use more modern cytological techniques to achieve a finer chromosomal characterization. The finding of appropriate chromosomal markers might allow to investigate on the proposed ancestry of *P. formosa*, and on chromosomal diversification since the original hybridization event. This may shed light on whether or not chromosomes play a role in maintaining *P. formosa* as a species and whether chromosomal introgression exists among the unisexual and bisexual species, possibly through the triploids as genetic bridge.

Results on the heterochromatin distribution point out a complex situation of sex chromosomal determinations in the genus: both male and female heterogametic species, karyologically identifiable as such, coexist along with species having no sex chromosomes.

C-banding patterns and NORs location are discussed in view of the pcytotaxonomical interrelationships between the species.

C2

EFFECT OF NUTRIENT AVAILABILITY ON INBREEDING DEPRESSION AND SEED PATERNITY IN A NORTH AMERICAN ANNUAL LEGUME. CHAMAECRISTA FASCICULATA.

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Previous work on Chamaecrista fasciculata has demonstrated that progeny from outcross pollen show greater fitness than progeny from self pollination. The first goal of this study was to determine whether nutrient availability affected the extent of inbreeding depression illustrated by the difference between self and outcrossed seeds. It was expected that inbreeding depression would be more severe with limited resources. The second and third goals were to determine whether nonrandom paternity favoring outcross progeny resulted from pollen mixtures of self and outcross pollen and whether seed paternity was affected by nutrient availability. It has been hypothesized that some plants may have the ability to selectively mature progeny of higher fitness.

A greenhouse experiment was conducted using low and high levels of fertilizer on two groups of 7 pollen recipient plants which were pollinated with self, outcross, and mixture of self and outcross pollen sources. Fruit abortion, seed number, and seed mass were measured. In addition, seed and parental allozyme genotypes were determined using starch gel electrophoresis. Results demonstrated that the expression of inbreeding depression was affected by nutrient availability: differences in seed number and seed weight between self and outcross progeny were much greater under the high rather than low fertilizer treatment--a result opposite of expectation. We also found that seed paternity was affected by nutrient availability: the progeny in the high fertilizer group were more likely to show a significant bias toward outcross paternity than those in the low fertilizer group. However, the bias was not strong. This study demonstrates that, even when the differences between self and outcross progeny are great, nonrandom fertilization favoring outcross pollen is not a significant factor for this species.

W2

Inversion Polymorphisms in the Drosophila obscura group.

D. Sperlich (Tübingen)

NOT RECEIVED

C1

WHEN DOES IT PAY TO FORGET? :

ENVIRONMENTAL VARIABILITY AND OPTIMAL MEMORY LENGTH

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Most optimal foraging models simply identify optimal strategies for given characterisations of the environment but ignore how foragers may achieve such optima. By contrast learning models attempt to model processes by which animals gain information while foraging and make most efficient use of this information. In variable environments it might seem reasonable to expect that recent events will have greater relevance to foraging decisions than distant ones, thus many learning models have memory components, either as memory windows or as exponential weighting in favour of recent events. This paper discusses the relationship between environmental variability and memory length. The general case of a forager with an exponentially decaying memory and using an arbitrary learning rule is considered. It forages in a variable environment where two types of prey may be encountered and the encounter rates with these types are normally distributed about a long-term mean. The forager has a fixed lifespan and maximises its fitness gain over this period. It is shown that the memory which maximises the forager's fitness declines both with increasing variance in the mean encounter rates and with increasing lifespan. It is also shown that there is threshold variance (or lifespan) over which it no longer pays to have a decaying memory.

P4

THE PROBABILITY OF FIXATION OF UNDERDOMINANT CHROMOSOMAL REARRANGEMENTS IN SMALL POPULATIONS

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A detailed analysis has been carried out in order to determine, as precisely as possible, the value of the probability of fixation of a chromosome rearrangement causing partial sterility of the heterozygote. The analysis has been performed both in the case of a species with separate sexes and in the case of a species with completely random mating (i.e. including the possibility of self-fertilization). A number of Montecarlo simulations were done with a computer. The results obtained in these tests have been compared with the estimates obtained (Spirito, unpublished results) using the genotypic transition matrices.

Moreover, some preliminary results on the probability of fixation of a chromosome rearrangement in a multi-deme model are presented. This model consists in several isolated demes subject to extinction and successive re-colonization by individuals coming from the other demes.

