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No effect of larval experience on adult host preferences in *Polygonia c-album* (Lepidoptera: Nymphalidae): on the persistence of Hopkins' host selection principle

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Abstract. 1. The possible effect of juvenile imprinting or 'chemical legacy' on the subsequent oviposition – often called the 'Hopkins' host selection principle' – has been a controversial but recurrent theme in the literature on host-plant preference. While it appears possible in principle, experimental support for the hypothesis is equivocal. The present study points out that it is also important to consider its theoretical implications, and asks under what circumstances, if any, it should be favoured by natural selection.

2. Following this reasoning, it is predicted that host preference in the polyphagous butterfly *Polygonia c-album* L. (Lepidoptera, Nymphalidae) should not be influenced by larval environment. This was tested by rearing larvae on three natural host plants: the high-ranked *Urtica dioica* and the medium-ranked *Salix cinerea* and *Ribes uva-crispa*, and exposing the naive females to oviposition choices involving the same set of plants.

3. It was found that larval host plant had no effect on oviposition decisions of the adult female. Hence, the Hopkins' host selection principle does not seem to be applicable in this species.

4. Based on recent insights on how accuracy of environmental versus genetic information should affect the control of developmental switches, the conditions that could favour the use of juvenile cues in oviposition decisions are discussed. Although the Hopkins' host selection hypothesis cannot be completely ruled out, we argue that the circumstances required for it to be adaptive are so specific that it should not be invoked as a general hypothesis for host selection in plant-feeding insects.

Key words. Chemical legacy, environmental cues, genetic cues, host-plant preference, *Polygonia c-album*, phenotypic plasticity, pre-imaginal conditioning, specialisation.

Introduction

The idea that oviposition preferences of insects is directly influenced by larval experience is an old one that is often attributed to Hopkins (1917), although his original formulation was actually rather vague. The hypothesis has later come to be known as 'Hopkins' host selection principle' (HHSP).

The main rationale behind the hypothesis is that larval experience of its feeding environment provides reliable information on host quality and availability during subsequent oviposition. The female herself has evidently survived to adulthood on the plant, and hence the plant is a suitable resource that exists in the locality (provided that the female ecloses reasonably close to her feeding site).

There appears to be some disagreement on how the HHSP should be formulated, especially with respect to mechanisms (Barron, 2001). For that reason, we will begin by stating that we will use the term to describe the general observation that information on host availability and suitability is transferred from the larva through the pupa and used by the ovipositing female during oviposition. This is purposefully a non-mechanistic usage, as we believe it is important to separate observation of the phenomenon from mechanistic and evolutionary explanations of it. Thus, with our usage, any mechanism that causes larval host-plant experience to affect oviposition decisions will qualify as satisfying HHSP.

The hypothesis has some intuitive appeal, but has received little empirical support. However, for a hypothesis whose 'life and death' has been reviewed (Barron, 2001), and that has received 'another nail in its coffin' (van Emden *et al.*, 1996), it is amazingly persistent. Indeed, for a researcher working on host selection by

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phytophagous insects, questions on HHSP are very predictable during peer review of manuscripts and following oral presentations. What is it about this hypothesis that is so appealing?

We believe that there are several reasons for this refusal to die. One is, as already mentioned, that it is intuitively appealing. Another reason is that the mechanisms proposed to be involved in the transfer of information from the larva, through metamorphosis, to the adult insect are conceptually interesting in themselves (e.g. Corbet, 1985; Rietdorf & Steidle, 2002; Gandolfi *et al.*, 2003). Finally, of course, the hypothesis may be correct, at least under some circumstances.

This paper has two objectives. One is to test the applicability of the hypothesis for our primary study system, the polyphagous butterfly *Polygonia c-album* and its diverse array of hosts. In addition, as we feel the subject has received more mechanistic attention than theoretical, we will also provide a theoretical discussion on whether HHSP is a plausible general hypothesis for host selection, or alternatively, under which specific circumstances it should be expected to work.

