

SHORT COMMUNICATION

Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse

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Introduction

As Thompson (1988a) remarks, the relationship between adult oviposition preference and offspring performance is the crux of the problem of understanding the evolution of insect/plant associations. Females often display a hierarchy of preferences for different hosts, so that they use a host lower in the hierarchy when the preferred species is not available (e.g. Wiklund, 1981; Thompson, 1988b). The preference hierarchy may be more or less well correlated with larval performance; here used as a composite term for offspring growth rate, survival and reproduction (Thompson, 1988a). A good correlation suggests that plant characteristics, including plant chemistry and nutritional value, is the most important factor that influences larval performance, limits host plant range and promotes specialization on only a few host plants – the general pattern in insects. This is the core of both coevolution theory and sequential evolution theory for the evolution of insect–host plant interactions (Ehrlich & Raven, 1964; Jermy, 1984; Ronquist & Nylin, 1990). Conversely, poor correlations can be used as evidence by those who consider other ecological factors, such as selection for enemy-free space, to be of great importance in the evolution of host plant choice and specialization (e.g. Atsatt, 1981; Bernays & Graham, 1988; see also Strong, 1988).

Thompson (1988a) and Thompson & Pellmyr (1991) review some of the evidence on preference–performance relationships, and note that the correlations range all the way from good to poor. Surprisingly often, poor correlations are found (e.g. Chew, 1977; Courtney, 1981; Williams, 1983; Penz & Araujo, 1991; Valladares & Lawton, 1991). There is evidence that a number of factors may cause poor correlations between preference and performance (Thompson, 1988a; Thompson & Pellmyr, 1991). These include: (1) selection for enemy-free space;

(2) the preferred plant may be rare; (3) the poor host plant may be a recent addition to the habitat, and selection may not have had time to eliminate oviposition on the poor (or even fatal; Chew, 1977) plant species; (4) a favourable host may grow in unfavourable habitats. Some additional factors may be of importance in more specific cases.

Most of the studies on preference–performance relationships have been performed on oligophagous species. However, Nylin (1988) showed that the polyphagous comma butterfly, *Polygonia c-album* L., displays a marked preference, well correlated with larval performance (in terms of survival and development time), for hosts in Urticales (including the herbs *Urtica* and *Humulus* as well as the tree *Ulmus*), over hosts in Salicales (*Salix*), Rosales (*Ribes*) and, especially, over those in Fagales (*Betula*, *Corylus*). Thus, there is a hierarchy of preference for different host orders, similar to the preference hierarchy for species found in *Papilio* (Wiklund, 1975, 1981; Thompson, 1988b) and other oligophagous butterflies. This work provided the basis for the present study. Here, we demonstrate that the preference hierarchies and preference–performance correlations are found also in more rigorously designed experiments, with simultaneous presentation of four potential host plants. We then focus on the lower end of the preference and performance hierarchies: Is there a difference in larval performance on two species of the lowest-rated genus, *Betula*? Do females discriminate between them, despite the fact that there should be only very slight selection in favour of discrimination among insignificant host plants? In short, has the hierarchy evolved to perfection even at the lower levels and, if so, how and why?

Methods

Host plant choice in P.c-album. (1) In the earlier study on host plant choice in *P.c-album* (Nylin, 1988) potential hosts were presented together with *Urtica dioica*, which

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was used as a reference. A population-level preference for a specific host was calculated as the ratio of total number of eggs laid by all females on this host over the number of eggs laid on *U.dioica*. As a complement and test of this relative measure of preference, in the present study four hosts were simultaneously presented to five females of *P.c-album* wild-caught in the Stockholm area at the very beginning of the flight season (after adult hibernation), between 4 and 12 May. The plants used were *U.dioica*, *Ulmus glabra*, *Salix caprea* and *Betula pubescens*.

The females were kept in separate cages of about $0.5 \times 0.5 \times 0.5$ m. In each cage, the host plants (freshly cut twigs of roughly equal size, placed in bottles of water) were presented at equal distance from the central light source and food source, forming a square in the cage. Eggs were counted every 2 days (females of *P.c-album* almost always lay their eggs singly, so each egg can be seen as representing a choice of host) and a new presentation of fresh hosts was then made, in a random manner. This procedure was repeated for the total life-span of the females, so that almost all eggs laid by these five females were sampled.