C3

POPULATION STRUCTURE AND GENETIC DIVERGENCE IN THE EUROPEAN STREAM LIMPET, *ANCYLUS FLUVIATILIS*

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Anchylus fluviatilis is a benthic freshwater pulmonate found throughout Europe. It has received considerable attention in studies of molluscan shell growth patterns, ecophysiology, bioenergetics, and ecotoxicology, providing a wealth of data that make it a 'model' organism for aquatic benthic macroinvertebrates. Recent cytogenetic work indicates that *A. fluviatilis* is a tetraploid species.

We have used allozyme patterns for 13 loci, all of which were polymorphic in at least one population, in order to elucidate the genetic structure of local populations in central and southern Germany. A total of 45 lotic sites have been sampled in an effort to include geologically different habitats.

A striking population genetic feature is the existence of gross linkage disequilibria among loci: We have found distinct multi-locus associations of alleles. To date, three major 'strains' can be recognized, each of which is composed of several very similar multi-locus genotypes. About 60 % of all local populations harbor individuals of only one or the other strain, whereas 40 % are composites in this regard.

The partitioning of genetic diversity into a limited number of multi-locus genotypes resembles the genotypic characteristics of many known asexual organisms. Possible contributions of tetraploidy, mode(s) of reproduction, and selection to the maintenance of observed patterns of genotypic diversity are currently under investigation.

C10

MOLECULAR EVOLUTION AT THE POPULATION LEVEL

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Predictions of the neutral theory about genetic variation in natural populations are compared with restriction map and DNA sequence data from *Drosophila*. Several instances are known in which the neutral theory does not provide an adequate explanation, whereas models based on natural selection are in qualitative agreement with the data. The level of DNA polymorphism within a population is to a large extent determined by genetic mechanisms, such as recombination and DNA repair, which interact with selection. Studying the standing variation in natural populations at the DNA sequence level provides an excellent tool to precisely characterize variation and to distinguish the forces involved in the evolutionary process.

S6

THE EVOLUTIONARY SIGNIFICANCE OF PHENOTYPIC PLASTICITY

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Phenotypic plasticity has until recently not played a role in evolutionary theory commensurate with its importance. This talk introduces a symposium on the evolutionary biology of phenotypic plasticity, which takes different forms - either continuous reaction norms or discontinuous polyphenisms. The history of these concepts is briefly sketched, then examples of evolutionary studies of plasticity are discussed. Reaction norms can be either adaptive or nonadaptive. Much adaptive plasticity involves reactions to prey, parasites, or predators. Variation among the reaction norms of different genotypes modulates the expression of genetic variation and covariation in heterogeneous environments. Developmental mechanisms are involved in much of the variation found within populations. Genetics and demography must be combined with the mechanisms that generate phenotypic plasticity before the sources of variation and the response to selection can be understood.

S8

MORPHOLOGICAL AND BIOCHEMICAL TRAITS: THEIR INTER-RELATIONSHIPS AND SELECTIVE RELEVANCE

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The most interesting characters for the study of evolutionary change are usually those for which the contribution of a single gene makes only a slight difference. Mean, variance, skewness and kurtosis of morphological traits are normally examined in order to define the genetic component, if any, and the possible selective relevance. The collection of data from relatives, twins included, is classically considered the first step, even if the amount of really useful information can be relatively low, also in the most favourable cases. The availability of a number of polymorphic mendelian traits has made possible the partition of phenotypic variance, which has been in many cases successful. More recently, with genome almost completely covered with evenly distributed restriction fragment polymorphic sites, the direct mapping of loci involved in determination of quantitative traits has become possible and some results are very promising. On the other hand, the environmental component can be better studied in changing environments, and some secular trends in humans have been used to evaluate selective relevance of quantitative traits.

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According to molecular clock hypothesis, tempos of molecular evolution are approximately constant and do not depend on rates of morphological evolution. According to alternative point of view, evolution of informational macromolecules has periods of acceleration and deceleration, which are parallel to those of organismal evolution.

