

ORIGINAL ARTICLE

Host plant choice in the comma butterfly–larval choosiness may ameliorate effects of indiscriminate oviposition

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Abstract In most phytophagous insects, the larval diet strongly affects future fitness and in species that do not feed on plant parts as adults, larval diet is the main source of nitrogen. In many of these insect–host plant systems, the immature larvae are considered to be fully dependent on the choice of the mothers, who, in turn, possess a highly developed host recognition system. This circumstance allows for a potential mother–offspring conflict, resulting in the female maximizing her fecundity at the expense of larval performance on suboptimal hosts. In two experiments, we aimed to investigate this relationship in the polyphagous comma butterfly, *Polygonia c-album*, by comparing the relative acceptance of low- and medium-ranked hosts between females and neonate larvae both within individuals between life stages, and between mothers and their offspring. The study shows a variation between females in oviposition acceptance of low-ranked hosts, and that the degree of acceptance in the mothers correlates with the probability of acceptance of the same host in the larvae. We also found a negative relationship between stages within individuals as there was a higher acceptance of lower ranked hosts in females who had abandoned said host as a larva. Notably, however, neonate larvae of the comma butterfly did not unconditionally accept to feed from the least favorable host species even when it was the only food source. Our results suggest the possibility that the disadvantages associated with a generalist oviposition strategy can be decreased by larval participation in host plant choice.

Key words host plant choice, insect–host plant interaction, mobility, oviposition behavior, parent–offspring conflict, specialization

Introduction

In plant feeding insects, there is a great variation in the relative role played by ovipositing mothers and their offspring in locating and recognizing a suitable host plant for larval growth. In many systems, such as the free feeding sawflies (Price, 2003), leaf beetles (Futuyma, 1990) and in most butterflies (Thompson & Pellmyr, 1991), the ovipositing female plays the important role of selecting

suitable host plants, whereas the neonate larvae are subject to the choice of the mother. However, on the other hand, there are insect systems where the mothers make quite a poor job in host plant selection, but this is often compensated by comparatively mobile larvae who themselves are able to find suitable hosts (Chew, 1977; Bernays & Chapman, 1994; Berdegué *et al.*, 1998). In some extreme examples, such as in some Hesperids and Noctuids, the females oviposit on inedible substances, or drop eggs in the air, quite far from a host plant (Dethier, 1959, and references therein).

In most butterflies, the larval diet is of crucial importance for their future fitness as it affects growth rates and is the main source of nitrogen throughout the life. Female butterflies should therefore choose hosts where

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larval performance is the best to maximize larval fitness (Thompson, 1988; Jaenike, 1990), and experimental studies generally confirm a correlation between the oviposition preference of mothers and larval performance (Wiklund, 1975; Nylin & Janz, 1993; Gripenberg *et al.*, 2010). However, female preference and larval performance do not always correlate perfectly (Rausher, 1979; Underwood, 1994; Gripenberg *et al.*, 2010). This could happen in situations when other factors, such as predation, parasitism and pathogens, affect larval fitness more than growth performance (Thompson & Pellmyr, 1991) or when there is a trade-off between female fecundity and larval fitness (Nylin & Janz, 1996). In the latter case, a larva may end up on a suboptimal host where its fitness is low.

The Swedish population of the comma butterfly (*Polygonia c-album*) is polyphagous with a well-known host preference hierarchy in ovipositing females (Nylin, 1988; Janz *et al.*, 1994). In the field, *P. c-album* larvae can be found on plants belonging to a whole range of families in four different orders (Rosales, Betulales, Salicales, and Urticales; Seppanen, 1970). The female host preference is in general agreement with larval performance (Nylin, 1988; Nylin & Janz, 1993). According to the “mother knows best” paradigm (Thompson, 1988), in such species larvae should not put much effort into host selection apart from fine-tuned decisions about preferable leaf tissue within hosts. However, larvae of *P. c-album* are not completely left to their mothers’ good or bad choices. When allowed to choose among different hosts, neonate larvae show preferences that reflect their performance (Nylin & Janz, 1996) and they abandon unsuitable hosts (Nylin *et al.*, 2000). This is interesting because it suggests that larvae of this species are capable of evaluating their food on a similar basis as the adult females. Similarly, it has recently been shown that neonate larvae of the cabbage white butterfly (*Pieris brassicae*) are more choosy than mothers and prefer high-performance aphid infested host plant individuals over noninfested individuals, when mothers do not differentiate (Soler *et al.*, 2012).

