

Research article

Frequency dependence of host plant choice within and between patches: a large cage experiment

NIKLAS JANZ*, ANDERS BERGSTRÖM and JOSEFIN JOHANSSON

Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden (*author for correspondence, tel.: +46-8-164-048; fax: +46-8-167-715; e-mail: niklas.janz@zoologi.su.se)

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Abstract. Oviposition preference is considered to be one of the most important factors behind patterns of host use among herbivorous insects. However, preference is defined as host plant choice under equal host abundance and availability, and it is likely that frequency-dependent effects will alter the actual pattern of host use beyond what preference trials reveals. The effects of such alterations are poorly known but could be important for the understanding of specialization and host shifts. We investigated how changes in frequency of a preferred and a less preferred host affected movement patterns and egg deposition within and among patches in a polyphagous butterfly, *Polygonia c-album*. Two experiments were carried out in large (8 × 30 m) outdoor cages, artificially divided into distinct patches with different frequencies of the two hosts: one that allowed for limited movement between patches and one that did not. There was a clear effect of frequency on patch selection; females spent more time in and laid more eggs in patches with a high frequency of the preferred host, which will potentially have a large effect on host use by modifying encounter rates in favor of the preferred host. However, there was no significant frequency-dependent plant choice within patches in any experiment. Instead, results indicate that females are distributing their eggs among plants species according to specific likelihoods of oviposition, independent of encounter rates, which is compatible with a strategy of risk-spreading.

Key words: bet-hedging, habitat selection, host range, host use, oviposition preference, specialization

Introduction

Female oviposition preference is recognized as a prime determinant for the pattern of host plant use in herbivorous insects, particularly in those insects that do not normally feed as adults (apart from on carbohydrates), such as butterflies (Thompson, 1988). Preference is typically measured under (and is indeed defined in terms of) equal host plant availability and/or encounter rates (Wiklund, 1974; Singer, 1986; Thompson and Pellmyr, 1991; Singer, 2000). Preference measurements are useful to understand the behavioral and evolutionary mechanisms behind host use, but there are a number of other factors that can alter the effect of female preference as a determinant of host use.

Singer (2000) has suggested the terms “electivity” and “host use” to better account for these factors. Electivity is an emergent property of the interaction that incorporates both female preference and plant acceptability; it describes the proportional use of a plant as a function of its relative abundance. Hence, females with identical host preferences can show different electivity, primarily due to differences in plant acceptability. Finally, the term “host use” can be defined as the actual proportions of food plants in the diet without reference to relative abundance or availability (Singer, 2000).

Of course, females do not normally encounter hosts at equal rates, which can significantly alter the actual pattern of host use. Unfortunately, the factors affecting encounter rates are by no means simple and straightforward. Perhaps the most obvious reason for unequal encounter rates is variation in host plant abundance. Hence, even if preference hierarchies appear to be “fixed” among populations of *Papilio zelicaon* in the northwestern USA, populations differ in host use due to differences in local plant availability and abundance (Thompson, 1993; Wehling and Thompson, 1997).

Apart from the direct effect of frequency, encounter rates can be further modified by frequency-dependent host choice through a modification of the preference hierarchy, e.g. by learning (Rausher, 1978; Prokopy *et al.*, 1982; Papaj and Prokopy, 1989; Allard and Papaj, 1996; Cunningham *et al.*, 2001). The most common effect of frequency-dependent host choice is to increase encounter rates and/or preference for the most common host or prey type (Rausher, 1978; Sherratt and Harvey, 1993; Smithson and MacNair, 1997), a phenomenon known as apostatic choice. The reverse, an increased preference for a rare host type (anti-apostatic choice) appears to be more rare (Sherratt and Harvey, 1993). Anti-apostatic host choice has been suggested to be beneficial when there is a benefit of diet mixing (Greenwood, 1984), which is not applicable to most butterflies and other herbivorous insects where the larvae usually feed on a single plant during its development.

