ABSTRACTS
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Host migration and the prevalence of a protozoan parasite in monarch butterfly populations

Seasonal migration is exhibited by many groups of animals, and may exert strong effects on host-parasite interactions. Among populations of monarch butterflies infected with the protozoan parasite, *Ophryocystis elektroscirrha,* I have found that disease prevalence is inversely related to host migratory distance. Long-distance movement by monarchs may directly reduce disease prevalence if infected hosts are less likely to successfully migrate. Migration may also select for increased host resistance or decreased parasite virulence if heavily infected hosts are unable to migrate and survive between reproductive intervals. Using a series of cross-inoculation experiments, I have shown that host and parasite strains from different populations vary, with resistance highest and virulence lowest in the population that migrates the farthest distance. To assess the genetic basis for these differences in host resistance, I constructed a line cross experiment using parental and F1-hybrid lines from two North American monarch populations. As predicted, families derived from the longest-distance migrants were more resistant to disease strains from both populations. In addition, parasite strains were less able to infect the F1-hybrid crosses compared to hosts from either parental population. These results suggest that loci with both additive and non-additive effects are responsible for genetic divergence in host resistance, and that novel host genotypes in general may be more likely to resist infection.

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Conservation genetics of the Karner blue butterfly (Lycaeides melissa samuelis)

The Karner blue butterfly *Lycaeides melissa samuelis,* currently recognized as one of several subspecies of the more widespread Melissa blue butterfly *L. melissa,* was recently listed as federally endangered. A number of factors are believed to have led to the dramatic decline of the Karner blue, the most important being the fragmentation and loss of its native habitat. Remaining populations are thus widely separated, increasing the probability of local extinction in the absence of colonization from neighboring areas. Although this butterfly has been the subject of intense conservation efforts, little if anything is known of its population genetic structure. Moreover, its taxonomic status remains unclear. We are therefore interested in: (1) assessing the phylogenetic position of the Karner blue in relation to other closely related butterflies and (2) examining genetic variation within and among Karner blue populations. To address these aims, we have developed a set of DNA-based markers including the A+T rich region and COI/COII genes from the mitochondrial genome as well as several nuclear microsatellite loci. Results

collected to date from a range of North American *Lycaeide*s populations (*L. melissa, L. idas*) will be discussed.

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Habitat structure and butterfly community patterns in an age-heterogeneous **Eucalyptus** *plantation*

Eucalyptus plantation has strong economic importance and is increasingly expanding both in world and local scales. In Rio Grande do Sul, south Brazil, it occupies at least 600,000 hectares. In spite of its enormous impact in natural habitats, hardly anything is known about its impact in native faunas. Patterns of butterfly communities in three successional stages of *Eucalyptus* (*Eucalyptus salina*) were studied in a 10,153 ha plantation at Barra do Ribeiro, Rio Grande do Sul (30º 23'S 51º 12'W GR), where *Eucalyptus* is grown as a mosaic of plots of different ages and fragments of native vegetation. From September 1997, fortnightly, records of butterfly diversity and abundance are made along transects (1 km x 10 m) in plots of *Eucalyptus* 2-3, 5-6 and 8 years old. Potential food plants, general floristic composition and vertical profile of the understory are registered. A dramatic reduction in species richness was observed in all plots as compared to recent records in a nearby (100 km) large urban center. Preliminary analyses indicate a decrease in butterfly diversity as *Eucalyptus* age increases; Margalef, Simpson complementary, Shannon-Wiener and Berger-Parker indexes all support this result, even though they are based on quite different theoretical assumptions. Whittaker dominance curves and quantitative similarity analysis (Euclidian distance) are also consistent with this pattern; a qualitative-only index (Jaccard), however, fails to point in the same direction. Sampling proceeds till August 1998 and further analyses on the association between the environmental variables and diversity patterns and the influence of the fragments of native vegetation as sources of species are being carried on.

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*Viability analysis of the Cranberry Fritillary (***Boloria aquilonaris***), an endangered species in Belgium*

The Cranberry Fritillary has a distribution range typical of boreo-alpine species: abundant in Fennoscandinavia, its populations are scattered on mountains and uplands in western Europe. In this part of its range, *Boloria aquilonaris* is located in raised peat bogs, where the Cranberry (*Vaccinium oxycoccos*) is its only larval foodplant. The natural patchiness of bogs has been increased by drainage and Norway spruce *Picea abies* plantations since the end of World War II. In Belgium, on the 20 populations monitored in 1996-1997, 14 were located on the same upland, the Plateau des Tailles (220 km square). A PVA (population viability analysis) was carried out on this priority area: (1) population size and habitat characteristics were monitored; (2) individual movements between populations were investigated; (3) the genetic structure of the populations was assessed. From this data set, we predict the future of the populations with a spatially-explicit model. Results show that the system of populations is stable. However, the long-term persistence of all the habitats is highlighted.

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How can we define a population in butterflies?

Butterfly populations were usually divided between open and closed, loose and tight. However, the analysis of spatially structured population systems showed that at the landscape scale we must rather consider a continuum ranging from isolated populations to species showing a continuous mixture of individuals in space and time. In this talk, we compare 4 species showing a contrasted population structure. We investigate whether individual movements, life-history strategies and habitat distribution can be used to explain the genetic structure of populations.

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Solitary display in the tropical butterfly, **Heliconius sara** *(Nymphalidae)*

Although lek-like mating systems are well documented for butterflies, solitary displays on unaggregated arena territories have not been reported previously. In a study conducted along a linear 3.2-km-long forest edge in southeast Brazil, we observed 155 marked male *Heliconius sara* butterflies defending territories on 444 occasions during 57 daily censuses over a 13-month period. The 74 territory sites used by butterflies at least once during the study were randomly distributed, as were the 26 more preferred sites defended on six or more survey days, and were seemingly unassociated with larval or adult resources. At least one territory was present in 29 of the 32 (91%) contiguous 100-m stretches of forest edge comprising the study area. In an analysis of the spatial distribution of occupied arenas on six well-separated dates having many (10-18) territorial males, butterfly spacing was no different than random. Also, using data from all 57 daily surveys, the frequency of territories did not increase with increasing proximity to focal individuals. We interpret the random dispersion of territorial *H. sara* as solitary display: an exploded lek lacking significant aggregation in the display habitat. This butterfly is also a pupal-mating species, suggesting that arena matings may be restricted to females that go unfound at pupation sites and to those mating more than once; both situations seem uncommon. We relate the territorial spacing in *H. sara* to inter-male competition for spatially unpredictable receptive females in the context of the postulated mating ecology of this species.

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Is there a future for the handmaid, **Dysauxes ancilla** *(Syntomidae), in Sweden?*

The moth *Dysauxes ancilla* breeds in an isolated population consisting of 2,000-2,500 individuals, restricted to an area of 6 ha on the Baltic island of Öland. The preferred habitat is edge zones of dry meadows with short vegetation and stands of junipers and oaks. During the last decades there has been a reduction of this habitat and the species has become less abundant. The species is listed as endangered in Sweden. Rearing of *D. ancilla* larvae shows that the larvae are polyphagous, although there is a strong hierarchical order in suitability amongst food plants. Survival and weight of enclosed imagines are significantly higher on *Calluna vulgaris* and a mixed diet, followed by *Thymus serpyllum*, *Hieracium pilosella* and *Brachytecium* sp. On several other food plants no larvae survive. Warm edge zones oriented to the south have a great importance for adult activity (shown by transect counts) and oviposition. This indicates crucial needs for a warm microclimate. Further, mark-recapture studies indicate that the species has a limited dispersal ability (mean= 40 m and observed maximum= 160 m). Extinction risks are mainly due to deterministic threats, i.e. habitat loss or succession. Demographic stochasticity is of minor importance and genetic deterioration is also a minor threat since preliminary results from allozyme electrophoresis show a higher genetic variability in the isolated Swedish population compared to a population from Germany within the main distribution area. A conservation strategy should therefore focus on maintaining, and manage the continuity of, warm edge zones oriented to the south. If possible, new suitable habitat in the surroundings should be created thus reducing risks from certain kinds of environmental stochasticity.

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Allocation, environmental variation and population dynamics

The environment varies over space and time. Abiotic factors, such as weather, and/or biotic factors, such as community composition, may change. Such variation affects an organism’s allocation of time and/or nutrients. Allocation patterns are one component determining life histories and hence linking environmental variation to population dynamics. To effectively link environmental variation that affects resources and their use to population dynamics, we need a set of generalizations regarding allocation. For example, under what conditions do organisms buffer environmental variation? How effective can that buffering be? I explore these questions using a case study from *Speyeria mormonia.*

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Eupyrene and apyrene sperm dynamics in spermatophore of the swallowtail butterfly, **Papilio xuthus** *(Lepidoptera: Papilionidae) after copulation*

Spermatophores ejaculated into the bursa copulatrix in female swallowtail butterfly, *Papilio xuthus*, using hand-pairing method were examined. Mean copula duration was about 54.9 min (n=39) under the constant room temperature (ca. 26.2 C). After copulation termination, all females were dissected. Eupyrene sperm was packed in a bundle and ejaculated, whereas the apyrene sperm were ejaculated individually. The former type of the sperm was twice in size as long as the latter, and had gentle wavy shape. The latter had fractionally wavy spiral. Since each eupyrene bundle had free 256 eupyrene spermatozoa, there were about 8000 eupyrene spermatozoa in a spermatophore immediately after copulation termination multiplying by 256. The number of apyrene spermatozoa was about 10-fold of the number of eupyrene spermatozoa. Then the number of eupyrene sperm bundles decreased, and disappeared 2 hours after copulation termination. However, the number of free eupyrene spermatozoa did not increase in the spermatophore, suggesting that most of them moved to the spermatheca. The number of apyrene sperm also decreased in the spermatophore, though a few apyrene sperm still stayed there at 2 hours after copulation termination. Copula duration and the volume of spermatophore did not affect the number of each type of sperm. The eupyrene and apyrene sperm dynamics in the spermatophore will be discussed in view point of the role of apyrene sperm for the male fitness.

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Latent sources and alternative states in a butterfly metapopulation

Often an assumption of source-sink theory is that the source/sink role of each habitat patch is fixed. I studied a metapopulation of the Edith's checkerspot butterfly that violated that assumption, and consequently had two alternative states. Previous work by C.D. Thomas, M.C. Singer and myself had shown that forest clearings functioned as source habitat for the butterfly, until an anomalous frost killed all the larvae in 1992. Meanwhile, rock outcrops functioned as sink habitat, but this role was density-dependent. After 1992, these outcrops stabilized at lower densities and became sources of migrants. Subsequently, I studied recolonization of the vacant clearings, and a set of experimentally-vacant outcrops. Yearly censuses of larval web densities showed that the butterflies re-colonized outcrops ten times faster than clearings, with initial densities a hundred times higher. This discrepancy was unexpected, because clearings had formerly functioned as source habitat, and a census of adult densities showed that immigration rate in vacant patches was the same for both habitats. The discrepancy was explained by a study of larval survival. In clearings, resident populations oviposit early in the flight season, and experience high success. Immigrants arrive later, but fail to reproduce because hostplant senescence has begun. Thus, vacant clearings functioned as sinks, but were really latent sources. Occasionally, small resident populations were established, and these underwent rapid population growth. If this growth continues, they will soon become source populations again. The study illustrates how details of the insect-plant relationship can lead to complex dynamics at scale of the landscape.

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The evolution of butterfly eyespot patterns

Our research has focused on the evolution of morphological diversity in butterfly eyespot patterns using the African satyrine, *Bicyclus anynana*. I will illustrate how we have used approaches at several levels of biological organization, from the molecule, through genotype and phenotype, to the population. This has provided novel insights about the ways in which genes modulate developmental processes to provide the basis of evolutionary change in pattern. This type of integrated study is vital to improve our understanding of evolutionary constraints and to be able to make predictions about biases in the directions taken by evolution.

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***Molecular diversity of visual pigments in the butterfly,* Papilio glaucus**

Vision is important for many organisms. In butterflies, feeding, ovipositing, drumming and the escape response are all wavelength-dependent behaviors that have been shown to be driven by the presence of multiple spectrally-distinct classes of photoreceptors. The difference in spectral sensitivity between photoreceptors is due primarily to changes in the amino acid composition of the visual pigment proteins (opsins) expressed within those photoreceptor cells. Using a 3 and 5 RACE (rapid amplification of cDNA ends) strategy, I have isolated six distinct opsin-encoding cDNAs from the a single female tiger swallowtail butterfly, Papilio glaucus. An alignment of insect amino acid sequences was used to reconstruct an opsin gene tree. The opsin gene family pattern of duplication and diversification in butterflies has an evolutionary history markedly different from that of *Drosophila*. Butterflies have, at a minimum, four visual pigment genes descended from the insect long wavelength clade, while *Drosophila* has only one. These differences extend to the clade of ultraviolet- sensitive visual pigments as well: *Drosophila* have two UV genes, while butterflies appear to have only one, and, though flies and butterflies share homologous genes descended from a common blue-sensitive clade, flies have two additional blue-sensitive visual pigments in a clade with no known homologue in butterflies or any other insect. The branching pattern of the insect long wavelength clade of visual pigments suggests a further surprising possibility: older lepidopteran lineages (*Manduca sexta*) may have additional long wavelength-sensitive visual pigments, although presently only three major visual pigments are known from either molecular biology or electrophysiology.

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Phylogenetic relationships among nymphalid butterflies inferred from sequences of the wingless gene

One hundred nymphalid genera were sequenced for a 345 bp region of the wingless gene. The sequences were analyzed using equal-weighted parsimony analysis, followed by successive approximations weighting. These results are compared with prior hypotheses of nymphalid relationships based on morphological features. The molecular data support traditionally recognized groups of nymphalids, such as Danainae+Ithomiinae, Satyrinae+Morphinae+Brassolinae, and the monophyly of the Heliconiinae. Other traditional subfamilies, such as "Limenitidinae," are shown to be unnatural, polyphyletic assemblages.

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Assessing butterfly diversity and abundance in two National Parks of Rio de Janeiro, Brazil

We assessed overall butterfly abundance at two parks in the Atlantic rain forest of Rio de Janeiro by walking timed transects along similar habitats at the interface of forest and cleared areas and counting the number of individuals seen. To assess diversity, we collected butterflies along the same transects. The parks are at similar elevations, but have different climatic conditions and levels of disturbance. There was a consistent and significant correlation between abundance as measured by non-collecting transect counts and diversity as measured by collecting, the latter not appearing to alter the magnitude of the non-collecting counts. Data on 318 species collected during 90 person/hours show that total and most monthly species abundances fit the log series distribution for one park but not for the other, where both number of species and abundances were lower. Similarity between the parks was low when calculated through both quantitative and presence-absence indices, suggesting that these areas have undergone differentiation in their butterfly faunas through time. Because conservation and management plans are often based on diversity patterns of vertebrates and plants, the results obtained with this method potentially provide an independent, and possibly different, data set on which to base management plans.

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Phylogenetic relationships of the Riodinidae

Although the Riodinidae comprise more than 1200 species, the systematics of this family and its relationship to other butterfly families remain unresolved. A phylogenetic estimate based on nucleotide characters from three sources, the nuclear wingless and elongation factor 1-alpha genes and the mitochondrial cytochrome oxidase I gene, supports the monophyly of the Riodinidae and their sister taxon relationship to the Lycaenidae. Moreover, relationships of subfamilies and tribes within the riodinids largely conform to the morphological hypothesis of Harvey (1987). The implications of this phylogeny to our understanding of larval ant association in the riodinids and lycaenids, and the age and biogeography of the Riodinidae are discussed.