Nylin and Janz (1996) showed that larvae of *P. c-album* in general choose to feed on host leaves in the same rank-order as expected from the ovipositing frequencies of females. However, the data seemed to suggest that the lowest ranked hosts, *Salix caprea* and especially *Betula pubescens*, were accepted to a greater degree by the females than the larvae, as only about half of the larvae actually fed from these plants, whereas almost all females laid some or many eggs on them. Also, the growth rate of the larvae that actually do establish on low-ranked plants follow the same pattern, where especially the birch diet results in a considerably lower per day weight gain

(Nylin & Janz, 1993) with a small final size and also high mortality compared to other hosts (Janz *et al.*, 1994). Taken together, these data may hint at a discrepancy between female willingness to oviposit on low-ranked hosts and larval fitness, and suggest a parent–offspring conflict.

The aim of the present study was twofold. To increase the understanding of the relationship between female oviposition behavior and larval performance, we aimed to investigate the concordance of host acceptance between life stages on a family and individual level by comparing both female and larval acceptance of low-ranked hosts. Further, we aimed to investigate the behavior of neonate larvae of the comma butterfly and their possible inclination to influence their own fitness. By studying acceptance instead of preference, we aspired for a more natural situation where animals make consecutive accept/reject choices rather than simultaneously choosing among several alternatives. This is especially true for the larvae, which primarily encounter the plant they hatch on and may decide whether to start feeding or search for better food, but female oviposition in butterflies is also better described as a sequence of acceptance choices than as a preference among alternatives (Courtney *et al.*, 1989). Thus, in two experiments, we investigated the acceptance of low-ranked hosts, both within individuals (as a larva and as an adult female), and between mothers and their offspring.

Material and methods

We conducted two separate experiments of host plant acceptance, during the spring of 2009 (Experiment 1) and 2012 (Experiment 2). Experiment 1 was designed to primarily investigate the degree of acceptance of low-ranked hosts on an individual level, between life stages, whereas Experiment 2 was designed to test acceptance between generations to compare mother and offspring acceptance levels. In both experiments, we used wild-caught gravid females from the Stockholm area and their offspring. As hosts we used *Urtica dioica* (stinging nettle), *Salix cinerea* (gray willow), and *B. pubescens* (downy birch) where *U. dioica* is the highest ranked and *B. pubescens* is at the very bottom of the host plant preference hierarchy of both females and larvae.

Female acceptance

We studied female oviposition behavior in flight cages measuring approximately 50 cm × 50 cm × 50 cm (length × height × width) with net walls and plastic roof

(L : D 8 : 16; 28 °C). The cages were heated and lit with individual light bulbs outside over the cages. Females were kept singly in the cages and they were provided with sugar solution in a highly positioned cup with an immersed sponge to sit and feed from. They also had access to one (Experiment 2) or several (Experiment 1) cuttings of host plant placed in the cages in bottles of water.

Larval acceptance

Newly hatched, unfed larvae (2–16 h old) were placed individually in Petri dishes (ø 9 cm, 22 °C, L : D 12 : 12) with damp filter paper. Larvae were provided with circular cutout pieces of host plant leaf (ø 1 cm), and their acceptance was scored if they had fed from the plants after 24 h (both experiments) and after 48 h (Experiment 2).

Rearing

After the scoring of acceptance, all larvae were reared singly on *U. dioica* in plastic jars that provided a water culture for the host plants. Plants were replaced with fresh ones when needed. Light and temperature conditions were set to induce the light directly developing morph (Nylin, 1989). Adult individuals were sexed and individually marked.