Most work on frequency-dependent food choice in insects has dealt with predation, where quality differences between alternative preys are relatively limited (Sherratt and Harvey, 1993). Herbivorous insects typically use plants that differ substantially in quality, which will have consequences for what the optimal solution will be when the relative frequencies of host plants change. There are several models that have tried to address this problem, but predictions are not always straightforward as there are so many factors at play that can potentially affect the outcome. A recent model by West and Cunningham (2002) tries to handle this variability by using an explorative approach where various factors such as search efficiency or discrimination ability can be incorporated into the basic model. Not surprisingly, the outcome will differ depending on the specific factors that are incorporated into the model, but the general prediction seems to be that under many scenarios, learning will increase

efficiency in host utilization by allowing the insect to concentrate on the most abundant host species (apostatic choice), to some degree even if it is of lower quality (cf. Roitberg *et al.*, 1999).

The efficiency of host choice with changing frequencies can be further complicated by incorporating the cost of acquiring information required to differentiate between hosts, and under some circumstances this can lead to rather unintuitive outcomes (Fox and Lalonde, 1993; Kotler and Mitchell, 1995; Larsson and Ekblom, 1995). This further emphasizes the difficulty of modeling an interaction that depends on so many disparate features, such as plant chemistry, plant abundance and distribution, natural enemies, information costs and adult feeding (c.f. Thompson and Pellmyr, 1991; Nylin *et al.*, 1996; Roitberg *et al.*, 1999; Scheirs and De Bruyn, 2002; West and Cunningham, 2002). Yet another complicating factor is that frequency-dependent host choice can be expressed both within patches (e.g. searching for the most abundant host type in the patch) and between patches (e.g. searching for and/or staying in patches with high abundance of the preferred host) and these effects may or may not be correlated (Thomas and Singer, 1987; Kuussaari *et al.*, 2000; Hanski and Singer, 2001; Nakashima and Hirose, 2003). Furthermore, patch or habitat selection will also be influenced by other factors than host plant density, such as availability of adult food sources (Wiklund and Åhrberg, 1978; Murphy *et al.*, 1984; Brommer and Fred, 1999). In spite of these difficulties, it is important to understand the effect of changing relative frequencies of potential host plants on female preference and/or host use, because it could hold an important key to understanding how evolutionary changes in host use come about, such as changes in specificity and host shifts. There is phylogenetic evidence that suggests that host shifts are mediated by periods of lowered host specificity (Janz *et al.*, 2001), something that could perhaps be triggered by changes in host plant availability and frequency-dependent host choice.

Unfortunately, movements between patches with different frequencies of alternative hosts of different quality, and the subsequent partitioning of eggs between and within these patches, are difficult to study both experimentally and in the field. Hence the lack of empirical investigations of the problem. For the present study, we have been able to create experimental arenas using very large outdoor flight cages, which made it possible to explore the effects of frequency-dependent host plant choice on two levels (patch and individual plant). On the level of the patch, it seems clear that the butterflies should show a preference for patches where the preferred host is abundant. Within patches, predictions are less clear. Apostatic host choice should be favored when the preferred host is most abundant, but models differ in whether this should also hold when it is the less preferred host that is more abundant (Kotler and Mitchell, 1995; Larsson and Ekblom, 1995; Roitberg *et al.*, 1999; West and

Cunningham, 2002). Hence, we test the predictions that (1) females should aggregate in, and lay more eggs in, patches with high frequency of the preferred host, and that (2) females should show apostatic host choice within patches, concentrating on the most abundant host, at least when the abundant host is the most preferred.

Methods

Study organism

Polygonia c-album (the comma butterfly) is a widely distributed polyphagous butterfly in the tribe Nymphalini (Lepidoptera, Nymphalidae). It occurs throughout most of the Palearctic in semi-woodland and around forest edges. Northern populations are univoltine while in the south they produce a brighter colored directly developing summer generation (or several). The summer morph is not developed in Sweden, but can be experimentally induced by manipulating the photoperiod during larval growth (Nylin, 1989).