(2) To investigate the extent of discrimination between the species of *Betula*, the two birch species *Betula pubescens* and *B.pendula* were simultaneously presented in four different cages to groups of three to five female *P.c-album*. The females represented three different stocks originating from females caught in the Stockholm area. Eggs were counted after 3 days. A presentation was then made in the same cages of only *B.pendula* for 2 days, whereafter eggs were counted.

Larval performance in *P.c-album*. (1) Larvae (offspring of the five wild-caught females used in preference experiment 1) were divided among the host plants used in this experiment. Thirty larvae from each female were reared singly on each of these plant species. Larvae were reared until pupation in environmental chambers under long-day conditions (22 h), fifteen larvae from each female at 20–22°C and the remaining fifteen at 26–28°C. For comparison with a host plant known to be poor for larval growth (Nylin, 1988), a small number of larvae also were reared on *Corylus avellana* at both temperatures. Rearings took place in plastic jars in which the host plant could receive water from a lower jar. Plants were changed at frequent intervals and whenever they showed signs of senescence. Development time and weight at pupation were noted, and from these data and data on hatchling weights larval relative growth rates were calculated (% mean daily weight gain), i.e.: $((\exp((\log(\text{pupal weight}) - \log(\text{hatchling weight}))/\text{larval time})) - 1) \times 100$

(2a) Eggs laid on *B.pendula* and *B.pubescens* in preference experiment 2 were allowed to hatch *in situ* and larval performance followed during the first instar. (b) Forty eggs laid on other hosts were removed and allowed to hatch in plastic jars, after which the larvae were immediately transferred to *B.pendula* (twenty larvae) and *B.pubescens* (twenty larvae) and an attempt was made to rear the larvae individually on twigs of *Betula* spp. (c) To investigate if older larvae could survive on *B.pendula*,

ten healthy larvae (reared on *U.dioica*) was placed on *B.pendula* at the beginning of the final (fifth) instar.

Results

Host plant choice in *P.c-album*

(1) The results of simultaneous presentation of four hosts to five wild-caught females of *P.c-album* (% of all eggs laid on each plant) can be seen in Fig. 1. As in a previous study (Nylin, 1988), where host plant choice was measured only relative to *U.dioica*, the hosts in Urticales (*U.dioica* and *U.glabra*) were preferred hosts. The host in Salicales, *S.caprea*, and especially the host in Fagales, *B.pubescens*, were less preferred hosts. There was some variability in the preference hierarchies between females, but four out of five females had *U.dioica* or *U.glabra* as the most preferred host, whereas the fifth preferred *S.caprea*. All females had *B.pubescens* at one of the two lowest places in the hierarchy. This paper is concerned only with the lower levels of the hierarchy, and we will not here discuss correlations between preference and performance at the level of individual females. This result was very similar to earlier results (Nylin, 1988) and thus it appears that pairwise choices can be acceptable alternatives to simultaneous presentations in experimental design. The former technique is useful because it is often impractical or impossible to present all potential host plant species at the same time.

(2) When the two species of *Betula* were presented together all eggs but a single exception were laid on *B.pubescens* in the four cages (Table 1). When only *B.pendula*

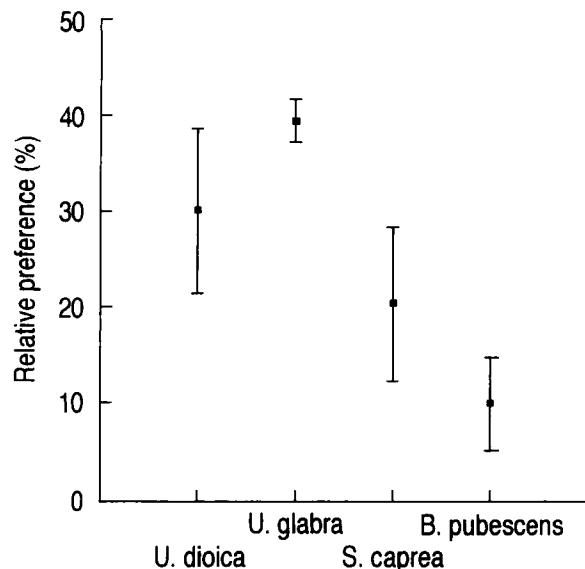


Fig. 1. The relative preference (i.e. the percentage of eggs laid on a particular host) for four host plant species, when presented simultaneously to females of *Polygona c-album* kept singly in cages. Data given are means \pm SE based on $N=5$ females. N (number of eggs) for females 1–5 were 207, 234, 166, 191 and 323, respectively.