The HHSP has been tested several times over the years and, up until quite recently, most of these studies found no support for the hypothesis (Wiklund, 1974; Tabashnik *et al.*, 1981; Williams, 1983; van Emden *et al.*, 1996; Rojas & Wyatt, 1999; Solarz & Newman, 2001; e.g. Kerpel & Moreira, 2005). However, there has been a surprisingly large number of fairly recent studies that have claimed to have found direct or indirect evidence for the HHSP (Anderson *et al.*, 1995; Rietdorf & Steidle, 2002; Akhtar & Isman, 2003; Gandolfi *et al.*, 2003; Chow *et al.*, 2005; Hora *et al.*, 2005; Olsson *et al.*, 2006; Facknath & Wright, 2007). These findings have ignited new sparks for the hypothesis and have caused Hopkins to rise from the coffin once again.

It is clear that, in principle, transfer of information from the larva to the imago is possible. In a recent review, Barron (2001) pointed at several possible mechanisms that can account for this. Preimaginal conditioning of the nervous system is often mentioned, but rarely clearly demonstrated. However information can also transfer through the pupa by means of external chemical compounds derived from the food, as a 'chemical legacy' (Corbet, 1985), and thus provide a means for imaginal conditioning, which has been more convincingly demonstrated (see Barron, 2001). If such chemical legacy is included in the definition, the HHSP could be possible, but is it plausible? We need to ask when and why insects should be expected to make use of such preimaginal information in their oviposition decisions.

Leimar *et al.* (2006) has recently argued for the view of the genome and the environment as different sources of information for future conditions. Developmental switches that influence development of phenotypic variants will usually make use of the most reliable information. They showed that strong selection acting on phenotypic alternatives will favour the use of genetic cues as predictors for upcoming selective conditions, but they also pointed out that under some circumstances, environmental cues can be more reliable (Leimar *et al.*, 2006).

Genetically determined preference hierarchies are common features among plant-feeding insects, and the basic function of these hierarchies is to ensure that the best possible plant is used for oviposition (Wiklund, 1975, 1981; Courtney *et al.*, 1989; Thompson & Pellmyr, 1991; Thompson, 1993). Ideally, females should always oviposit on the host that can provide the best offspring performance, but there are several factors that can cause females to spread their eggs over other plants further down in the hierarchy (Thompson, 1988). Predation, variation in plant abundance, risk spreading between alternative hosts (or years or patches) and proximity of adult feeding resources, are but just a few (Mayhew, 1997; Scheirs *et al.*, 2000; Scheirs & De Bruyn, 2002; Janz, 2005; Janz *et al.*, 2005a,b).

The HHSP is a specific form of phenotypic plasticity, where an early source of environmental information will influence behaviour at a later developmental stage. What is somewhat unusual about it, is that the environmental information used to modify oviposition behaviour is pushed back in time, long before the trait itself is expressed. Hence, the environmental information, rather than modulating an existing pattern of expression, must alter the expression of a trait before it is actually expressed. It follows then that we must ask under what circumstances the larval environment can be a more reliable predictor of future conditions, than the genome and current environment combined.

The value of cues from the larval feeding environment will be highly dependent on spatial and temporal variation in host availability and suitability. For example, in bi- or multivoltine insects, larval cues may be a useful source of information to allow it to respond to predictable changes in host suitability (such as induced defences), but not in a situation where temporal variation in host suitability is small or unpredictable (because the information content of the cue will be low). Moreover, large differences between hosts in offspring performance would mean that females that have grown on a poor host would do better searching for a better plant for her offspring, than to look for her own larval host. Taken to its extreme, HHSP would under such circumstances cause the offspring of such a female to remain always on this inferior host, a strategy that will hardly be favoured by natural selection. For this reason, we should also expect HHSP to be less favourable in situations where alternative hosts vary greatly and consistently in quality as larval food.

