

The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis

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SUMMARY

Recent theoretical studies have suggested that host range in herbivorous insects may be more restricted by constraints on information processing on the ovipositing females than by trade-offs in larval feeding efficiency. We have investigated if females from polyphagous species have to pay for their ability to localize and evaluate plants from different species with a lower ability to discriminate between conspecific host plants with differences in quality. Females of the monophagous butterflies *Polygona satyrus*, *Vanessa indica* and *Inachis io* and the polyphagous *P. c-album* and *Cynthia cardui* (all in Lepidoptera, Nymphalidae) were given a simultaneous choice of stinging nettles (*Urtica dioica*) of different quality. In addition, the same choice trial was given to females from two populations of *P. c-album* with different degrees of specificity. As predicted from the information processing hypothesis, all specialists discriminated significantly against the bad quality nettle, whereas the generalists laid an equal amount of eggs on both types of nettle. There were no corresponding differences between specialist and generalist larvae in their ability to utilize poor quality leaves. Our study therefore suggests that female host-searching behaviour plays an important role in determining host plant range.

1. INTRODUCTION

The problem of resource specialization versus generalization among plant-feeding insects has been a long-standing enigma in the field of insect–host plant interactions. The puzzle, as Futuyma has pointed out (Futuyma 1991), is why there are so many specialists. What is the advantage of a restricted host range, or, alternatively, what is the cost of a wide host range? There are many apparent advantages of a wide host range: decreased search time, a more balanced diet, a buffer against fluctuating or otherwise changing environments, a way of spreading the risks, to name a few. Therefore, the predominance of specialists over generalists suggests that there must exist a fundamental trade-off between a wide host range and some aspect of insect–host plant utilization. To date, quite a few studies have looked for a physiological trade-off with some measure of offspring performance (i.e. survival, growth and reproduction), assuming that performance is negatively correlated on different host plants. However, in most cases performance on different hosts has turned out to be uncorrelated or even positively correlated (e.g. Futuyma & Wasserman 1981; Futuyma & Philippi 1987; Carriere & Roitberg 1994; Fox & Caldwell 1994); Via (1991), Mackenzie (1996) and a reanalysis by Fry (1992) of data from Karowe (1990) being the only studies to our knowledge that have actually been able to demonstrate a negative correlation.

Although there may be many reasons why such physiological trade-offs have been so hard to demonstrate (Joshi & Thompson 1995; Fry 1996), it appears profitable to start looking for explanations in other places. In this paper we wish to focus on the role of the ovipositing female and point at a possible behavioural cost of a broad host range that has been less explored than the trade-off in performance on different plants, and that can add to the understanding of both host range expansion and specialization.

The potential host range of the larvae is often wider than the range of plants actually oviposited on by females (e.g. Wiklund 1975; Smiley 1978; Roininen & Tahvanainen 1989), which in itself suggests that the limits to host range are set by female behaviour rather than by larval feeding capacities. Some authors have also pointed out that there may exist constraints on information processing (e.g. Courtney 1983; Futuyma 1983), and more recently several theoretical studies have shown how this could contribute to the evolution of diet specialization (Fox & Lalonde 1993; Bernays & Wcislo 1994; Kotler & Mitchell 1995; Larsson & Ekbom 1995; Bernays 1996).

An egg-laying female must possess an identification system that correctly separates acceptable oviposition sites from non-acceptable sites. Errors in defining the boundary between these groups (i.e. decisions to oviposit on a plant that will not support growth and survival of her offspring, and decisions not to oviposit on a plant that would) can be very costly. In addition,

she needs a system to rank the acceptable plants or plant parts according to their profitability (see, for example, Courtney *et al.* 1989). To correctly identify all acceptable host plants from other plants (indeed, from all other objects) and to rank the acceptable plants and plant parts will be increasingly difficult with an increasing host range. Each plant has its own identification problems; for example, there may be specific enemies associated with certain plants (Price *et al.* 1980; Bernays & Graham 1988; Bernays 1989) that need to be identified and adapted to, or there may be risks of confusion with other non-acceptable plants (Fox & Lalonde 1993; Nylin & Janz 1993; Larsson & Ekbom 1995). As polyphagous insects often feed on phylogenetically and chemically separated plants, inclusion of a new host plant into the repertoire will not simply involve an expansion of the boundaries defining what is an acceptable host, it will call for completely new boundaries, wholly new sets of identification rules to correctly separate this novel plant from the background noise.