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Adult acquired resources and cyanogenesis in **Heliconius** *butterflies*

Cyanoglucosides are the putative chemical defense of aposematic *Heliconius* butterflies. Most heliconiines synthesize low levels of cyanoglucosides from amino acids present in the larval diet. *Heliconius* species, however, also feed on amino acid rich pollen as adults and show increased cyanogenesis and decreased palatability. We hypothesize that increased cyanogenesis in *Heliconius* is a consequence of pollen feeding. To test this, we assigned fresh imagos of *H. ethilla* and *H. charitonia* to one of two diets: an amino acid-sugar diet and a sugar-only diet. Butterflies were hand fed for 20 days, frozen, and analyzed for cyanoglucoside content. Amino acid fed *H. charitonia* synthesized more cyanoglucosides than conspecifics fed sugar only. Cyanogenesis in *Heliconius ethilla,* however, did not differ between treatment groups. Fieldwork in Mexico supports the association between pollen feeding and increased cyanogenesis. *H. charitonia* and *H. erato*, species which collected high levels of pollen, synthesized more cyanide than *Heliconius ismenius*, a species with low levels of pollen collection. These data show that some but perhaps not all *Heliconius* species respond to increased amino acid availability by increasing cyanoglucoside levels. The documented ability of adults of primitive heliconiine species to synthesize cyanoglucosides from stored amino acids suggests that this preceded the evolution of pollen feeding. We propose that pollen feeding accounts for increased levels of cyanoglucoside synthesis in *Heliconius* and is implicated in the evolution of unpalatability in these butterflies.

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Allozyme variability and genetic subdivision in the scarce heath (**Coenonympha hero*****)***

Allozyme electrophoresis is useful for analysing geographic population structure in insects. It has been widely used for butterflies and the level of genetic variation has often proved to be high. The scarce heath, *Coenonympha hero* (Nymphalidae: Satyriane) is an internationally threatened species in Europe. Its total distribution ranges from northeast of France, eastward through Russia, to Amur, Korea and Japan. In central Sweden it is locally abundant and appears in a network of more and less isolated forest meadows of varying size. However, the meadows are continuously being reforested as they are abandoned and planted with spruce or overgrown. I conducted a pilot study of allozyme variability in the scarce heath, *Coenonympha hero* in 1996. Out of 18 loci scored, only two (Sod and Pgi) were polymorphic as defined using the 0.95 common allele frequency criterion. The small number of polymorphic loci can be an indication of a severe bottleneck at the time for colonization to Scandinavia. Despite the low variation observed, indications of isolation effects were found. For example, two populations separated by only a 150 meters wide forest strip showed significant genetic subdivision. Samples from other parts of Sweden, as well as from Estonia and Russia, are currently analyzed and will be included in the presentation.

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Predators attack the cephalic portions of caterpillars: field experiments with artificial prey

It is generally believed that predators prefer to attack the cephalic region of prey. In this study, we investigated the distribution of attacks on different body regions using artificial caterpillars set out in natural vegetation in tropical southeast Brazil. Imitation caterpillars consisting of 20mm long X 1.5mm diameter cylinder of green modeling clay were glued to leaf tops and examined after 5 days for bird and wasp damage. Three prey types were used: models i) with a gray head, ii) with green head and iii) without cephalic differentiation. In each experiment we randomly placed 30 models of each prey type on plants 10m apart along vegetation margins. The experiment was repeated in April, July and December of 1997. We recorded the frequency of predators attacks on prey body extremities (recording data separately for the cephalic and caudal thirds) and on the center third of the body. Combined results from the three experiments showed that i) attacks were more frequently directed to prey extremities than expected by chance (76.5% vs. 23.5%: G=16.4; df=1; p<0.001), ii) no difference existed among the three prey types in the relative preference for attacking body extremities (G=0.047; df=2; p>0.05), iii) for models whit heads, more attacks were directed towards the cephalic than caudal extremity (65% vs. 35%; G=16.50; df=1; p<0.001), and iv) 96% of the attacks were made by wasps. Our results demonstrate that predators, particularly wasps, have a marked tendency to attack caterpillar prey at their extremities and to concentrate these attacks near the head.

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Effects of a naturalized weed on native Pieris *caterpillars*

When a native butterfly encounters a naturalized weed related to its normal hostplants, several butterfly/caterpillar responses are possible. These yield several potential evolutionary outcomes from incorporation of the novel plant into a broadened diet to exclusion of the plant from oviposition choices. Growth and assimilation responses of caterpillars from several *Pieris napi* subspecies to a widely naturalized weed in eastern North America, *Alliaria petiolata* (garlic mustard) are reported. These are compared to responses for eastern Massachusetts *Pieris rapae*. Caterpillar feeding on garlic mustard is widely variable. Post-ingestive effects slow growth substantially, but have no residual effects if individual caterpillars leave garlic mustard and move to a normal hostplant.

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The systematics of Sparganopseustis *(Lepidoptera: Tortricidae) and the use of the internet*

The genus *Sparganopseustis* Powell & Lambert was first described in 1986, which included 12 species including the newly described type for the genus, *Sparganopseustis martinana* Powell. We revised this genus and found more than 20 new species. However, due to extreme sexual dimorphism, we are sequencing a part of the COI gene in order to associate different sexes of the same species. In addition to writing a manuscript, we put keys for males and females of *Sparganopseustis* on the World Wide Web as Web documents allow us to make these keys immediately and widely available and to include color illustrations.

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A.B.R.I. A focal point for African Butterflies

A poster explaining the mission of ABRI:
Helping develop database on African butterflies
Support breeding programs for molecular biology and genetic work
Publications support on African Rhopalocera
Coordination point for African Lepidoptera
Center for visiting scientists

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The effects of niche breadth and population mobility on density-distribution relationships in British butterflies

Positive relationships between local population densities and regional distributions of species have been observed for a wide variety of taxa. Despite the important theoretical and practical implications, both the pattern itself and the underlying mechanisms generating the pattern remain poorly understood. We use a new detailed data set to test the effects of population mobility and niche breadth on density-distribution relationships in British butterflies. The data consist of presence/absence in one hundred and fifty 500m squares and relative densities from one hundred and fifty four transects, located in sixteen habitat types in Western Britain. Including all species, local population density is not significantly correlated with regional distribution. If species are separated according to relative mobility, then only mobile species show a significant density-distribution pattern. The lack of a pattern amongst the sedentary species suggests that meta-population dynamics may be important in determining species distributions, but they do not generate a density-distribution pattern. At the level of the whole landscape, niche breadth is significantly related to species distribution, but not density. Within individual habitats, all density distribution correlations were positive, and most were significant, suggesting that niche breadth may be influencing this pattern.

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Risk sensitive foraging for mates in a pupal mating butterfly

A central theme in sexual selection theory is that there are costs associated with mate choice. Individual behavior, therefore, should reflect changes in the associated costs and benefits. For example, when response to predation risk alters male interactions with future potential mates, male response should depend on the relative value of the resource, i.e. mating opportunity. This study examines the mate locating and risk taking behavior of a pupal-mating butterfly, *Heliconius hewitsoni*, as a function of changing pupal maturity. Male *H. hewitsoni* locate female pupae and 24-36 hrs before female eclosion compete for access to the pupae and the teneral females. Male *H. hewitsoni* assess pupal maturity and adjust their searching and risk taking behavior according to changes in the opportunity for mate acquisition. Males visited pupae throughout the nine day pupal phase and visits increased in frequency and duration as the pupae aged. Male response to simulated predation attempts at the pupal site depended on changing mating opportunity as reflected by changing pupal maturity. Time to return to site of capture was significantly less when pupae were close to eclosing than when pupae were days from eclosing. Captured males and uncaptured control males differed significantly in time to return to site, indicating that in response to predation risk males shift from a risk-averse to a risk-prone strategy as pupae increase in value.

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Preliminary approaches to the conservation of Parnassius apollo

Parnassius apollo is endangered in all states of the European Union. In France, a strong regression of marginal populations has been observed. Studies on the features, extent and possibly causes of the regression have been carried out using comparison of collection and literature data with present distribution and field and laboratory observations.
Population dynamics: *P. apollo* presents a typical metapopulation structure with large, stable source populations and less permanent satellites. A minimum area of 500m2 is necessary to shelter a colony. Typical size of a source population is between 1000 and 5000 individuals. Adults are able to cover distances up to 7 km. Yearly variation of population size can vary within a factor of at least two.
Habitat characterization: *P. apollo* is linked to open sunny mountain landscapes. Invasion by scrubby vegetation is the main factor of extinction in regions under ocean influence. Climate warming is likely to cause a rise of the inferior limit of the habitat.
Larval foodplants: The main foodplants of *P. apollo* are Crassulaceae: *Sedum album* on limestone substrate and *Sempervivum* sp. on acidic soil. Laboratory experiments suggest that life-cycle regulation and relations with foodplants are primordial in breeding success.
Conservation: For conservation, habitat maintenance and restoration are paramount. Mechanical clearing and grazing may be used. Grazing intensity must be controlled and the state of colonies must be regularly monitored. The future of lower colonies, threatened by climate warming, is rather somber. Restoration of suitable habitats is a preliminary to reintroduction.

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Comparative species diversity of two Amazonian fruit-feeding butterfly communities in vertical, horizontal, and temporal dimensions

Butterfly diversity studies have been important to our understanding of community ecology and conservation biology, but they seldom measure diversity in multiple dimensions of space and time, or employ sampling methods that are comparable among areas. At two Amazonian forest sites (one strongly disturbed, the other little disturbed) we used a standardized trapping regime in the canopy and understory at monthly intervals for one year to show that fruit-feeding nymphalids are not randomly distributed in space and time. Partitioning total species diversity into additive components within and among community subdivisions (vertical, horizontal and temporal dimensions) showed that each subdivision made significant contributions to diversity. Based on individual abundance and observed species richness both sites had fewer species in the canopy than in the understory, and a greater number of species were found in more disturbed habitats. However, we show that such observed differences in diversity may be seriously misleading due to the effects of disparate sample sizes. We show that samples from a single habitat, height and time contain only a small fraction of the total species richness in a sample community, and we demonstrate the feasibility and necessity of performing long-term sampling in multiple dimensions. Finally, we emphasize the need for similar studies from other sites to compare diversity among tropical forests because even though rapid assessments are widely used in conservation, their ultimate contribution must be assessed against long-term studies documenting the variation of many species through space and time.

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Patterns of hostplant specialization and cyanogenesis in passion vine butterflies

The larvae of *Heliconius* butterflies feed exclusively on leaves of *Passiflora* plants. Although we have studied many dimensions of host-plant relations, we know very little about the chemical basis for these interactions. However, it is well known that *Heliconius* manufacture aliphatic cyanogenic glycosides, and it is generally assumed that they do not sequester cyclopentyl cyanogens from *Passiflora* plants. Chromatography, nuclear magnetic resonance and cyanide quantitation methods were used to investigate the fate of hostplant cyanogens in greenhouse populations of *Heliconius* butterflies. Our results indicate that *Heliconius* butterflies can sequester cyanogenic glycosides from passion vine plants, but sequestration is specific for monoglycosidic cyclopentyl cyanogens. We identified the sequestered cyanogen by *Heliconius sara* from its specific host, *Passiflora auriculata*, as epivolkenin. Quantitation studies show that sequestration is more efficient in a derived and extremely host-specific clade of *Heliconius* butterflies known as the *sara-sapho* group. As specialists store greater quantities of cyanogens than generalists reared on their specific hosts, we hypothesize that the physiological mechanisms involved in sequestration may have restricted *Heliconius* specialists to *Passiflora* plants of a particular cyanogenic chemistry.

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Effects of **Hypoestes phyllostachya** *(Acanthaceae), an introduced plant, on* **Anthanassa** *spp. (Nymphalidae: Melitaeinae), a native butterfly in Monteverde, Costa Rica*

Hypoestes phyllostachya (Acanthaceae), from Africa, was introduced to Monteverde, Costa Rica over 40 years ago. Five to 15 years ago, it spread along roadsides and pastures. *Anthanassa ardys* and *Anthanassa tulcis* (Nymphalidae: Melitaeinae) were observed using these exotic plants as oviposition sites. However, *Hypoestes* does not support larval development beyond the first instar. *Anthanassa* spp. use native acanths as larval hosts. In laboratory two-choice oviposition preference tests, *A. ardys* showed a preference for *Dicliptera unguiculata*, a native, over *Hypoestes*. Field data for oviposition so far do not show a preference for either plant species. In 1998, I conducted a series of studies to determine why behavioral traits had not evolved to prevent this apparently maladaptive behavior. Perhaps oviposition on *Hypoestes* affords eggs greater protection from predation and parasitism than oviposition on native acanths. For this to be advantageous, larvae must be able to crawl from *Hypoestes* to a native acanth and then feed successfully. In the lab, larvae crawled later and with lower mortality from a dead *Dicliptera* to a live *Dicliptera* than in an experimental treatment where larvae crawled from a live *Hypoestes* plant to a live *Dicliptera* plant. Some larvae were able to crawl 20 cm in lab and still survive when placed on a plant. However, larval ability to crawl in the field was not assessed. The mean distance from eggs on *Hypoestes* to the nearest native acanth in the field was 137 cm. Data so far show little difference between egg predation/parasitism on natives and on *Hypoestes*. There appears to be little advantage to ovipositing on this exotic.

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Life-histories of Indo-Australian* Arhopala *butterflies (Lycaenidae): specialization, plasticity, and diversity

Arhopala (including genus-level taxa of doubtful rank such as *Flos*) constitutes the most speciose clade among the Indo-Australian Lycaenidae butterflies comprising more than 230 described species. Life-history data are now available for 41 species. From this data set, four major ecological groups emerge. (1) The larvae of most species with recorded life cycles feed on young foliage of Fagaceae trees (*Quercus, Lithocarpus, Castanopsis*), where they build characteristic shelters and are facultatively and unspecifically attended by a variety of arboreal ants belonging to four subfamilies. All are narrowly oligophagous; shifts to non-fagaceous hosts appear to be rare. (2) Larvae of *Flos* species also mainly feed on young Fagaceae foliage, where they build shelters of a different type and are obligately and specifically attended on by numerous *Dolichoderus* ants. (3) One subset of at least 6 species feeds on *Macaranga* pioneer trees (Euphorbiaceae). Their larvae do not build shelters, but feed in a characteristic way on the youngest apical leaf of their host tree. Most larvae live on myrmecophytic *Macaranga* species, where they are constantly and specifically attended by numerous *Crematogaster* ants inhabiting the host tree. These butterflies are narrowly specialized with regard to hostplants and host ants. At least one species, however, lives on a non-myrmecophytic *Macaranga* and has facultatively myrmecophilous larvae. (4) Larvae of species in the *A. centaurus* group are polyphagous on a variety of trees, but are obligately bound to the weaver ant *Oecophylla smaragdina*. These contrasting patterns of specificity and life-cycle diversity now call for a phylogenetic exploration.

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Pitfall or panacea? Assessing butterflies as tools for land management

Land managers seek scientifically valid short cuts to guide their planning efforts. These include delineating human activities, assessing ecosystem health, and maintaining critical habitats and ecosystem processes. Butterflies often have been suggested as tools for conservation planning. Using recent data from the Great Basin, we are examining how butterflies can inform ecosystem management in that region. Butterflies in the Great Basin tend to be extirpated by habitat fragmentation in a predictable order. Therefore, surveys of butterflies within mountain ranges can help evaluate how human activities might perturb current species distributions. Across the Great Basin, elevational gradients significantly affect species richness and elevational distributions of butterflies. Thus, we can predict which species are at greatest risk of being lost from individual mountain ranges. To test empirically whether butterflies can provide information about the health of habitats or ecosystem processes, we are evaluating the effects on butterflies of variation in the scales at which management alternatives are implemented; measuring the extent to which the distribution and abundance of butterflies vary in space and time; and testing whether human activities in sensitive habitats influence the viability of certain taxa. Rare butterfly species sometimes may need to be conserved on their own merits rather than as surrogate measures of ecosystem health. To identify short cuts for ecosystem management, we must consider which biological attributes might link species viability to that of particular areas or processes; then test the hypothesis that potential surrogate taxa actually can function in that context.

