Butterfly Host Plant Choice in the Face of Possible Confusion

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We tested predictions from the theory that ovipositing females of phytophagous insects are limited by their neural capacity for information processing. Previous studies have found that relatively specialized insects make faster and/or more accurate identifications of host plants compared to generalists. The study species was the polyphagous comma butterfly, Polygonia c-album *(Nymphalidae). We compared females originating from two populations (Sweden and England) which differ in degree of specialization on the preferred host* Urtica dioica *(Urticaceae). Females were given a choice between this plant and a very similar nonhost, white dead nettle,* Laminum album *(Lamiacease), or a choice between a relatively poor host,* Betuala pubescens, *and the nonhost* Betula pendula *(Betulaceae). Oviposition rate was lower in cages with* Betula *compared to cages with* Urtica, *demonstrating that* P. c-album *females will withhold eggs when preferred hosts are not available. As predicted, females originating from the Swedish generalist population oviposited more often on the nonhost* Lamium. *However, females of both populations discriminated very strongly against oviposition on* B. pendula. *We found that newly hatched larvae have some ability to move from herbaceous nonhost to hosts. Although alternative interpretations are possible, the results give further support to the hypothesis that there are trade-offs between diet breadth and the ability to discriminate among plants.*

KEY WORDS: oviposition; information processing; host plant preference.

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INTRODUCTION

The idea that phytophagous insects may be constrained in host plant choice, by the amount of information from the environment that they are able to process, is an old one in the theory of host plant choice (Levins and MacArthur, 1969). More recently, however, this idea has received increasing attention (Fox and Lalonde, 1993; Bernays and Wcislo, 1994; Larsson and Ekbom, 1995; Bernays, 1996, 1998; Janz and Nylin, 1997; see also Mayhew, 1997).

Levins and MacArthur (1969) pointed out that the need to avoid risk of confusion between good and poor hosts might be one important reason for the high incidence of monophagy in phytophagous insects. Bernays (1996, 1998), Bernays and Wcislo (1994), and Janz and Nylin (1997) recently took up this idea again, now more specifically in terms of neural constraints resulting in a trade-off between diet breadth and the ability to discriminate among hosts. If there is a limit to information-processing capacity, as seems reasonable, generalists and specialists may allocate such capacity differently. Generalists (with the exception of those with totally nondiscriminating oviposition) must be able to identify and often also rank many different plants and may, for this reason, be slower or less accurate in each individual decision.

Comparative empirical evidence for such a trade-off has recently been forthcoming. It has been found that females of more specialized species and populations may make faster and/or more accurate decisions regarding whether or not to accept a plant as a host (for a review see Bernays, 1998). In one of these studies, females originating from two populations of the comma butterfly [*Polygonia c-album* (L.)] was given a choice between two individuals of stinging nettle (*Urtica dioica* L.), differing in quality (Janz and Nylin, 1997). Females of the English population are more specialized on using nettle as a host compared to females of the more polyphagous Swedish population (Nylin, 1988; Janz and Nylin, 1997; Janz, 1998); the difference is genetic and carried on the X chromosome (Janz, 1998). As predicted, English females were found to make more accurate choices. They preferred highquality nettles for oviposition, whereas Swedish females did not discriminate significantly between nettles of different quality.

In the present study we report results from experiments where we instead gave females originating from these two butterfly populations choices between two plant species that could potentially be confused: one host and one nonhost. The first choice was between the preferred host *U. dioica* (Urticaceae) and "white dead nettle," *Lamium album* (Lamiaceae). These two species very often grow together, intermingled in dense stands, and to the human eye their leaves are morphologically very similar in shape, texture, glossiness, and color. *L. album* flowers late in summer and the white flowers are insignificant at the time of the year when *P. c-album* females are

ovipositing. It is quite possible that white dead nettles actually mimic the stinging nettles to capitalize on their strong defense against vertebrate herbivores, but this does not seem to have been investigated properly. Whatever the cause, the situation creates a risk of confusion for ovipositing females, and from the information-processing theory we predicated that a set of females originating from the English population should be more accurate in determining which plants are really *U. dioica*. They would be likely to represent a genotype that has evolved to devote most of their available neural capacity to fast and accurate identification of nettle identity and quality. Swedish females must also be able to cope with identifying and ranking an entire hierarchy of commonly used alternative hosts in several plant families (see Materials and Methods) and may have to pay for this by a poorer ability to identify nettles.

