

## Conservative resource utilization in the common blue butterfly – evidence for low costs of accepting absent host plants?

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We studied host plant preference of the common blue butterfly, *Polyommatus icarus*, and larval performance on two different host plants, *Oxytropis campestris* and *Lotus corniculatus*. The study species is a small lycaenid butterfly believed to be relatively sedentary. The study populations originated from two different and widely separated geographical areas. In one area both hosts are naturally occurring, with *O. campestris* being most abundant at the study sites, in the other area only one of the host plants, *L. corniculatus*, is present. There was no difference in oviposition preference or larval performance between populations from the two different areas. Hence, *P. icarus* from sites dominated by *O. campestris* has not evolved a higher preference for or better performance on this host plant. More surprisingly, *P. icarus* from the area where *O. campestris* is completely absent has retained not only good larval performance on this host plant but also high female preference for it. This conservatism at a large geographical scale is seen even though there seems to be genetic variation present in both populations, at least for preference but perhaps also for performance. We suggest that such lack of variation in resource utilization between populations may be evidence for weak selection against “preferences” for plants that are rare or absent. A combination of other constraining factors may also contribute to some degree, especially stepping-stone gene flow between populations.

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Several studies have shown that habitat heterogeneity affects genetic variation (Jaenike and Holt 1991, Sandoval 1994) and that distinctness of resources even can play a significant role in fostering resource polymorphism, with distinct intraspecific morphs showing differential resource use (Smith and Skúlason 1996). More commonly found is intraspecific geographic variation in resource utilization behaviour, which has been demonstrated in a number of animal species (Arnold 1981, Boinski 1999, Foster 1999). In those animals where variations in habitat preference, such as for food resource use and oviposition sites, have been most extensively studied it is clear that genetic variation for

such traits is common (Jaenike and Holt 1991). This is not surprising considering the high spatial and temporal variation in habitat between different areas, and the fact that behaviour is the link between physiology and ecology of animals (Bernays 2001). Resource related selection leading to local adaptation seems to be the norm rather than the exception. Phytophagous insects have proven to be excellent organisms to study this phenomenon, and rapidly evolving local adaptation in resource use has been shown in a number of studies on herbivorous insects (Diehl and Bush 1984, Singer et al. 1993, Kuussari et al. 2000). In insects the use of different host plants in different populations can lead to large

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changes in gene frequency (Diehl and Bush 1984) and host dependent selection can lead to divergent host adaptations (Funk 1998).

In this light studies showing conservatism over large geographic areas and time spans stand out as being the exceptions. One study that has drawn attention to conservatism in resource use is Wehling and Thompson 1997, concerning the butterfly *Papilio zelicaon* (Lucas) in North America. Such conservatism in resource use is not only of theoretical interest but can also potentially be a danger to the preservation of a species, especially when many environmental changes occur rapidly due to e.g. changes in human land practises. An increased knowledge and understanding of the evolutionary dynamics of host plant use can thus be of importance in conservation biology; especially concerning recovery plans for threatened species.

In the present study we investigated whether any differences in female host plant preference and/or offspring performance can be found between two populations of the common blue butterfly, *Polyommatus icarus* (Rottemburg), inhabiting areas with different resource availability. *P. icarus* is a small lycaenid butterfly believed to be relatively sedentary. The study populations originated from two different geographic areas (Fig. 1). In one area (the Baltic island of Öland)