With a host repertoire that includes plants from seven families and five orders, it is among the most polyphagous butterflies. The focus of the present study is the host choice between *Urtica dioica* (Urticaceae) and *Salix caprea* (Salicaceae), two host plants that are fairly abundant in the habitat types where *P. c-album* is found. *U. dioica* is among the highest ranked hosts in terms of both preference and performance (together with other hosts in Urticales) and *S. caprea* is intermediately ranked (Nylin, 1988; Janz *et al.*, 1994). While the ranking of hosts appear to be similar between populations (at least in Europe) host specificity is highly variable (Nylin, 1988; Janz and Nylin, 1997; Janz, 1998; Nylin *et al.*, 2000). There is also substantial individual variation, at least among Swedish butterflies, with occasional butterflies actually preferring *S. caprea* over *U. dioica* (Janz *et al.*, 1994). However, females of the directly developing summer morph, used in this experiment, are generally more strongly specialized on plants in Urticales (Nylin, 1988). Larval performance has little variation between families and years, and corresponds well with the female's preference hierarchy (Nylin, 1988; Nylin and Janz, 1993; Janz *et al.*, 1994). However, if overall performance is broken up into its components, some individual performance components can diverge from the general pattern so that e.g. adult size is actually maximized on *Salix* rather than on *Urtica* (Nylin *et al.*, 1996). The butterflies used in this study were from the F1 generation of females that were wild-caught in May. Eggs from the wild-caught females were collected and the larvae were reared on *U. dioica* under conditions that are known to produce directly developing butterflies (cf. Nylin, 1989). There is no effect of larval host plant on the subsequent female host preference (cf.

Wiklund, 1974; Williams, 1983; Janz, 2002). Larvae were kept in plastic jars covered with insect net, with constant access to a fresh stalk of *U. dioica*, two larvae in each jar. They were reared in environmentally controlled growth rooms. After eclosion, the butterflies were moved to mating cages, 1 × 1 × 1 m and were given long-day (L/D: 19/5 h light regime) conditions to facilitate mating.

General experimental set-up

The experiments were carried out in large cages of oblong shape with a dome shaped cross section (dimensions W × L × H: 8 × 30 × 4 m) during July of 2003 and 2004. The cages were situated in an open pasture near the Tovetorp Research Station, 100 km southwest of Stockholm, Sweden, with an east-westerly orientation. The cages were covered with fine-meshed net that reduce solar radiation by approximately 25%. The bottom of the cages consisted of natural grassland vegetation, cut to about 1 dm along the cage edges to decrease predation from bugs and spiders. Plant material for use in the experiments were freshly collected each day from a small set of individuals (or clones) growing in the vicinity of the cages.

There were two experimental set-ups. The first was designed to test frequency dependence of host choice on two levels of resolution – patch and plant – hence the cage was divided into two patches with a barrier that allowed some movement between treatments. In the second set-up we used a closed design, where females were confined to one of the treatments without any possibility to move between them. We will henceforth refer to these set-ups as the “movement” and “no-movement” experiments.

Movement experiment

In the movement experiment, the cages were divided into two patches by free hanging camouflage nets, hung in a maze-like fashion in a 2 m wide barrier zone in the center of the cage. The barrier zone served the function of creating two distinct, equally sized patches, while still allowing some migration between the patches. Ample sources of adult food were provided in both compartments in the form of potted nectar plants as well as sponges with a diluted sucrose solution. Host plants were presented in bottles, standing in a 3 × 4 + 3 grid, making a total of 15 plants in each patch. There were two treatments: one with a high frequency of the preferred host *U. dioica* and a low frequency of the lower ranked *S. caprea* (hereafter referred to as the HU treatment), and one with the reversed frequencies (the HS treatment). The ratio between high and low frequency was 1:4 (3:12). Two adjacent cages were used in parallel to control for possible effects of day and position. The east-westerly orientation of

the treatments was switched every day in each cage and the two cages always received reciprocal set-ups.

Ten mated and individually marked females were released into each cage compartment at 11.00 A.M., five in each patch. They were released from a cooler onto a sponge with diluted sugar. At 13.00, 15.00 and 18.00 the location (compartment) of each female in the cage was recorded. After the final recording at 18.00, the females were removed from the cage and the eggs were counted. On the next day, the plants were exchanged for fresh ones, treatments were switched and 10 new females were released into the cage. The trial was repeated 6 times.