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Do adult female and larval behavior influence habitat suitability of alpine meadows for the butterfly, **Parnassius smintheus***?*

Female *P. smintheus* do not oviposit on their larval hostplant, stonecrop (*Sedum lanceolatum*), therefore, upon hatching larvae must move to the hostplant. Although *S. lanceolatum* is not an oviposition site, observations of mated females indicate *that S. lanceolatum* is an important nectar source and an indirect cue for oviposition in caged individuals. The interactions between oviposition site selection by adult females, the ability of hatching larvae to detect and orientate to the larval hostplant, and the spatial arrangement of *S. lanceolatum* in meadows are likely important in determining the suitability of alpine meadows for *P. smintheus*. As part of a larger project studying the population dynamics of *P. smintheus*, I am attempting to determine what influences the suitability of alpine meadows in the Eastern Canadian Rockies portion of its range, by comparing characteristics of meadows with and without *P. smintheus*. The potential effects of the interaction between the density and dispersion of *S. lanceolatum*, and both adult female and larval behavior, on habitat suitability will be explored.

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Forest canopy structure and habitat restoration for over-wintering monarch butterflies in California

Over-wintering monarch butterflies seek a very narrow range of microclimatic conditions that are met by a relatively few forest groves along the California Coast. Many of these groves are threatened by development and changes in forest structure from tree senescence, disease, and insect pests. Using fisheye photography, we have measured key characteristics of canopy structure that determine light and wind penetration, and have correlated those characteristics to patterns of use by monarch butterflies. These measurements are then related to maps of trees and understory, and have been used to develop habitat restoration plans that create proper microclimates for the butterflies. Detailed examples from several sites illustrate the procedures.

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The relationship between egg size and adult body size in butterflies: a comparative study

A number of variables have been proposed to explain the interspecific patterns of egg to body size relationship in butterflies, involving non-adaptive allometry, climate, fecundity, or features related to hostplant structure or ecology. Attempts to determine such relationships have generally focused on selected taxa within more or less local geographical scopes. This study attempts to determine whether a basic allometric relationship explains egg size patterns in these insects. Once that such relationship has been estimated, an attempt is done to measure the possible dependence of size (adult, and egg size) on some basic life history and broad climatic variables. The present approach is based on linear estimates of egg and body sizes from over one thousand butterfly species from all families (Hesperiidae and Papilionoidea) and faunal regions. On the whole, the results confirm the idea that egg size is primarily dependent on adult butterfly size.

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Introgression and evolutionary novelty in Heliconius *wing patterns: Evidence from developmental genetics and synthetic hybrid zones*

Heliconius butterflies exhibit an exceptional degree of differentiation in wing pattern 1) within species across regions, and 2) within habitats across species. Conversely, sets of diversely patterned species of one clade of the genus are precisely mimicked by a corresponding array of sympatric species from a distinct clade. This paper addresses the source of variation that allows natural selection to drive pattern evolution in this system.

Studies of development, mendelian genetics, and simulated hybrid zones involving species and races of the *H. cydno/melpomene* group suggest that recent wing pattern evolution in this clade arises from genetic exchange between races or species and is based on a shared toolbox for generating wing pattern. I provide a phenomenological and metaphorical description of this toolbox and show the ease and rapidity with which this pattern generating system can produce successful new mimetic forms.

Points of discussion include: 1) What circumstances might cause cross-species recombinational variants to occur in nature? 2) What is the relative contribution of mutation vs. introgression in pattern evolution? 3) Why there are so few wing patterns in *Heliconius*? 4) Does one clade typically drive evolution of novel patterns? 5) How might evolving *Heliconius* populations jump

from one adaptive peak of wing pattern to another without crossing the fitness valleys between? 6) Do *Heliconius* possess fundamentally different developmental genetic mechansims for generating wing pattern?

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A new twist in the interaction of moths and spiders: the case of **Eudulophasia invaria** *(Geometridae, Eudulini).*

In Corcovado Park Costa Rica, brightly colored diurnal adults of the geometrid moth *Edulophasia invaria* Walker, oviposit exclusively in silk webs, usually of spiders but occasionally those of *E. invaria* larvae on or near the hostplant, *Spigelia anthelmia* L. The host is an herbaceous member of the family Loganiacea, a group known for such toxic plants as *Strynos* and medicinal plants such as *Spigelia* itself. In the laboratory, adult moths readily oviposit into spider webs and possess morphological and behavioral traits that suit them for safely moving about spider webs with spiders present. Adult moths are capable of surviving attacks of several families of spiders tested. These predators quickly reject adults after brief contact. Various aspects of the evolution and ecology of this system are discussed, including the role of these moths as distasteful models for tiny mimetic butterflies of the family Riodinidae.

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Butterflies as environmental indicators at a local scale

Butterflies are widely recognized as potentially valuable indicators of habitat change due to their sensitivity to variation in the physical and biological environment. However, the importance of different factors in determining species distributions may be sensitive to the scale of study. Most previous surveys have been carried out at regional or geographical scales, where because of their relative sedentariness, the absence of particular butterflies might indicate site histories and dispersal limitations, as much as current conditions. Butterflies might potentially be good indicators at smaller spatial scales (local scale), where dispersal is unlikely to be a problem. To assess the indicator properties of butterflies at the local scale, numbers of species, total abundance and the quantitative species composition of butterflies were examined in a 300 m by 300 m area in the Picos de Europa (northern Spain). The number of species was significantly higher in sites with higher expected insolation values. These results emphasize the importance of microclimate in limiting species microdistribution, and the utility of butterflies as indicators for monitoring the response of biodiversity to climate change. Species composition was strongly influenced by vegetation height, by variation in total flower density, and by flower species composition, but not by geographical distance between sites (over such short distances). We conclude that butterflies can be used for monitoring the biotic effects of changes in land management that result in variation in vegetation and floral heterogeneity in relatively small areas.

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A comparative metapopulation approach to assess the vulnerability of the declining butterfly **Erynnis tages** *(Hesperiidae) in North Wales*

Most recent population viability studies of threatened butterflies involve a single-species metapopulation approach, focusing on their spatial distribution, habitat specificity, dispersal ability and population size. Habitat specialists with relatively limited dispersal abilities presumably have much lower threshold of sensitivity to habitat fragmentation than generalist and relatively vagile species, which may perceive the landscape as functionally connected across a greater range of levels of fragmentation. We identified key factors affecting the rarity and vulnerability of *E. tages* in North Wales, by comparing its distribution, habitat specificity, dispersal ability and population size with those of the butterfly *Polyommatus icarus*, that is still widespread but which feeds on the same hostplant*, Lotus corniculatus*. *E. tages* showed a restricted distribution relative to that of the hostplant, whereas *P. icarus* occupied nearly all 500m grid squares that contained *L. corniculatus. E. tages* was more selective when choosing plants for oviposition than *P. icarus*. Distances moved by both species were similar, but the estimated number of individuals in the landscape was far higher for *P. icarus*, generating more potential colonists. These results suggest that the vulnerability of *E. tages* to habitat changes could be the result of high oviposition specificity, which lead to a more patchy perception of the habitat, as well as a relatively low absolute frequency of migration, which reduces the probability of patch colonization.

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Biology of extinctions in butterfly metapopulations

Population ecologists have traditionally studied the processes that contribute to population regulation and long-term persistence. Persistence is relative, however, as any population has a finite lifetime, and one may as well turn the matter the other way round and ask about the processes that influence population extinction. I review here local and metapopulation-level processes that influence the risk of extinction of local populations and entire metapopulations of butterflies. A large-scale study on the dynamics of the Glanville fritillary butterfly (*Melitaea cinxia*) provides many instructive examples. Metapopulation-level processes influencing local extinction include coupled interactions with specialist natural enemies, influence of migration on extinction risk, and the magnification of demographic and genetic stochasticities in small local populations in metapopulations. Entire metapopulations may go extinct because of habitat loss and fragmentation, but the risk of metapopulation extinction is also increased by two forms of stochasticity, extinction-colonization and regional stochasticities, analogous to demographic and environmental stochasticities in local dynamics. Metapopulation extinctions are likely to involve a long delay. An extended view of population extinction is needed especially for species, such as many butterflies, which have highly fragmented population structures. There is a great

opportunity for butterfly population biologists to contribute fundamental results on the ecological, genetic and evolutionary consequences of population extinction in metapopulations.

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Population dynamics and conservation: an analysis of a long-term butterfly data set

Long-term population and demographic analyses, gleaned from long-term monitoring, can be important tools of conservation and species-specific management; they are also fairly rare. Results from a long-term study of the threatened bay checkerspot butterfly, *Euphydryas editha bayensis*, at the Jasper Ridge Biological Preserve, Stanford University, California are reported here. Annual population estimates were calculated from 35 years of mark-release-recapture data on the univoltine, serpentine-obligate insect. The long-term population trend shows a marked decline to probable extinction for two demographic units within the preserve. Male and female population estimates show congruence, but significant differences exist between the sexes with respect to catchability, mortality, dispersal, date of peak flight, and flight season duration. Related differences were also found between demographic units. These long-term results may generalize to other systems so that exhaustive work in related taxa may be avoided.

Henning, Graham
Lepidopterists' Society of Africa

Lepidopterists' Society of Africa

Founded in 1983, the Lepidopterists' Society of Africa has gained considerable respect through its conservation initiatives. This poster details some of the efforts and achievements of the Society with some indication of the objectives still to be reached. The conservation policies of the society are outlined. The primary policy being that habitat destruction is considered to be the only threat to butterfly populations in Africa. Butterfly conservation is outlined in an historical perspective with two case histories to illustrate the efforts made by Lepidopterists in South Africa. These two histories are the Brenton blue (*Orachrysops niobe*) and the Roodepoort copper (*Aloeides dentatis*). The South African Government has involved itself in butterfly conservation. This is briefly discussed and the role of the Provincial Government Conservation bodies is outlined. The role of the *Red Data Book* in South African butterfly conservation is discussed.

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Small-male advantage in territorial **Heliconius sara***: a paradoxical strategy?*

Heliconius sara males observed defending mating territories in southeast Brazil are unusual in having wings that are on average 3% shorter than those of males caught away from territories. This is both new and unexpected, since large size is often decisive in territorial disputes. Marking studies showed that size differences persist over the entire year, and that for individuals resident for more than 30 days, shorter-winged butterflies return to territories over longer time-spans. Field experiments additionally showed that intruders retreat quicker when encountering smaller residents, suggesting that small size may impart superiority in these territorial confrontations. However, the situation in *H. sara* also seems consistent with a 'paradoxical strategy' (Maynard Smith & Parker 1976, Anim. Behav., 24,159-175), an ESS in which individuals with inferior resource holding power are favored in war-of-attrition contests against superior adversaries when V/K (resource value/rate of cost accrual) is greater for small contestants. It is relevant that *H. sara* has a second, seemingly much more important mating system in which males are chemically attracted to female pupae, and in which large males may be more successful in winning mates. Because it is unlikely that small males are intrinsically superior fighters (or that they receive greater territorial gains), we propose that large *H. sara* males, supposedly favored in pupal mating, may risk losing more in terms of future reproductive success through chance injury in territorial fights (large K) and thus avoid combats with small opponents who, because of their diminished mating prospects (small K), risk little.

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Expanding distributions of speckled wood* Pararge aegeria *butterflies: interacting effects of climate and habitat fragmentation

Potential effects of predicted future climate change on butterfly distributions are unclear, but are likely to involve latitudinal shifts of ranges northwards. We use a 'climate response surface' to model the relationship between present climate and the European distribution of the speckled wood butterfly *Pararge aegeria* (Satyridae). This species has undergone marked changes in its UK distribution over the past 150 years, which are thought to be related to climate. We include several bioclimatic variables into the model, chosen to reflect principal limitations on *P. aegeria* growth and survival (warmest and coldest month mean temperatures, sum of summer sunshine hours, temperature sum above 5°C, and moisture). We test the model using historical distribution data, and also present data showing potential range changes under alternative climate change scenarios. Recent anthropogenic changes in the distribution and availability of habitats, however, may result in butterfly distributions being unable to track changing climates, if new habitats are fragmented and too isolated to be colonized. Following contraction and subsequent re-expansion of *P. aegeria*'s UK range, many previously-occupied areas have not yet been re-colonized, indicating that recent habitat loss may be affecting re-colonization and hence range shifts. We have also incorporated current distribution of habitat (woodland) into the climate model using remotely-sensed data. We discuss recent and predicted future range changes in this species in the UK in relation to climate, dispersal and spatial distribution of habitat.

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Ecological specialization and the abundance and distribution of lycaenid butterflies

Many researchers have documented a positive correlation between local abundance and geographic distribution in groups of closely related organisms. Three main hypotheses have been proposed to account for this widely observed correlation: sampling artifact, metapopulation dynamics, and ecological specialization. The ecological specialization hypothesis consists of two parts. It proposes 1) that species that are able to utilize a wide range of resources and habitats will become locally abundant and 2) that these same species will also be able to tolerate conditions across a larger geographic region and will therefore become more widely distributed. This study examines whether hostplant specialization is a factor in determining the relative abundance and distribution of lycaenid butterflies. In 15 sites, we censused the adults and eggs of nine lycaenid species and the availability of hostplants. For each butterfly species at each site, we tried to determine on how many plant species the butterflies were ovipositing. Finally, we compared the information about hostplant specialization and local abundance to the local, regional, and continental distributions of the butterfly species.

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Sex-linked inheritance of hostplant specialization in a generalist butterfly

I investigated the genetic background of intraspecific variation in oviposition specificity in the generalist butterfly *Polygonia c-album*. Using reciprocal crosses between two populations that differ in degree of specialization, I show that specificity is strongly sex-linked. This indicates that genes determining this difference are primarily located on the paternally inherited X-chromosome. The results suggest that intraspecific differences in specificity are caused by the same genetic mechanisms that have been shown to determine interspecific differences in hostplant ranking in other butterflies. Accordingly, the common assumption that specialization and ranking are determined by fundamentally different mechanisms was not supported.

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The benefit of Müllerian mimicry and the diversity of S. American Heliconius *butterflies*

Natural selection favors bright colors or bold patterns that advertise unpalatability. In a noxious polymorphic species frequency-dependent selection should lead to fixation of the common morph, because rare morphs suffer higher relative attack rates by naive predators. This generally leads to warning coloration that is monomorphic within species and shared between species (Müllerian mimicry). However, several unpalatable species of *Heliconius* butterflies (Lepidoptera: Nymphalidae) exhibit polymorphic warning coloration in a population. One possible explanation is that divergent selection may favor different color-pattern morphs of a single unpalatable species if they match two or more unpalatable Müllerian mimic species (comodels) which possess different warning colours and patterns.

I test for the presence of divergent selection operating on a polymorphic species (*H. cydno*) using a multi-site transplant experiment in western Ecuador. Yellow *H. cydno* survives longer when moved into sites with yellow *H. eleuchia*, and white *H. cydno* survives longer when moved into sites dominated by white *H. sapho*. This pattern of higher survival in the presence of the putative matching comodel provides unique experimental evidence for the benefit of Müllerian mimicry.

I also found the frequency of yellow or white *H. cydno* correlates with the density of their respective comodels at different locales, suggesting that the divergent selection identified by the selection experiment helps maintain polymorphism in *H. cydno*.

My results suggest that between-site divergent selection is generated by Müllerian mimicry. This process may explain the inexplicably high amounts of genetic variation seen in these and other polymorphic Müllerian mimics.

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Reproduction, resource allocation and nuptial gifts in butterflies

Many insects have a mating system where males transfer nutrients to females at mating, referred to as "nuptial gifts". Butterflies with nuptial gifts are polyandrous (females mate several times) and have large male spermatophores. Females of the polyandrous butterfly *Pieris napi* use male-transferred nutrients to increase their pool of nutrients used for egg production and show a positive relationship between amount of ejaculate material received and lifetime reproductive output. A budget calculation reveals that nitrogen derived from male nuptial gifts is essential for maximum egg production. Furthermore, multiply-mated females use more of their resources from the thorax than single-mated females. Consequently, multiply-mated females have a relatively higher reproductive investment than singly-mated females, i.e., they transform a larger part of their body reserves to egg production. Thus, the value of the nuptial gift is determined on the function within the female rather on the nutritional value of the gift itself.