Assuming that there is a limit to the amount of information an egg-laying female can receive and process while searching for a good oviposition site (e.g. Bernays 1996), it follows that a polyphagous female must divide her neural capacities between the different host plants in her repertoire, whereas a monophagous female can allocate all her capacities to evaluate intraspecific variation in host plant quality. Thus a polyphagous female should have to pay for her ability to evaluate a greater number of host plant species with a decreased capacity to evaluate intraspecific host plant variation. Assuming that time is a scarce resource it is more likely that this decreased capacity is manifested as a higher error rate, rather than a longer decision time.

In this paper we test the prediction that polyphagous butterflies should have a higher error rate than monophagous butterflies when choosing between conspecific host plants with differences in quality. We perform both a comparative study using five species in the tribe Nymphalini, and an intraspecific study of two populations of *Polygona c-album* (the comma butterfly) with varying degrees of specificity.

2. MATERIALS AND METHODS

(a) Study species

All species in the study belong to the tribe Nymphalini, a group containing species with both tropical and holarctic distributions.

The Eurasian comma butterfly, *Polygona c-album*, is polyphagous and feeds on plants from seven families: Urticaceae, Ulmaceae and Cannabidaceae, Salicaceae, Grossulariaceae, Betulaceae and Corylaceae. Of these, the plants in Urticales (the first three families) are generally preferred by the ovipositing females, and they also support the highest larval growth rate (Nylin 1988; Janz *et al.* 1994). The North American *P. satyrus*, the golden anglewing, is a specialist on *Urtica*. Some populations have been reported to feed on Salicaceae as well (Scott 1986), but this did not seem to be the case for the females used in this study; they refused to lay eggs on *Salix* and the larvae did not survive on it (personal observation).

Vanessa indica (the Indian admiral) is a specialist on plants in the Urticaceae, most notably on *Urtica* and *Parietaria*. It has a disjunct distribution, with a main area in Asia and isolated populations on the Canary Islands and on Madeira, off the African Atlantic coast. *Cynthia cardui*, the painted lady, is a generalist, feeding on plants in the Asteraceae, Urticaceae and Malvaceae, along with a number of other plants (Ackery 1988). It has an extremely cosmopolitan distribution, occurring on all continents except South America. The Eurasian peacock, *Inachis io*, is a specialist on *Urtica*. Unlike any of the other species, however, it is also a clutch layer, laying hundreds of eggs in each batch.

All temperate species are potentially multivoltine and hibernate as adults. *C. cardui* is a migrant that does not overwinter in the temperate zones it migrates into over the summer months. All butterflies used in this study came from the first generation of laboratory stocks stemming from wild-caught females, with the exception of *C. cardui* and the English *P. c-album*, that were obtained from commercial butterfly providers.

The *P. c-album* females used in the first experiment were taken from a population near Stockholm, Sweden, in May 1994, and the *P. satyrus* females were caught in the Blue Mountains, Washington, USA, also in May 1994. The original *V. indica* females were caught in the Tokyo area of Japan in April 1996, and *I. io* were caught in the vicinity of Stockholm, Sweden, in May 1996. The Swedish *P. c-album* used in the intraspecific study originally came from the same population mentioned above, near Stockholm, Sweden, in May 1995.

Directly developing (non-diapausing) individuals of all species were used in the experiments.