For the empirical test of the applicability of the HHSP in our model system, larvae of the polyphagous butterfly *P. c-album* were reared on three natural host plants, the high-ranked *Urtica dioica* and the intermediate-ranked *Salix cinerea* and *Ribes uva-crispa*. These were chosen to be able to produce pairwise comparisons that did and did not differ in preference and performance (suitability) ranking. The prime goal of the experiment was to be able to demonstrate an effect of larval rearing plant on adult oviposition decisions (the HHSP), and not how such an effect might be accomplished (preimaginal conditioning, chemical legacy etc.).

In Sweden, *P. c-album* is univoltine and as it hibernates in the adult stage, there is at least 9 months between larval feeding and adult oviposition. Moreover, weather conditions during oviposition and larval growth are highly variable and unpredictable. Hence, in this system, the larval feeding environment should provide little information that can improve oviposition decisions. It has also previously been shown that there is a strong genetic component to host preference in this species. Differences between geographically separated populations are largely influenced by major genes on the X chromosome (often called Z in the Lepidoptera) (Janz, 1998, 2003; Nygren *et al.*, 2006), while differences within and between geographically connected populations appear to be influenced by several autosomal genes, some with additive effects (Nylin *et al.*, 2005). However, the preference hierarchy can apparently be modified following environmental input: oviposition decisions can be altered by frequency and availability of alternative host plants (Janz *et al.*, 2005a; Johansson *et al.*, 2007), and possibly by proximity of adult feeding resources (Janz, 2005). Still, following the reasoning above, we predicted that females of this butterfly should not make use of larval cues in its oviposition decisions. In other words, HHSP should not apply for this species. Alternatively, if such an effect is found, it should be between the two similarly ranked hosts, because if there is a clear difference in quality between the hosts, it should not pay to retain an elevated preference for the poor host.

Material and methods

Study organisms

Polygonia c-album (Lepidoptera: Nymphalidae) is a widely distributed polyphagous butterfly, occurring across most of the Palearctic. It has one of the widest host ranges among butterflies, using plants from seven families and five orders as hosts. It has a well developed preference hierarchy, where plants in Urticales (*Urtica*, *Humulus*, *Ulmus*) are the highest ranked, and support the best offspring performance. Further down in the hierarchy we find *Salix*, *Ribes*, *Betula* and *Corylus*. The preference hierarchy correlates well with larval performance on the population level, even though individual variation is substantial (Nylin, 1988; Janz *et al.*, 1994). Populations in different parts of the geographical range vary greatly in specificity, but the ranking appears to be similar (Nylin, 1988; Janz & Nylin, 1997; Janz, 1998, 2003; Nygren *et al.*, 2006). On a more local scale, populations across a 110 km large area around Stockholm, Sweden showed large variation in preference within populations, but no significant variation between populations, implying an open population structure (Nylin *et al.*, 2005).

Butterflies used in the present study were the F1 offspring of butterflies that were wild-caught in Åkersberga, 20 km north of Stockholm, and Jörva, 10 km north-west of Stockholm, as well as outside the Stockholm University Campus, Sweden.

Three naturally occurring plants were chosen for the experiments: the high-ranked *Urtica dioica* (stinging nettle) and the two medium-ranked hosts *Salix cinerea* (grey sallow) and *Ribes uva-crispa* (gooseberry). Three plants were used to be able to detect potential plant-specific effects.

Larval rearings

Larvae from each female were split evenly between plants and reared individually in plastic jars on stalks of natural host plants standing in water. All plant material was collected from natural stands in the area around the Stockholm University campus. Larvae were checked daily and wilting foliage was replaced by fresh foliage.

During growth, larvae were kept in rearing rooms with a controlled constant temperature and day length. Rearing conditions were initially set to a temperature of 17 °C and a photoperiod of LD 12:12 h. After moulting into the third instar, larvae were transferred into another room with a temperature of 26 °C and a photoperiod of LD 22:2 h, a procedure that is known to induce direct development in the Swedish population of *P. c-album* (Nylin, 1989).