The second choice given to females was between the two common species of birch trees in Sweden and England, *B. pubescens* Ehrh. and *Betula pendula* Roth (Betulaceae). The first species is a relatively poor host, but one that is very abundant and (although low in preference ranking) commonly used in Sweden. On the second birch species growth and development of *P. c-album* larvae are not possible (Nylin and Janz, 1993). The distinction between birch species is often not evident to the human eye without intense scrutiny of several leaves on a tree. Regarding this risk of confusion, the prediction from the information-processing theory is not equally straightforward, as predictions and tests of the theory so far have dealt only with choices involving plants which are preferred by both of the investigated populations or species. Perhaps the most logical prediction is that the Swedish females, despite their wider diet breadth, should be more accurate when given a choice of birch species. The task of identifying *B. pubescens* is one which genotypes of this population are continuously selected to perform, in contrast to the situation in the English population.

The experimental setup also made it possible to test whether *P. c-album* females will withhold eggs when a preferred host plant is not available (as had been suggested by earlier pilot studies). Such data will give some information on the degree of selection for high oviposition rate in *P. c-album*.

MATERIALS AND METHODS

Study Species and Stock

The holarctic genus *Polygonia* is a member of the tribe Nymphalini, together with genera such as *Nymphalis* and *Vanessa*. The only representative of the genus in northern Europe is the comma butterfly, *Polygonia c-album*, which occurs widely across the whole of the Palearctic.

Larvae of this species feed on herbs, vines, bushes, and trees in several families and orders: Urticales—stinging nettle *Urtica dioica* (Urticaceae), elm *Ulmus glabra* (Ulmaceae), and hop *Humulus lupulus* (Cannabidaceae); Salicales—sallow *Salix caprea* (Salicaceae); Rosales—currants *Ribes* spp. (Grossulariaceae); and Betulales—birch *Betula pubescens* (Betulaceae) and hazel *Corylus avellana* (Corylaceae) (Ackery, 1988; Nylin, 1988; Ebert, 1993). This list is roughly in decreasing order of female preference and larval performance (Nylin, 1988; Nylin and Janz, 1993, 1996; Janz *et al.*, 1994). Larvae can initiate and complete development on all of these hosts (Nylin, 1988), and females of the Swedish population seem to oviposit naturally on all of them (S. Nylin and C. Wiklund, personal observation). The English population is evidently much more specialized on the hosts in Urticales (Nylin, 1988; Janz and Nylin, 1997; Janz, 1998), in the field situation especially on *U. dioica* (Pratt, 1986). We made use of this difference between populations to produce two sets of individuals (genotypes) differing in specialization.

The Swedish stock used in the experiments originated from six females caught wild north of Stockholm, Sweden, in May 1997. Females of the summer form, which develops directly to sexual maturation without adult hibernation diapause, was produced following the procedure described by Nylin (1989, 1992). Larvae were reared on *U. dioica* or *S. caprea* in a regime of increasing day length and temperature. It has been shown that the plant used for rearing does not affect the preferences of the resulting adult females (Nylin and Janz, 1996). The English stock originated from adults caught wild in southeastern England in the spring of 1996 and females used in the experiment were of the fourth generation raised (after hibernation in the third generation). Offspring of hibernating adults were reared on *U. dioica* in a long-day regime to produce the summer form.

Individually marked males and females were kept in large flight cages for mating. Matings take place in the afternoon and the mating pair stays in copula until after lights out, thus mating pairs could be isolated in the evening.

Eggs are laid singly or in small clutches on the host plant. As the plants used are large and the clutch sizes small, it is likely that larvae often complete development on a single plant individual. In other words, female host plant choice directly determines offspring life history and fitness (Nylin and Janz, 1996; Nylin *et al.*, 1996).