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Hormonal control of life history and morphological traits in the butterfly **Bicyclus anynana**

The African satyrid butterfly *Bicyclus anynana* occurs in two different seasonal forms: the wet-season form with large ventral eyespots and a conspicuous transverse band, and the dry-season form with small eyespots and no band. This plasticity can be induced in the laboratory by the respective use of constant high (24°C) or low (20°C) temperatures during larval growth and early pupal development. Temperature also influences development-time and the size of pupae and adults. Truncation selection on ventral eyespots at 20°C resulted in two different selection lines: a ventral LOW-line (vLOW), expressing the dry-season form across all rearing temperatures and a ventral HIGH-line (vHIGH), which always produces the wet-season form.

We showed that the hormones controlling seasonal morph formation are ecdysteroids. We measured ecdysteroid-production at low and high rearing temperature during the early pupal stages in the stock population of *Bicyclus anynana*, in the selection lines vHIGH and vLOW and in two lines, which were selected for fast or slow development. In the same lines we also measured life-history traits including growth rate and fat content. The results show that the ecdysteroid hormone system is involved both in the control of plasticity and the regulation of development time. While the dry season form has a much higher fat content than the alternative form, correlated responses are weak or not observed in this trait when selection occurs on wing pattern or development time. We propose that the physiology of fat-production may be under control of another hormone-system.

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Dispersal and gene flow in the alpine butterfly **Parnassius smintheus***: an analysis using microsatellite DNA markers*

For species occupying fragmented habitats, rates of dispersal and concomitant gene flow among local populations have important implications for both ecological and evolutionary dynamics. Dispersal may in turn be affected by landscape structure (size and isolation of habitat patches and the nature of intervening matrix) that is subject to alteration by human activity. In montane areas for example, fire prevention and global warming may be leading to a rise in tree line and altering the alpine landscape. The butterfly *Parnassius smintheus* is, for the most part, restricted to alpine meadows. We are investigating the effects of landscape structure on gene flow and dispersal in *P. smintheus*. This is done at two spatial scales. Seventeen populations are studied at a small scale (less than 12km separating most distant populations) where an extensive mark-recapture study has also been conducted, providing direct estimates of dispersal, and fourteen populations are studied at a large spatial scale (approx. 140km separating most distant populations). We characterized four microsatellite DNA markers to assess the degree of genetic differentiation among local populations of *P. smintheus*. We assess the ability of these highly variable genetic markers to resolve population genetic structure at both spatial scales. We determine the effects of landscape structure on the spatial distribution of genetic variation. At the fine scale, we also examine the relationship between the degree of genetic differentiation and observed dispersal among populations.

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Experimental analyses of wing and body size, flight, and survival in temperate pierid butterflies

Comparative analyses have identified a suite of wing and body traits associated with the evolution of palatability and unpalatability in tropical butterflies. We have used experimental manipulations of wing and body size and shape to determine how such traits affect flight and survival within populations of temperate butterflies. We used mark-release-recapture (MRR) experiments to study two pierids, *Pontia occidentalis* and *Colias philodice/eurytheme*, that co-occur at study sites in south-central Washington state (USA): our studies show that *P.*

occidentalis has lower flight speeds and lower palatability to bird predators than *C. philodice/eurytheme*. Experimental reductions of wing area with *P. occidentalis* increased the probabilities of recapture (suggesting decreased evasive flight ability) in one MRR study, and reduced probabilities of survival in a second study. Experimental increases of body mass with *P. occidentalis* increased recapture probabilities and decreased survival probabilities in one MRR study, but not in a second study. Similarly, experimental increases of body mass with *C. philodice/eurytheme* had no significant effects on either recapture or survival probabilities. Experimental rodeos indicate that neither reducing wing area nor increasing body mass significantly affected the rate of recapture by human 'predators' for either *P. occidentalis* or *C. philodice/eurytheme.* These results suggest that differences in wing area or body mass do not consistently generate differences in evasive flight or survival in palatable or unpalatable butterflies in this system, contrary to the predictions of previous comparative analyses.

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Conservation and utilization of wild silkmoths in East Africa

The species diversity of indigenous silkmoths and their habitats in Africa are declining due to the rapid human population growth that has led to increased demand for agricultural land and fuel wood. To save this situation, there is need to provide some economic incentives to the communities to instill some voluntary positive change for conservation of these species. This study was designed to investigate the existing diversity of wild silkmoth species in Kenya, Uganda and Tanzania and the possibility of establishing wild silk production for income generation. Wild silk production is an eco-friendly, agro-based venture with a great potential for environmental amelioration and income generation. A survey was done and a number of silk spinning genera were listed in the families Saturniidae, Lasiocampidae and Thaumetopoeidae. Further studies in farmers' fields on population dynamics of selected species, *Argema mimosae* Boisduval (Saturniidae) and *Gonometa* sp. (Lasiocampidae) revealed that these species had two generations in a year. Different predators and parasitoids attacking the silkmoths were identified. A questionnaire response and information obtained from farmers at various sites indicated the communities' willingness to participate in wild silkmoth farming. These findings and implications of this study towards conservation and sustainable utilization of wild silkmoths are illustrated.

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Paralucia spinifera*- an endangered lycaenid from New South Wales; biology, conservation and controversy*

Paralucia spinifera, the Bathurst copper, is a myrmecophilous lycaenid of very restricted distribution in southern New South Wales, Australia. Its historical range is unknown, but is now inhabits half a dozen sheltered, woodland edge sites where its foodplant, *Bursaria spinosa* co-occurs with the ant, *Anonychomyrma itinerans* group. Like other species of *Paralucia*, it is a nocturnal feeder and groups of larvae return to ant byres at the base of the food plants during the day. It egress from and ingress to the ant byre is in the company of ants but the exact nature of the mutualism is not clear. As in other myrmecophiles, the larvae have well-developed Newcomer's and tentacular organs, and are well-supplied with pore cupolae. The adults fly in late winter and again in February each year.

Colonies comprising a few hundred adults are commonly found in sheltered gullies where fire frequency is such that their food plant is at half growth and where herbaceous nectar sources are abundant. The few scattered colonies are hedged in by exotic conifer plantations, threatened with overgrowth by blackberry, their food plants are variously grazed by stock and rabbits, and urban sprawl interferes with natural fire and regeneration patterns.

Designated an endangered species about four years ago, some of the species localities are listed on the National Estate, one is a designated nature reserve. Protection of the butterfly as a named endangered species has lead to vigorous debate in the entomological community about the 'threat' of over-collection, the alienation of amateur effort in documenting the relatively poorly known Australian fauna, and the appropriateness of IUCN categories for uncritical application to invertebrate species.

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Butterfly wing pattern formation: dopa decarboxylase expression in wild type and melanic tiger swallowtail butterflies

The phenotypes displayed in cryptic coloration and mimicry form the direct interface between the complex developmental pathways underlying colour pattern formation and natural selection. We are therefore interested in understanding the developmental regulation of colour pattern formation in butterflies, and in elucidating how such a complex trait can be controlled by a single major locus in melanic mimics. Here we use the Eastern Tiger Swallowtail *Papilio glaucus* as a model of Batesian mimicry. In this species, females are either wild type (yellow and black) or melanic (where most of the yellow color is replaced by black). Our experimental approach combines the analysis of the temporal order of wing pigment synthesis, precursor incorporation studies, enzyme assays, and in situ hybridisation to mRNA encoding a key synthetic enzyme, dopa decarboxylase. We show that dopa decarboxylase provides dopamine to both of the two major colour pigments, papiliochrome (yellow) and melanin (black). Interestingly, however, dopa decarboxylase activity is tightly spatially and temporally regulated, being utilized early in presumptive yellow tissues and later in black. Further, in melanic females, both dopa decarboxylase activity and early papiliochrome synthesis are suppressed in the central forewing and this formerly yellow area is later replaced by atypical melanisation. These results show that the differential enzyme regulation observed in the yellow/black pattern of a single wing, is similar to that involved in melanism. We infer that dopa decarboxylase activity must be regulated in concert with downstream enzymes of either the melanin and/or the papiliochrome specific pathways, forming part of a complex developmental switch between yellow or black. This modification of multiple enzyme activities in concert is consistent with a model of melanisation involving coordinate regulation of the underlying synthetic pathways by a single Y-linked (female) factor.

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Butterfly distributions and conservation planning in Madagascar

We describe biogeographic patterns in butterfly distributions at two spatial scales in Madagascar (the rain forest biome and the Masoala peninsular landmass), and show how this information could or has been applied in the selection and design of protected areas.
The mycalesine satyrine butterflies, representing ca. 21% of Madagascar's butterflies, underwent a spectacular radiation in the rain forest biome, which is distributed in a narrow band stretching nearly the length of the island (ca 12° latitude). Species richness in mycalesine butterflies showed a parabolic distribution against latitude with a peak at mid-latitude. The best explanation of this pattern is a null model of the distribution of species ranges within a bounded biome. This species richness pattern is also demonstrated by a collection of approximately 700 other endemic rainforest-restricted species of other Lepidoptera, beetles, birds, herptiles and mammals. Many species can therefore be included in reserve networks by protecting forests in the mid-latitudinal region. However, at least in the mycalesines, it is the narrow-ranged species that deviate most from the null pattern and require additional reserves for their protection. Since we do not know the degree to which local endemism may co-vary between taxonomic groups, it is prudent to select a suite of ß-diverse indicator taxa for gap analyses.
On the 4,000 km^2 Masoala Peninsula, the butterfly community demonstrated substantial turnover along known or suspected environmental gradients, and the presence of rare butterfly species was concordant with the presence of threatened or endangered birds and primates. We describe how this information was used in conjunction with other biological and socio-economic data to prioritize regions for protection and to justify the design of Madagascar's largest protected area.

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Do montane taxa tend to occur at more temperate latitudes than lowland taxa? Evidence from the largest radiation of butterflies in Madagascar

Evolutionary radiation into habitats at higher elevation inevitably involves adaptations to montane climate. It might be expected that these adaptations would allow and favor range shifts to more temperate latitudes for elevationally restricted species facilitated during cycles of global cooling. For a large adaptive radiation, distributional patterns along the latitudinal gradient should reflect past asymmetric range expansions. Madagascar seems an ideal place to test this idea, because it is an island that still has a long chain of montane rainforest aligned with a monotonic latitudinal climatic gradient. A species-rich radiation of satyrine butterflies in Madagascar for which a fully resolved phylogeny and range maps have been generated, and which contains derived montane clades, provides an opportunity to test this prediction.

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Why did **Hamearis lucina** *(Riodinidae) become extinct in North Wales, and could it be restored?*

We mapped the remnant hostplant (*Primula veris*) network of an extinct butterfly (*Hamearis lucina*) in North Wales. Logistic regression was used to identify that large *P. veris* plants were usually preferred for oviposition in surviving *H. lucina* populations in northern Britain. These regressions were then used to predict the potential carrying capacity of the remnant habitat network in North Wales leading to an estimate of roughly 4500 eggs, a population size that is potentially susceptible to stochastic extinction. We developed a spatially explicit grid based simulation model to mimic possible local extinction and colonization dynamics of the butterfly in the North Wales network. The model showed where the butterfly has the greatest capacity to persist within the network, but the scope for restoration may be limited. The work illustrates a practical approach to assess species reintroduction programs.

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Effects of selective logging on butterfly communities in Belize

Replicated experimental plots were set up in Belize's Chiqibul Forest Reserve in 1994 as part of a 40-year investigation into the effects of low-intensity timber extraction on tree mortality, growth rates and species composition. The plots also provide an opportunity to investigate parallel effects of selective logging on butterfly communities, and will allow long-term changes in the butterfly fauna to be monitored. I sampled butterflies using fruit-baited traps and transect counts in two pairs of experimental (logged in 1994) and control (unlogged) plots. I compared the two treatments using species richness statistics and species accumulation curves. The results have implications for the conservation management of forests in Belize, and for the design and analysis of similar investigations elsewhere in the tropics.

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Hybrid zones of **Heliconius** *butterflies as refugia of novel patterns against stabilizing mimetic selection*

Strong selection against a diversity of recombinant, non-mimetic phenotypes is thought to be the main population genetic process in hybrid zones between distinct mimetic races of *Heliconius*. Our studies suggest, to the contrary, that in the center of such contact zones selection on wing pattern is diminished. Two consequences of such selection-relaxed zones include 1) the maintenance of high variance in wing pattern and thus opportunity for rapid evolution of new mimetic associations, and 2) increased introgression between races, accounting for the relative lack of differentiation in non-wing pattern traits. We analyze a four-way hybrid zone in *Heliconius* involving three races of *H. cydno* and one of *H. melpomene*, in the Dagua region, Andes of Colombia. Evidence from wild-caught females and genetic crosses indicate that 6 major mendelian genes (15 alleles) control most of the wing pattern variation found within the hybrid zone and show that wild-caught individuals (within the contact zone) are hybrids between the three *H. cydno* races or between these and *H. melpomene*. We present evidence 1) that *H. cydno* and *H. melpomene* hybridize in nature, and 2) that introgression between these species plays an important role in the generation of naturally occurring wing pattern variation. A genetic model of the system shows that 216 true breeding novel patterns can be expected to appear in the Dagua hybridization zone. One such pattern is virtually indistinguishable from that of *H. heurippa*, a species described from the foothills of the Colombian Llanos. It is proposed that *H. heurippa* originated in a hybrid zone involving *H. melpomene* - *H. cydno*.

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Ontogenetic changes in leaf shelter construction by larvae of the Silver-spotted Skipper

Larvae of the silver-spotted skipper, *Epargyreus clarus* (Hesperiidae), construct intricate shelters from leaves of their leguminous hostplants. We investigated the pattern and process of this behavior through observation, videography, and experimental manipulation. Each larva builds and inhabits its own shelter, successively abandoning shelters and constructing new ones approximately 5 times across 5 instars. On kudzu (*Pueraria lobata*; Fabaceae), larvae produce shelters in 4 distinct styles that change predictably as the insects grow. The shape and size of structures produced by first instar larvae are almost invariant, while those produced by older larvae are quite variable. Young caterpillars, which commence shelter construction immediately upon emerging from their eggs, make precisely spaced cuts in leaf tissue and lay down 'hinges' and 'guywires' of silk to construct a peaked triangular structure; older larvae silk together 2 leaves or leaflets to form a domed pocket. Larval body size is directly related to shelter size. Deposition of silk in predictable locations on the leaf surface determines the location of the leaf cuts; removal of silk in key areas prevents shelter construction.

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Extraordinarily high rate of chromosomal mutations and speciation in some genera of the Palearctic butterflies (Lepidoptera, Papilionoidea)

In most cases, the chromosome number and the karyotype structure are stable species features. However, both intrapopulation and intraindividual chromosome number variability in spermatocytes I and II was found in our investigations of several species from genera *Agrodiaetus, Anthocharis, Aporia, Colias, Gonepteryx* and *Pieris*. In many cases, the causes of this variability are the chromosomal mutations (fragmentation and fusion of chromosomes). These mutations occur during spermatogenesis and affect not all, but only some of the sexual cells of the individual.

An extraordinarily high rate of these spontaneous chromosomal mutations was found in some species of *Agrodiaetus*. According to data obtained together with N. Kandul (St. Petersburg University), the frequency of the mutant spermatocytes in *Agrodiaetus damocles krymaeus* may be as high as 9%, that is some 2-3 orders of magnitude higher than a normally chromosomal mutations rate in other animals. This frequency can be compared only with one of rearrangements induced by transposable elements.

Thus, there is a permanent mutation pressure leading to the appearance of gametes with new chromosome rearrangements in the populations. Nevertheless no individuals were found in which all of gametes had the same new rearrangement(s). Presumably these chromosomal mutations have a negative heterotic effect and their transmission to the offspring have low probability.

The phenomenon discovered can be used for the explanation of the unusually high rate of changes of chromosome numbers in phylogenesis within some groups of butterflies. The strong mutation pressure may be one of the main factors of the chromosome speciation in *Agrodiaetus*.