Data were collected on larval development time and pupal mass, and the mean larval growth rate (pupal mass/larval development time) was calculated from these data. It has previously been observed that larval growth rate is the performance component that best corresponds to female oviposition preference in this species (Janz *et al.*, 1994; Nylin *et al.*, 1996).

After pupation, pupae were weighed and sexed and were kept in the final rearing room until eclosion. Newly emerged butterflies were transferred into mating cages (1 × 1 × 1 m) where they were allowed to mate. Couples were removed from the mating cage in copula and after separation, females were transferred to the egg-laying cages (0.5 × 0.5 × 0.5 m).

Oviposition trials

A total of 41 mated females were placed individually in the oviposition cages. Each female was given a series of pairwise trials with two of the three host plants, and each female was tested with all three possible combinations of pairs. The plant combination was changed each day and the order of the trials was randomised between females. Each female was also provided with diluted sugar solution (approximately 20%) on a sponge standing in the centre of the cage, and the experimental arena was illuminated by a light bulb (75 W), hanging approximately 0.5 m above the transparent cage roof. Daylight regime was LD 8:16 h. After each day, plants were removed from the cages and the eggs were counted.

Analyses

Larval growth rates on the three hosts were analysed with a one-way ANOVA. Preference data were analysed with nonparametric statistics due to a failure to meet the assumptions of parametric tests. First, general preference was analysed with a series of pairwise Wilcoxon signed-rank tests, to confirm that there was a general difference in preference between the presumed high-ranked and the two presumed medium-ranked hosts. To test the HHSP, separate two-sample Wilcoxon rank-sum (Mann–Whitney) tests were then performed for each plant species, comparing the number of eggs laid on this plant per day for females that had grown on the same plant, with females that had grown on any of the other two plants.

Results

Larval performance

Larval growth rate differed between host plants (ANOVA, $n = 188$, d.f. $= 2$, $r^2 = 0.21$, $P < 0.0001$). Similar to what had been reported in previous studies (e.g. Janz *et al.*, 1994), larvae reared on *U. dioica* grew fastest, followed by *S. cinerea* and *R. uva-crispa* (Fig. 1).

Oviposition preference

The plants were chosen to represent one high-ranked host (*U. dioica*) and two medium-ranked hosts (*S. cinerea* and *R. uva-crispa*), and this *a priori* assumption was confirmed with three pairwise Wilcoxon signed-rank tests (Fig. 2). As assumed, there were significant differences in the rankings of ovipositing females in pairwise comparisons of *U. dioica* with *S. cinerea* ($n = 41$, $z = 4.038$, $P < 0.001$) and *R. uva-crispa* ($n = 41$, $z = 4.044$, $P < 0.001$), respectively. However, there was no significant difference in the rankings of the two medium-ranked hosts *S. cinerea* and *R. uva-crispa* ($n = 41$, $z = -0.188$, $P = 0.85$).

Finally, there was no effect of larval host on female oviposition preference for any of the plants in the study (two-sample Wilcoxon rank-sum tests: $n = 41$, *Urtica*: $z = -1.435$, $P = 0.15$; *Salix*: $z = 1.083$, $P = 0.28$; *Ribes*: $z = 0.699$, $P = 0.48$; Fig. 3). Hence, no support for the HHSP was found in the data from the present study.

Discussion

Polygonia c-album is a polyphagous butterfly, and the difference in larval performance across hosts is relatively large. As relative quality of the alternative food sources may influence the applicability of HHSP, the three plants used in this study were chosen to represent one high-ranked (*U. dioica*) and two medium-ranked hosts (*S. cinerea* and *R. uva-crispa*), to increase the potential of finding a positive result. With a clear difference in quality between hosts, it should be less beneficial to retain an elevated preference for the poor host. The expected differences in larval performance between these plants were confirmed by the data obtained from this study (Fig. 1), and the female preference ranking corresponded well to these differences in performance (Fig. 2).