Experiment 1

We used a total of 399 newly hatched F₂-larvae, derived from 11 laboratory-reared F₁-females (daughters of four wild-caught F₀-females) in a larval host plant acceptance test. In this test, larvae were placed on top of a piece of leaf from a low-ranked host situated at 5 cm distance from a piece of nettle, the high-ranked host. Their acceptance was scored after 24 h, and they had to have consumed at least 10% of either host plant to be used as data. Fifty-five larvae were scored for acceptance of the lowest ranked host *B. pubescens*, and 344 larvae (between 17 and 46 larvae/F₁-female) were scored for acceptance of the intermediately ranked *S. cinerea*. When larvae had completed the acceptance trial, they were all individually reared on *U. dioica* as described above.

When the butterflies had reached the adult stage, they were randomly placed in mating cages and mated, after which the females were subjected to a host plant oviposition acceptance test. Females were presented simultaneously to *U. dioica*, *S. cinerea* and *B. pubescens*, put in glass bottles at nonequal heights in the cages: the low-ranked

B. pubescens and *S. cinerea* were placed near the ceiling and the light source, at the same height as the sugar solution, whereas the bottle containing *U. dioica* was placed on the cage floor. The setup was constructed so that females would encounter the low-ranked hosts more often than the high-ranked *U. dioica*, because butterflies tend to fly upwards toward the light and also since the food source was placed high in the cage. This setup has been used previously by us to score acceptance of low-ranked hosts by making it hard to find the *U. dioica* cutting, a plant that is strongly preferred in summer (e.g. Nylin *et al.*, 2009). The oviposition trial was completed when females had produced at least 10 eggs per day for 3 days. In total, 23 females laid a sufficient number of eggs to be included in the study.

Experiment 2

A total of eight wild-caught females were tested for their level of relative acceptance of birch, *B. pubescens*, the lowest ranked host, in no-choice tests. We used *B. pubescens* for these females because we wanted to be able to measure variation between individuals in their risk-spreading, generalistic tendency. We feared that in spring, the quality of *Salix* would be too good so that that the *P. c-album* females would be too accepting for us to be able to see much variation in acceptance. In the acceptance test, the females were subjected to one solitary fresh cutting of a *B. pubescens* every second day and a solitary cutting of a fresh shoot of *U. dioica*, the preferred host plant, every other day for a total of 14 days. We aimed to keep the total leaf area of the cuttings approximately the same between host species. Plants were exchanged at approximately the same time in the mornings. We collected data about the number of eggs oviposited on each plant each day and collected the eggs batchwise in small jars for hatching.

When hatched, 30–77 larvae from each female were subjected to an acceptance test. The number of larvae tested from each female varied because we aimed to attain about 30 adult offspring from each F₀-female, and we continued to test additional newly hatched larvae from females whose larvae died early during the rearing. They were placed on a solitary cutout piece of *B. pubescens* leaf as described above, and after 24 h, we checked if they had eaten from the cutting. If the larvae showed signs of feeding, i.e., if there was any leaf matter removed from the cuttings (often there were also some evidence of frass), they were scored as having accepted birch and moved to be reared on nettle. For those that had not eaten, they were placed on a fresh piece of birch and the procedure

was repeated for a second 24 h (a total of 48 h). After this time, all larvae were scored for their acceptance or rejection and reared to adults on *U. dioica*.

After eclosion, the adult butterflies were sexed and kept in a cold room (10 °C) until all had emerged. We then mated the butterflies, and attempted to select for high and low degree of acceptance, to further increase the variation in our sample. Thus, the F₁-generation butterflies were divided between three mating cages so that those with mothers that had no acceptance of birch were together in one cage and those whose mothers had only laid a few eggs on birch, and those with mothers that had laid more than a few eggs on birch, were placed in the other two cages, respectively. Matings usually take place during the afternoon in this species, so we shifted their light–dark cycle so that it corresponded to the actual morning hours to better be able to spot any matings. We checked the cages regularly for matings (the pair remains together for several hours) and when found, the pair was removed from the cage and, when naturally separated, the male was returned to his cage.

We tested 19 mated F₁-females' oviposition acceptance of willow, *S. cinerea*, as compared to nettle, *U. dioica*, in the same manner as described above for the F₀-females, but we only recorded ovipositions during 6 days in total. For these females, we used *S. cinerea*, a host of higher ranking than *B. pubescens*, because the quality of birch is too low later in the season to be acceptable. Again, the batches of eggs from each female were counted and collected each day and placed in small jars for hatching. When hatched, 30 larvae from each female were tested for their acceptance of *S. cinerea* as food in the same way as described above for *B. pubescens*, but the experiment was terminated after 24 h, when the acceptance or rejection was recorded.