(b) Oviposition experiment 1

In a first study, naive females of *Polygona c-album* and *P. satyrus* were placed in cages and given a simultaneous choice between two nettles (*Urtica dioica*) with selected differences in quality. One nettle was fresh and green, the other was older with partly yellowish-brown leaves. Plant pairs were taken from the same natural populations around the university campus, and the pairs were chosen so that the difference between the two plants was as large as possible (without using wilted plants) and was obvious to a human eye. Both nettles in each pair were cut to the same size and shape, thus making up pairs of nettles that resembled each other in every aspect except leaf colour/quality. The plants were placed at equal distance from the central light and nectar sources. Light bulbs (100 W) over each cage were used as the sole light source. Eggs were counted (and removed from the plants) once every day for 5–8 d, and the nettle-pairs were then rotated among all the cages (of both species) to compensate for relative differences in quality between the pairs. The positions of the nettle categories within the cages were also switched daily, to control for position effects. When the ‘good’ nettle in a pair showed signs of deteriorating or when the ‘bad’ nettle lost its turgor, the whole pair was replaced with a new one. The *P. c-album* females were kept individually in cages (0.5 × 0.5 × 0.5 m) but for practical reasons the *P. satyrus* females had to be kept two or three to a cage in larger cages (0.5 × 1 × 1 m). However, the distance between the plants in the cages was kept constant, and mean values for each cage were used as data points for the cages containing more than one female. The data were analysed with analysis of variance (ANOVA) using log-transformation to obtain homogeneity of variances, with each egg-counting occasion making a data point. This allowed for an estimation of the variance within and between females or cages as well as between species.

(c) Oviposition experiment 2

In this experiment we investigated the ability of females of the specialists *Vanessa indica* and *Inachis io* and the generalist *Cynthia cardui* to discriminate between nettles of good and bad quality. The following oviposition experiments were conducted in a similar way to that of experiment 1, with the difference that the total number of eggs oviposited by one female during the whole choice trial (normally 2 d of ovipositing) were used as a data point. The data for *V. indica* and *C. cardui* were log-transformed to obtain homogeneity of variances and then analysed using paired *t*-tests. Data for *I. io* were analysed with a sign test, as each female seldom laid more than one clutch during the choice trial. In these and all the following trials the females were kept individually in cages of $0.5 \times 0.5 \times 0.5$ m size.

(d) Oviposition experiment 3

In the intraspecific comparison of *P. c-album* we first conducted a choice trial with the high-ranked *Urtica dioica* and the lower ranked *Salix caprea* (cf. Nylin 1988; Janz *et al.* 1994) to assess a difference in specificity over host plant species. This choice trial was performed with an identical set-up to the trial with nettles of different quality, and the interaction between population and plant species were analysed in a two-way ANOVA with log-transformed data. The intraspecific comparisons of discrimination between nettles of good and bad quality again used the same set-up as was used in experiment 2, and were analysed with a paired *t*-test on log-transformed data.

(e) Larval rearings

We reared larvae on nettles belonging to the two categories mentioned above ('high' and 'low' quality) to control for the possibility that the predicted difference in discrimination may reflect a high capacity to utilize poor quality nettles. Larvae from Swedish and English *P. c-album*, *V. indica* and *C. cardui* were used in this experiment. The larvae were reared individually in jars containing a plant of either category in 12 h day length and at 17 °C. The plants were checked daily and were exchanged if wilted. We measured survival and weight after 8 d. For each species or population survival was analysed with a χ^2 test against the null hypothesis that there should be no difference in survival on the two categories of plants. Weight after 8 d was analysed with a non-parametric Mann–Whitney *U*-test, as the variances differed too much between groups to justify a parametric test, even after transformation.