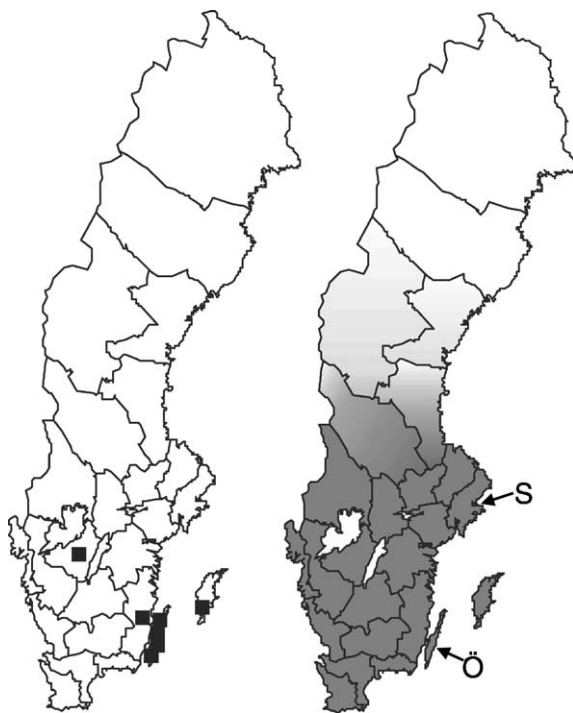


Fig. 1. Left: map of Sweden showing the distribution of *Oxytropis campestris* (indicated by squares), almost entirely restricted to Öland. Right: map of Sweden showing the location of the two study areas (S = Stockholm, Ö = Öland). The shaded area indicates the approximate distribution of *Lotus corniculatus* in Sweden.

both hosts are naturally occurring, with *Oxytropis campestris* (L.) being most abundant at the study sites, in the other area (Stockholm) only one of the host plants, *Lotus corniculatus* (L.), is present and *O. campestris* is completely absent. We predicted that a difference in relative preference for the two host plant species should be found between the populations, since gene flow between them should be slight and differences in selection on preference should exist. This expectation is based on the assumption that a relatively higher preference for a locally more abundant species should increase realized fecundity in the field, especially in comparison with high preference for a totally absent plant species. If the shift in preference is large enough to result in specialization on the locally abundant host there may be additional advantages, such as better ability to discriminate between plant individuals (within species) that differ in quality (Janz and Nylin 1997).

## Material and methods

### Study species

The common blue, *Polyommatus icarus* (Lycaenidae: Polyommatainae), is a Palaearctic butterfly. In Sweden it is partially bi-voltine. The species is loosely associated with ants (Fiedler 1990). *Polyommatus icarus* is an oligophagous species with larvae feeding on a large number of plant species within the Fabaceae family. The exact number and hierarchy of host plant species are not known. Preliminary tests have shown that females do discriminate between plant species within Fabaceae when given a choice (A. Bergström and S. Nylin, unpubl.); this is also supported by field observations of ovipositing females (Thomas and Lewington 1991).

*Lotus corniculatus* is often mentioned in the literature as being one of the preferred host plants (Thomas and Lewington 1991, Tolman and Lewington 1997, Asher et al. 2001). Most records are from areas where *Oxytropis campestris* is absent. In Sweden frequent oviposition on this species has been observed on the island of Öland, where the plant is abundant (O. Leimar, pers. comm.).

### Experimental procedures and statistics

Experiments were conducted during the summers of 1999 and 2000 with butterflies from a total of four local sites, from two geographically different areas. One study area is located on the island Öland in the Baltic Sea, off the south eastern coast of Sweden. The other area is in the province of Stockholm further to the north (Fig. 1). The distance between the two areas is approximately 450 km. Distances between study sites within the two areas are approximately between 10 and 35 km. These sites

were Alvaret and Tävelsrum on Öland, and Frescati and Husa in the Stockholm area.

Both larval performance and female oviposition preference experiments were conducted with two different host plants within Fabaceae, common bird's-foot-trefoil, *L. corniculatus*, and yellow oxytropis, *O. campestris*. *L. corniculatus* was collected at the university campus area in Stockholm and *O. campestris* came from potted plants originating from the study site Tävelsrum on Öland. *Oxytropis campestris* can be considered as a remnant species in Sweden, from the last ice age, and today has a very limited distribution. It is still locally common on Öland but restricted to only a few very small and fairly isolated sites on the adjacent mainland and one site on Gotland. At the two study sites on Öland it is abundant and outnumber *L. corniculatus*. In the Stockholm area *L. corniculatus* is abundant while *O. campestris* is completely absent. The current main distribution of *O. campestris* is to the east in Russia on the arctic tundra.