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Variation of the wing color pattern in* Heliconius erato phyllis *(Nymphalidae) from southern Brazilian populations: a balance between natural and sexual selection

Heliconius erato phyllis is a subspecies with a wide geographical distribution in Brazil, extending from Northeast to Southeastern; it occurs also in Northern Argentina and in Uruguay. Its wing color pattern is mainly composed of a black background with a red forewing band and a hindwing yellow bar. Measurements were made in the dorsal and ventral wing pattern comprising more than 100 variables, including area, linear and ratio variables from which 19 were used in the statistical analysis. Eight localities in the State of Rio Grande do Sul (the southernmost state in Brazil) were sampled; the offspring of two crosses were also included for comparison. The means of the main components of color pattern were found to be different between localities, whereas the ratio variables and thus the butterfly overall appearance were not significantly different. Some dorsal components were found to be less variable than the respective ventral ones, and the red wing area was less variable than the yellow area in the same wing surface, in all populations sampled. Further, the dorsal red signaling is larger than the ventral one; the yellow signaling however, is the same in both sides. Males were narrower than females, presented a greater dorsal yellow signaling and a greater distance between dorsal red band and yellow bar. The general picture that emerged from this investigation is compatible with a balance between natural selection maintaining monomorphism in the aposematic color pattern and sexual selection. This last one could involve intramale competition for mating through pattern signaling and thermoregulation.

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Molecular phylogeny of the European Satyrids (Lepidoptera : Nymphalidae)

Within the diurnal Butterflies, the subfamily Satyrinae is considered to be an homogeneous group with a diversification correlated with adaptation to Poaceae as the foodplant. This study, using two different mitochondrial genes, the NADH dehydrogenase subunit 1 (ND1) and the large ribosomal subunit (16s), leads to a better understanding of the phylogenetic relationships within the subfamily, especially for the European taxa. From an analysis point of view, the focus is particularly on the impact of nucleotide composition bias on the loss in phylogenetic signal. We used the absolute saturation test of Bremer, decay index, and constraint analysis for assessing the impact of species and sites on topology. The irresolution of the basal nodes is not due to a lack of informative sites (the total evidence approach yield an identical topology), but to a radiation. This analysis is confirmed by the congruence of phenetic (neighbor joining) and cladistic (maximum parsimony criterion) approaches (for the two genes). Furthermore, the branching pattern between species belonging to same genus seems to be reliable, supported by strong bootstrap values, showing a sufficient number of synapomorphies to solve phylogenetic relationships. Adaptative radiations took place in Mediterranean and arid regions, but also in mountain zones. Even if fossils dating from the Rupelian (Oligocene, 35-30 Mya) are known in south of France, the proliferation of species in several genera suggests a current expansion of the group.

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Life history studies of two races of **Heliconius erato** *which differ in body size*

Differences in body size between two races of *H. erato* were investigated by monitoring several aspects of life history including growth trajectories (size vs. larval developmental time), pupal and adult weight and growth rates of larvae fed a variety of natural and novel hostplants. The results suggest that nutritional effects do not affect body size differences between races, leading to the conclusion that such differences are genetic. In both races there seemed to be genetically based variation in growth rate. But *H. e. petiverana* proved to have a more plastic growth rate due to a variation in its average larval developmental time on the different hostplants. More canalized growth rate in *H. e. phyllis* across hostplants may reflect a broader host breadth in its natural populations, and a correlated capacity to handle broader ranges of plant chemical defenses. On the other hand, in *H. e petiverana* there were significant differences in growth rate between sexes. Male exhibit a higher growth rate than females when feeding on *P. talamancencis*, their natural hostplant.

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Molecular phylogenetics of the speciose oriental butterfly genus **Arhopala**

The genus *Arhopala* (Lycaenidae: Theclinae) is among the most speciose genera of butterflies; over 200 species are currently recognized. Its highest diversity occurs throughout the wet and seasonal tropics of South East Asia. Explaining the evolution of the genus and making an assessment of its diversity will enhance our understanding of both existence and degradation of tropical diversity. In our study we are reconstructing the phylogeny of part of *Arhopala*. We do this in order to make a historical framework that allows us to compare biogeographical and ecological features that may have played a key role in the diversification of the genus. A comparison is made of parts of different DNA sequences (cytochrome oxidase 1, small and large subunits of mitochondrial ribosomes, Internal Transcribed Spacer of the nuclear ribosomal genes). This is done for a number of species of *Arhopala* representing some of the major (basal) groups as well as recently evolved groups. We try to assess the suitability of each of these DNA sequences for uncovering the historical relationships within *Arhopala*.

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The genetic structure of **Parnassius mnemosyne** *populations in Northeast Hungary*

Population structure of *Parnassius mnemosyne* was investigated by mark-release-recapture studies and allozyme polymorphism in Northeast Hungary. Large differences were observed in the estimated sizes between different populations. The results of the genetic data suggest that even large populations may have small effective population sizes, due to biased sex ratio, recent bottlenecks and founder effect. The results of both the genetic and MRR studies indicated that the Bükk populations have a metapopulation structure. At the same time, populations from different geographical regions were highly differentiated indicating a restricted gene flow among them. Loss of genetic variability was observed in a small, isolated population.

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Viewing diversity through the eyes of phylogeny: case studies of the Australian genera **Jalmenus** *and* **Ogyris** *(Lycaenidae: Lycaeninae)*

Certain members of the family Lycaenidae participate in highly specific associations involving larvae, their hostplants, and attendant ants. Myrmecophilous lycaenids are subject to at least two major selective forces: a) constraint by the range and nutritional value of their hostplants; and b) freedom from parasites and predators via their ant guard. The Australian genera *Jalmenus* and *Ogyris* constitute excellent model systems within which to explore myrmecophily, because each displays remarkable diversity in their larva-plant-ant associations. Genealogical relatedness was inferred based upon molecular characters, both among species within each genus, and among genera within the tribe Theclini to which they both belong. Molecular sequence was gathered from the mitochondrial genes Cytochrome Oxidase I and II, and the nuclear gene Elongation Factor 1-alpha. Phylogenetic analyses indicated that (i) *Jalmenus* and *Ogyris* each constitute monophyletic groups within the tribe Theclini; (ii) different genes provide significantly different levels of resolution within and between these genera; (iii) patterns of

relatedness within both genera reflect patterns of observed biogeographic distribution and ant association.

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Evolution of wing pattern elements in the African genus **Bicyclus** *(Satyridae)*

Bicyclus anynana, an African satirid, has been used extensively as a model system to study the genetic and developmental architecture of wing pattern elements in butterflies such as eyespots and bands. Genetic or developmental constraints acting on serial homologous pattern elements in this species have been found by artificially selecting traits in one eyespot and looking at the responses to selection in the other eyespots. Now taking a broader view across representatives of the whole genus and making use of a preliminary molecular phylogeny, I will discuss the evolution of wing pattern elements and the evolution of constraints in this genus.

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Phylogenetic relationships of Ithomiinae (Lepidoptera, Nymphalidae) based on first instar larvae

The chaetotaxy (the study of setal distribution of the body) of the first instar larvae of 35 Ithomiinae and 3 Danainae species (143 individuals), based on examination of the head capsule, labrum, mandible and body was used to delineate 99 taxonomic characters. There are 17 pairs of long setae on the head of most Ithomiinae larvae, 5 of microsetae and 16 punctures, and 97 pairs of long setae on the body. PAUP and Hennig programs were used for the evaluation of the phylogenetic relationships. Some characters, mainly the cervical sclerite of the prothorax, were important in the discussion on the phylogenetic position of *Tellervo* (the only non-Neotropical Ithomiinae genus). Many characters, related to the head capsule, were not very consistent; others presented variation in the population or had anomalous states in some individuals (without symmetry, for example). The six large monophyletic groups identified here do not correspond to generally accepted tribes. Possibly the use of chaetotaxonomic characters are more useful for comparison among subfamilies (or superior categories) than for more recent radiation (generic) groups.

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Geographic variation of the life stages of **Methona** *(Nymphalidae, Ithomiinae) in central Brazil*

Geographic (phenotypic) variation of the larvae, pupae and adults was studied in *Methona* populations in central Brazil and the differences compared with other known Brazilian populations. *Methona* spp. are widely distributed on the Neotropics and they are among the most common butterflies on urban environments of much of Brazil. The larvae are monophagous on the leaves of *Brunfelsia* (Solanaceae); a common ornamental. Caterpillars were sought on 629 plants in 82 localities in central Brasil. A total of 614 larvae were collected, described and their geographic distributions were mapped. Substantial phenotypic and geographical variations were recorded and compared with other populations (southern, southeastern, northern and northeastern Brazil). The phenotypic pattern of the larvae of the town of Uberlândia suggest that is a hybridization zone between populations of the Central Brazilian Plateau and southeastern Brazil. The color pattern of the larvae and the pupae of many of the populations investigated leads one to question the phylogenetic and taxonomic relationships generally accepted in this genus.

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The phylogeny of the tribe Nymphalini. A total evidence approach

The Nymphalidae is one of the largest and most extensively studied butterfly families in the world. The phylogenetic relationships among tribes and genera are, however, poorly investigated. A phylogenetic hypothesis for the tribe Nymphalinii (sensu Harvey) is presented, based on morphology and mtDNA sequences for the protein-coding gene ND1.

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Foraging in **Heliconius** *butterflies: when does it pay to learn?*

Field observations indicate that *Heliconius* butterflies learn the spatial distribution of the resource locations in their home-range and repeatedly visit these sites on a predictable schedule. It has also been suggested that these insects possess a circadian memory with regard to floral resource availability. We performed a series of preliminary greenhouse experiments with *Heliconius* foraging on patches of artificial flowers to address questions related to movement patterns and learning. The results showed several instances of non-random foraging, suggesting efficient use of floral nectar and pollen under natural conditions. The main results can be summarized as (i) butterflies exhibit a variety of hard-wired rules for foraging within and between small-scale arrays of experimental flowers; (ii) these fixed behaviors tend to prevail over location learning in such small-scale settings; (iii) butterfly foraging efficiency increases with experience; (iv) butterflies learn colors relatively fast but fail to associate color with time of day. We discuss these results in the contexts of optimal foraging models and evolutionary ecology of these butterflies.

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Do Neotropical migrant butterflies navigate by a solar compass?

Many tropical butterfly species are well-known for their migratory behavior. Although these insects can maintain a constant direction throughout the day, physiological mechanisms of orientation are unknown. It has been argued that tropical migrant butterflies must use a time-compensated sun compass to accomplish their journey, but the crucial experimental manipulations to test this hypothesis had not been conducted. This study reports the results of clock-shift experiments performed with two species of migrating butterflies (Pieridae: *Aphrissa statira* and *Phoebis argante*) captured during flight across Lake Gatun, Panama. The observed constant flight bearing of natural controls suggests that these species are capable of performing time-compensated celestial navigation. Our clock-shift experiments suggest that a sun compass is involved. Individuals submitted to a 4-h advance shift took significantly different mean orientations on release compared to control butterflies. The direction of this difference was consistent with use of a sun compass. The magnitude was approximately half the predicted value if the vanishing bearing of released butterflies is used as the parameter to evaluate the effect of time-shifting, and approximately three-quarters of that predicted if estimated heading is the parameter used. Mean vanishing bearings of controls and experimentals did not correspond to predicted values. This difference can be largely attributed to the combined effects of wind and handling.

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Distributional and climatic changes in Europe and Central America over this century

We present time-referenced distributional data on multiple species of butterflies. Analyses showed general northward and upward movement of species' ranges of a magnitude consistent with the documented warming trends in Europe and the Americas during this century. Some species were stable. We discuss the value of comparisons between stable and moving species in fine-tuning predicted impacts of global warming on wild biota.

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Phylogeny of the tribe Lemoniini based on adult morphology (Lepidoptera, Riodinidae): a preliminary assessment

Field and laboratory studies on members of the riodinid tribe Lemoniini have provided major insights into understanding myrmecophily in riodinid and lycaenid butterflies. Despite their role as model organisms in ecological and evolutionary studies, the tribe Lemoniini has never been the subject of a modern phylogenetic analysis. To construct a phylogeny for the Lemoniini we studied 23 species from all 11 currently valid genera placed in the tribe. To test the monophyly of this tribe we studied 8 species from 5 genera in the putative sister tribe Nymphidiini, and one outgroup species from the tribe Stalachtini. Using cladistic methods we analyzed 102 adult morphological characters (the largest number ever assembled for a major group of riodinids) and re-evaluated many characters used traditionally in riodinid systematics. Four patterns emerged from our study: (1) the Lemoniini does not constitute a monophyletic group; (2) the genera *Thisbe, Lemonias* and *Audre* do not form monophyletic groups; (3) the high degree of homoplasy in our analysis indicates that adult characters are too plastic to infer higher level relationships within the tribes Lemoniini and Nymphidiini; (4) as currently understood the relationships among genera in the Lemoniini and Nymphidiini require reassessment. Our study suggests that a better understanding of riodinid phylogeny will come from future work that incorporates additional characters that supplement those derived from adult morphology (e.g., morphology of early stages, DNA sequence).

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*Monarch butterfly (*Danaus plexippus*) migratory orientation differs by continental region but does not compensate for displacement*

Monarch butterflies converge on their overwintering sites in central Mexico from widely disparate breeding grounds covering most of eastern North America. During the fall migration, butterflies are often blown off course within this broad range. It has been commonly believed that butterflies are able to compensate for these displacements with a continent-wide map sense. The monarchs' proposed map sense was tested by mimicking the within-population displacements commonly seen in the fall and observing the butterflies' subsequent flight orientation at the new release sites. Both body orientation in flight and vanishing bearing were measured upon release. Butterflies collected in different parts of the eastern United States behaved differently, but displaced butterflies continued to behave as appropriate for where they were collected rather than changing to a new orientation more appropriate for the new release site. This is the first study to demonstrate experimentally that monarch butterfly behavior differs by region and that the butterflies do not immediately compensate for displacements.

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Carnivorous and other aphytophagous Lepidoptera

The approximately 200 parasitic or predaceous species in the Lepidoptera are widely distributed throughout the order, implying multiple convergent origins of aphytophagy. The number of independent shifts suggests that transitions from herbivorous to carnivorous feeding habits can occur relatively easily, but that these origins rarely lead to adaptive radiations of species with parasitic and predatory lifestyles. A notable exception to this pattern is the butterfly subfamily Miletinae in the Lycaenidae. With an estimated 120 species in four tribes, all of whose larvae are thought to be carnivorous, the subfamily Miletinae is the most well-developed clade of carnivorous Lepidoptera. Phylogenetic and ecological analysis of the miletines and related taxa will help to resolve why this group has succeeded where others have failed.

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To eat or not to eat: an investigation of the putative mimetic relationship between the California Sister and Lorquin's Admiral utilizing Scrub Jays as model predators

In nature, unpalatable animals are often boldly and distinctly colored in patterns that are easily recognizable by predators. The expectation is that once a predator has been convinced of the unappetizing flavor of the prey, it will avoid consuming any organism that exhibits those particular coloration patterns. Under these circumstances, it is believed that Batesian mimetic relationships develop between an unpalatable species and a palatable one. This project investigated a putative mimetic relationship between two butterflies, *Limenitis lorquini* and *Adelpha bredowii* (Lepidoptera: Nymphalidae) by analyzing the feeding responses of a model potential predator Aphelocoma coerulescens (Passeriformes: Corvidae) to these insects. The data collected indicates a statistical difference in the incidence of bill-wiping and handling time between the two species. This supports a difference in palatability suggesting a Batesian mimicry relationship between *Limenitis lorquini* and *Adelpha bredowii*.