Patch occupancy was measured as the accumulated time each female spent in a patch, where two consecutive observations in the same patch were taken to mean that the female had spent the intervening time in that patch. When a female were noted from different patches in two consecutive recordings, her occupancy was “zeroed” and started anew in the new patch. The occupancy data were analyzed with the Wilcoxon matched-pairs signed-rank test. This analysis assumes that the butterflies did not freely move across the barrier between observations. This assumption was validated by testing if previous patch occupation was a good predictor for patch occupation in the next observation occasion, using a chi-square goodness-of-fit test. Oviposition data were collected at the end of each day. The oviposition data were analyzed with the two-sample Wilcoxon rank-sum (Mann–Whitney) test. As there was no way to differentiate the eggs oviposited by different females, we instead used plant individuals as data points. This design allowed us to evaluate population-level host choice on the level of the patch and of individual plants. However, it did not allow us to evaluate host preference of individual butterflies.

No-movement experiment

To be able to assess individual oviposition preference, and to safeguard against possible interactions between patch- and plant preference, we performed a second experiment where each female were flown individually. In this no-movement experiment, two adjacent cages were divided into three discrete compartments, completely separated from each other by walls of insect net, producing 6 equal arenas with a ground area of 10×8 m. In these arenas, host plants of the same types as in the first experiment were presented in a $2 \times 4 + 2$ grid, using the same 1:4 ratios between plant species. Again, the plant positions were randomly assigned at the beginning of each trial. On each day, one naive female was released into each cage compartment at 11.00 and removed at 18.00. Thus, each female only experienced one treatment (either HU or HS). Treatments were matched pair-wise in the two cages so that each compartment could be compared with an identically positioned compartment in the adjacent cage.

Eggs were counted after each treatment and data on both total egg deposition and eggs per plant (corrected for frequency) were analyzed with the Wilcoxon matched-pairs signed-rank test, using individual females as data points.

Results

Movement experiment: frequency dependence between patches

First, to test whether butterflies really perceived the barrier as an obstruction in the movement experiment, we tested if previous patch occupation was a good predictor of current patch occupation, and there were significantly fewer movements across the barrier than would be expected if butterflies moved freely throughout the whole cage ($\chi^2 = 76.13$, $df = 1$, $p \ll 0.001$). Hence, we found it justified to consider the treatments as distinct patches. The mean number of documented movements across the barrier was 1.15 per female over the whole day ($\pm SE$ 0.11), with no significant differences in direction of movement. There were also no significant differences in total number of movements between observation times, i.e. females were equally likely to cross the barrier at all times of the day.

Overall, the females spent significantly more time in the HU treatment, indicating a patch-level preference for patches with a high frequency of the preferred host (Wilcoxon signed-rank test, $n = 60$, $z = -2.065$, $p = 0.039$; Fig. 1a). The east–westerly orientation of the cage sections had no significant effect (Wilcoxon signed-rank test).

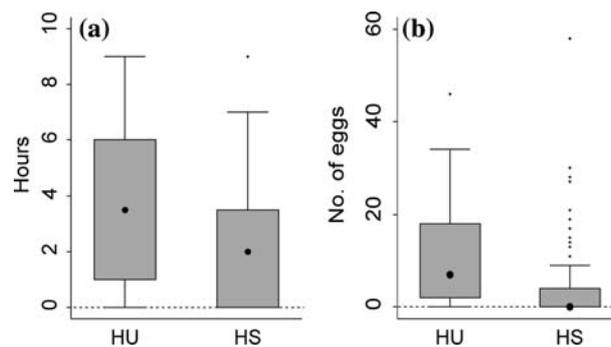


Figure 1. Frequency-dependent patch selection by ovipositing females of *P. c-album* in the movement experiment. HU = High *Urtica dioica* (high frequency of preferred host), HS = High *Salix caprea* (low frequency of preferred host). Medians with upper and lower quartiles, upper and lower adjacent values, and outside values. (a) Occupancy in the two treatments as measured by the accumulated hours each female spent in the two patches during the course of the trial. Each trial lasted for one day (7 h). n (number of females) = 60. (b) Total number of eggs deposited in the two treatments per plant and day. n (number of plants) = 180.

The higher patch occupancy in the HU treatment was also manifested in a higher egg output in patches with a high frequency of the preferred host; there was a significantly higher level of oviposition in the HU treatment (two-sample Wilcoxon rank-sum (Mann–Whitney) test, $n = 180$, $z = -5.701$, $p < 0.001$). The patch with a high frequency of the preferred *U. dioica* received on average 10.1 eggs/plant while the patch with a low frequency of *U. dioica* received 4.1 eggs/plant (Fig. 1b). There were no significant position effects between the eastern and western sides of the cage or of treatment day (Mann–Whitney and Kruskal–Wallis tests).