3. RESULTS

(a) Oviposition experiment 1

As predicted, ovipositing females of the monophaga-

Table 1. Two-way analysis of variance for preference of *Polygona satyrus* females

(Choice between good- and poor-quality stalks of nettle (*Urtica dioica*); $n = 44$ (number of measurements), dependent variable is log-transformed.)

source	SS	d.f.	MS	F	p
cage	1.885	2	0.943	0.782	0.465
nettle	18.673	1	18.673	15.492	0.000
cage \times nettle	1.297	2	0.649	0.538	0.588
error	45.803	38	1.205		

Table 2. Two-way analysis of variance for preference of *Polygona c-album* females

(Choice between good- and poor-quality stalks of nettle (*Urtica dioica*); $n = 92$ (number of measurements), dependent variable is log-transformed.)

source	SS	d.f.	MS	F	p
female	9.604	6	1.601	2.163	0.055
nettle	0.048	1	0.048	0.065	0.799
female \times nettle	4.688	6	0.781	1.056	0.396
error	57.715	78	0.740		

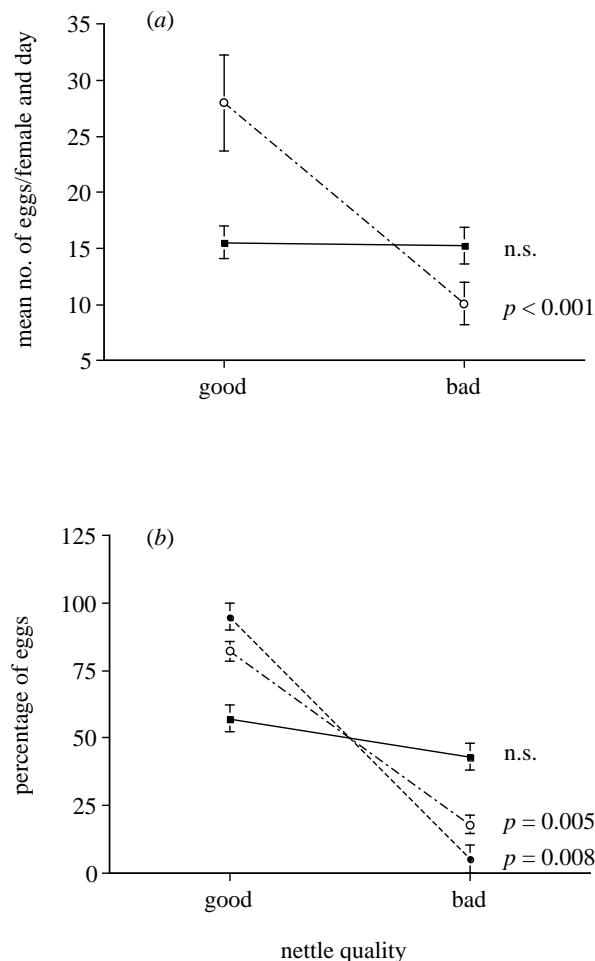


Figure 1. Results from interspecific comparisons of oviposition preference for nettle stalks of good and poor quality. (a) Number of eggs per female and day oviposited on the two categories of nettle by the Swedish population of *Polygona c-album* (generalist; filled squares, solid line) and *P. satyrus* (specialist; open circles, dot-dash line). (b) Percentage of eggs oviposited on the two categories of nettle by *Cynthia cardui* (generalist; filled squares, solid line), *Vanessa indica* (specialist; open circles, dot-dash line) and *Inachis io* (specialist and clutch-layer; filled circles, dash line). Means \pm standard error. See text for further explanation.

gous *Polygona satyrus* showed a marked preference for the good-quality nettles over the poor-quality nettles, whereas the polyphagous *P. c-album* females did not discriminate between the two types of nettle at all. *P. satyrus* females laid on average (\pm s.e.) 28.0 ± 4.3 eggs per day on the 'good' nettle and 10.1 ± 1.9 eggs per