Correlation and cluster analyses of antigenic (for serum proteins) and morphological (for body proportions) distances between species representing the majority of primate genera have been carried out. Using linear programming each distance matrix was forced onto the consensus phylogenetic tree of the order. We have compared the lengths of the same branches calculated for different character sets and normalized in such a way that the overall length of the tree was 1.0. The main trends in the variation of evolutionary rates for protein and body proportions at different stages of primate phylogenesis have been revealed. It is shown that molecular evolution is significantly more regular than morphological one. However, the results are consistent with the conception that progressive morphological evolution consists of acceleration and deceleration cycles parallel to those, which made molecular evolution, but in the latter case, these cycles are occurring against the background of total deceleration and in the former case, against the background of total acceleration.

C7

THE SHAPE OF A FITNESS CURVE: NESTLING WEIGHT AND
SURVIVAL IN THE GREAT TIT (*PARUS MAJOR*).J.M. Tinbergen and M. Boerlijst, Institute for Ecological Research,
Boterhoeksestraat 22, 6666 GA Heteren, The Netherlands.

Variation in clutch size between populations or in time may originate from variation in selection pressure and subsequent micro-evolution. In order to predict evolutionary response to selection pressures we should know, among other things, the relation between a trait and fitness in the natural environment. The shape of such a 'fitness curve' for the trait size is the subject of this paper.

In experiments to assess optimal brood size in the Great Tit, nestling survival was strongly related to manipulated brood size. Artificially increasing brood size results in a decrease in both nestling weight and subsequent nestling survival. This effect is for a substantial part responsible for the decrease in reproductive value (taken as a fitness measure) with increasing brood size.

We concentrate on estimating the relation between nestling weight and subsequent nestling survival in two free-living populations of Great Tits. Firstly we give a descriptive analysis of the shape of this curve. Then we collect evidence for the causality of this relationship, and we discuss the role of dispersal in determining the level and shape of the fitness curve. Finally the effect of the shape of this curve on optimal brood size is discussed.

C7

RESOURCE ALLOCATION, LIFE HISTORIES AND
DOMESTICATION IN SETARIA.

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Domestication, i.e. the processes that occur during the transformation of a wild plant into a cultivated one, include changes in several characters related to the seed itself (size, dormancy, shedding, etc.) but also changes in the growth pattern of the plant (life cycle and resource allocation to growth or reproduction).

Life histories and resource allocation were studied in the *Setaria* complex. The crop species, *S. italica* (foxtail millet), is cultivated either for its seeds (*S. italica maxima*) or for fodder (*S. italica moharia*). The maxima type has a typically annual life cycle, with a vegetative phase followed by spike production and maturation and death of the plant. Resource allocation to reproduction is high and very localised in time. Fodder millets and wild millets (*S. viridis*) have a second vegetative-reproductive phase. In this case, there is a tendency towards polycarpy, although the life cycle is still annual, as all plants die at the end of the growing season. Resource allocation to reproduction varies according to the variety or genetic family studied and occurs during a much longer period of the life cycle (vegetative and reproductive phases overlap).

Reproductive effort (measured by the proportion of tillers flowering) was studied on two crosses and a model describing this reproductive effort as a function of time was developed. The pattern of inheritance of this character was also investigated.

P6

GENETIC MARKERS AND MORPHOLOGICAL VARIABLES IN MAN

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Although human populations have often been studied for their morphologic variability and proteic variability considered separately, not enough attention has been given to analyzing their covariation. Furthermore, the few published data show often contradictory interpretations of the results, probably also due to the fact that the number of loci on which heterozygosity is calculated is not sufficient.

The present work tries to find a relation between biochemical variability and morphometric variability in an Italian population that could be particularly enlightening from this point of view because a large number of loci (about 30) and the main antropometric characters have been examined in it.

The families of about 3000 newborns were examined and the newborns themselves underwent regular checks for the first two years of their life.

The effects of heterozygosity have been evaluated for about 30 genetic loci on different morphologic variables, elaborating also the techniques of appropriate numeric analysis

C7

REPRODUCTION STRATEGY AND THE LIFE CYCLE IN GRAPTOLOID COLONIES

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Colonies of extinct graptoloids were clones composed of hermaphroditic zooids. Their breeding system approached that of amphicarpic plants, and combined selfing with distant outcrossing. The balanced coexistence of these extreme means of reproduction may be visualized as an evolutionarily stable strategy (ESS). Such breeding system might have accounted for overall high rates of graptoloid evolution as well as for rapid transformations in large populations.