Movement experiment: frequency dependence within patches

In the movement experiment, *U. dioica* received a substantially larger amount of eggs than *S. caprea* in both treatments (Two-sample Wilcoxon rank-sum (Mann–Whitney) tests, $n = 90$, $z_{HU} = 4.104$, $z_{HS} = 3.625$, $p < 0.001$). The mean number of eggs per plant was similar for each of the two plant species between patches, e.g. a nettle in the HS treatment received as many eggs in absolute numbers as a nettle in the HU treatment (Fig. 2a). This does not take into account that the total amount of eggs differed between patches. When doing so, by calculating the proportion of the total egg deposition in the patch found on each plant, there still were no significant frequency dependence (Fig 2b). The only effect that even came close to significance was for a higher

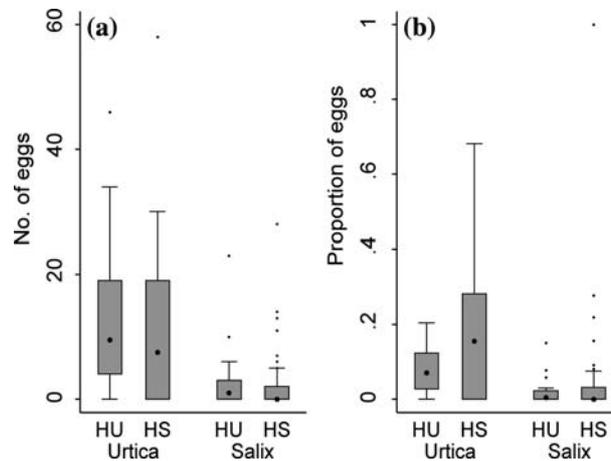


Figure 2. Egg deposition by ovipositing females of *P. c-album* on *Urtica dioica* and *Salix caprea* within patches in the movement experiment. HU = High *Urtica* (high frequency of preferred host), HS = High *Salix* (low frequency of preferred host). n (number of plants) = 180. Medians with upper and lower quartiles, upper and lower adjacent values, and outside values. (a) Total number of eggs deposited per plant and day. (b) Proportion of the total number of eggs laid in the patch that were deposited on each plant during one day of oviposition.

use of *U. dioica* in patches where this preferred host was rare (two-sample Wilcoxon rank-sum (Mann–Whitney) test, $n = 90$, $z = -1.67$, $p = 0.09$).

No-movement experiment

In the no-movement experiment, there was once again a higher total egg deposition in the HU treatment (Wilcoxon matched-pairs signed-rank test, $n = 16$, $z = -2.01$, $p = 0.04$). Thus, if females are confined to a habitat with mostly poor quality plants, they will lower their oviposition rate rather than increase oviposition on the poor hosts (Fig. 3). Moreover, there was no difference between treatments in relative electivity; the number of eggs per plant was not significantly different between treatments (Wilcoxon matched-pairs signed-rank tests $n = 16$, $p \gg 0.05$). Hence, the results of the two experiments agreed in that there was no significant frequency-dependent host plant choice within patches.

Discussion

Females of *Polygonia c-album* showed a clear frequency dependent patch selection with regard to host plants (Fig. 1). There was a significantly higher level of occupancy in the patch with high frequency of the preferred host in the movement experiment, and the total amount of eggs laid was also significantly higher in this treatment. The aggregation of females in the HU treatment could

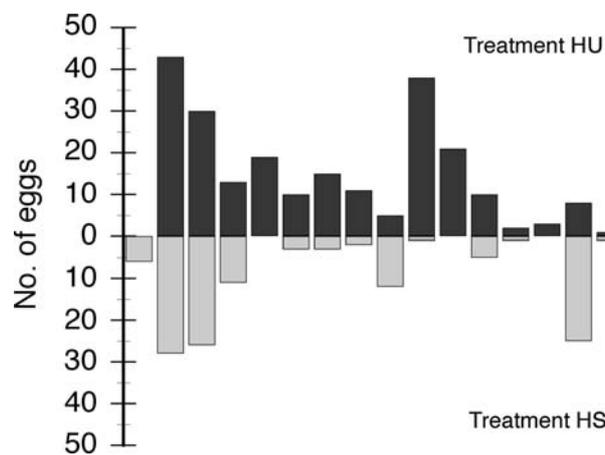


Figure 3. Total amount of eggs deposited by single females of *P. c-album* in the no-movement experiment. Each horizontal bar represents the total egg deposition by one matched pair of females, one in each treatment. HU = High *Urtica* (high frequency of preferred host), HS = High *Salix* (low frequency of preferred host). n (number of females) = 32.