Experimental Procedures and Statistics

Mated females were put in individual flight cages, $0.5 \times 0.5 \times 0.5$ m, where the host plant choice experiments were conducted. Each cage (wooden frame

with clear plastic top and front, sides and rear covered with cloth) was lit from above by a 75-W light bulb between 0830 and 1630. The floor of the cage was covered with paper, kept moist at all times, and the butterflies were fed a solution of sugar in water from a sponge placed directly under the light. The two plants making up the choice experiment were in bottles of water, placed in opposite corners of the cage.

Throughout the experiment, plants were circulated among all the different cages (to prevent cage effects) and replaced whenever they showed any sign of wilting. Their relative position inside the cages was changed frequently during the observation sessions (to prevent position effects). This was done several times daily in cages with much oviposition activity and in all cages at least daily.

Each individual female was used with one of the two pairs of plants (size-matched pairs of *U. dioica*/*L. album* or *B. pubescens*/*B. pendula*). Toward the end of the experiment some *L. album* had started to show more conspicuous flowers; they were removed to correspond more closely to the natural field situation in Sweden and for the first generation of butterflies in England. Direct development and summer flights normally do not occur in Sweden and in only a minority of the English population. Females were observed and ovipositions scored over a period of 3–6 days, depending on the oviposition rate.

Since many cages were in use simultaneously it was not possible to observe all cages continuously. Furthermore, females spent most of the time at rest on the cloth sides of the cages, interrupted by a period of oviposition only at long intervals. For this reason an observation scheme was adopted in which the observer followed a set path along the cages. An observation period was started whenever an oviposition event was observed. The female was then observed for 3 min. Landings and ovipositions on each plant in the pair were noted, as well as the clutch size. Eggs were taken to be of the same clutch (and the same "choice" of plant for oviposition) if the female did not take off between laying the eggs but moved around on the plant.

Even though landings were recorded only during periods when the females were actively ovipositing, some of these landings probably represented other activities, resting and basking. The impression from observations, however, was that a large proportion of landings on nonhosts represented actual "mistake" landings, where the female first responded to visual or odor similarity to the host and had to use contact cues to identify the plant further. See also Results, where it is shown that a large majority of landings on *U. dioica* resulted in oviposition. It could be possible to distinguish between these types of activities by closer scrutiny of female behavior, but in order not to limit further the number of females that could be observed at the same time, no such attempt was made.

As by no means all oviposition events could be observed, due to simultaneous activity in the cages, eggs were also counted daily. The eggs were saved until eclosion and used for survival and mobility experiments prompted by the results of the oviposition experiments:

For the survival experiment 20 larvae from each population were placed on each of *U. dioica* (as a control), *L. album*, and *B. pendula*, two larvae in each jar, and followed until the molting to the second instar.

A simple mobility experiment was conducted to assess the ability of newly hatched larvae to move from a nonhost to a host, after an oviposition "mistake." The bottom of a large tray (55×35 cm) was covered with a green porous material that retains water, Oasis Ideal Floral Foam. This material is commercially available for arranging and preserving cut flowers and plants. In two opposite corners of the tray plants of *U. dioica* were placed; in the other two corners, plants of *L. album*. The distance between plants was 20 cm, and the only way for a larva to reach a host plant was to go down the stem of *L. album* and over the floral foam surface to a stem of *U. dioica*. In each experiment 20 newly hatched larvae were placed on each of the two *L. album* plants, and the position of larvae was investigated after 24 h. This was done for both of the two populations, each in three replicates.

Degrees of freedom in statistical tests are based on the number of females, not the number of observed events. Population means are presented in the figures and text as means of means from individual females $\pm$ SE, but nonparametric significance tests were used throughout because most measurements deal with proportions.

RESULTS

Landings on Nettles and "Dead Nettles"

There were 10 Swedish females in cages with a choice between *U. dioica* and *L. album* from which at least 10 landings were observed, during observation periods (defined as under Materials and Methods, always starting with oviposition). Pooling data from all observation periods for each female, all females alighted more often on *U. dioica* than on *L. album* (Fig. 1; range, 52.4–68.3%). The probability of obtaining this difference in the predicted direction from random landings in all 10 females is $0.5^{10}(P < 0.001)$.