Sexual reproduction of graptoloid colonies was completed by fragmentation of colonies and their regeneration. Fragmentation followed by regeneration and only later by sexual reproduction of regenerated fragments constituted the so-called great cycle while regular course of events initiated by sexual reproduction in undisturbed (complete) colony resulted in normal colony formation and is termed the small cycle. Thus the adaptive significance of the sexual process in the life cycle is in the restoration of the "perfect" pattern of the complete colony which offered the highest fitness.

C7

EVOLUTION OF LIFE CYCLES IN ALGAE

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Three types of life cycles are found in nature:

- (1) Haploid life-cycles, like those observed in mosses (the individuals are haploids and the diploid stage is achieved as epiphyte of the haploid individuals)
- (2) Diploid life cycles like those observed in higher plants (the individuals are diploids and the haploid stage is achieved as epiphyte of the diploid individuals)
- (3) and haplo-diploid life cycles, like those observed in some algae (an alternation of haploid and diploid individuals is observed).

The question is to determine, what are the conditions on the relative haplo/diploid fitness, for the maintenance of an haplo-diploid life cycle towards the two others possible haploid or diploid life cycles. A simulation model has been built to answer this question.

The results show that an haplo-diploid life cycle can be maintained in a population without any ecological niche differentiation between haploid and diploid individuals. This results is in agreement with observations of red algae populations.

C3

DIFFERENTIATION OF 'GLACIAL RELICT' CRUSTACEAN POPULATIONS IN RELATION TO LATE- AND POST-GLACIAL GEOLOGICAL HISTORY

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The so-called glacial relict crustaceans of Northern Europe are characterized by a weak dispersal capacity; their lacustrine distribution is determined by former standing-water connections, and thus confined to areas which once were covered by late-glacial ice-dammed waters or which have emerged from the former phases of the Baltic Sea through post-glacial crustal uplift. They provide an opportunity to study genetic differentiation in populations whose isolation history and subsequent directions of gene flow are well known.

We studied gene frequency variation in 50-100 populations of each of three 'relict' crustacean species (*Mysis relicta*, *Pallasea quadrispinosa*, *Pontoporeia affinis*) in Fennoscandia. Common patterns of variation across loci and species reveal the existence of anciently diverged and differentially distributed stocks, originating in distinct late-glacial refugia, and now mixed in parts of the Finnish lake district. Against the knowledge on geological history, patterns of differentiation can be discerned into phenomena preceding and following the isolation of lakes, and the time-scale of stock mixing be rather accurately determined.

C2

RESTORER GENE DYNAMICS IN GYNODIOECIOUS SPECIES.

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Gynodioecy is usually defined as the simultaneous occurrence of female plants and hermaphrodites in natural populations. The phenomenon is best understood as the expression of an evolutionary conflict between cytoplasmic genes and so-called restorer genes, situated on the nuclear chromosomes. In most studies of this system restorer genes are considered (1) to give complete restoration of male fertility, and (2) to be alleles of sex loci with typically two alleles, one restorer allele and one male sterility allele.

The occurrence of partial restoration of male fertility is common in gynodioecious species. Previous crossing studies in *Plantago lanceolata* had shown that this phenomenon may result from incomplete dominance of restorer alleles. In this paper evidence will be presented that in this species there also exist restorer alleles with a partial restoration effect, and that restorer loci can carry more than two alleles. The impact of alleles with partial restoration effect on the dynamics of gynodioecy was studied with the help of computer models. In these models emphasis was put on short term changes and on the relative importance of the size of the restoration effect in these changes in relation to the other forces that are thought to be important, i.e. the pleiotropic advantage of females through ovule production, inbreeding depression and the cost of restoration.

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The consequences of systematic environmental effects on gene expression for all equilibria in a two-locus model with additive inheritance are investigated. A simple model is analysed with two diallelic loci under optimizing selection, with discrete, non-overlapping generations, random mating, without mutation and random genetic drift, and different, discrete environments. The alleles contribute additively to both the intercept and slope of a linear reaction norm, which maps the genotype to phenotype in every specific environment. Explicit expressions are found for all the equilibria and it is shown that a small shift in the environment can have a large effect on the nature of these equilibria. These results are evaluated numerically and discussed in relation to the maintenance of genetic variation by genotype-environment interaction.