be a result of active inspection of the available habitat before oviposition, or it could be caused by a more passive effect of different motivation to stay in the present patch. The observed minimum number of movements between patches was rather low and most butterflies remained in the same patch for much of the experiments. This would suggest that the reason for the aggregation in the HU treatment is more due to different motivations to stay or leave, than by an active inspection of all available habitat.

Within patches, the pattern was less clear. As expected, females did prefer *U. dioica* to *S. caprea* in both the HU and HS treatments, but there was no clear evidence for frequency-dependent host choice (Fig. 2). In particular, there was no support for apostatic host choice in either of the treatments. The only trend that bordered to statistical significance was towards anti-apostatic host choice in the HS treatment of the movement experiment, i.e. an increased preference for the preferred host when it was rare. However, there was no corresponding trend in the no-movement experiment, so any anti-apostatic effect on host choice is speculative at best. Still, the conclusion that no apostatic host choice occurred appears well founded.

It was in fact quite striking that the butterflies appeared to distribute the eggs in a very uniform manner in both experiments; within plant species, the amount of eggs deposited per plant did not differ much between treatments. Indeed, the larger amount of eggs found in the HU treatments can entirely be explained by the higher frequency of the preferred host. Interestingly, the fact that the total number of eggs oviposited differed between treatments also in the no-movement trial implies that the females are withholding eggs rather than increasing oviposition on the less favorable host. Consequently, patch selection must be more important for the total egg output than host plant selection within patches.

Why did we not see any apostatic host choice, at least for the preferred host? Why did they persist in laying equal amounts of eggs on the inferior plant (*S. caprea*) even when it was rare?

On the face of it, this does appear counterintuitive. It is possible that conditioning requires longer time, and hence did not have time to develop in this experimental set-up. Another way to explain this behavior is that it serves as a means to spread the risks between several hosts if host profitability is subject to unpredictable variation between seasons (bet-hedging). Under such circumstances genotypes may favor lower variance in fitness at the expense of lower arithmetic fitness. Risk-spreading could potentially select for the use of several hosts, although its effect remains uncertain and will depend on the magnitude of environmental variation and the difference in profitability between hosts (cf. Hopper, 1999). It has even been suggested that bet-hedging could favor specialization on the best host under some circumstances, as long as this reduces variance in geometric fitness, which would be the case if the difference in

profitability between hosts is large and the preferred host is abundant (Roitberg *et al.*, 1999). The circumstances under which *P. c-album* flies in Sweden can probably be characterized as unpredictable with regard to abiotic factors such as temperature and humidity, and relative host plant abundance also varies substantially between patches in their natural habitat. The relative profitability of the hosts in the current study is a complex relationship in itself (Nylin *et al.*, 1996). While *U. dioica* provides higher growth rate and shorter development time (Janz *et al.*, 1994), a higher propensity for direct-development (Wedell *et al.*, 1997), and more nitrogen-rich spermatophores (Wedell, 1996), *S. caprea* allows larger adult size and higher female fecundity (Janz *et al.*, 1994). Even if *U. dioica* will offer higher overall offspring performance in most circumstances, some individual performance components will actually be higher on *S. caprea*. From the female's point of view, it may be possible to predict the effects that each plant will have on different aspects of performance, but it will be much more difficult to predict the external conditions that the offspring will meet during growth and after successful eclosion and hence the relative influence that the different performance components will have on offspring fitness. Taken together this makes risk-spreading a relatively plausible factor behind the egg-laying pattern of *P. c-album*.