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The importance of floral scent and visual cues in hawkmoth foraging

Nectar-feeding hawkmoths constitute an important class of pollinators worldwide, especially for night-blooming plants with pale, tubular flowers, sucrose-rich nectars and strong, sweet fragrances. A survey of 13 hawkmoth-pollinated plants from Arizona's Sonoran Desert revealed that floral reflectance spectra were strongly convergent, while the complexity, chemical constitution and relative emission rates of fragrance varied markedly, with no ubiquitous compounds or classes thereof. In wind tunnel assays, naive *Manduca sexta* moths flew upwind in response to diverse scent blends (but never to single compounds) in the absence of visual cues, but did not attempt to feed. In greenhouse assays, naive *M. sexta* were visually attracted to arrays of artificial flowers, but would not feed unless floral scent was present, and fed more avidly if individual flowers were scented. Finally, we modified *Datura wrightii* plants such that only three options were available to wild foraging hawkmoths; (1) flowers bagged with dark cheesecloth (scent only), (2) artificial flowers with a nectar reward (visual only), and a combination of (1) and (2). Moths approached the bagged flowers without attempting to feed, visited the artificial, scentless flowers in small numbers, and fed more avidly at the artificial flowers associated with floral scent. These results suggest that scent attracts moths from a distance, that different odorant classes are functionally redundant, that scent and visual cues are required to elicit feeding, and that once feeding has begun, scent is not required on an individual flower basis. Future experiments will address the potential for scent-based associative learning in hawkmoths.

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Climate change and the northward expansion of a skipper butterfly--detecting connections

The geographical distributions of many species are widely expected to change as the predominant biological response to global warming. The Pacific Northwest has warmed 2-3 C over the past 50 yrs, which may be sufficient to affect the distributions of vagile and temperature sensitive organisms. *Atalopedes campestris*, the Sachem skipper, has expanded ~500 miles northward over the past 35 yrs. In this study I explore the hypothesis that the northern range edge is limited by climate factors, and therefore this may be a model system in which to study ecological effects of global warming. To test whether this species is close to its lower thermal limit along its northern range edge, I measured survivorship and freezing of winter-acclimated larvae exposed to 4 & 24 hr cold periods. Survival dropped off sharply and freezing was detected below –10 C. Transplant experiments monitored overwinter survival and microclimatic conditions both within and beyond the current range. I detected very low survivorship at all sites, which is consistent with an expectation of little cold tolerance in this species.

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Patterns of nuclear and mitochondrial gene evolution in the swallowtail butterfly genus Papilio

Although much attention has been given to combining morphological and molecular data, it is now apparent that attention must also be given to combining different types of molecular data. We gathered sequence data from twenty-three species of the swallowtail butterfly genus *Papilio*, as well as two outgroup species from the genera *Eurytides* and *Pachliopta*. Sequence data consisted of 1010bp of the nuclear protein-coding gene elongation factor-1 alpha (EF-1a) as well as the entire sequences (a total of 2211bp) of the mitochondrial protein-coding genes cytochrome oxidase I and II (COI and COII). We used a differential weighting method to locate sources of phylogenetic error in a combined parsimony analysis. We also implemented a multi-partition maximum likelihood analysis that allowed insight into the evolutionary patterns of various subsets of the data. We found that COI and COII have substitution rates much higher than EF-1a and that to effectively combine all of these genes in a simultaneous parsimony analysis it is necessary to downweight COI and COII in order to minimize the effects of random error caused by homoplasy. Ultimately we generated a very well supported hypothesis of relationships between the major lineages of *Papilio*.

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Countryside biogeography of moths in a fragmented landscape: species diversity in the agricultural matrix

Human-dominated landscapes are often characterized by fragments of remaining habitat embedded in a complex matrix of agricultural and other human land uses. Island biogeography and metapopulation theories have dominated the study of such landscapes, setting up a binary model of “habitat” and “non-habitat” and focusing almost exclusively on the former. In most terrestrial systems, however, the area between patches of original habitat is not water or some other wasteland, but a variety of land uses that may have widely differing, and considerable, abilities to support the original native faunas. We term this model Countryside Biogeography. In this paper, we report on the results of moth surveys both within a large remnant of original forest and in a variety of local agriculture land uses in a recently fragmented area of southern Costa Rica. We light-trapped moths in coffee, shade coffee, cattle pasture, and finely mixed agricultural plots, both near (<1km) and far (>4km) from the large forest remnant.

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*Mayhem in the monarch’s court: Viceroy (*Limenitis archippus*) mimicry revisited*

In its most familiar manifestation, defensive mimicry involves an otherwise defenseless prey species (the mimic) that gains protection from predators through its resemblance to a protected prey species (the model). The Viceroy butterfly (*Limenitis archippus*) is well known as a striking and purportedly defenseless mimic of two chemically defended and aposematic models, the Monarch (*Danaus plexippus*) and the Queen (*Danaus gilippus*). However, a decade’s worth of laboratory and field studies have revealed unanticipated dimensions of complexity in the viceroy’s mimicry relationships. Here, I assess spatiotemporal variation in the “aversive conditioning potential” of viceroys, monarchs, and queens (i.e., each butterfly’s ability to serve as a model, educating predators to avoid it and its look-alikes). Seasonal and geographical patterns of relative abundance and palatability are quantified, and those data are used to calculate an aversive conditioning index for each species in several southeastern U.S. locales. Results reveal that viceroys, queens, and to a lesser extent monarchs all switch between being “models” (strong aversive conditioners) and “mimics” (weak aversive conditioners), depending upon ecological context. Consequently, viceroy-queen and viceroy-monarch relationships in different areas comprise a spatial mosaic of local model-mimic relationships differing in character and symmetry. This has important implications for understanding the dynamic selective forces involved in this and other predator-prey relationships.

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To conserve or not to conserve forest fragments: case study using butterflies at the Kenya coast

Throughout the tropics, deforestation is destroying the forest resource base, leaving only forest fragments. A case in point is the eastern coastal forest of African, which once stretched from northern Natal to southern Somalia. In Kenya, only a few large tracks of this forest remain, such as the Arabuko-Sokoke (40,000 hectares) and Shimba Hills (14,000 hectares) forests. More common are the very small fragments like the Muhaka (180 hectares) and Mrima (350 hectares) forests. The species richness of butterflies was surveyed in the two forest fragments of Muhaka and Mrima in order to provide a preliminary assessment of the effectiveness of remnant tropical forest fragments to support biodiversity. Butterflies from each forest were collected from three sites: the forest interior, the edge and the support zone, consisting of agricultural areas surrounding the forests. Both Muhaka and Mrima forests was characterized by a fairly even density of butterflies in all zones. The interior of the forest had the most number of butterflies, but 60% of these were savannah non-forest species, evidence of the high degree of disturbance mainly caused by logging. Compared to the larger forest reserves of the Arabuko-Sokoke forest, Mukaka and Mrima forest fragments contained about one third as many species. However, the two patches were found to contain several species not recorded in the large forest reserves found in the same geographical area. Clearing the small forest fragments would therefore lead to local extinction of some forest butterflies.

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Dispersal of **Parnassius smintheus** *among shrinking alpine meadows*

Rising tree line in the Canadian Rockies is reducing size and increasing isolation of alpine meadows by the encroachment of forest. The effect of intervening forests on dispersal of *Parnassius smintheus* (Papilionidae) was assessed among 26 meadows over a 12 km study area in Kananaskis, Alberta, Canada in 1995/96, using mark-recapture techniques. A total of 2774 captures of *P. smintheus*, in the two years, were used to estimate movement. Statistical models were used to assess the effect of landscape variables, including distance through forest, on dispersal rate between pairs of meadows. Fitted models, combined with landscape variables estimated from aerial photos from both 1952 and 1993 suggest that there has been a net reduction in dispersal by 40 percent over that interval, while the amount of alpine meadow habitat has declined by about 70 percent.

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The effectiveness of the California gnatcatcher as an umbrella species for three coastal sage scrub dependent lepidopterans

The federally listed California Gnatcatcher has been used as an umbrella species for the conservation of the southern California coastal sage scrub fauna. This action is commensurate with a general conservation paradigm of using vertebrates and vertebrate-based reserve designs to de facto protect invertebrate cohabitants. Over the past four field seasons I have monitored 28 patches of coastal sage scrub in northern San Diego County on which gnatcatchers are known to occur. I have surveyed each patch repeatedly for three species of sage-scrub dependent lepidoptera: *Apodemia mormo* (Mormon metalmark), *Euphilotes bernardino* (Bernardino blue), and *Hemileuca electra* (Electra buckmoth). Initial results indicate that the presence of the gnatcatcher may not be a good indicator for the presence of these insects; only the largest habitat patches supported all three species of Lepidoptera. Future conservation plans, not only in the sage scrub but also in any biological community where invertebrate conservation is important, take insect preservation for granted at their peril.

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Eurema elathea *seasonal phenotypes and the ecological correlates of polyphenism and gregarious night-roosting in butterflies*

Eurema elathea adults were censused weekly in six night-roosts around a forest fragment in Uberlândia (Central Brazil), and in two roosts in a suburban area. Males were classified in six phenotypes ranging from the presence of a conspicuous wide black bar at the dorsal forewing inner margin (wet season dark morphs) to the absence of that bar (dry season light morph). Body mass and wing area of co-occurring morphs showed similar means. Butterfly abundance and morph frequencies varied in close relation to humidity (rainfall); in the wet season few individuals were captured (always the dark morph); at the peak of population size (dry season) the light morph predominated. A "move to a roost -stay for some days - move again" pattern of dispersal was recorded; a lower fraction (15.6 %) of recaptured butterflies and a higher recruitment was recorded compared to other night-roosting butterflies. Dispersal potential was similar between the sexes and varied seasonally. The maximum residence time recorded was 91 days for a female and 84 for a male. Pooled males and pooled females showed similar means for residence time, the same being true for different morphs. The fraction of individuals that moved from one roosting site to another was similar between the sexes and between the male morphs, although higher in the forest fragment than in the suburban area. A higher fraction (21.3 %) of marked butterflies were recaptured in the latter, suggesting a behavioral modification for sedentary behavior in those individuals

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Visual ecology of butterflies

Perennial issues in sensory biology are questions about nature of the proximate and ultimate interactions between visual system structure, behavior, and the environment. Butterflies offer a fine arena for answering these questions because (1) they are highly visual animals, (2) they are diverse in reproductive and foraging behavior, and habitat preferences, and (3) their visual system is relatively easy to study. Studies of the butterfly visual system indicate that, like other insects, acuity and spectral sensitivity vary across the visual field, and that eye structure limits the distances at which butterflies can detect small objects and pattern elements to a few meters. However, detection distance will depend on eye size, which correlates positively with body size both within and among species. I examine the relationship between visual system performance, behavior, and ecology in tasks faced by adult butterflies, including directed flight and the detection and recognition of nectar sources, oviposition sites, and mates. This review tentatively concludes that some eye features can be interpreted as adaptations to specific problems and that behavior patterns reflect and can help overcome limitations of the visual system. However, firmer conclusions will require more information on (1) diversity in eye structure within butterflies, (2) the parts of the visual system that are used most in each of these tasks, (3) details of the behavior during visual detections and assessments, and (4) the details of the ambient light in which these tasks are performed.

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Diversity of butterflies in the agricultural landscape determined by management practices or landscape heterogeneity?

Organic farming has often been assumed to enhance diversity. Rather few comparisons of diversity in different farming systems have been made and those that exist mainly focus on a small part of the farm as the unit for comparison. To investigate the importance of management practices and landscape structure on diversity of butterflies 16 farms were censused during 1997. The farms were between 30-150 hectares in size (forests not included) and were paired according to management practices with the aim to control for landscape structure on farm level. The pairing was done with the help of the Bray-Curtis dissimilarity index based on the farms' area of cereals, lays, peas and beans, oil plants and other crops, non used and used pastures and forests. The farms were located in the central part of Sweden in two different regions with the same species pool. On each farm a transect route was walked six times during July and the beginning of August. No differences in diversity, number of species or number of observations were noted between farms managed differently. However, a significant difference in the number of species between the regions was found. This is suggested to depend on landscape structure since one region had a more heterogeneous landscape than the other region. The initial condition by the landscape is in this case more important for diversity of butterflies than the farming system per se.

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Predation and defense of **Euptoieta hegesia** *(Nymphalidae)*

Anolis predators have a large impact on the population biology of *Euptoieta hegesia*, a butterfly of coastal scrub habitats on Jamaica. A population study of adults of this species revealed that these predators have greater impact on the larger females. Predator selectivity may be partially responsible for skewed sex ratios in *E. hegesia*. The effects of *Anolis* predators are also apparent in two other butterfly species, as well as between years, in this habitat but are absent from a population of the sister taxa, *E. claudia*, which only occurs above 1200 m elevation in the Blue Mountains. Larvae of *E. hegesia* use *Turnera ulmifolia* (Turneraceae), a species with a genetic polymorphism for the elaboration of hydrogen cyanide, as their primary host. Larvae that were reared on cyanogenic morphs of the host were consumed less frequently by *Anolis* spp. predators. Importantly, 70% of larvae that were attacked but not consumed survived to pupate normally. Larvae reared on cyanogenic secondary hosts (*Passiflora foetida* and *P. suberosa*; Passifloraceae) had lower survival and longer development times but higher pupation masses than those reared on either morph of *T. ulmifolia*. Together, our studies suggest that tradeoffs between larval performance, chemical defense and size-related adult mortality may mediate hostplant use.

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Dispersal behavior, metapopulation dynamics, and critical habitat for the Fender's blue butterfly

Although the general concept of metapopulation dynamics is now widely accepted by practicing conservation biologists, application of metapopulation theory to management of specific rare species is not always straightforward. For example, habitat management and recovery plans for rare species often identify key habitat based on static estimates of population size or conclusions from generic metapopulation models, which may not capture the relevant biology of particular species. We explore relationships among dispersal behavior, patch size and location, and population viability for an endangered butterfly, the Fender's blue (*Icaricia icarioides fenderi*) in Oregon, USA. Based on dispersal behavior (movement rate and turning angle relative to distance from patch edge), demographic rates (estimated from annual censuses of eggs and adult butterflies), and maps of existing and potential Fender's blue habitat near Eugene, Oregon, we construct an individual-based model of metapopulation dynamics to ask: How much, if at all, does a metapopulation approach (which targets a network of habitat patches linked by "stepping stones") improve population persistence over a static approach (which targets the largest existing populations)? Results are interpreted in light of general metapopulation theory and compared with the structure and dynamics of other butterfly metapopulations.

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Burning prairie to restore butterfly habitat? A modeling approach to management tradeoffs for the Fender's blue butterfly

Designing strategies to restore endangered species habitats may involve trade-offs that include negative short-term impacts to achieve positive long-term success. In managing grasslands, fire is a powerful tool to control invasive weeds and stimulate native plant growth, but it may decimate the invertebrate fauna. We present an empirically-based mathematical model to rank potential burn strategies for Fender's blue butterfly (*Icaricia icarioides fenderi*) habitat. Potential strategies include combinations of times between burn (1, 2, 3, 4 or 5 years) and fractions of a habitat to burn in each fire (1/8, 1/4, 1/3, or 1/2) as well as a strategy of never burning. Burning 1/3 of the habitat every two years maximizes the average annual population growth rate, but 8 of 21 strategies led to 95% of simulated butterfly populations persisting 100 years. However, in simulations based on parameters' lower confidence limits, there were some cases in which no strategies led to populations persisting 100 years. In this uncertainty analysis (the effect of changes in parameters based on our confidence in them) the rank order of the strategies was also investigated. This analysis indicates that the rank order of burning strategies is most sensitive to our confidence in rates of habitat change after a burn (number of "good" years after a fire and time for habitat to return to pre-burn conditions). Surprisingly, the rank order of strategies changes little over a wide range of butterfly demographic rates. We conclude that

better knowledge of rates of habitat change after a burn would improve our ability to make management decisions significantly more than better knowledge of the butterfly's vital rates.