P5

Direction of changes of quantitative characters
along great geographical distances

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It is a well-known fact that the quantitative characters can vary within the area of different species. The increase of clutch size northward in great tit is such an example. The changes are analysed by calculating correlation coefficients between clutch size and geographical location, if we accept the linearity of the connection. The well-known south-north trend is only a special case, we have to find the best correlation between the feature and geographical points. A method is given to compute this value. The analysis of data shows that the change of clutch size has a south-west north-east direction. The distribution of points influences the value of the correlation coefficient and the direction of the change, as well. A way is given to correct this effect.

In the following some other examples are presented: the clutch size trends of swallows and house martins.

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Experimental crosses demonstrated that diploid (2X) and autotetraploid (4X) *Plantago media* are reproductively isolated by post zygotic barriers: triploid hybrids (3X) are inviable due to endosperm collapse. Population genetical theory predicts a rapid elimination of the minority cytotype under random mating, resulting in parapatry.

The macro distribution of the cytotypes in the Pyrenees is indeed almost mutually exclusive. However in the contact zone, sympatric cytotype populations of considerable size occur. Near Formigal extensive cytotype sympatry was found, without any apparent population structure. Under these conditions selection for pre zygotic reproductive isolation is to be expected. This could also explain stable cytotype sympatry. Therefore the existence of pre-zygotic reproductive barriers between the cytotypes was studied in sympatry. The results are discussed in relation to the recent debate on sympatric speciation.

S6

Field experiments on the quantitative genetics of reaction norms in the Great Tit.

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In ringed bird populations with known pedigrees, significant amounts of genetic variation for traits such as body size, clutch size and the timing of egg-laying have been demonstrated. At the same time and in the same population, significant correlations can be found between the phenotypic values for these traits and environmental factors mainly the abundance and timing of caterpillars which form the main prey.

Using the concept of reaction norms, these two aspects can be integrated in a single model. This opens the way to address new questions. After positively answering the question that nearly all individuals show the phenotypic plasticity responsible for the difference in means between populations or years, the main questions are concerned with the mechanism and the adaptiveness. Especially traits such as clutch size and the timing of egg laying are very interesting, because the critical period in which the selection takes place occurs four to five weeks later. The selection for these traits is reflected in nestling growth. At the same time growth is interesting as the ontogeny of body size. Using a split brood design it is possible to unravel some of the genotype environment interactions for body size. A number of new problems, e.g. sib competition, and phenotypic variation in the parents related to the brood size manipulations hinder a straightforward interpretation of the experimental results. We are however beginning to understand the ecological interactions, or in genetic terms the environmental variance a bit better.

S3

MORPHOLOGICAL VARIATION IN *PLANTAGO LANCEOLATA*: LIMITS OF PLASTICITY.

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Hayfield and pasture populations of *Plantago lanceolata*, a perennial rosette plant, were studied to find out whether and how populations differed in response to environmental conditions.

Population differentiation - Transplant experiments in natural habitats revealed that the seed yield of transplants in an alien environment can be less than 10 per cent relative to native plants. Experiments simulating competition, grazing and trampling showed that hayfield plants have a higher tendency to invest in shoot growth, while pasture plants invest more in reproduction. Only when seed set is limited to a short period, e.g. due to an early haycut, and competition increases during the growing season, it appears that plants from hayfields have the advantage, because the fewer spikes that are formed mature earlier in the season. In contrast, pasture plants seem to produce excess spikes: many seeds do not mature, when none of the spikes are predated.

Canalization of development - The morphology of the species ranges from phenotypes with an erect growth habit, relatively long leaves, few daughter rosettes, and few but large spikes (hayfield-types) to prostrate plants with short, broad leaves, more rosettes, and more but smaller spikes (pasture-types). Both external stimuli, such as competition for light, and population differences are responsible for shifts in this growth pattern. Apparently, the developmental system causes canalization in the expression of many traits, resulting in a limited range of possible phenotypes. There is evidence that hormones that affect apical dominance play an important role in the existence of these phenocopies.

Conclusion - The low performance of transplants in alien habitats shows the importance of genetic specialization in *P. lanceolata*. Still, a genotype from a pasture can switch from a pasture- to a hayfield type of growth when brought under competitive conditions. The change may be in the right direction, yet, it just does not suffice, when compared to genotypes from a hayfield that have a genetic disposition to do so.