A common feature of models of host choice, and of foraging theory in general, is that they typically assume an all-or-none response; females should either accept or reject all plants from a given category. There should be no intermediate responses, where a female has a probability between 0 and 1 of accepting a plant for oviposition. This cannot be strictly true, as we typically find that females oviposit on a lower-ranked plant in simultaneous choice trials, even when there is a higher-ranked plant available. In fact, if oviposition were an all-or-none decision, simultaneous choice trials would not work; females should always lay all their eggs on the most preferred plant in the trial. Instead, we typically find that eggs are distributed across plants according to rather fixed ratios. The results, although not quantitatively comparable, also appear to agree qualitatively with no-choice trials, so it does not appear to be an artifact of the method (Janz and Thompson, 2002). In itself, this indicates that oviposition cannot simply be an all-or-none decision. The results from this study reinforces this impression, as the females appeared to spread their eggs across the potential host plants with relatively fixed ratios across patches, regardless of frequency. A simple mechanism to explain this behavior would be that each plant species is represented by a certain probability of oviposition, upon encounter, that could be anywhere between 0 and 1. This probability may be further adjusted during the female's life time by learning, or motivation. An interesting side-effect of the oviposition strategy revealed by our experiments would be that females confined to poor habitats, with low abundance of the preferred hosts, would have lower

realized fecundity. We would therefore expect that under such circumstances, the probability of accepting the abundant lower-ranked plant would indeed be adjusted upwards with time. The important difference between this mechanism and the classical “threshold model” first formally described by Courtney *et al.* (1989) is that the probability of oviposition is tied to specific plant species and could conceivably be independently modified on different host species during a female’s life time. With time, small evolutionary (between generation) modifications of these probabilities will lead to changes in specificity, larger modifications will lead to host shifts. With this view, host shifts and specificity are different manifestations of the same underlying process, differing only in the magnitude of the change (cf. Janz, 1998, 2003). Thus, by altering the probabilities of oviposition tied to each plant species, changes in plant abundance and patchiness can initiate evolutionary changes in specificity and host shifts.

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References

- Allard, R.A. and Papaj, D.R. (1996) Learning of leaf shape by pipevine swallowtail butterflies: a test using artificial leaf models. *J. Insect Behav.* **9**, 961–967.
- Brommer, J.E. and Fred, M.S. (1999) Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. *Ecol. Entomol.* **24**, 125–131.
- Courtney, S.P., Chen, G.K. and Gardner, A. (1989) A general model for individual host selection. *Oikos* **55**, 55–65.
- Cunningham, J.P., West, S.A. and Zalucki, M.P. (2001) Host selection in phytophagous insects: a new explanation for learning in adults. *Oikos* **95**, 537–543.
- Fox, C.W. and Lalonde, R.G. (1993) Host confusion and the evolution of insect diet breadths. *Oikos* **67**, 577–581.
- Greenwood, J.J.D. (1984) The functional basis of frequency-dependent food selection. *Biol. J. Linnean Soc.* **23**, 177–199.
- Hanski, I. and Singer, M.C. (2001) Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. *Am. Nat.* **158**, 341–353.
- Hopper, K.R. (1999) Risk-spreading and bet-hedging in insect population biology. *Ann. Rev. Entomol.* **44**, 535–560.
- Janz, N. (1998) Sex-linked inheritance of host-plant specialization in a polyphagous butterfly. *Proc. Royal Soc. Lond. Ser. B Biol. Sci.* **265**, 1675–1678.
- Janz N. (2002) Evolutionary ecology of oviposition strategies. In M. Hilker and T. Meiners (eds) Blackwell, Berlin, pp. 349–376.
- Janz N. (2003) Sex-linkage of host plant use in butterflies. In C.L. Boggs, W.B. Watt and P.R. Ehrlich (eds) University of Chicago Press, Chicago, pp. 229–239.