Only four English females could be scored in the same way, because activity was concentrated to rare and brief periods and often went undetected. Three of these four females landed more often on *U. dioica*, the exception being the female with the smallest number of observations (Fig. 1; range, 33.3–90.5%). Thus a preference for landing on *U. dioica* cannot be demonstrated
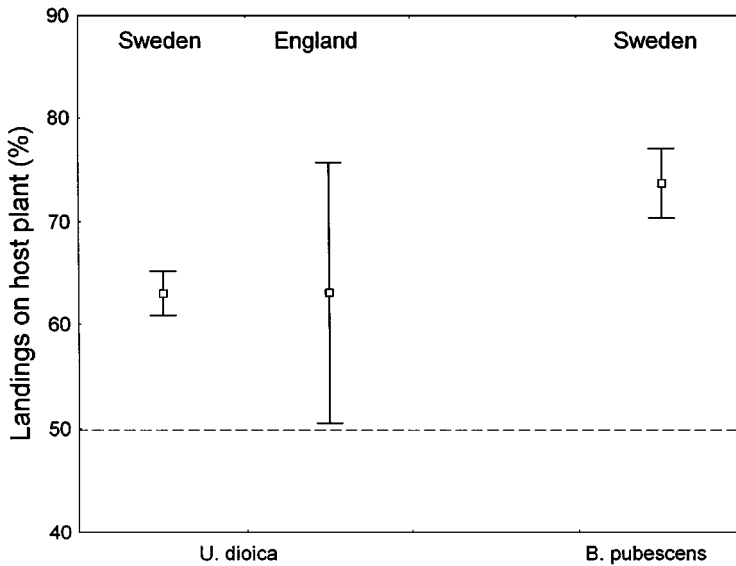
Fig. 1. The proportion of all observed landings by *Polygonia c-album* females that took place on the host plant, compared to the expectation from randomness of 50% (dashed line). Left: Choice between host *Urtica dioica* and nonhost *Lamium album* by Swedish ($N = 10$) and English ($N = 4$) females. Right: Choice between host *Betula pubescens* and nonhost *B. pendula* by Swedish females ($N = 6$). The variation shown is means of means from individual females $\pm$ SE.

for females originating from this population, but the very similar means give no reason to expect that the genotypes differ in this respect. There were no obvious trends over time, trends that would suggest that females learned to avoid landings on *L. album*.

Oviposition on Nettles and "Dead Nettles"

In a large majority of all observed landings on *U. dioica*, oviposition followed (Fig. 2). This suggests that most such landings indeed represented exploration of possible sites for oviposition. The mean proportion of landings resulting in oviposition was $76.2 \pm 3.4\%$ for the Swedish females ($N = 10$ females observed to land on *U. dioica* at least 10 times) and $85.5 \pm 1.7\%$ for the English females ($N = 3$ females). The tendency for the English females to accept *U. dioica* more readily after landing was significant in a Kruskal–Wallis ANOVA median test ($P < 0.05$) but not in a Mann–Whitney U test.

As predicted, the Swedish females made more "mistakes" in oviposition. Swedish females were sometimes observed to oviposit after landing on
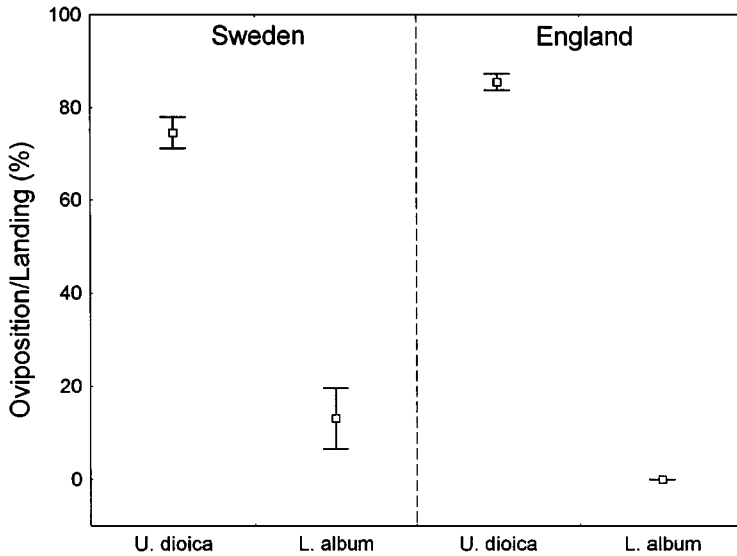
Fig. 2. The proportion of observed landings by females originating from the Swedish ($N = 10$) and English ($N = 3$) populations that resulted in oviposition on host *U. dioica* and nonhost *L. album*. The variation shown is means of means from individual females $\pm$ SE.