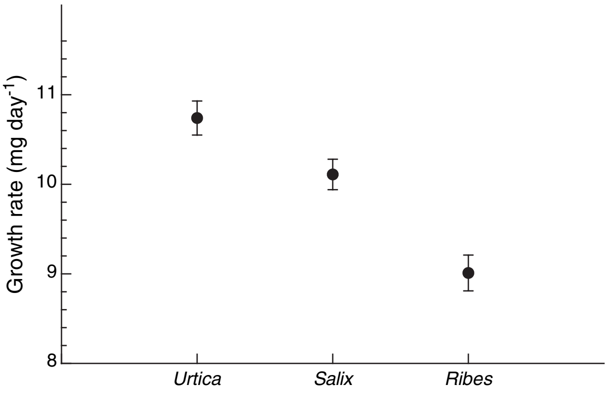

Fig. 1. Mean growth rates (mean daily weight gain) for individual larvae of *Polygonia c-album* feeding on *Urtica dioica*, *Salix cinerea*, and *Ribes uva-crispa*. Means ± SE.

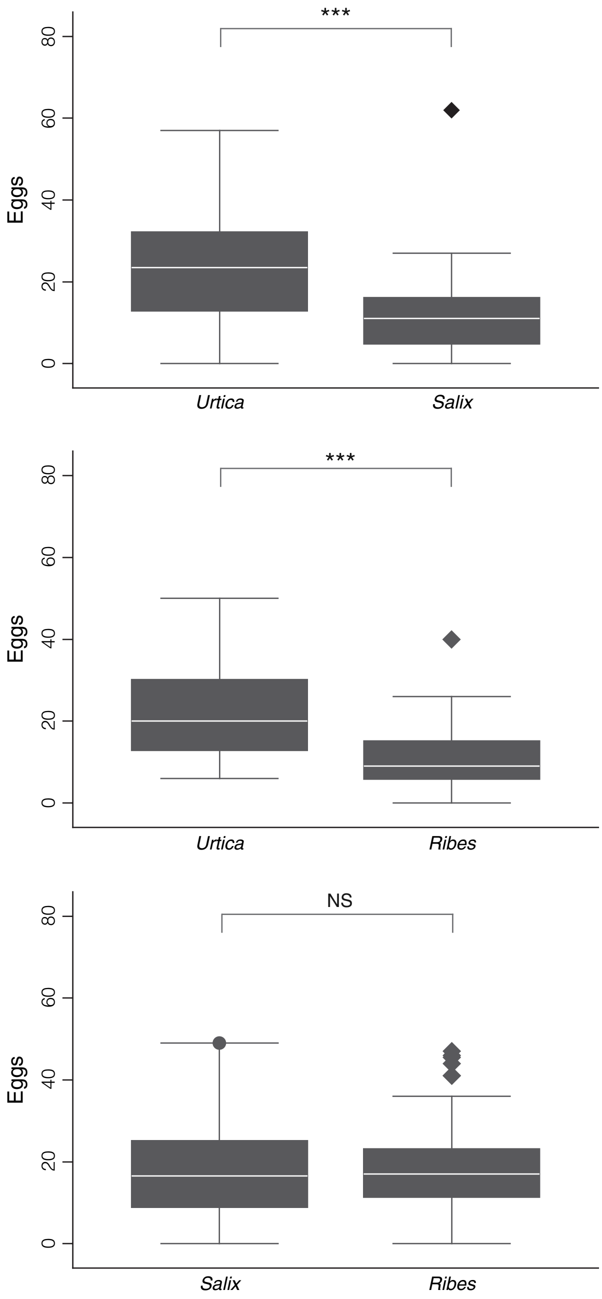

Fig. 2. Oviposition preference of females of *Polygonia c-album* for *Urtica dioica*, *Salix cinerea*, and *Ribes uva-crispa*, as revealed by pairwise choice trials. ***$P < 0.001$; NS, non-significant. White lines show medians, boxes show the lower and upper quartiles, whiskers show total range (excluding outliers, that are shown as circles and diamonds).