- 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. Royal Soc. Lond. Ser. B Biol. Sci.* **264**, 701–707.
- Janz, N. and Thompson, J.N. (2002) Plant polyploidy and host expansion in an insect herbivore. *Oecologia* **130**, 570–575.
- Janz, N., Nylin, S. and Nyblom, K. (2001) Evolutionary dynamics of host plant specialization: a case study of the tribe Nymphalini. *Evolution* **55**, 783–796.
- 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.
- Kotler, B.P. and Mitchell, W.A. (1995) The effect of costly information in diet choice. *Evol. Ecol.* **9**, 18–29.
- 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.
- Larsson, S. and Ekbom, B. (1995) Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos* **72**, 155–160.
- Murphy, D.D., Menninger, M.S. and Ehrlich, P.R. (1984) Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. *Oecologia* **62**, 269–271.
- Nakashima, Y. and Hirose, Y. (2003) Sex differences in foraging behaviour and oviposition site preference in an insect predator, *Orius sauteri*. *Entomol. Exp. Appl.* **106**, 79–86.
- Nylin, S. (1988) Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae). *Oikos* **53**, 381–386.
- Nylin, S. (1989) Effects of changing photoperiods in the life cycle regulation of the comma butterfly, *Polygonia c-album* (Nymphalidae). *Ecol. Entomol.* **14**, 209–218.
- Nylin, S. and Janz, N. (1993) Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. *Ecol. Entomol.* **18**, 394–398.
- Nylin, S., Janz, N. and Wedell, N. (1996) Oviposition plant preference and offspring performance in the comma butterfly: Correlations and conflicts. *Entomol. Exp. Appl.* **80**, 141–144.
- Nylin, S., Bergström, A. and Janz, N. (2000) Butterfly host plant choice in the face of possible confusion. *J. Insect Behav.* **13**, 469–482.
- Papaj, D.R. and Prokopy, R.J. (1989) Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.* **34**, 315–350.
- Prokopy, R.J., et al. (1982) Associative learning in egg-laying site selection by apple maggot flies. *Science* **218**, 76–77.
- Rauscher, M.D. (1978) Search image for leaf shape in a butterfly. *Science* **200**, 1071–1073.
- Roitberg, B.D., Robertson, I.C. and Tyerman, J.G.A. (1999) Vive la variance: a functional oviposition theory for insect herbivores. *Entomol. Exp. Appl.* **91**, 187–194.
- Scheirs, J. and De Bruyn, L. (2002) Integrating optimal foraging and optimal oviposition theory in plant-insect research. *Oikos* **96**, 187–191.
- Sherratt, T.N. and Harvey, I.F. (1993) Frequency-dependent food selection by Arthropods – a review. *Biol. J. Linn. Soc.* **48**, 167–186.
- Singer, M.C. (1986) The definition and measurement of oviposition preference in plant-feeding insects. In J.R. Miller and T.A. Miller (eds) Springer-Verlag, New York, pp. 65–94.
- Singer, M.C. (2000) Reducing ambiguity in describing plant-insect interactions: “preference”, “acceptability” and “electivity”. *Ecol. Lett.* **3**, 159–162.
- Smithson, A. and MacNair, M.R. (1997) Density-dependent and frequency-dependent selection by bumblebees *Bombus terrestris* (L) (Hymenoptera: Apidae). *Biol. J. Linn. Soc.* **60**, 401–417.
- Thomas, C.D. and Singer, M.C. (1987) Variation in host preference affects movement patterns within a butterfly population. *Ecology* **68**, 1262–1267.
- Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol. Exp. Appl.* **47**, 3–14.
- Thompson, J.N. (1993) Preference hierarchies and the origin of geographic specialization in host use in swallowtail butterflies. *Evolution* **47**, 1585–1594.
- Thompson, J.N. and Pellmyr, O. (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Ann. Rev. Entomol.* **36**, 65–89.

- Wedell, N. (1996) Mate quality affects reproductive effort in a paternally investing species. *Am. Nat.* **148**, 1075–1088.
- Wedell, N., Nylin, S. and Janz, N. (1997) Effects of larval host plant and sex on the propensity to enter diapause in the comma butterfly. *Oikos* **78**, 569–575.
- 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.
- West, S.A. and Cunningham, J.P. (2002) A general model for host plant selection in phytophagous insects. *J. Theoret. Biol.* **214**, 499–513.
- Wiklund, C. (1974) Oviposition preferences in *Papilio machaon* in relation to the host plants of the larvae. *Entomologia Experimentalis et Applicata* **17**, 189–198.
- Wiklund, C. and Åhrberg, C. (1978) Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). *Oikos* **31**, 169–183.
- Williams, K.S. (1983) The coevolution of *Euphydryas chalcedona* and their larval host plants. III. Oviposition behavior and host plant quality. *Oecologia* **56**, 336–340.