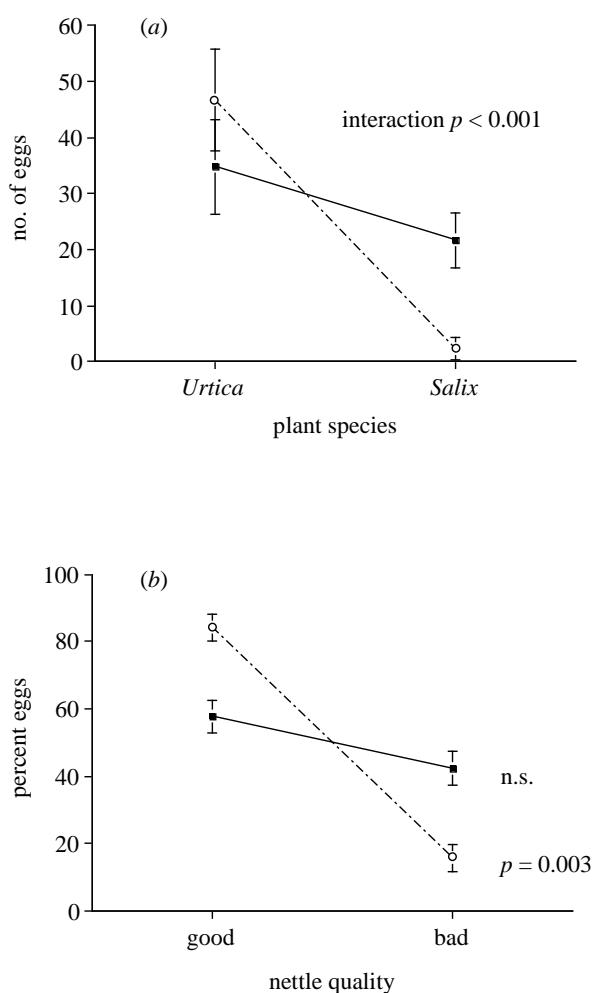


Figure 2. Results from the intraspecific comparison of oviposition preference of Swedish (filled squares, solid line) and English (open circles, dot-dash line) populations of *Polygona c-album*. (a) Number of eggs oviposited on *Urtica dioica* (stinging nettle) and *Salix caprea* (sallow). (b) Percentage of eggs oviposited on good and bad quality stalks of stinging nettle. Means \pm standard error. See text for further explanation.

day on the 'bad' nettle ($p < 0.001$, ANOVA; table 1), and *P. c-album* laid a mean of 15.6 ± 1.5 eggs per day on the 'good' and 15.2 ± 1.6 eggs per day on the 'bad' nettle ($p = 0.451$, ANOVA; table 2). Thus the two species differed significantly in how they responded to within-species variation in host plant quality (figure 1a). There were no significant differences between the females or cages in either of the two butterfly species (tables 1 and 2).

(b) Oviposition experiment 2

The results of the comparison between the specialists *Vanessa indica* and *Inachis io*, and the generalist *Cynthia cardui*, were similar to the results of the first experiment (figure 1b). Whereas females of the generalist showed no discrimination between the two categories of nettle (paired t -test, $n = 14$, $t = 1.48$, $p = n.s.$), both specialists clearly did (*V. indica*: paired t -test, $n = 10$, $t = 7.48$, $p < 0.001$; *I. io*: sign test, $n = 10$, $z = 2.665$, $p = 0.008$).

Table 3. Two-way analysis of variance for female preference. Females belonging to Swedish and English populations of *Polygona c-album*

(Choice between *Urtica dioica* and *Salix caprea*, $n = 36$, dependent variable is log-transformed.)

source	SS	d.f.	MS	F	p
plant	36.580	1	36.580	39.553	0.000
population	5.265	1	5.265	5.692	0.023
plant \times population	12.347	1	12.347	13.350	0.001
error	29.595	32	0.925		

(c) Oviposition experiment 3

The patterns obtained in the interspecific comparisons persisted on an intraspecific level as well. Our results confirmed previous observations that the English population of *P. c-album* is more specialized than the Swedish population (figure 2a; two-way ANOVA, $p_{\text{interaction}} < 0.001$; table 3). As predicted, this difference was also reflected in a significant ability of the English females to discriminate between conspecific differences in host plant quality (paired t -test, $n = 11$, $t = 6.69$, $p < 0.001$), whereas the Swedish females again showed no discrimination at all (paired t -test, $n = 7$, $t = 1.53$, $p = n.s.$; figure 2b).