The statistical analyses were performed using STATISTICA 10.0.228.2 (Statsoft Inc., Tulsa, OK, USA) and Stata Statistical Software: Release 12 (StataCorp LP, College Station, TX, USA). To compare oviposition rates between three hosts, we used the Freeman–Halton extension of the Fisher exact probability test for 2 × 3 tables (Freeman & Halton, 1951). The relationship between the proportion of larvae that accepted a poor host and the proportion of eggs that were laid on these hosts by their mothers was tested with a GLM using the binomial family and a logit link and robust standard errors (Papke & Wooldridge, 1996). We also used Mann–Whitney *U*-tests to compare oviposition acceptance in adult females who as larvae had accepted or rejected *S. cinerea* (Experiment 1), and the difference in acceptance of the two hosts in both females and larvae (Experiment 2). Additionally, we compared the degree of oviposition accep-

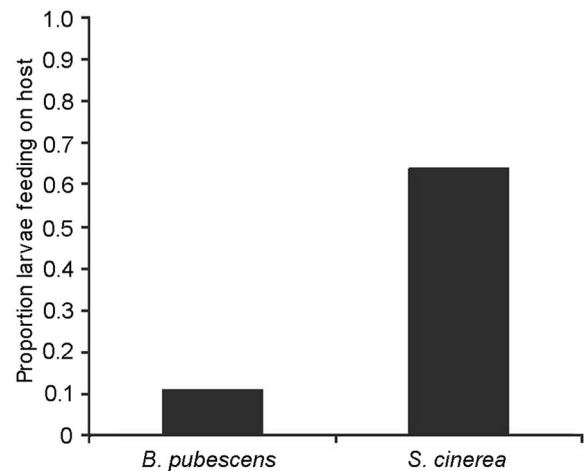


Fig. 1 Larval acceptance of lower ranked hosts. The proportion of larvae staying to feed on *B. pubescens* or *S. cinerea*, respectively, as opposed to rejecting them for feeding *U. dioica*.

tance between families in Experiment 1, using Kruskal–Wallis tests.

Results

Experiment 1

In the larval acceptance test, very few larvae accepted to feed at all on the low-ranked host, *B. pubescens*, and left to feed on nettle, *U. dioica* (Fig. 1). A significantly greater proportion of larvae accepted the willow, *S. cinerea*, as food (Fisher exact test: $P < 0.0001$).

Also, in females, the acceptance of birch was very low as compared to both willow and nettle (Fig. 2). This could be seen in the proportions of females ovipositing at least one egg on the different hosts (Fig. 2A, Freeman–Halton extension of Fisher Exact test for 2 × 3 tables, $P < 0.0001$), and in the number of eggs oviposited on the different hosts (Fig. 2B; Friedman test: $\chi^2 = 18.98$; $df = 2$, $P < 0.0001$). Of the seven females accepting *B. pubescens*, five laid less than 10% and two laid a majority of their eggs on birch (58% and 100%, respectively).

The within individual, between life stages comparison of the degree of relative acceptance of *S. cinerea*, a lower ranked host, unexpectedly revealed a negative relationship between the degree of acceptance as a larvae and the later acceptance as a female (Fig. 3). Individuals that had accepted and fed from *S. cinerea* showed a lower ovipositing acceptance of that same host as adults, as compared to individuals that had rejected *S. cinerea* (Mann–Whitney *U*-test: $U = 80$, $P = 0.047$).