Table 1. Number of eggs laid on the two species of *Betula* by groups of female *Polygonia c-album* of three stocks. P = statistical significance as determined by χ^2 -tests.

| Stock | Eggs on <i>B. pubescens</i> | Eggs on <i>B. pendula</i> | P |
|-------|-----------------------------|---------------------------|--------|
| 1 | 48 | 0 | <0.001 |
| 1 | 67 | 0 | <0.001 |
| 2 | 100 | 1 | <0.001 |
| 3 | 99 | 0 | <0.001 |

was presented no eggs were laid in three of the cages, whereas fifty eggs were laid in the remaining cage. This is an exceptional event, unparalleled before or since, but demonstrates that strong oviposition on this plant sometimes do occur, at least in the laboratory when there is no alternative. In all cages oviposition occurred again when more highly preferred hosts were introduced after the experiment. This suggests that oviposition rate was suppressed by the lack of preferred hosts, but the experiments were not designed to rigorously demonstrate this pattern.

Larval performance in *P. c-album*

(1) As in the earlier study (Nylin, 1988), performance correlated well with preference at the population level (Fig. 2). At both experimental temperatures, growth rates

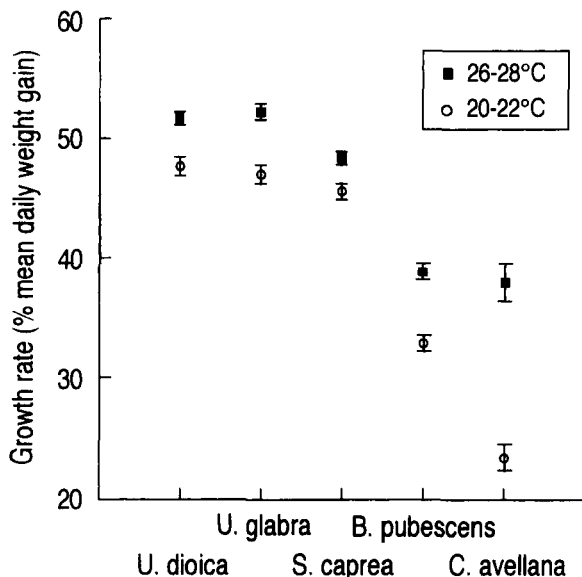


Fig. 2. Relative growth rates of larvae (means \pm SE; sexes pooled; families pooled) on five host plants of *Polygonia c-album*, when larvae were kept in two temperatures. N (number of larvae) for the five plant species at the two temperatures were (high temperature given first): *Urtica dioica* 72, 72; *Ulmus glabra* 70, 71; *Salix caprea* 68, 66; *Betula pubescens* 68, 58; *Corylus avellana* 21, 6.

were high on the preferred hosts *U. dioica* and *U. glabra*, intermediate on the less preferred host *S. caprea* and low on the species lowest in the preference hierarchy, *B. pubescens* (and also on *C. avellana*; a host for which females also have low preference; Nylin, 1988). As in the earlier study, this was seen mostly as variation in development time, since pupal weights (not reported here) were rather similar on the four hosts. Data on survival can be seen by comparing the N -values of successfully pupated individuals (given in the figure legend to Fig. 2) with the number of larvae established on each of the four plant species used in the preference experiment (i.e. seventy-five). Survival was high on all four of these hosts, including *B. pubescens*, once larvae were established on the plants (they were exchanged for new specimens until this was the case), and the few cases of mortality in almost all cases was due to larvae drowning. Survival data from *C. avellana* are not comparable since fewer larvae were used and larvae that failed to establish themselves were not always replaced.