P7

CONSERVATION GENETICS OF PLANT POPULATIONS. GENETIC DIFFERENTIATION IN RELATION TO POPULATION SIZE IN *SALVIA PRATENSIS* AND *SCABIOSA COLUMBARIA*: ALLOZYME VARIATION.

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- (2) Institute for Ecological Research, Boterhoeksestraat 22, 6666 GA Heteren, The Netherlands

As a consequence of restricted gene flow and genetic drift, small and isolated populations are expected to show decreased levels of genetic variation which eventually may lead to genetic erosion causing inbreeding depression and loss of favorable alleles. Ultimately this may lead to extinction of the population or species. A genetical and ecological study of two endangered plant species in The Netherlands was started to examine the relevance of genetic erosion for the process of extinction. We started out to measure the amount of allozyme variation in relation to population size. Significant correlations were found between population size and proportion of polymorphic loci and mean observed number of alleles per locus respectively. An analysis of genetic diversity showed substantial genetic differentiation between populations for both species. The extent of differentiation was larger among small than among large populations. Furthermore differentiation occurred in apparently homogenous environments within relatively short distances, indicating low levels of gene flow between populations.

P7

GENE DUPLICATION AT THE PGD AND GPI LOCI IN THE PLANT SPECIES *SCABIOSA COLUMBARIA*.

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An electrophoretic study of the amount of allozyme variation in *Scabiosa columbaria* revealed complex patterns for the enzymes glucose phosphate isomerase (GPI, E.C. 5.3.1.9.) and phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.44.). For both enzymes three loci were observed. A genetic analysis showed that heterodimers are formed between the polypeptides coded by GPI-1 and GPI-2 and by PGD-1 and PGD-2 respectively. Crosses showed that the GPI-2 and PGD-1 loci are tightly linked: recombination between these loci is estimated to occur at a frequency of 6%. The amount of recombination between GPI-1 and PGD-2 could not be established at the moment. The results so far suggest that a small chromosome segment, containing these loci, has been duplicated in the past. Further research will be done to establish the origin of the duplication, the extent of the duplicated segment and the evolutionary importance.

C3

PATTERN OF GENETIC VARIABILITY IN CHESTNUT (*Castanea sativa* Mill.) POPULATIONS FROM TURKEY.

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Multilocus electrophoresis analysis based on 17 enzyme loci is used to study the genetic structure of *Castanea sativa* Mill. from Turkey, supposed main centre of origin of this species. The data are compared with those observed in populations from Italy. The genetic variability of *C. sativa* from Turkey ($H_e=0.26, P=0.79, N_e=1.47$) is higher than that observed in Italy ($H_e=0.21, P=0.52, N_e=1.39$). Genetic differentiation among Turkish populations is also higher than that found in the Italian ones (average Nei's $D=0.114$ within the former ones; $D=0.027$ within the latter ones). The genetic divergence between *C. sativa* from Turkey and Italy shows a value of $D=0.155$. Among the populations from Turkey three main clusters which differentiate respectively the populations from the Eastern, Middle and Western region can be detected. The Western Turkish populations are more similar to the Italian ones ($D=0.099$) than to the Middle and Eastern populations ($D=0.165$). This suggests that Western populations could be the evolutionary intermediates between Italian and Turkish areas of *C. sativa*.

The *Asellus aquaticus* L. Crustacea Isopoda ecdysis links the male reproductive success to an unique courtship pattern.

Vitagliano G., Fano E.A., Marchetti E.

The duration of precopula has been correlated with: 1) the fitness of the ♂ (Parker 1979, Gwynne 1984, Tsubaki and Sokey 1988); 2) sex-ratio of the population (Manning 1981); 3) photoperiod (Migliore et al. 1982). Its genetics determination has been studied (Palmer and Dingle 1986, Gromko 1987/1989). In *Asellus aquaticus* ♂♂ have daily mature sperms as demonstrated with 3H-thymidine (Rocchi and Vitagliano 1969). ♀♀ are fertilisable only after birth ecdysis (Unwin 1920, Ridley 1983). ♂ carry ♀ in precopula for many days (Vandel 1925). *A. aquaticus* is sympatric with *P. coxalis* in south Europe and with *A. meridicanus* in north-west Europe. Censuses and data-tions on laboratory populations and on those caught in field (Italy, Holland, Scotland) show that ♂♂: 1) identify ♀♀ of their own species (etherspecific or homosexual pairs are $\approx 1/10000$) but 2) not the receptive ones (♂♂ have precopulas ranging from 1 to 60 days, even if other ♂♂ are absent) and 3) do not chose for other free, receptive ♀♀. Male's reproductive success depends on the unprefix female's birth ecdysis (in spite of his daily production of sperms and of the presence of other receptive ♀♀). No significant difference exists among all the populations at the same photoperiod.