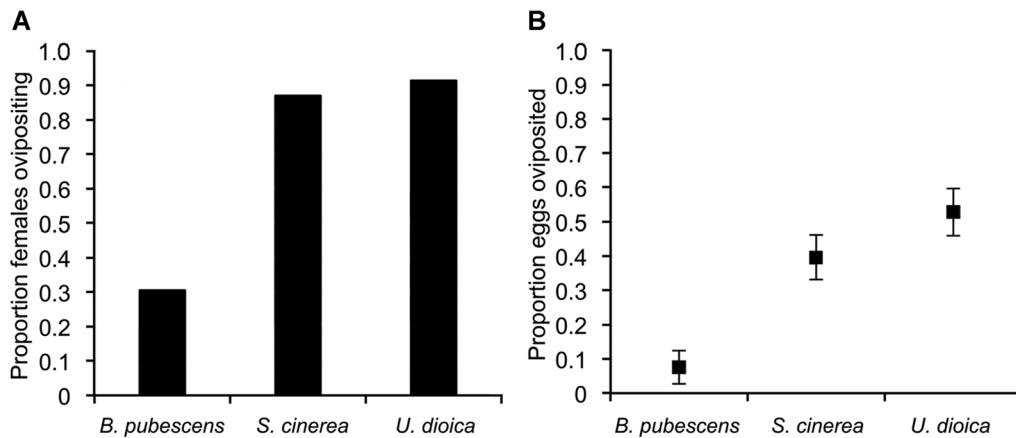


Fig. 2 Female host plant oviposition acceptance. (A) The proportion of females laying at least one egg on the host plant and (B) the mean (\pm 1SE) proportion of total amount of eggs laid by females on each host plant *B. pubescens*, *S. cinerea* and *U. dioica*, respectively.

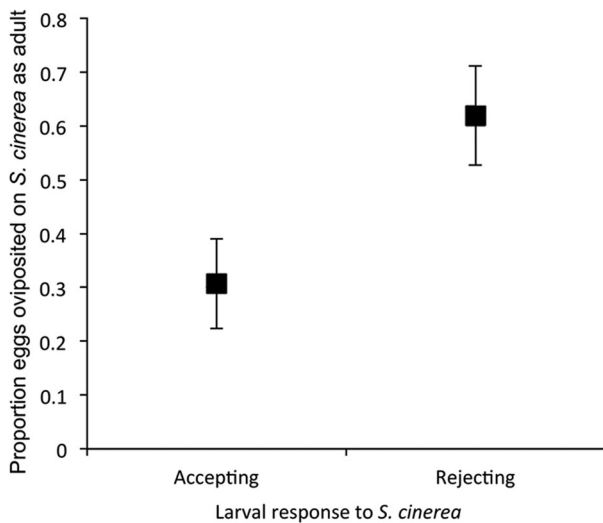


Fig. 3 The acceptance of *Salix cinerea* for oviposition in female *P. c-album* in relation to her acceptance of the same host as a neonate. Data represent the mean proportion (\pm 1SE) of total egg numbers that were oviposited on *S. cinerea* as opposed to *U. dioica* and *B. pubescens*.

Since previous results from *P. c-album* have shown heritable differences in oviposition preferences (Janz, 1998; Nylin *et al.*, 2005), we compared the F_2 -female acceptance of lower ranked hosts between families as the proportions of eggs oviposited on *B. pubescens* and *S. cinerea*, but the difference was not statistically significant between groups of sisters (Kruskal–Wallis tests: $H(7;23) = 11.95$, $P = 0.102$) or on the level of grand mother (Kruskal–Wallis tests: $H(3;23) = 6.73$, $P = 0.081$).

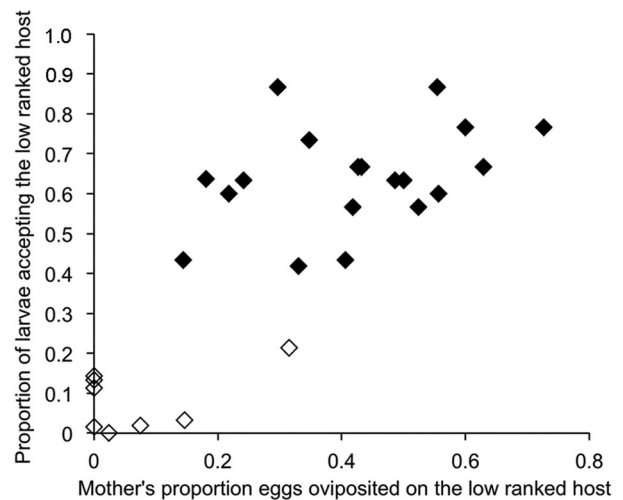


Fig. 4 Larval acceptance in relation to mother acceptance of lower ranked hosts in *P. c-album*. Open diamonds represent the proportion of F_1 larvae accepting *B. pubescens* after 24 h in relation to the proportion eggs oviposited by their F_0 mothers ($n = 8$), and closed diamonds represent the proportion of F_2 larvae accepting *S. cinerea* after 24 h in relation to the proportion eggs oviposited by their F_1 mothers ($n = 19$).