(2a) Out of ninety-five larvae hatched *in situ* on *B. pubescens*, the great majority (78%) survived and seemed healthy at the time of moulting to the second instar (they were not followed after this stage). Out of fifty larvae hatched *in situ* on *B. pendula* and kept under the same conditions, not one started eating. Instead all died after a couple of days (many had by that time fled the plant). (b) The results with transferred larvae were similar. Most (70%) of the twenty larvae reared on *B. pubescens* pupated successfully, with mortality being primarily due to failure of newly hatched larvae to establish themselves on the plant. All twenty larvae on *B. pendula* died early in the first instar. (c) However, out of ten larvae placed on *B. pendula* in the beginning of the final instar six survived to pupation. Two died accidental deaths from drowning (possibly while searching for better food) whereas three apparently starved to death. Pupal weights (and adult size) in the surviving individuals were very low (pupal weights \pm SE; 211.8 ± 20.3 ; normal weights range from 300 to 325 mg, cf. Nylin 1988), suggesting that growth was terminated prematurely.

Discussion

Thompson (1988a) notes that there is a problem in determining which component of larval performance to use in correlation analyses, because the components are not always positively correlated with each other. A fact which has not received enough attention is that this is to be expected from theoretical considerations, since female preferences can be expected to be correlated not with any individual trait but with offspring fitness (Reavey & Lawton, 1991). Here, we seek correlations primarily with the most clear-cut and inclusive components of larval performance, i.e. survival and growth rate.

In *Polygonia c-album* there is a general correspondence between female preference and larval performance (in terms of survival and growth rates), suggesting that host plant quality is the most important factor for host plant

Table 2. Host plants used by species of *Polygonia* and related genera. Sources: Seppänen (1970), Larsen (1974), Scott (1986), Ackery (1988). 'Dubious' records (Scott, 1986) omitted. Butterflies of uncertain species status or with unknown hosts omitted.

| Species | Host plants |
|----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Polygonia c-album</i> | <i>Ribes, Ulmus, Urtica, Humulus, Salix, Populus, Betula, Corylus</i> |
| <i>P.faunus</i> | <i>Ribes, Urtica, Salix, Betula, Alnus, Rhododendron, Vaccinium</i> |
| <i>P.gracilis</i> | <i>Ribes, Rhododendron</i> |
| <i>P.egea</i> | <i>Ribes, Ulmus, Parietaria, Urtica, Corylus</i> |
| <i>P.progne</i> | <i>Ribes, Betula, Rhododendron</i> |
| <i>P.c-aureum</i> | <i>Humulus</i> |
| <i>P.satyris</i> | <i>Urtica, Humulus, Salix</i> |
| <i>P.interrogationis</i> | <i>Ulmus, Celtis, Urtica, Boehmeria, Humulus</i> |
| <i>P.comma</i> | <i>Ulmus, Urtica, Boehmeria, Laportea, Humulus</i> |
| <i>Kaniska canace</i> | <i>Smilax</i> |
| <i>Nymphalis vau-album</i> | <i>Ribes, Ulmus, Salix, Populus, Betula, Fagus</i> |
| <i>N.polychloros</i> | <i>Pirus, Prunus, Ulmus, Celtis, Salix, Populus</i> |
| <i>N.californica</i> | <i>Ceanothus</i> |
| <i>N.antiopa</i> | Rosales: * <i>Pyrus, Sorbus</i> ; Urticales: * <i>Ulmus, Celtis</i> , Salicales: <i>Salix, Populus</i> ; Fagales: <i>Betula, Alnus</i> |
| <i>N.xanthomelas</i> | <i>Salix</i> |
| <i>Aglais urticae</i> | <i>Urtica</i> |
| <i>A.milberti</i> | <i>Urtica</i> |
| <i>Inachis io</i> | <i>Urtica</i> |

* From these two host orders there are only Nearctic reports. Several other hosts reported in Scott (1986), also in plant orders other than those included.

choice in this species. Hosts in Fagales, i.e. species of *Betula* and *Corylus*, are the least preferred hosts in the range of hosts used by *P.c-album* (Nylin, 1988; this study). Presumably the reason for this is that these hosts lack the special chemical properties (whatever they are) which makes hosts in *Salix*, *Ribes* and, especially, Urticales the preferred hosts for *Polygonia* spp. (Larsen, 1974; Scott, 1986; Nylin, 1988). Nevertheless, *Betula* spp. have been recorded as a host of *P.c-album* in the field (Seppänen, 1970; C. Wiklund, pers. comm.) and, as has been shown here, some eggs are occasionally laid on them in the laboratory, especially when there is no alternative. To what extent has the preference hierarchy evolved to correlation with larval performance at these lowest levels of the hierarchy?