### Larval performance

Eggs were collected from wild caught females and larvae were placed upon cuts of one of the two host plants as they hatched. 15 larvae (5 from each of 3 different females) from each area were raised on *O. campestris* and the same numbers were raised on *L. corniculatus* (60 in all). These larvae were weighed every third day and then as pupae, for a total of four times. Larval growth rates were calculated according to the formula:  $\log r = (\log_{w_1} - \log_{w_0})/d$ , where  $r$  is the daily growth rate,  $w_0$  and  $w_1$  initial and final weights in each time interval, and the number of days between measurements (Nylin 1991). For the larval performance analysis larval growth was calculated as the mean value of the two obtained larval growth rates. Another 197 larvae were raised on *L. corniculatus* to be used for the preference experiment, all of these individuals were weighed as pupae. All larvae were tended to every day and supplied fresh plants when needed. All inflorescence were excluded from the diet in order to avoid inequalities. Larvae were kept individually in plastic cups with stalks and leaves of host plants standing in water and covered with mesh. They were kept through all instars in a climatic room at 26°C and L:D set at 22:2. Positions of the cups were randomly moved on, and between, shelves in order to prevent possible temperature and light differences within the room.

### Oviposition preference

After adult eclosion all butterflies were sexed and individually marked before being put into cages for mating. After mating, females were put individually into

small plastic cages, 20 × 20 × 10 cm, for preference testing. All tested females were given a choice between sprigs of *L. corniculatus* and *O. campestris*. At the end of each day, after 8 hours, all eggs were counted. To be included in the analysis a female had to oviposit a minimum of 10 eggs per day for three days in total. Preference values were calculated by dividing the number of eggs on a host plant by the total number of eggs laid by a female. Host plants presented were randomly circulated between cages and changed regularly for freshness. Cages with ovipositing females were kept outside if sunny and under artificial light when cloudy. Throughout the day all cages were repositioned to avoid differences in light emission and temperature. All preference values were Arc-Sin transformed before statistical analysis.

### Statistics

Statistical analysis used was Nested design ANOVA (when not otherwise indicated) in STATISTICA '99 Edition, Kernel release 5.5. Sites were nested in areas, and families (offspring of a single mating) within years, sites and areas. Families and sites were treated as random factors, but because of the small number of levels (which leads to uncertain estimates of variance in these factors) we also explored the consequences of treating them as fixed factors.

### Oviposition preference for individual plants

In an additional experiment we controlled for possible differences in female oviposition preference based on host plant individuals rather than host plant species. This was done in a preference test with 18 females using 16 individually marked potted plants, 8 of each host plant species. These plants were randomly chosen from potted plants originating from the populations actually used by the tested butterflies. This preference test was conducted in the same way as previously described.

## Results

### Larval performance

Larval performance (growth rate and pupal weight) was analysed in two models including geographical area, site, family, sex and host plant (nested ANOVA, total N = 43 larvae, N = 43 pupae).

There was a significant difference in larval growth ( $p < 0.001$ ) between the two host plants. Larvae raised on *L. corniculatus* grew faster. Female and male larvae did not differ in larval growth rate up until pupation

( $p > 0.73$ ). There was no difference in growth rates between the sites ( $p > 0.35$ ) or areas ( $p > 0.62$ ), but families tended to differ ( $p = 0.08$ ). We also performed three factorial ANOVAs with sexes pooled ( $N = 54$ ), in order to study any interactions between host plant and family, site and area, respectively that could indicate variation in relative performance on the two hosts. No such interactions were found, for family ( $p > 0.37$ ), site ( $p = 0.49$ ) or area ( $p > 0.23$ ).

Performance on the two host plants were subsequently analysed in separate models including area, site, family and sex (nested ANOVA, total  $N = 26$  larvae on *L. corniculatus*,  $N = 17$  larvae on *O. campestris*). Interestingly, the results differed between the two host plants. On *L. corniculatus* there was no significant differences between areas ( $p > 0.65$ ), families ( $p > 0.92$ ) or sexes ( $p > 0.52$ ). However, sites within areas did differ ( $p < 0.001$ ). On *O. campestris*, areas, sites and sexes did not differ ( $p > 0.49$ ,  $p > 0.70$  and  $p > 0.77$ , respectively). There were however significant differences between families ( $p < 0.01$ ).