No effect of larval host plant on adult oviposition was found, regardless of preference or performance ranking (Fig. 3), and removing the high-ranked *U. dioica* from the analyses of the lower-ranked plants did not improve the results. Hence, it appears safe to conclude that for *P. c-album* the HHSP does not

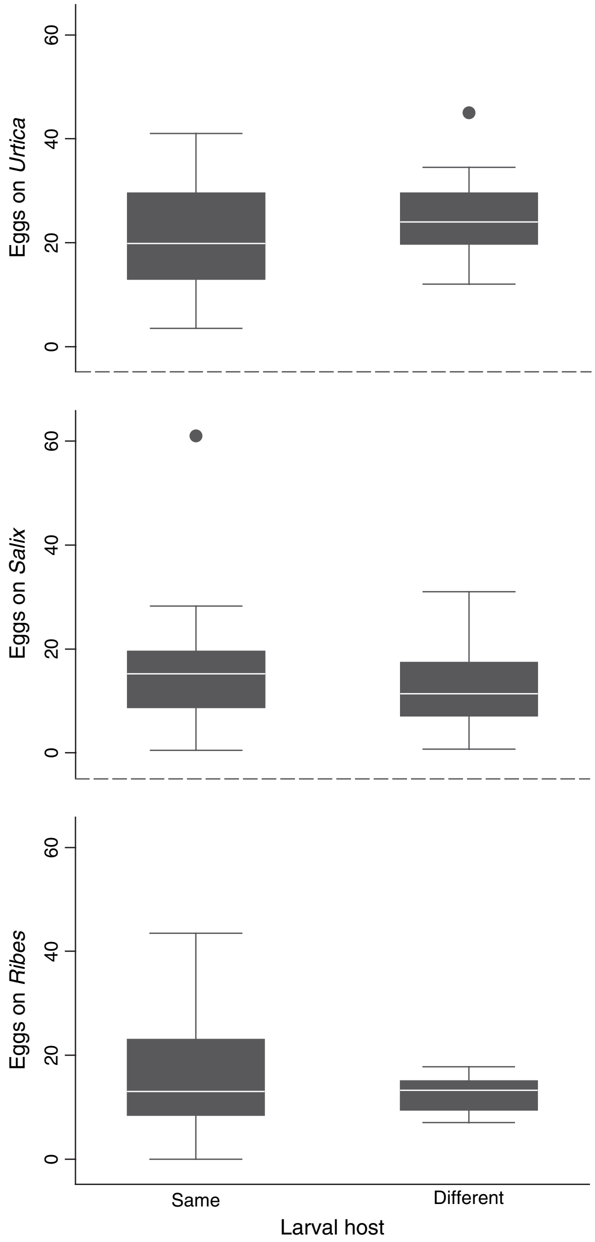

Fig. 3. Number of eggs laid on the three host plants, comparing females that had fed on the same plant as larvae with females that had fed on one of the other plants. None of the comparisons were significant. White lines show medians, boxes show the lower and upper quartiles, whiskers show total range (excluding outliers, that are shown as circles). Number of females reared on *Urtica* = 15, on *Salix* = 16, on *Ribes* = 10.

apply. This is in line with many other studies that have investigated the hypothesis, but failed to find any support for it (e.g. Wiklund, 1974; Tabashnik *et al.*, 1981; Williams, 1983; van Emden *et al.*, 1996; Rojas & Wyatt, 1999; Solarz & Newman, 2001; Kerpel & Moreira, 2005).

Curiously, as mentioned earlier, a number of recent studies have found effects of larval feeding experience on patterns of adult oviposition (Anderson *et al.*, 1995; Rietdorf & Steidle, 2002; Akhtar & Isman, 2003; Gandolfi *et al.*, 2003; Chow *et al.*, 2005; Hora *et al.*, 2005; Olsson *et al.*, 2006; Facknath & Wright, 2007). Even if the underlying mechanisms have often been difficult to unambiguously nail down, these are intriguing findings, and the discordant results require us to ask under what circumstances a 'Hopkins effect' should be expected for theoretical reasons.