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Impacts of habitat fragmentation on the fruit-feeding butterfly community of Venezuelan dry forest

Although pioneering studies indicate that tropical butterfly communities are affected by forest fragmentation, nature of the impacts remain unclear in quantitative terms and require further investigation. I evaluated the effects of fragmentation on the diversity and composition of the frugivorous butterfly community with special reference to the role of isolation, in a set of dry forest fragments formed by the damming of the Caroni River in eastern Venezuela. My study was carried out over three growing seasons, using eleven small fragments (0.1 to 1.2 ha) and nine control sites. Overall abundance of bait-trapped butterflies on fragments was significantly reduced as compared to control sites and showed decline with distance from colonizing sources (ranging from 0.1 to 2.7 km). Analysis indicated a general trend of reduced species richness on forest fragments that was accentuated with isolation. Overall community composition significantly differed amongst control sites, near islands and far islands. Species abundance analysis indicated that the observed changes in community composition were due to significantly lowered population densities or absence of 50% of the recorded species on islands. 44% of species showed no change in abundances while 6% showed modest increase on fragments. Our results indicate that morphines, medium-sized satyrines, and charaxines may be vulnerable to extinction after habitat fragmentation while small satyrines and some fast-flying nymphalines may be relatively unaffected. Thus we found significant effects of isolation on diversity and composition of the fruit-feeding butterfly community which can be attributed to the differential responses of species to forest fragmentation.

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Phenofaunistics: seasonality as a property of butterfly faunas

A decade ago, Henk Wolda lamented the intellectually primitive state of insect phenology as an area of eco-evolutionary study. It seems obvious that phenology at the faunal, as well as the individual species level, reflects adaptive processes, but we do not actually *know* that. Using a multiyear database for two nearby sites in the North Inner Coast Range of California, we develop and test quantitative approaches to phenology as a property of entire butterfly faunas. Specifically, we address these questions: How site-specific, reproducible and variable are such patterns? How can they be concisely characterized in quantitative terms? How much of inter-site variance is attributable to site, year, and species composition? Are there broad, regional phenological patterns comparable to plant life-form spectra as a function of climate? How site-dependent is the specific sequence of species flight periods? Are there coherent sets of phenologically-associated species across sites? How can phenologocial null models be constructed to test for non-randomness?

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The role of wing color and pattern in habitat use by Palearctic butterflies

Butterfly wing color affects thermal stability and hence flight times and reproductive output. Wing color and pattern affects the vulnerability of species to predator avoidance and evasion and influences intra-specific communication. On any wing surface these requirements may conflict and limit the habitat types and climatic regimes in which particular species may persist. Studies of microhabitat use by butterflies in southern and northern Europe have raised three key questions:

1. How specific are particular morphologies to specific habitat structures?
2. Does a phylogenetically constrained wing morphology restrict species to certain types of habitat?
3. Does the interaction of conflicting constraints on adjustments of wing color and pattern influence the geographic distribution of specific wing color and pattern types?

Data from field work and image analysis of wing morphology is presented which addresses these questions and raises issues of whether there are distinct morphological pattern groupings, which comprise groups of closely associated species, which are associated with particular habitat structures, and which might form semi-stable evolutionary units.

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Rapid assessment of butterfly diversity patterns: A methodology for landscape evaluation

As part of a landscape-scale investigation of diversity patterns involving multiple biological groups, I developed and tested methods for the systematic inventory of butterfly diversity. A rapid assessment was made of butterfly diversity patterns in the 754 hectare (ha) Beaver Meadows pilot study area in Rocky Mountain National Park, Colorado. I measured butterfly richness and relative abundance at multiple scales using a stratified random sampling design. Twenty-four 0.1 ha multi-scale plots were sampled four times during June, July, and August 1996. I recorded 49 butterfly species (~40% of the butterfly species documented from the 1074 km2 Park) in the 2.4 ha area within the plots. Although butterflies were recorded in all vegetation types, certain vegetation types contributed disproportionately to the butterfly diversity in this landscape. Species richness, diversity and the number of unique species were highest in aspen (*Populus tremuloides*) areas, which occupy only a small proportion of the landscape. Patterns in butterfly richness were positively correlated with vascular plant species richness (r2 = 0.469). However, considerable within-type variance and high between-type overlap in butterfly species composition suggested that remotely sensed patterns in major vegetation type are not the most appropriate criteria for landscape stratification. This unbiased, spatially explicit method of systematic butterfly inventory provides a rapid, cost efficient approach for landscape evaluation.

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Spatial pattern in butterfly-hostplant associations

Butterfly diet often varies spatially. This variation may take the form of local adaptation on the part of the insect in response to selection associated with plant quality, plant abundance and/or the interactions of plant traits with insect life history. Host preference may also fail to vary adaptively, because selection is countered by gene flow, and/or because there are constraints on the evolution of preference hierarchies. Insect population founding and extinction may both be influenced by diet, thereby influencing the spatial distribution of host use as well as the frequency of use of each host species. Most of these effects can be found in a small group of closely-related butterflies, the checkerspots: I shall present data from *Melitaea cinxia*, *Euphydryas aurinia*, and *Euphydryas editha*.

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The naming of names. Or, why the oldest profession is still needed

According to the biblical account, taxonomy - the naming of animals and plants - antedates even the creation of women. "Modern" taxonomy, using the Linnaean binominal system, dates back nearly two and a half centuries. Taxonomists are often challenged as to why, after all this time, they still keep changing the names of even quite familiar species. On this poster, I use an example from my work on a conspicuous African papilionid butterfly, *Graphium policenes* and its relatives, to show some of the obstacles in the way of stability. These include the historical and quasi-legal as well as incomplete attempts to resolve earlier problems. Moreover, further study of more material with new techniques yields new information--even new taxa--that thickens the plot still further. This process is likely to continue while there are still unexamined specimens in collections and while a vestige of the natural world still survives. The oldest profession--now, of course, practiced by both sexes--still has a future.

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Genetic differences at the species boundary in butterflies

Butterfly species often maintain their genetic integrity in spite of hybridization and some gene exchange. Genes that mirror species boundaries in spite of occasional exchange of other genes are likely to provide information about the genetic architecture and process of speciation. One group of genes that is particularly prone to conform to species boundaries are sex-linked genes, which comprise one of 30 pairs of chromosomes in Lepidoptera, and yet contain over half of mapped genes for species differences. Mitochondrial DNA is also a good marker of species boundaries in butterflies, and this may be related to Haldane's rule and the fact that butterfly females are the heterogametic sex. Based on the relatively few well-worked examples known so far, it appears that a small subset of the total butterfly genome, biased in chromosomal location, may be sufficient to initiate speciation, even when populations are sympatric.

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*Redwing blackbird reproductive behaviour and the palatability, flight performance, and morphology of temperate pierid butterflies (***Colias, Pieris***, and* **Pontia***)*

In presentation experiments to redwing blackbirds in eastern Washington, palatability of pierid butterflies varied over the birds' breeding season. The cloudless sulphur *Colias eurytheme/protodice* was always more palatable than the cabbage white *Pieris rapae* and the western white *Pontia occidentalis*. *P. occidentalis* and *P. rapae* had similar palatabilities when demand for resources by the nestlings was relatively low. When demand for resources increased at the height of the birds' breeding season, the palatabilities of all three species increased. Moreover, the palatability of *P. occidentalis* increased disproportionately such that it was intermediate in palatability between *C. eurytheme/protodice* and *P. rapae.* Differences in palatability were associated with differences in capturability in artificial predation experiments. *C. eurytheme/protodice* flew for a greater durations and distances than the other species prior to capture. The three species did not differ in flight speed. However, *C. eurytheme/protodice* was missed more often, suggesting that the species differed in maneuverability. Two indicators of flight performance in tropical butterflies, flight muscle ratio (thoracic mass/body mass) and the position of center of body mass, ordered with capturability of the species as predicted. However, capturability was also associated with differences in body size among the species.

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Locomotor mimicry in **Heliconius** *butterflies*

The study of locomotor mimicry in butterflies focuses attention on morphological design and its biomechanical consequences in the context of mimetic flight behavior. Evolutionary convergence in the flight behavior of butterfly species via selection on mimetic similarity may be used to test whether attributes identified through biomechanical and aerodynamic theory are truly relevant to flight behaviors. Sit-and-wait predators such as the rufous-tailed jacamar probably base decisions to pursue insects on motion as well as coloration. The remarkable color congruence of mimetic *Heliconius* from the sylvaniform and pupal-mating lineages has made them the focus of a number of studies in mimicry, and hence these lineages were suitable subjects to extend the investigation of mimicry into flight. In an analysis of the morphology and kinematics of four distasteful species of passion-vine butterflies *Heliconius* that comprise two mimicry pairs, I found that flight-related morphology (centers of body and wing mass and wing shape) diverged among species within lineages and converged among species within mimicry groups. As predicted from biomechanical theory, wing beat frequency also diverged among species within lineages and converged within mimicry groups. This is the first evidence of behavioral mimicry arising in a mutualistic, Mullerian-mimetic context.

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Sperm precedence in multiply mating Papilio *species*

Multiple mating has been well documented in *Papilio*. This raises the possibility of sperm competition and cryptic sexual selection, especially where the ranges of two species overlap. We double mated *P. glaucus* and *P. canadensis* females with conspecific and heterospecific males to determine that precedence is a common pattern of sperm usage in *Papilio*. We are investigating the possibility of cryptic sexual selection or other departures from precedence in and near the *P. glaucus* and *P. canadensis* hybrid zone in Michigan. We are also using western *Papilio* species to determine the effect of increased phylogenetic distance on patterns of sperm usage.

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The gradation from capital breeding to income breeding as a major determinant of life-history and population dynamics in Lepidoptera

Importance of adult derived resources in reproduction varies greatly among different groups of Lepidoptera. Non-feeding adults have evolved in numerous independent cases, whereas adult feeding is crucial in some other groups, some butterflies and sphingids, for example. Applying the terminology of vertebrate ecology, forms that mainly rely on resources derived during the larval life can be called capital breeders whereas those relying on adult foraging in their reproduction can be labeled as income breeders. It is proposed that the position of each species on the axis formed by the gradation from capital to income breeders is a major determinant of both life history and the type of population dynamics of the species. In capital breeders, there is a straightforward positive correlation between female size and fecundity that leads to evolution towards heavy abdomens. In turn, heavy abdomens impede adult mobility that results in simplification of adult behavior. In contrast, in income breeders, fitness may be critically dependent on adult mobility and sensorial abilities, selection may thus favor light rather than heavy abdomens. This is a fundamental difference with far-reaching consequences to several aspects of life-history evolution. Furthermore, as the females of capital breeding moths show a simplification in adult behavior, no regulation of population density is expected to occur at the level of adult behavior that may be a precondition for eruptive and cyclic population dynamics.

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Systematics of an endemic radiation of Madagascan butterflies (Lepidoptera: Satyrinae: Mycalesina) based on total evidence.

Studies of adaptive radiations of insects on islands have had a profound influence on development of ideas within the fields of evolutionary biology and biogeography, but early studies focused principally on geologically recent island archipelagoes. We present here the first results from a modern phylogenetic study of the largest adaptive radiation of butterflies on Madagascar, a group of mycalesine satyrines potentially isolated biogeographically for a very long time. These results are based on an extensive morphological dataset and sequence data for the cytochrome B and COII genes. Trees resulting from total evidence analyses are well resolved but morphological and molecular data show considerable conflict. It is apparent that these mitochondrial genes are most useful for clarifying alpha-taxonomic problems and for resolving the more derived species groups within this group of butterflies. There is strong evidence from all datasets that most currently recognized generic entities are paraphyletic, including *Henotesia*, classically treated as occurring in Africa. It is also clear that data from more slowly evolving genes will be need to provide a robust phylogeny.

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On the consequences for butterfly conservation: stochasticity and genetics in metapopulations, a pedigree approach

Only a few studies have analyzed the effects of both genetic and stochastic processes on the risk of extinction or the vulnerability of butterfly populations. Typically, studies concentrate either on genetic effects (inbreeding depression, loss of genetic variation, accumulation of deleterious alleles) or stochastic effects (environmental, catastrophic, demographic). In the present study we explore the combined effects of inbreeding and demographic stochasticity on the viability of laboratory metapopulations of the butterfly *Bicyclus anynana*. Pedigrees were determined for six metapopulations and one large panmictic population over a period of eight generations with inbreeding. Each metapopulation consisted of four subpopulations that varied in effective population size (Ne) and amount of gene flow. Fitness traits were measured to quantify the effects of inbreeding depression. Computer simulations were run to explore the stochastic effects of biases in sex ratios, variance in progeny number and differences in mating success. The loss in molecular genetic variation at six allozyme loci has been analyzed and compared to the expected loss. Interestingly, small populations loose more than expected genetic variation, possibly due to background selection. Large populations, however, maintain most variation due to significant heterozygote advantage. The effects of heterozygote selection (overdominance) cannot be observed in small populations because of the large impact of stochastic processes swamping the effects of selection.

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Adaptive morphological variation in the speckled wood butterfly: Mate-locating, a matter of design?

The behavioral strategies adopted by an animal, may depend directly on its phenotype (or *design*) and on the way it interacts with the environment. In the case of flying ectotherms, like butterflies, different flight patterns may have different consequences for both thermoregulatory and biomechanical requirements. I studied the relationships between morphological variation and behavioral variation in males of the speckled wood butterfly (*Pararge aegeria* L.). This satyrine butterfly mainly occurs in different types of woodland and males either perch in a territorial way, or patrol to locate mates. Darker males were more likely to patrol through the forest, while paler males mainly perched in sunlit patches on the forest floor. Field measurements of thoracic temperature and a warming experiment in the laboratory showed that thermal requirements differ between the behavioral strategies and that behavioral differences between color types relate to differences in thermoregulation. Additional insights were gained by using natural and manipulated speckled wood specimens as dummies on thermoprobes. Differences in relative thorax size were also found: perchers had larger thoraxes than patrollers. This points to differences in biomechanics and power-output of the two flight patterns and coincides with interspecific comparisons. Finally, I present preliminary results on the relevance of the behavior-morphology relationships to a context of larger scale mobility (dispersal) and habitat fragmentation. Relative thorax size increased with degree of fragmentation. This leads to the question whether designs change in a changing landscape.

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Is the whole more than the sum of parts? Values, evidence and identity in butterfly systematics

Knowledge of butterfly phylogenetic relationships continues to be a mosaic of near certainty and extreme doubt. The higher classification of butterflies, still based largely on morphology, will be reviewed, and its importance for ecology, evolutionary biology and conservation briefly discussed. Examples will be given of classifications based on morphology and other data (e.g. molecular) suggestive that "total evidence" is preferable for general classification, and that morphological data will continue to play a key role in Lepidoptera systematics.

A special concern is the application of butterfly systematics to conservation issues. If butterflies are to be used as a part of a surrogate for biodiversity as a whole, then we need (in theory at least) to be able to model character or genetic diversity so that the relative values of different subsets of species (local faunas or assemblages), alone and in combination, can be assessed. In relation to area selection, due to the many conflicting distribution patterns exhibited by terminal taxa, it turns out that species richness for a globally extensive group comprising more than 18,000 species is likely to be an excellent first-order surrogate for almost any measure of genetic or character diversity. Species richness is definitely not, however, a suitable criterion for area selection. Efficient area selection in conservation planning depends on complementarity: the combination of sets of attributes enumerated at some agreed level of abstraction—typically terminal taxa (i.e. families, genera or species). Patterns of complementarity are determined, therefore, by accurate identity or non-identity of all taxa under consideration, and thus reliable presence or absence records for the chosen terminals, over the entire set of areas being compared.

The notion of identity, or the implications of stating that two or more discrete populations belong to the same taxon, is a neglected subject in biology, coming at the interface of pattern and process (part of the two "world views" discussed by Olivier Rieppel). This is especially true at species-level, where evolutionary biologists seek to establish a series of singularities based on knowledge of reproductive processes, while taxonomists try to derive whole systems from general hierarchical patterns. If Hennig's three-taxon statement can be extended to the question of identity, then taxonomic separation and recognition become relative, not absolute criteria. I will argue that this is a better approach for the construction of classifications for use in conservation evaluation, as it enables us to apply complementarity without being hostage to special pleading based on quirks of reproductive biology. For the purposes of conservation management, however, such taxonomy may not be the most appropriate. Here we may see how fundamental divisions that have affected major branches of biology throughout this century may have practical consequences. Thus it may be necessary to admit a plurality of approach without losing sight of the need to set clear values, goals and objectives that will determine the types of taxonomy to which we need to attend.