Pupal weights also differed between host plants ( $p < 0.001$ ; nested ANOVA, total  $N = 26$  pupae on *L. corniculatus*,  $N = 17$  pupae on *O. campestris*). Individuals grown on *L. corniculatus* attained larger pupal weights. Pupal weights also differed between the sexes, with males being heavier than females ( $p < 0.001$ ). For this reason we performed different analyses for the sexes (nested ANOVA,  $N = 16$ , males,  $N = 27$ , females). There was no significant difference in pupal weight between larvae from different areas (males  $p > 0.73$ , females  $p > 0.07$ ), sites within areas (males  $p > 0.33$ , females  $p > 0.58$ ) or families (males  $p > 0.61$ , females  $p > 0.55$ ). For this reason we did not perform factorial analyses on pupal weights.

### Oviposition preference

Oviposition preference was analysed in a model including year of capture, geographical area, site and family (nested ANOVA, total  $N = 49$  females). No difference in female preference between the two years was found ( $p > 0.94$ ). There was also no significant difference in oviposition preference between the sites ( $p > 0.87$ ; Fig. 2) or between the two different areas ( $p > 0.46$ ). There were statistically significant differences between families ( $p < 0.05$ ). This difference was not significant when excluding (from the complete model) families where only one female could be tested ( $p = 0.06$ ,  $N = 35$ ; Fig. 3). However, when years, areas and sites were pooled in a non-nested one-way ANOVA (as suggested by the non-significance of these factors) the family differences were again significant ( $p < 0.02$ ,  $N = 35$ ).

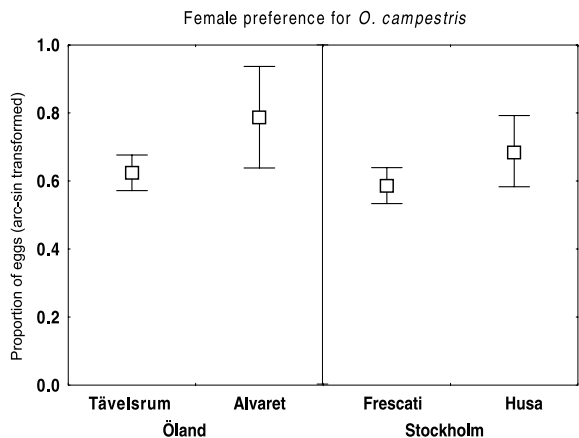


Fig. 2. Preferences of *Polyommatus icarus* females (originating from different areas and sites) for *Oxytropis campestris* in a choice between this plant and *Lotus corniculatus*.  $N = 49$  females: Tävelsrum  $N = 20$ , Alvaret  $N = 5$ , Frescati  $N = 18$  and Husa  $N = 6$ .

### Oviposition preference for individual plants

Preference for individual plants was analysed using nested ANOVA with plant individuals nested within plant species. Plant individuals were treated as random factor. There was no difference in preference between plant individuals ( $p > 0.61$ ).

### Discussion

The results of this study show that *P. icarus* is evolutionarily conservative in its utilization of the two tested host plants, *L. corniculatus* and *O. campestris*, at the population level. Why are *P. icarus* from Öland and Stockholm so similar in their performance and prefer-

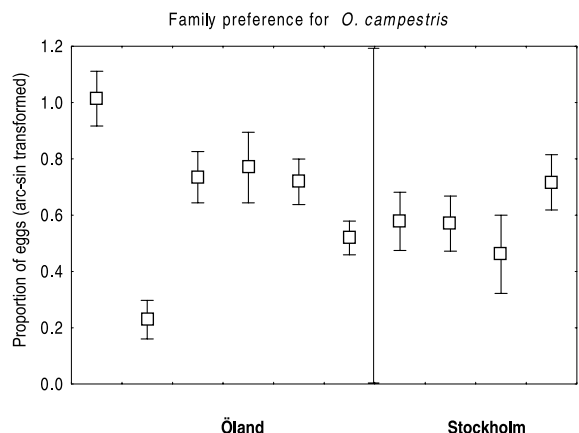


Fig. 3. Preferences of *Polyommatus icarus* females from different families for *Oxytropis campestris* in a choice with *Lotus corniculatus*. Total  $N = 35$  females (2–8 females in each family).

ences, despite the differences in plant communities between the two studied populations?