(d) Larval rearings

The results from the larval rearings reveal no difference between the species in their ability to grow and survive on bad quality nettles. All species tested grew significantly slower on these nettles than on fresh and green nettles, and *V. indica* and *C. cardui* also suffered significantly higher mortality on the bad quality nettles (table 4). Apparently all tested species suffer a cost for feeding on the bad quality nettles.

4. DISCUSSION

All specialist species tested showed a significant preference for good quality nettles, whereas the two polyphagous species did not discriminate between the two categories of nettles at all. This difference was not paralleled by a corresponding higher ability of polyphagous larvae to utilize low-quality leaves as food. Interestingly, the same pattern was present on an intraspecific level as well, suggesting that constraints on female search efficiency may be an important causal factor in the evolution of host range.

Even if this outcome is exactly what we predicted from the information processing hypothesis described in §1, there is at least one alternative hypothesis, framed in terms of maternal care, that is also compatible with the data. This hypothesis, however, also focuses on oviposition behaviour rather than on larval feeding efficiency. We will describe and discuss the implications of these hypotheses in turn.

According to the information processing hypothesis, polyphagous females pay a cost for being able to discriminate between and evaluate a larger number of

Table 4. Larval survival and weight after 8 days on nettles of different quality

species (population)	survival				weight mg			
	N (g+b)	good quality	bad quality	p (χ^2)	N (g+b)	good quality	bad quality	p (U-test)
<i>Polygona c-album</i> (Swedish)	20+20	60 %	50 %	n.s.	12+10	8.78	5.37	0.018
<i>Polygona c-album</i> (English)	30+30	73 %	50 %	n.s.	22+15	6.03	4.14	0.002
<i>Cynthia cardui</i>	30+30	53 %	20 %	0.033	16+6	6.43	3.47	0.039
<i>Vanessa indica</i>	30+30	70 %	20 %	0.004	21+6	6.47	4.44	0.041

g, good quality nettle; b, bad quality nettle. See text for further explanation.

plant species in terms of a reduced capacity to perceive intraspecific differences among individuals of one of its preferred host plants. The ability to correctly evaluate differences in quality among conspecific host plants will then restrict the evolution of wide host ranges. This constraint to intraspecific oviposition accuracy will be counterbalanced by a number of factors acting to increase host range. In some situations the effect of these factors will be strong enough to overcome the constraint, resulting in polyphagous species or populations. Under what circumstances then should this cost of a more indiscriminate oviposition strategy be relaxed enough to allow for evolution of a wider host range?

In general terms the answer must be any factor that reduces the correlation between oviposition site selection and offspring performance (cf. Thompson 1988). In a previous study, the degree of preference–performance correlation among different host plant species varied from very high to very low among females of *P. c-album*, showing a possible relationship with specificity (Janz *et al.* 1994). General factors that probably play an important role in the correlation between oviposition site selection and offspring performance are the relative abundance of the favoured host and the time available for oviposition. In models where the female has to pay a cost in order to acquire information to discriminate between two hosts, predictions on how abundance patterns affect the degree of discrimination can be complicated (e.g. Kotler & Mitchell 1995; Larsson & Ekbom 1995). Furthermore, the effect of the time available for oviposition will probably interact with that of the abundance patterns, making the situation even more complex. However, as long as the female can increase the probability of encountering an acceptable host by including an alternative plant in the repertoire, a shorter time available for oviposition should favour inclusion of the alternative host. The time available for oviposition can be restricted by high adult mortality rate or any circumstance that restricts the number of days when flight is possible, such as harsh weather conditions. This means that wide host ranges and indiscriminate oviposition should be likely to evolve in highly seasonal environments, such as in the temperate regions, where spring weather can be cold and unpredictable and where the length of the summer does not permit additional generations to be fitted into the season (cf.