Experiment 2

In the wild-caught F_0 -females, the acceptance of *B. pubescens* as a host in the no-choice experiments was low (Fig. 4). Of the eight females, four totally rejected ovipositing any eggs on *B. pubescens*, whereas two laid <10% and the other two 15% and 31% of their eggs, respectively. However, the acceptance of *S. cinerea* by the F_1 -females was higher. All females oviposited on

S. cinerea and with a higher proportion of eggs than on *B. pubescens* (0.393 ± 0.0355 , mean \pm 1SE; Mann–Whitney $U = 146$, $z = -3.69$, $P = 0.0002$; Fig. 4). The larvae showed a similar pattern as the females and had a lower acceptance of *B. pubescens* as compared to *S. cinerea* after 24 h (Fig. 4, Mann–Whitney $U = 152$, $z = -4.01$, $P < 0.0001$). Still after 48 h, the larval acceptance of *B. pubescens* was very low as 79% still refused feeding at all on *B. pubescens*, and 13 of the rejecting larvae died (probably from starvation).

Figure 4 shows the relationship between larval acceptance of low-ranked hosts to the acceptance of their mothers. Thus, there is a correlation between the proportion of larvae accepting the low-ranked host and the proportion of accepted ovipositions on that same host by their mothers (GLM, generally: $z = 2.39$, $n = 27$, $P = 0.017$; *S. cinerea* only: $z = 2.11$, $n = 19$, $P = 0.035$; *B. pubescens* only: $z = 1.57$, $n = 8$, $P = 0.118$). This suggests that females that are not so discriminating in host plant choice also give rise to less discriminating larvae.

As very few larvae accepted birch as host, we only managed to rear and mate three females that had accepted birch as larvae. Thus, in this experiment, a within individual comparison of acceptance could not be attained.

Discussion

This study shows that neonate larvae of the polyphagous comma butterfly, *P. c-album*, do not unconditionally accept to feed from any host they find themselves on, even though it is within their natural host plant range and there is no alternative food present. Moreover, the relative acceptance in neonates of the low-ranked hosts, birch (*B. pubescens*) and willow (*Salix cinerea*), shows the same general pattern as female oviposition acceptance (this study) and the average preference ranking of larvae and females (Nylin & Janz, 1996), with a low acceptance of birch and a somewhat higher acceptance of willow.

The comma butterfly utilizes only a few plant species from four different orders and could be regarded as a polyspecialist rather than a true generalist (Nylin & Janz, 2009). The degree of specialization in female oviposition preference varies between populations (Nylin, 1988; Janz & Nylin, 1997), but also a great variation within population can be found, and it is at least partly heritable (Nylin et al., 2005). Our study shows great individual variation in acceptance of birch especially. In Experiment 1, only 30% of the females laid any eggs at all on birch despite its exposed position in the cages, and the number of eggs varied between only a few to 100% of the eggs. Likewise in Experiment 2, more than half of the females refused

birch, although they were exposed to birch alone every second day for a total of 7 days.

Although some females seem to be rather accepting of birch, it is interesting to note that most larvae strongly rejected feeding from this host. As much as 79% refused to start feeding at all, even though forced to starve for more than 48 h. This time is close to the general survival limit from starvation of *P. c-album* neonates, which is reported to be 2.92 ± 0.87 days (Reavey, 1992), and some larvae in this treatment actually died. This behavior suggests that the larvae of *P. c-album* do not blindly accept the food source chosen by their mother. As mentioned above, staying and feeding on the inferior host *B. pubescens* results in a lower survival, lower growth rate and smaller final size (Nylin & Janz, 1993; Janz et al., 1994). An alternative would be to dismiss the mothers' choice and leave the unpreferred host in search for a better suited one, a strategy that would involve great risks even though other host species could sometimes be found in the vicinity. Whether or not *P. c-album* neonates ever undertake this endeavor in nature is unknown, but in a laboratory setting, some larvae (ca. 27%) did successfully manage to shift from a nonhost (*Laminum album*) to *U. dioica* when found close by (Nylin et al., 2000). However, these observed host switches in laboratory conditions could be a side effect of the tendency in neonates to search for the most digestible leaves within the host plant they hatch on, rather than them abandoning an unpreferred host.