That there is no difference in larval performance between the populations is perhaps less surprising than the lack of preference differences. In general it seems that most insects are more conservative in physiological traits than in behavioural, so that often there are weak or no relationship between oviposition preference and offspring performance among populations or genotypes (Futuyma et al. 1984, Janz et al. 1994, Craig et al. 1999). However, the variation in growth rate observed between families from the same sites on *O. campestris*, and instead between individuals originating from different nearby sites on *L. corniculatus*, shows that evolution in performance variables is occurring and that there is potential for evolution also in relative performance on the two hosts.

Relative host plant quality (performance) could be expected to often influence host plant utilization: if one host plant is of higher quality there should be some degree of selection for preferentially using that host. This does of course assume that there is a genetic component to host plant preference, which often seems to be the case (Jaenike 1983, Fox 1993). Our results in the present study would seem to indicate that *L. corniculatus* is a more suitable host, but some uncertainty remains. There might be factors in the field – making *O. campestris* a superior host – that cannot be controlled for in the laboratory. Furthermore, our result could partly be an artefact of a better supply of plants with higher quality, since we had better access to fresh *L. corniculatus* towards the end of the rearing period. Based on results of a more recent study using potted plants (A. Bergström, G. Nygren and S. Nylin, unpubl.), we believe that the two plants actually are of more similar quality than indicated here. It does seem unlikely that two host plant species are ever exactly equal in quality, but for the purposes of the following discussion both plant species can be considered as high-quality hosts.

Females from the Stockholm area have retained a high preference for a plant, *O. campestris*, which is never encountered in the wild. Conversely, females from Öland have not evolved local adaptations for preferentially using *O. campestris*, which is common in that area. There are several possibly contributing factors that could in part explain such a result.

Firstly, could it be that differences between the populations cannot evolve, because of lack of genetic variation? Zangerl et al. (2002) describes a case of paradoxical preference for a low-quality host, possibly explained by lack of genetic variation following a colonization event 150 years ago. That there is in fact genetic variation in preference present in the gene pools of *P. icarus* is however suggested from the experimental result that families did show differences in host plant preference.

Secondly, *Oxytropis* and *Lotus*, and perhaps all Fabaceae, might contain identical or very similar chemical cues that reveal them as suitable host plants. Females might not discriminate between plant species but between different levels of chemical cues. A recent study done by Singer and Lee on the butterfly *Melitaea cinxia* (L.) showed that some females discriminate between individual host plants rather than between host plant species (Singer and Lee 2000). A preliminary cafeteria experiment (A. Bergström and S. Nylin, unpubl.) as well as field observations (Thomas and Lewington 1991) indicate that females do discriminate between species within Fabaceae, all plant species are not equally accepted. If *O. campestris* and *L. corniculatus* contain similar amounts of the triggering substance(s), then this could perhaps help explain the obtained results – although this is very difficult to reconcile with the observed variation among families in relative preference for the two species. In addition, there was no indication that individual plants were consistently preferred.

Thirdly, gene flow between areas and populations can counteract local adaptations for host use. Immigration of individual butterflies between Stockholm and Öland within a season is highly unlikely, but the species is common in most parts of Sweden. In a study on distribution and abundance of lycaenid butterflies in Colorado, USA, the study sites were at least 0.5 km apart. This, the researchers claimed, was likely to minimize migration since lycaenids are weak-flying butterflies (Hughes 2000). Personal observations (A. Bergström) suggest that the common blue is a fairly strong flyer for a lycaenid, a view supported by Asher et al. (2001). It is not unlikely that individuals are capable of migrating between the local sites within the two compared areas. If individuals from sites without *O. campestris* on Öland migrate to the experimental sites local adaptation can be precluded at the source sites for this study, where the plant is very abundant. The amount of gene flow between the two compared areas (Öland and Stockholm) is however probably small, but it cannot be ruled out that some “stepping-stone” gene flow contributes to the lack of local adaptation (Peterson 1996).