L. album (Fig. 2; mean proportion of landings, 13%; $N = 8$ females where at least 10 landings on *L. album* were observed during oviposition periods), but never English females. However, only two English females were observed to land on *L. album* at least 10 times, and so no conclusion regarding differences between the genotypes can be drawn based on observation data alon (Mann–Whitney *U* test, n.s.).

Results from counting all the eggs laid, with or without observation, were clearer in this respect. Pooling all eggs from each female (38–221 eggs per female), the Swedish females laid a significantly larger proportion of eggs on *L. album* (Fig. 3; Mann–Whitney *U* test, $P < 0.05$). With the exception of a single egg, all English females totally avoided oviposition on *L. album* (total $N = 6$ females). Note, however, that the range for the Swedish females was from 0 to 23 % of the eggs on *L. album* ($N = 11$ females). In other words, a few of the Swedish females discriminated as strongly against *L. album* as did the English females.

Landings on Birches

There were six Swedish females in cages with a choice between *B. pubescens* and *B. pendula* from which at least 10 landings were observed,
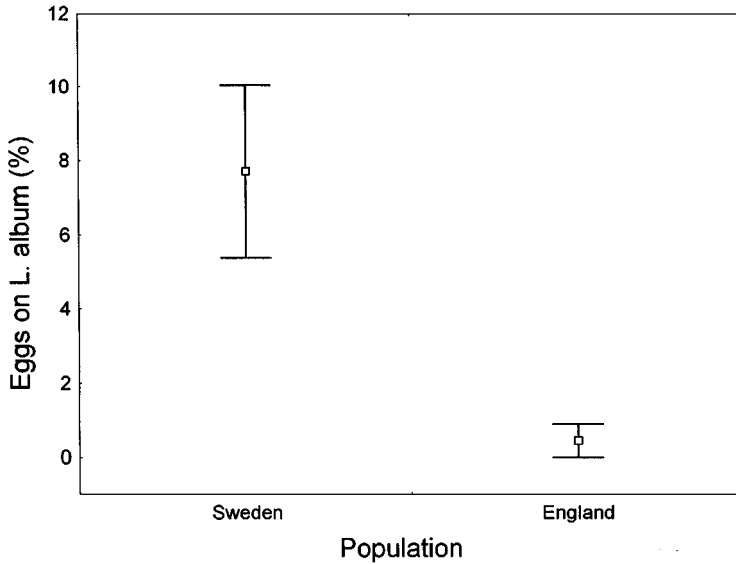
Fig. 3. The proportion of all eggs (in cages with *U. dioica* and *L. album*) that were laid on nonhost *L. album*, by Swedish ($N = 11$) and English ($N = 6$) females. The variation shown is means of means from individual females $\pm$ SE.

during observation periods. Pooling data from all observation periods for each female, all females alighted more often on *B. pubescens* than on *B. pendula* (Fig. 1; range, 63.6–87.1%). The probability of obtaining this difference in the predicted direction from random landings in all six females is $0.5^6 (P < 0.05)$. The Swedish females in fact made fewer landing "mistakes" on *B. pendula* than on *L. album* (Fig. 1; Mann–Whitney U test, $P < 0.05$).

The English females showed very little activity, and even less oviposition, in eight cages with only *Betula*. For this reason, no "observation periods," as defined above could be initiated, and no comparison between the populations could be made.