For evident reasons, but perhaps unfortunately, almost all studies on host plant choice in butterflies and insects with similar ecologies have been done with female ovipositing decisions in mind (but see Nylin & Janz, 1996; Fred & Brommer, 2010). Thus, too little is known about the behavior of neonate larvae, their ability to actually search for and evaluate a replacement host, and under what natural circumstances, such behavior could be useful. Studies now accumulate showing that larvae do have opinions on their food and that they are able to select food sources that benefit their performance in controlled preference experiments (Nylin & Janz, 1996; Soler et al., 2012; this study). However, the spatial scale on which these preferences may act in nature is unknown. Interestingly, we found a correlation in the acceptance of low-ranked hosts between mothers and her larvae so that a greater proportion of larvae of females that accept lower ranked hosts also accept to feed from that host. At this point, it is hard to evaluate possible reasons for this correlation, but it opens for the possibility that larvae may use a similar host recognition system as females, and that it may have a genetic basis.

The most striking result in this study is perhaps the seemingly disparate behavior between life stages within

individual females in Experiment 1. Females that as a larva had rejected *S. cinerea* and chosen to feed from *U. dioica* showed a much higher inclination to oviposit on *S. cinerea* as compared to those who had accepted *S. cinerea* as a larva (Fig. 3). It should be noted here that all larvae after the acceptance test were reared on *U. dioica*, and that there is in any case good evidence that the larval host plant does not affect the subsequent oviposition choices of adults in this species, i.e., there is no ‘‘Hopkins effect’’ (Janz *et al.*, 2009). We would have expected the opposite pattern, given previous findings of larvae showing the same host plant preference hierarchy as do ovipositing females (Nylin & Janz, 1996), the observed correlation in acceptance of low-ranked hosts between mother and her larvae (Experiment 2 in this study), the evidence for a genetic component in oviposition preferences in this species (Janz, 1998; Nylin *et al.*, 2005) as well as the tendency of a family effect of oviposition acceptance of *S. cinerea* (Experiment 1). The answer to this paradox may lay in our experimental design. It is perhaps not possible to measure host plant acceptance in a similar manner for larvae and adults. Perchance by using the setup of Experiment 1, we did not primarily measure larval acceptance of *S. cinerea*, but their mobility instead, resulting in a higher degree of mobile individuals ending up on *U. dioica*. The pattern we see in this study may rather reflect variation in individual strategies, where a mobile larva correlates with a more risk-spreading generalist female strategy.

In conclusion, our study shows that larvae of phytophagous insects, although generally subjected to their mother’s choice of host plant, do not always accept their mothers’ bad choices. Having a generalist or a specialist host plant strategy involves various trade-offs between, for instance, recognition of several suitable hosts contra sensitivity of individual host plant quality or female fecundity and risk-spreading contra larval individual performance. Our results suggest the possibility that the disadvantages associated with a generalist oviposition strategy can be decreased by larval participation in host plant choice. However, there is a prominent lack of knowledge about larval behavior and what sensory and decision mechanisms they may use. Hopefully, future work will provide more information about what different cues influence larval host plant choice and what possibilities they have to act on them.

Acknowledgments

We thank Vlad Dinca and H el ene Audusseau for their help in catching butterflies and  asa Sundstr om for her help in rearing the larvae. This study was financed by

grants from The Swedish Research Council (VR) to SN (grant 2011–5636) and Stockholm Faculty of Sciences to NJ. We also acknowledge support from the Strategic Research Programme Ekoklim at Stockholm University.

Disclosure

The authors declare no conflict of interest.

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Accepted August 30, 2013