We suggest, however, that the most relevant interpretation of results such as those presented here is that they challenge the basic assumption behind predictions regarding adaptation to the local plant community. It may well be that there is no or little cost of retaining preference for a host plant never encountered in the wild. If there is no cost then there is no direct selection against retaining an absent host plant in the repertoire, and evolution of host plant range would occur only through genetic drift and other indirect evolutionary processes that do not necessarily produce local adaptation. Several potential costs have been suggested for organisms being

generalists – in this case utilising several different host-plant species – compared to specializing on a narrow range of resources (Janz and Nylin 1997). However, most of these are not relevant as costs of having preferred but absent potential hosts, instead they are typically costs of actually utilizing several hosts.

Some more relevant costs in the present context that have been discussed in the literature recently are: less efficient search images, longer search and handling times, increased risk of predation during search and oviposition and an increased risk of oviposition mistakes (Bernays 2001). The mechanism for these costs might be found in the information processing theory which states that organisms are limited by their neural capacity for information processing (Janz and Nylin 1997, Nylin et al. 2000, Bernays 2001). It has been suggested that efficiency factors could influence both diet breadth and changes in host plant use (Bernays 2001). We suggest that future studies of conservative host plant ranges should include preference studies in situations where also the search behaviour over larger distances can be included. This is because it is possible to imagine that costs of wide host plant ranges occur only or mostly in terms of information processing by ovipositing females searching for plants. Preference differences among populations may be found in more natural situations even though they are not revealed in relatively small cages, such as those typically used in the laboratory.

The lack of local adaptation for resource use in some butterflies (present study, Nylin, S., Nygren, G. and Windig, J., unpubl., Wehling and Thompson 1997) is a phenomenon that we believe is worthy of more attention. It is at present not at all clear how general such patterns are. Recent results (Novotny et al. 2002) suggest that phytophagous insects even in tropical areas may be less specialized than has previously been thought (impacting strongly on estimates of global biodiversity). In other words, it now seems probable that most phytophagous insects have host plant repertoires including several plant species. The degree of conservatism of such host plant ranges will have clear and important consequences for theory on the evolutionary dynamics of host plant utilization, including the possibility of speciation and biodiversity being influenced by host plant use.

In conclusion, we would like to stress that conservatism in host plant use is not necessarily non-adaptive. Retaining a conservative and relatively wide host plant range (including also absent plants), rather than quickly specializing on locally abundant hosts, might be adaptive in a changing environment. Such a species could be pre-set for use of other host plants than the ones being locally abundant at present (cf. Wiklund 1981 on the function of preference hierarchies). In other words, what seems like a conservative trait – under evolutionary constraints – can actually turn out to be a mechanism that enables flexibility under changing circumstances.

The wide and conservative host plant range observed in e.g. *P. icarus* may not be an adaptation for this function in the strict historical sense of the word, i.e. that selection has acted to form and preserve it because it serves as a safe-guard against environmental change. It may be purely due to genetic and other constraints on evolution. Ironically, however, such constraints may clearly have adaptive consequences.