Oviposition on Birches and Oviposition Rate

Regarding the Swedish females, oviposition followed after landings on *B. pubescens* in $68.5 \pm 5.6\%$ of the cases ($N = 5$ females). As explained in the previous section, no formal "observation periods" could be initiated for the English females due to very few ovipositions, and for this reason no direct comparison of acceptability of *B. pubescens* was made. The oviposition rate (from counting eggs daily) in cages with English females and only *Betula* was only 1.1 ± 0.5 eggs/day ($N = 5$), compared to 10.5 ± 3.1 for the Swedish females ($N = 8$). In contrast, the oviposition rate was 27.5 ± 3.0 eggs/day

for the Swedish females ($N = 12$) and 36.9 ± 6.2 eggs/day for the English females ($N = 6$) when *U. dioica* was present. The differences in oviposition rate between plants are statistically significant for females from both populations (Mann–Whitney *U* test, $P < 0.01$). The differences between females originating from the two populations are significant for *Betula* cages (Mann–Whitney *U* test, $P < 0.05$) but not for *Urtica* cages, consistent with a higher acceptability of *B. pubescens* for the tested Swedish females. Several English females tested with *Betula* were moved to cages with *Urtica* after the experiment, and they then oviposited at rates normal for *Urtica*.

Discrimination against *B. pendula* was total for females of both populations. Not a single egg was laid on *B. pendula* (note, however, that only 23 eggs were laid in total in *Betula* cages with English females).

Survival and Mobility

In view of the results reported above, a survival experiment was performed as a check on an earlier pilot study and earlier published results (Nylin and Janz, 1993) which suggested that *L. album* and *B. pendula* (respectively) are lethal for newly hatched larvae. All 40 larvae died in the first instar on *L. album* (Swedish, all dead after 3 days; English, all dead after 2 days) and *B. pendula* (Swedish, all dead after 8 days; English, all dead after 4 days), whereas all survived to the second instar on *U. dioica*. They were not followed further.

The mobility experiments demonstrated that newly hatched larvae of *P. c-album* have some ability to move from nonhosts to hosts. The mean percentage of Swedish larvae that had moved from *L. album* to *U. dioica* after 24 h was $27.5 \pm 5.2\%$ ($N = 3$ replicates); that of English larvae, $15.8 \pm 3.6\%$ ($N = 3$ replicates; difference between larvae from the two populations not significant, Mann–Whitney *U* test).

DISCUSSION

Females of *Polygonia c-album* evidently have some ability to distinguish between hosts and nonhosts already in flight, even when the plants are very similar, as demonstrated by the fact that more than 50% of landings took place on host plants (Fig. 1). Visual cues, plant odors, or both could be involved in this phase of host plant choice. No differences between the sets of females originating from the two populations could be established during this phase. This may well be due to high variance and small sample sizes, which were limited by the need to observe landings as well as by the availability of mated females.

However, as predicted from the information-processing theory, the Swedish females (which originated from a more polyphagous population and, as expected, displayed much higher acceptance of *Betula* in the trials) oviposited more readily on the nonhost *L. album* than did the more specialized English females (Figs. 2 and 3). This supports earlier results from this butterfly and other insect systems, suggesting a trade-off between diet breadth and accuracy or speed in identification of preferred hosts (Bernays and Wcislo, 1994; Bernays, 1996, 1998; Janz and Nylin, 1997).

It must be stressed at this point that alternative explanations for the observed patterns could be construed, e.g., differences in thresholds for acceptance of a plant for oviposition. Threshold explanations and information-processing explanations are generally not mutually exclusive. However, the comma butterfly is a model species particularly well suited to disentangle the two. This is because even females from the "generalist" population do not at all have indiscriminate oviposition. They have a clearly defined hierarchy among the distantly related and chemically very different accepted hosts, and do not accept even close relatives of some hosts (as in the case of *Betula*). A single difference in the threshold for acceptance between the two populations thus cannot be the whole explanation. Moreover, threshold explanations and information-processing explanations operate at somewhat different levels. The latter is an attempt to explain what is gained by specialization, regardless of how specialization is mechanistically achieved.

We made use of the rather well-established difference in host plant specificity between the populations to produce two sets of individuals differing in specialization, to test predictions regarding the relationship between specialization and accuracy. However, as several independent samples were not taken from each population, the results regarding oviposition mistakes should not be seen as necessarily reflecting true population differences, but only differences between these two sets of individuals. Nevertheless, the difference in specificity between populations has been shown to have a genetic basis (Janz, 1998), and it prevailed in the genotypes studied. Thus, it seems likely that differences in accuracy between the two sets of individuals studied here reflect differences between two genotypes that are somewhat representative of their source populations.