There are two common tree-forming birch species in the western Palearctic, *B.pubescens* Ehrh. (including the arctic subspecies *tortulosa* Ledeb.) and *B.pendula* Roth (syn. *B.verrucosa* Ehrh.). The similarities between them, and their tendency to form hybrids, have often been stressed in the past (Linnaeus considered them a single species, *B.alba* L.). As a consequence the two species are often (although by no means always) lumped in insect host plant records (e.g. Seppänen, 1970; concerning *P.c-album*). However, the two species are in fact morphologically and ecologically rather distinct, and in fact it is now thought that about five speciation events divide the two species (Roskam, 1985). They belong to different species 'series' (*Pubescentes* and *Verrucosae*), and are more closely related to other species in the Nearctic and in the eastern Palearctic than to each other. Other insects are known to distinguish between *B.pendula* and *B.pubescens* (e.g. Roskam, 1985; Claridge & Nixon, 1986). Larval performance and oviposition preference in *P.c-album* is very different on

the two species. *B.pendula* is fatal to larvae, whereas growth on *B.pubescens* is poor to intermediate (worse than on *S.caprea*, but better than on *C.avellana*). Females apparently use chemical cues to distinguish between the species of *Betula*. This is the only reasonable explanation for the high degree of discrimination against *B.pendula*. It is interesting to note that such discrimination has been able to evolve despite the apparently very minor role of *Betula* as a host. The penalty for a mistake is obviously high for each particular egg, but should be of significance for the fitness of ovipositing females only if oviposition on *Betula* takes place at a reasonably high rate in the field. Field studies are needed to clarify this point, but will be very difficult in the case of *P.c-album* because females are hard to follow for any extended periods of time. At present all evidence suggest that *Betula* is an unimportant host genus for *P.c-album* (e.g. Pratt, 1986, 1987; Nylin, 1988).

The probable reasons why total discrimination (and perfect preference–performance correlation) has been able to evolve in the case of *P.c-album* can be found by reversing the two causes of poor preference–performance correlations (see Introduction; Thompson, 1988a; Thompson & Pellmyr, 1991) which we find relevant in this case, i.e. the abundance hypothesis (based on optimality criterions) and the time hypothesis (based on the assumption of evolutionary constraints to optimal choice). The abundance hypothesis states that when the best hosts are rare, poorer but more abundant hosts should be used instead. All of the plant species investigated in the present study are common in Sweden. Moreover, both species of *Betula* are very abundant in the typical open forest habitats of *P.c-album*, which (when coupled with the certainty of death of offspring on *B.pendula*) means that it is likely that

females cannot afford to waste an egg on, or even alight on, every *B.pendula* they come across. At the same time, *B.pubescens* is so abundant, and not poor enough as a host, that it may pay females not to discriminate against all *Betula*.

The time hypothesis states that there may not always have been time enough for perfect preference–performance correlations to evolve. In the case of *P.c-album*, however, phylogenetic analysis suggests that the species and its ancestors have used all of the studied plants, or their ancestors, for a very long time. This opinion is based on the fact that the same range of plant genera (*Urtica*, *Ulmus*, *Humulus*, *Salix*, *Ribes*, *Corylus*, *Betula*) are important hosts for all *Polygonia* and also for the related *Nymphalis*, *Aglais* and *Inachis* (Table 2; e.g. Larsen, 1974; Scott, 1986; Ackery, 1988). Note from Table 2 especially that *P.faunus*, the probable sister-species to *P.c-album* (Scudder, 1889), feed on the same range of plants, including *Betula*. These plant genera are neither very closely related, nor an assortment of the most abundant plants in habitats of *Polygonia*. Therefore the only plausible explanation for this pattern is a long history of associations with these genera, reaching back at least to the time before the latest several speciations in this butterfly group. Nearer to the present, the hosts in Fagales may well have been more important as hosts for *P.c-album* in prehistoric days, when *Betula* and *C.avellana* were highly abundant in comparison with *U.glabra* (Southwood, 1961), whereas the ‘follower of man’ *U.dioica* and the generally cultivated *Humulus lupulus* must have been much rarer than today.

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