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## References

- Arnold, S. J. 1981. Behavioral variation in natural populations. I. phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. – *Evolution* 35: 489–509.
- Asher, J., Warren, M., Fox, R. et al. 2001. The millennium atlas of butterflies in Britain and Ireland. – Oxford Univ. Press.
- Bernays, E. A. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. – *Annu. Rev. Entomol.* 46: 703–727.
- Boinski, S. 1999. Geographic variation in behavior of a primate taxon: stress responses as a proximate mechanism in the evolution of social behavior. – In: Foster, S. A. and Endler, J. A. (eds), *Geographic variation in behavior*. Oxford Univ. Press, pp. 95–120.
- Craig, T. P., Abrahamson, W. G., Itami, J. K. et al. 1999. Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. – *Oikos* 86: 119–128.
- Diehl, S. R. and Bush, G. L. 1984. An evolutionary and applied perspective of insect biotypes. – *Annu. Rev. Entomol.* 29: 471–504.
- Fiedler, K. 1990. Effects of larval diet on myrmecophilous qualities of *Polyommatus icarus* caterpillars (Lepidoptera: Lycaenidae). – *Oecologia* 83: 284–287.
- Foster, S. A. 1999. The geography of behaviour: an evolutionary perspective. – *Trends Ecol. Evol.* 14: 167–208.
- Fox, C. W. 1993. Host confusion and the evolution of insect diet breadths. – *Oikos* 67: 577–581.
- Funk, D. J. 1998. Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. – *Evolution* 52: 1744–1759.
- Futuyma, D. J., Cort, R. P. and van Noordwijk, I. 1984. Adaptation to host plants in the fall cankerworm (*Alsophila pomataria*) and its bearing on the evolution of host affiliation in phytophagous insects. – *Am. Nat.* 123: 287–296.
- Hughes, J. B. 2000. The scale of resource specialization and the distribution and abundance of lycaenid butterflies. – *Oecologia* 123: 375–383.
- Jaenike, J. 1983. Genetic variation for host preference within and among populations of *Drosophila tripunctata*. – *Evolution* 37: 1023–1033.
- Jaenike, J. and Holt, R. D. 1991. Genetic variation for habitat preference: evidence and explanations. – *Am. Nat.* 137: 67–90.
- Janz, N. and Nylin, S. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a

- test of the information processing hypothesis – Proc. R. Soc. Lond. B Biol. Sci. 264: 701–707.
- Janz, N., Nylin, S. and Wedell, N. 1994. Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. – *Oecologia* 99: 132–140.
- Kuussaari, M., Singer, M. and Hanski, I. 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. – *Ecology* 81: 2177–2187.
- Novotny, V., Basset, Y., Miller, S.E. et al. 2002. Low host specificity of herbivorous insects in a tropical forest. – *Nature* 416: 841–844.
- Nylin, S. 1991. Butterfly life history adaptations in seasonal environments. – PhD thesis, Dept. of Zoology, Stockholm Univ.
- Nylin, S., Bergström, A. and Janz, N. 2000. Butterfly host plant choice in the face of possible confusion. – *J. Insect Behav.* 12: 469–482.
- Peterson, M. A. 1996. Long-distance gene flow in the sedentary butterfly, *Euphilotes enoptes* (Lepidoptera: Lycaenidae). – *Evolution* 50: 1990–1999.
- Sandoval, C. P. 1994. The effects of the relative geographic scale of gene flow and selection on morph frequencies in the walking-stick *Timema cristinae*. – *Evolution* 48: 1866–1879.
- Singer, M. C. and Lee, J. R. 2000. Discrimination within and between host species by a butterfly: implications for design of preference experiments. – *Ecol. Lett.* 3: 101–105.
- Singer, M., Thomas, C. D. and Parmesan, C. 1993. Rapid human-induced evolution of insect-host associations. – *Nature* 366: 681–683.
- Smith, T. B. and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. – *Annu. Rev. Ecol. Syst.* 27: 111–133.
- Thomas, J. and Lewington, R. 1991. The butterflies of Britain & Ireland. – Dorling Kindersley.
- Tolman, T. and Lewington, R. 1997. Collins field guide: butterflies of Britain & Europe. – HarperCollins Publishers.
- Wehling, W. F. and Thompson, J. N. 1997. Evolutionary conservatism of oviposition preference in a widespread polyphagous insect herbivore, *Papilio zelicaon*. – *Oecologia* 111: 209–215.
- Wiklund, C. 1981. Generalist vs specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. – *Oikos* 36: 163–170.
- Zangerl, A. R., Huang, T., McGovern, J. L. et al. 2002. Paradoxical host shift by *Depressaria pastinacella* in North America: is enemy-free space involved? – *Oikos* 98: 431–436.