Oviposition on nonhosts might seem puzzling, but it is not an unusual phenomenon (Thompson, 1988; Mayhew, 1997). It occurs when insects or plants are new to an area and there has not been enough time for insects to evolve perfect correlations between female preference and offspring performance (Chew, 1977), when larval mobility is higher than female mobility (Tammaru *et al.*, 1995), or when the adult life span is too short to permit very discriminating host plant choice (Larsson and Ekbom, 1995). None of these explanations applies very strongly in the present case, but it is possible

that milder versions of the last two are applicable, together with the neural constraint explanation tested in the present study. There is no reason to believe that the problem of distinguishing between *U. dioica* and *L. album*, or *B. pubescens* and *B. pendula*, is a new one for either Swedish or English *P. c-album*. None of the plants are recent colonizers in either area; all four occur widely over the whole distribution area of *P. c-album*.

Given enough time, it certainly seems possible for an insect to evolve the means for certain identification of a given host plant, but perhaps not all possible host plants at the same time. Host plant choice is the evolutionary outcome of several trade-offs and must be considered in the context of the whole ecology and life history of the population. In the English population a second generation is possible most summer, and this may be the factor which selects for specialization on host plants such as *U. dioica*, permitting fast growth and development (Nylin, 1988; Janz *et al.*, 1994; Janz, 1998). The Swedish population is univoltine, and in this situation several other hosts will result in a similar or even higher offspring fitness (Janz *et al.*, 1994; Nylin, 1988; Nylin *et al.*, 1996). In other words, a set of abundant alternative hosts is available, and it may not be feasible or even possible to evolve the means for certain identification of all of them. With a range of rather distantly related host plants such as those of *P. c-album*, the cues used for identification (whether visual or chemical) will most likely be unique to each host. If neural constraints are of importance, the capacity for information processing that can be devoted to each such identification task will be limited.

One possibility would be to extend the time investigating each possible host plant, but this would limit realized fecundity, and lifetime reproductive success may well be higher if some "mistakes" are accepted (Larsson and Ekbom, 1995). In this study we observed that the oviposition rate in *P. c-album* is retarded when only low-ranked hosts are present. This would seem to indicate that selection for fast oviposition is not severe in this species. Nevertheless, there is necessarily a trade-off at some point between the number of eggs that can be placed and the quality of each oviposition site.

Another evolutionary possibility would be to exclude a host plant from the repertoire when there is a risk of confusion with a nonhost (Fox and Lalonde, 1993). In the case of *U. dioica* this would mean excluding one of the most preferred and best host plants, and this would be favored only if the cost of confusion is very high. This leads us to the consequences of "mistake" ovipositions on *L. album*. Given that this plant is lethal for young larvae, the cost is certainly not trivial. However, it may be somewhat reduced by the fact that newly hatched larvae show some mobility from nonhosts to hosts (this study). If this also happens in nature, the fact that *L. album* often grows in close proximity to *U. dioica* both causes the problem and helps to solve it.

Most comparisons between sets of females from the two populations were not possible regarding *Betula*, but, nevertheless, there were some fascinating results from this experiment. The choice between *B. pubescens* and *B. pendula* was given attention in a previous study on the Swedish population (Nylin and Janz, 1993). We found it interesting to investigate the level of perfection in an identification task involving a nonhost and a plant that is low in the preference hierarchy and poor in terms of offspring performance—a "choice betwen had and worse." We found perfect identification of *B. pubescens* and rejection of *B. pendula* in oviposition trials and suggested that this might be because *B. pubescens* (despite its low rank) is commonly used in the field due to its abundance and for this reason an important host to identify.

The results of the present study reinforce this picture. The Swedish females distinguished between the two congeneric birch species even before landing and performed this task even better than the task of distinguishing nettles from "dead nettles," members of different plant families (Fig. 1). Moreover, the females originating from England also showed perfect discrimination between the birches in oviposition, even though they must be of very minor importance as hosts in the English population. There is a long history of association with *Betula* in the genus *Polygonia* and the related *Nymphalis*, suggesting the possibility that neural machinery specialized for this task may have evolved as a fixed species characteristic (Nylin and Janz, 1993).

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