Nylin 1988; Scriber & Lederhouse 1992; Janz *et al.* 1994).

Another factor that would decrease the correlation between oviposition site selection and offspring performance is a higher ability of the larvae to search for good feeding places after hatching. Even if larvae of all species used in this study generally remain on the same plant on which they hatch, it is clear that the first instar larvae of *P. c-album* have a certain ability to choose a better feeding place by themselves (Nylin & Janz 1996), and there are some observations indicating that this ability does vary in the genus and is more limited in the more specialized *P. satyrus* and *P. gracilis* (personal observations). Moreover, species with more mobile larvae show even more indiscriminate oviposition (e.g. Marques *et al.* 1994; Tammaru *et al.* 1995).

An egg-laying pattern such as that of the generalists *P. c-album* (Swedish population) and *C. cardui*, will select for more mobile larvae and perhaps even a higher capacity to efficiently feed on suboptimal plant parts. In contrast, the greater carefulness in oviposition site selection shown by the specialized *P. satyrus*, *V. indica* and the English *P. c-album*, will select for low larval mobility and a high efficiency in utilizing high-quality plant parts, but not necessarily for a high capability to feed on suboptimal plant parts.

Larval mobility and feeding efficiency can be seen either as adaptations to the egg-laying patterns of the females, or, alternatively, as traits that have evolved for other reasons and pre-adapted the female for a particular egg-laying strategy. In the latter case the decreased discrimination of within-host differences would not necessarily constrain the evolution of a broad host range, as it would be an adaptation to an already existing larval feeding habit. *A priori*, however, it seems more logical to view the female traits as preceding and causing the larval traits, as the females are often better equipped to make choices between potential host plants (Price 1994) and as oviposition preference appears to be more ecologically and evolutionary labile than larval performance (Wasserman & Futuyma 1981; Janz *et al.* 1994). It is likely that once evolution takes the path towards more indiscriminate oviposition, this selects for higher larval mobility, which in turn pre-adapts the female for even more indiscriminate egg-laying. This ‘coevolution’ between the female and larval strategies or capacities

may eventually result in females with almost totally undistinguishing oviposition strategies and, accordingly, larvae that can localize and select suitable host plants entirely on their own (cf. Marques *et al.* 1994; Tammaru *et al.* 1995). The repeated evolution of flightless females among polyphagous forest macrolepidoptera (Barbosa *et al.* 1989; Hunter 1995) can be seen as extreme endpoints of this process, possible only when female choice of oviposition site is totally decoupled from larval fitness.

An alternative to the information processing hypothesis can be formulated in terms of maternal care. Here the specialists and generalists simply represent different outcomes of the offspring quality versus quantity trade-off. The specialist female should then spend more time evaluating each plant to assure that it offers good conditions for larval feeding and survival. A generalist female on the other hand should maximize offspring quantity and will to a higher degree tend to accept suboptimal oviposition sites. This hypothesis is compatible with the data, and much of the discussion above could also apply to this scenario. It is not clear, however, that the results presented here should have been predicted from this hypothesis alone. One could, for example, have predicted that the generalist female should respond differently when she encounters a nettle of suboptimal quality than when she encounters a plant species of suboptimal quality. If she encounters a nettle of low quality, chances are high that there will be a nettle of better quality in its immediate vicinity, as nettles grow in clusters. It should thus pay for her not to oviposit on the poor quality nettle and keep searching for a better one. On the other hand, encountering a plant species of lower quality provides no information at all about the chances of finding a better quality plant species in the future. In this case it would probably pay for the generalist female to oviposit before setting out to search for another host plant. It is important to note that the two hypotheses are not necessarily mutually exclusive; it is quite possible to incorporate the maternal care hypothesis into the more general information processing hypothesis. Clearly more studies are needed that are directly designed to disentangle these hypotheses.

The most important conclusion from this study is that the predictions from the information processing hypothesis were met, even if there may be other explanations for the data. The results suggest that female host-searching behaviour plays an important role in determining host plant range.

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