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Substrate-borne sound production by larvae of the lycaenid butterfly **Hemiargus isola***: communication with tending ants*

Larvae of the lycaenid butterfly *Hemiargus isola* are facultatively tended by ants. Tended larvae have higher survivorship and higher growth rates than their untended counterparts. We characterized substrate-borne vibrations produced by butterfly larvae and tested the hypothesis that the vibrations function to call tending ants. Silent larvae could be induced to call by touching them with a paintbrush, suggesting that larvae produce calls when disturbed. Calls were attractive to ants. In choice experiments, ants were much more likely to approach and tend larvae whose calls were not muted than equally-sized larvae whose calls were muted. The results suggest that larvae produce vibratory calls when in need of protection, and that the calls may help ants to locate butterfly larvae on the hostplant. Preliminary results suggest that calling is energetically expensive; therefore, future research will explore the relationship between the cost of communication and patterns of growth in tended and untended caterpillars.

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A comparative study of spatial population structure and movements in five species of butterflies

Migration (movements between habitat patches) is a critical feature of the life cycle of many species, and migration often has a fundamental influence on the dynamics of local populations and metapopulations. We have conducted a comparative study of migration in five species of butterflies belonging to the tribe Melitaeini. In Finland, two of the five species are endangered (*Melitaea diamina* and *Euphydryas aurinia*), two species are threatened (*M. cinxia* and *E. maturna*), and one species (*Mellicta athalia*) is still common. Each species has a population structure made up of more or less discrete local populations. We investigated whether the different species have different migration behaviors and whether this is related to for example the rarity of the species. Mark-recapture studies were conducted in different years, in different landscapes and with different sampling intensities. In all five cases, however, a metapopulation of ca. 20 local populations was studied. To allow comparisons between the data sets we used a model recently developed by I. Hanski, J. Alho and A. Moilanen. This model has 6 parameters that describe daily mortality rate within populations, daily emigration rate, the probability of death during migration, the effect of distance on migration, and the scaling of emigration and immigration rates to patch area. The results show interesting differences between the species and the sexes. The results also demonstrate the feasibility of estimating migration mortality with the kind of data we have sampled.

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Influence of egg maturation on mate-avoidance behavior in monoandrous females of the little copper, Lycaena phlaeas *(Lepidoptera: Lycaenidae)*

Females of the little copper, *Lycaena phlaeas*, were captured in the field and dissected to investigate the mating frequency and reproductive output. As shown by spermatophore counts in the bursa copulatrix, most females were generally monandrous. The single spermatophore constantly occupied about a half of the bursa copulatrix in volume though the size decreased with the female age. A young female had 250 immature eggs in the ovaries. They were estimated to lay 150 eggs throughout the course of their lives. Mate avoidance behaviors were frequently observed in either experienced or virgin females. In the laboratory experiments, virgin females loaded a few mature eggs immediately after the eclosion and gradually increased with age. Young females loading a few mature eggs exclusively fed on nectar in a whole day and few of them accepted to copulate with males. The size, age and mating history of male did not inhibit the releasing of mate avoidance behavior of the virgin females. However, females accepting copulation loaded significantly more mature eggs than those avoiding mating. When a female loaded more than 40 mature eggs feeding on enough nectar in the laboratory, she solicited courtship. Copula duration was about 16 min irrespective of male age. All the females avoided males after mating. Egg maturation in ovaries is seen to be important for mating behavior of such monandrous species.

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Identified genes as tools for testing butterfly adaptations

Adaptation is a central concept in the argument for Darwinian natural selection, explaining why natural selection occurs: why fitness differences among variants of organisms exist. Butterflies have been used as test systems for studying adaptation for many years. Such work was originally limited to the use of "the comparative method," but recently has begun to become experimental. The study of mimicry is a case in point: it began as "comparative speculation," but in the 1950s, experimental approaches transformed it into an area of rigorous study, and it is now one of the best understood aspects of the evolutionary process.

The "method of identified genes" is one important experimental approach to the study of adaptation. It derives from the ability of modern molecular biology to identify genes of known, or knowable, molecular and physiological function. Variation at such genes can then be used to probe the adaptive nature of phenotypes, assessing how genetic changes in phenotype do or do not change organismal performance, hence the adaptive relations between organisms and their environments, and may or may not lead to net fitness differences. This method often considers variation in genes specifying metabolic enzymes—"allozymes"—because these were the first class of genes for which functional characterization became widely feasible. The method has been applied successfully to other butterfly allozymes. Identifiable genes which control the expressions of other genes can also now be studied in butterflies, as other contributions in this symposium show.

A new experimental focus in our program to study evolutionary mechanisms, using pierid butterflies as model systems, starts from earlier work by Burns on the dimeric esterase gene, Es-D, of *Colias*. This enzyme may be involved in detoxifying the defensive chemicals of *Colias*' larval hostplants. The gene shows a large number of allelic variants in many North American *Colias* species, and Burns found patters of similarity and difference among species' Es-D profiles that may reflect both taxonomic relatedness and variation in hostplant use. He also found some unusual genetic transmission patterns of Es-D variation in *C. eurytheme,* which we can now interpret in terms of natural variation at regulatory genes controlling the expression of this enzyme.

Further study of this system thus can examine the following important general issues in adaptive evolutionary biology:

- the importance of the co-segregation of structural gene variation and variation in multiple regulatory loci controlling structural gene expression in the wild;
- the potential genetic manipulablity of hostplant coevolutionary adaptive scenarios in relation to predictions of the original Ehrlich/Raven coevolutionary models;
- the disentangling of similarity and difference among taxa bases on "phylogenetic constraints" from that based on lineage predisposed differential adaptations.

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Butterfly sperm polymorphism: A role for eunuchs in sperm competition?

Males of several species of insects, molluscs and various other invertebrates produce several sperm types; some of which do not fertilize the female's eggs. The function of these non-fertile sperm has remained enigmatic ever since their discovery nearly 100 years ago. Butterflies produce two types of sperm: fertile, 'eupyrene' sperm, and non-fertile 'apyrene' sperm, which represent 90-95% of total sperm number. Several explanations for the function of apyrene sperm have been suggested. They may have a physiological role by activating or aiding transport of the fertilizing sperm inside the female, or represent nutrients for the eupyrene sperm or the female. In 1984, Silberglied and co-workers suggested that the apyrene sperm instead play a role in sperm competition either by blocking the site of sperm storage, displacing or inactivating rival males' sperm, or delaying female re-mating. We investigated these explanations for apyrene sperm function in the polyandrous green-veined white butterfly, *Pieris napi* (Pieridae). We found no support for the physiological explanations as the proportion of the two sperm types varied both with male and female mating history. Instead, apyrene sperm appear to reduce the risk of sperm competition by acting as a filler of the female's sperm storage organ delaying female re-mating

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Evolutionary conservation of oviposition preference in a widespread polyphagous insect herbivore: **Papilio zelicoan**

We analyzed geographic differentiation in oviposition preference in the anise swallowtail butterfly, *Papilio zelicaon* Lucas, which is one of the most widely distributed and polyphagous butterflies in western North America. Among 13 populations that span 1200 km of the range of *P. zelicaon* in the Pacific Northwest of North America, the overall oviposition preference hierarchy has not diverged significantly, even though these populations differ in the plant species they use in the field. The results indicate that differences in host availability and use have not favored major reorganizations in the preference hierarchy of ovipositing females. Instead, this butterfly has a conserved preference hierarchy that varies within a narrow range among populations. All populations ranked the four test plant species in the same overall relative order, even though these populations differ in the plant species they use in the field.

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Color learning in butterflies

Color plays an important role in butterflies' lives, as it is involved in mate recognition, hostplant location, and food selection. We have used *Agraulis vanillae* (Nymphalidae) and *Battus philenor* (Papilionidae) to investigate innate color preferences and color learning in the context of both nectar foraging and oviposition behavior. Naive butterflies of both species demonstrate color preferences that can be modified by associative learning. Individuals readily learn to associate color with a nectar reward within just a few flower visits; continued experience results in greater discrimination in favor of the rewarding color. Most individuals quickly shift their foraging behavior when the color of the rewarding flower is changed. In addition, *B. philenor* females are able to learn to associate one color with an oviposition stimulant, and a different color with the presence of a nectar reward. A capacity for such dual conditioning may be important for female butterflies who must learn to recognize one color in association with a hostplant, and another with a nectar source. An overall ability to learn to associate environmental stimuli with colors is likely to be adaptive for butterflies living in a spatially or temporally variable environment.

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Warming drives local range shifts in a threatened checkerspot butterfly

The response of species to global warming will include distribution shifts at many spatial scales. Populations of the bay checkerspot butterfly, *Euphydryas editha bayensis*, exhibit numerical declines with warmer weather coupled with local shifts toward cooler slopes. The magnitude of the spatial shifts corresponds closely to the change in air temperature. The patterns are readily explained by phenological patterns of butterfly and hostplant development. This study suggests that such local range shifts may foreshadow broad latitudinal shifts in response to global warming. Given predictions of rapid climate change, the degree to which species distributions can shift along topoclimatic gradients is an essential component of understanding ecological responses to climate change, as well as establishing design guidelines for nature reserves.

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Intraspecific phylogeography of an alpine butterfly

Using 2.3 kb of the cytochrome oxidase gene in the mitochondria we have reconstructed the historical relationships between alpine populations of three subspecies, *Colias meadii meadii*, *C. m. elis*, and *C. m. lemhiensis*. Observed patterns of relationship are interpreted in light of Pleistocene glacial advances.

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Sexual selection and the evolution of butterfly mating systems

Sexual selection is the evolutionary process proposed by Darwin to explain traits whose primary function appears to be that of ensuring an individual's success in courtship and mating, and hence has a strong effect on the evolution of animal mating systems. In this review of sexual selection in butterflies, I pay particular attention to its effect on male and female mate location patterns, courtship and mating behavior, sperm competition and life history character traits. The mate-location behaviors of male butterflies have been reasonable well studied, and males typically one of two strategies; either searching (patrolling), which means that males range widely in search of mates, or perching, which means that males are quite localized in space (and often defend territories) to obtain a mate. However, female mate location behaviors have been considerably less well studied, a shortcoming that is beginning to be realized by many workers. I argue that the evolution of butterfly mate location patterns is the combined result of male and female behaviors, and hence a full understanding requires detailed understanding of male, and female, behaviors.

The observation that male butterflies are more brilliantly colored than females in species that exhibit sexual color dimorphism, led Darwin to suggest that female preference for gaudy males was the underlying driving force. However, the weight of the evidence strongly suggests that Darwin was wrong, and repeated attempts to show that female butterflies are attracted to particularly colorful males have failed, and it seems that olfactory cues are quite dominant when it comes to stimuli governing female choice.

Some thirty years have now passed since the first demonstration that the second males generally enjoyed higher fertilization success than the first males in doubly mated females of the checkerspot butterfly *Euphydryas editha*. Second male sperm precedence is still the prevailing pattern, but recent research has begun to focus on understanding the strong individual variation in sperm precedence; although the second male on an average may fertilize some 80 % of the doubly mated female's offspring, variation in second male fertilization success usually ranges from 0 to 100%. It has been shown that male size is associated with success in sperm competition, because large males transfer more sperm, but recent interest is also directed towards female post-copulatory choice, holding the issue open that females can somehow influence which male's sperm will be used for the fertilization of her eggs.

Sexual selection and mating systems have manifold effects on male and female life history traits. Under polygamy, relative males size increases with the degree of female polygamy, and males typically deliver large nutritious ejaculates which serve as nuptial gifts, whereas males in monandrous systems typically are smaller than females, and deliver small ejaculates that seem to contain little nutrients. Mating systems also strongly affect female life history traits, and females in monandrous species exhibit capital breeding where virtually all of the nutrients devoted to reproductive effort derive from reserves assembled during the larval stage, whereas females in polyandrous species, which receive repeated nuptial gifts during their lifetime, exhibit a kind income breeding. Capital, or income, breeding can be viewed as integrated parts of different life history syndromes, and may interact with other life history traits, such as male and female habitat preference, displacement behavior, and hostplant choice.

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Two nymphalid butterflies and the measurement of oviposition preferences

Are the same oviposition preferences produced by different experimental methods? Preferences are often assessed by providing two or more potential hostplants in a cage; then giving females time to explore and oviposit. The eggs are then counted on each plant after some designated time. In contrast, Singer (1982, *Oecologia* 52:224) measured preference in a clutch-laying species by placing females sequentially on alternate hosts and counting acceptance behaviors while preventing oviposition. This procedure increases the sample size of oviposition choices for clutch layers. We measured the oviposition preferences of the Aster-feeding, clutch-laying nymphalid butterflies *Chlosyne harrisii* and *Phyciodes tharos* using both methods and compared the results. *C. harrisii* females accepted only one plant, *Aster umbellatus*, regardless of method. Both methods gave the same preference hierarchy for *P. tharos*, with *A. lanceolatus* being the most preferred hostplant, but the magnitude of the difference among plants - Singer's specificity - differed between methods. Nevertheless, the preference hierarchy appears robust enough to be seen regardless of how it is measured, with free-flight cages being the easiest to use. For *Aster*-feeding butterflies, oviposition preferences determine usage of plants in the field.

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How landscape structure affects estimates of butterfly dispersal

Good estimates of dispersal are important in many areas of population ecology and genetics. Unfortunately, empirical estimates of dispersal contain sources of bias. Results from a Mark-Release-Recapture experiment with the Brown Argus, *Aricia agestis* (Lycaenidae), show how landscape structure affects estimates of butterfly dispersal. The dimensions of the study area determine which movements can potentially be recorded. Correcting raw data to take account of the distribution of potential movements alters dispersal estimates. Dispersal rates within habitat differ from dispersal rates between habitat patches.

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Fluctuating asymmetry in butterflies

Butterflies provide excellent opportunities for analyzing fluctuating asymmetry (FA). Despite claims that FA is a good indicator of "general health" or "overall quality", many studies did not find a relationship between FA and "other" quality measures. Correlations between FA in different traits are typically low. Considerable controversy exists on the questions whether FA is heritable. High heritabilities (h^2s) have been reported, but these are disputed. Generally h^2s are low or absent. An important question is whether there are categories of traits that 1) have relatively higher FA, 2) have a (higher) h^2 of FA and 3) where FA and quality are more closely related. I discuss the possible roles of development, plasticity, genetic architecture and natural selection on the trait itself and on its FA. The role of these factors will be illustrated with the results of a large-scale experiment in the speckled wood *Pararge aegeria*, and measurements on the eyespot of the peacock *Inachis io*.

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Molecular phylogeny of the Fritillaries

The so-called "Fritillaries" of English lepidopterists include two subfamilies of Nymphalid butterflies, the Argynninae and Melitaeinae. Both groups are widespread and diversified in the palaearctic and nearctic regions, but the relations between the taxa at a holarctic scale are not yet well defined. A thorough morphological study of the Melitaeinae has been carried out by Higgins but resulted in strong generic splitting.

Using mtDNA sequencing and enzyme electrophoresis (ND1 and COX1 genes and about fifteen polymorphic loci), we found that both subfamilies correspond to clearly monophyletic assemblages. Some genera, such as *Eurodryas*, *Hypodryas*, *Mellicta* in Melitaeinae and *Boloria*, *Clossiana*, *Brenthis*, *Fabriciana* in Argynninae are also monophyletic. There is an opposition between these plurispecific genera, with a clear structure, and monotypic or paucispecific genera (either lumped in paraphyletic genera, *Melitaea s.l.* and *Argynnis s.l.*, or split), which branch at the base of the trees in a confused tangle. Some formerly postulated affinities between genera of palaearctic and nearctic region (e.g. *Speyeria* and *Mesoacidalia*) are confirmed.
The evolutionary patterns associated with the disclosed phylogenetic relations will be discussed.