L

GENOTYPIC DIVERSITY AND COEXISTENCE OF SEXUAL AND CLONAL FISHES

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Most theories about the maintenance of sexual reproduction in higher plants and animals assume that sexual populations contain abundant genetic diversity and that asexual populations do not. Yet, this is not always true. Asexual populations are often composed of multiple clones and sexual populations may suffer local population bottlenecks leading to a loss of genotypic diversity among individuals. Furthermore, true clones are protected from inbreeding and other processes that tend to erode heterozygosity within individuals. Competitive interactions between closely related sexual and asexual lineages in a mixed reproductive complex should be affected by genetic diversity if such variation alters the niche-breadth of the constituent reproductive groups.

Field and laboratory studies of small livebearing fishes in the genus *Poeciliopsis* (Poeciliidae) support this scenario. The ecological success of the asexual portion of these complexes varies with clonal diversity. An assemblage of ecologically specialized clones can usurp a broad portion of the food and spatial resource spectrum from coexisting sexual lineages, but a single clone cannot. Competitive interactions between the sexual population and individual clones tend to be asymmetrical, with the sexual population being ecologically broader and its fitness being significantly less susceptible to local variance in food and environmental quality. However, competitive abilities of the sexual portion of these mixed reproductive complexes also seems to vary with genotypic diversity. Local population bottlenecks and founder events can erode genetic variability in a sexual lineage rendering it more susceptible to local environmental effects and consequently to replacement by clonal lineages. Loss of heterozygosity in the sexual population may decrease fitness through inbreeding depression, and simultaneously decrease the genotypic diversity that allows sexual individuals to survive in their seasonally and spatially variable desert stream environments. Clearly, the levels of genetic variation in both constituents plays a strong role in affecting the outcome of competition between sexual and asexual lineages.

IN THE SEARCH FOR THE NEW STRATEGY OF EVOLUTIONARY SYNTHESIS

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The integral approach to evolution by I.I. Schmalhausen (1938, 1982) may be regarded as an alternative to the STE strategy. According to it evolution presents a cybernetic cycle with feedback connection including the zygote, ontogenesis, phenotype, population, biocenosis. Evolutionary process starts from the ontogenetic level where considerable role belongs to epigenesis. The stabilizing selection (S.S.) provides normalization (canalization) of development, leads to the encrease of ontogenetic autonomization and to the decrease of population dynamic or plasticity (D). On the other hand reserve of plasticity provides population stability (S). The relation D/S we consider as evolutionary factor (Vorobyeva, 1987, 1989). Unlike S.S. the "creative" form of selection (C.S.) provides increase of plasticity and accumulates population diversity. In the case of S.S. diversity protects the stable norm, while in the case of C.S. it is used to form a new point of stabilization. This strategy permits us to treat micro- and macroevolution as different scales processes with similar mechanisms and factors. The biocenosis presents an arena of primary evolutionary transformation. The intraspecific "struggle for survival" stands as an evolutionary factor directly linked with selection and providing improvement of species structure.

S7

DEVELOPMENTAL CONSTRAINTS AND HOMOLOGY

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Homology between structures from different species implies their identification as "the same" organ under every variety of form and function. It is argued that the homology relation should only be applied to developmentally individualized parts of the phenotype. The parts are expected to possess certain conservative features to allow their identification in different species in spite of variation of structure, position and function. Thus a biological explanation of homology is expected to explain three properties of homologs: 1) the conservation of those features which are used to identify a homolog; 2) the individualization of the homolog with respect to the rest of the body; 3) the uniqueness of the homolog, i. e. its specificity to monophyletic groups. The main obstacle to describing a mechanistic basis of homology consists in the variability of developmental pathways of undoubtedly homologous characters. It is concluded that not all aspects of the developmental system are of equal importance. Only those features of the developmental system matter, which have been historically acquired and cause developmental constraints on the further evolutionary modification of the characters.

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P13

Stability of Arctic goose population.

L. WITTING, Aarhus, Denmark

not received

P11

Life history strategy of *ASELLUS AQUATICUS* (L.) in Tevere river, (Rome).

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Asellus aquaticus (Crust. Isop.) has a wide distribution area (Fano 1977) although recently overcome, but not completely excluded, by his competitor *Proasellus coxalis*.

We have analyzed some biological parameters of a population of *Asellus aquaticus* collected from Tevere river (Rome); in this biotope until 1960 (Stella pers. comun. 1971) *A. aquaticus* was the dominant detritivorous species, now it is rare and *P. coxalis* is the dominant one.

Results show that *A. aquaticus* is more aged at first reproduction, presents a longer mating time and development time (from eggs to larvae in the maternal brood pouch) and a smaller clutch size than *P. coxalis*, on the contrary it shows a more uniform age distribution than *P. coxalis* and the survival curve fit with IV type of Slobodkin (1962).

Therefore the modulation of some different biological features determines a life history tactics which explains:

- the numerical supremacy of *P. coxalis* in Tevere river
- the stable presence of *A. aquaticus* in this biotope although as rare species
- the non-exclusion of *A. aquaticus* by *P. coxalis* from Tevere river.

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P10

A THREE LOCUS MODEL FOR A QUANTITATIVE TRAIT
UNDER CONSTANT AND FLUCTUATING SELECTION

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A quantitative trait has been modelled as determined by three loci and an environmental component in an infinite, panmictic population with discrete generations. The phenotypic expression of each genotype is defined by a Gaussian distribution: the loci influence the distribution mean additively, independently of each other, and the contribution of the two alleles at each locus is either 0 or 1. The effects of constant and cyclic zygotetic selection regimes, which are also modelled by means of normal fitness functions, have been studied numerically for different recombination rates between the loci. The phenotypic optimum under constant environment has been chosen as to coincide with the mean of the trihybrid; the alternating functions are symmetrical with respect to it. Selection intensity is identical for the alternating functions, while the variance of the constant selection function to be compared with them is equal to the total variance of the variable environment. With completely linked genes, both constant and variable selection regimes attain six chromosome equilibria, the chromosomes with minimum (0) and maximum (3) contribution being lost. In general, for incomplete linkage or total independence, eight chromosome equilibria can be attained under constant selection, while one locus polymorphisms are present at equilibrium under variable selection.

P8

ADAPTATION OF MALE PHENOTYPE TO VARIATIONS OF
INTENSITY OF SEXUAL SELECTION IN *Gambusia holbrooki*

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Laboratory experiments have shown that the most successful size of males in mating is related to the intensity of intrasexual selection. Field studies confirmed the predicted changes in average male body length with the temporal or spatial variations in the intensity of male competition. The influence of the paternal genotype on size at maturity was found to be small, and adaptation appeared to be due mainly to developmental plasticity. We present evidence for possible mechanisms allowing immature males to gather information on the intensity of competition and on the success of their own phenotype in the population where they happen to be growing.

P12

Evolutionary genetics in Leishmania infantum group
(Protozoa, Kinetoplastida).

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The peculiar organization of mitochondrial DNA (Kinetoplast, K, DNA) of Kinetoplastida Protozoa suggests the existence of a molecular clock regulating the genetic divergence inside and between different species.

A large amount of non coding sequences may account for the accumulation of a high degree of variability even in the same strain (variable region) although some constant regions are conserved at genus level.

Studies on the genetic variability in Leishmania infantum s.l. species through restriction enzyme analysis of kDNA suggested us the existence of an active genetic evolution inside this group.

Cladistic and multifactorial analyses of kDNA characters (together with those from isoenzyme data) discriminate different genetic groups. In particular we have isolated a sequence from the variable region of L. infantum kDNA which was found useful as species-specific diagnostic probe and which shows different degrees of hybridization with the different cladistic groups.

Sequencing of this fragment revealed the presence of short and scattered repetitions of each base pair which probably occur at different degree in the strains probed.

All these observations let us to hypothesize a peculiar mechanism of molecular evolution in L. infantum s.l. species.

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