As pointed out by Barron (2001), the Hopkins' host selection principle has appeared in many disguises over the years, which is a little problematic. One such complication is that some of the observed 'Hopkins effects' may not be caused by the transfer of information on host suitability through life stages, but rather by maternal effects that affect general vigour or egg size (Mousseau & Dingle, 1991; Mousseau & Fox, 1998; Wolf, 2000). General vigour, influenced by larval host plant may alter oviposition preferences in several ways. A small female with low amounts of nutrients to allocate to egg production could accept lower-ranked hosts to a higher degree, as the expected lifespan would be shorter and the chances of finding enough high-quality hosts may be lower. In this case, the result would appear to be similar to a 'Hopkins effect'. Alternatively, allometric effects could cause the egg size of lower-quality females to be smaller. In this case, oviposition on high quality sites will be more important and the result would be an inverse 'Hopkins effect': higher specialisation on higher-quality hosts in females that have grown on lower-quality hosts. An effect of this type has been reported for the seed beetle *Stator limbatus*, where successful expansion onto a novel host was dependent on the larval host plant of the mother, mediated through differences in egg size and composition (Fox *et al.*, 1997; Fox & Savalli, 2000).

A true Hopkins effect, i.e. where information on host suitability/availability is transferred from the larva to the adult female (by neurological or chemical means), requires rather special circumstances to be adaptive. It all boils down to what can provide the most reliable information on future host availability and suitability of alternative hosts (Leimar *et al.*, 2006). As mentioned earlier, HHSP is a form of phenotypic plasticity, and the most distinctive difference between HHSP and a genetically determined preference hierarchy that can be modulated by adult experience, is that the proposed environmental cue is shifted upstream in development, to a time long before the trait is expressed. It has been pointed out that such a time delay between induction and expression of a trait is problematic for the evolution of phenotypic plasticity (Padilla & Adolph, 1996).

Larval experience can only provide reliable information on host-plant availability if the emerging female is likely to experience a similar environment to the one she grew up in, i.e. temporal heterogeneity should be low. On the other hand, if spatial heterogeneity is also low, genetic cues will be as accurate as the environmental cues, as selection will have favoured the same variants across time and space, and under such circumstances genetic cues are likely to be favoured over environmental (Leimar *et al.*, 2006). However, in some cases, temporal variation in host suitability can be predictable, such as when attack by an insect herbivore with a short generation time triggers inducible defences among plants. Cues from the larval environment may then function as cues for imminent change in host-plant suitability. Obviously, genetic information would not be very useful in predicting such a change, and this is probably one situation where HHSP might work.

Interestingly, this is also one of the types of situations where HHSP has been demonstrated. Notably, these cases do not involve shifts in host-plant use as such (i.e. a shift from host A to host B), but rather a reduced deterrence of a chemical compound that can be associated with plant defence or increased insect density, such as larval frass (e.g. Anderson *et al.*, 1995; Akhtar & Isman, 2003; Chow *et al.*, 2005). It is a change in acceptance of a feature of a single host when conditions change. When synchronised changes in host quality occurs over regular intervals, and where early cues during larval feeding can reliably predict changing conditions, reduced deterrence could be an adaptive means of making the best out of a bad situation. As insect densities increase, crowding and induced plant defences may reach levels that would have to be avoided under normal circumstances. However, avoiding them under high insect densities could lead to a refusal to oviposit at all, since all available oviposition sites would be considered to be poor under normal circumstances. Under such cases, larval experience could provide more reliable cues than the genome alone. The question remains, however, why larval cues should be favoured over adult cues. Information on increased larval densities and increased induced defences are available to the ovipositing female as well, and these cues will be closer in time to the actual expression of the trait (cf. Padilla & Adolph, 1996) and arguably more accurate. However, the outcome will depend not only on the accuracy of the cue, but also on the relative costs of gathering the information. The ovipositing female would have to probe available oviposition sites before the same information could be obtained, and if time or female mobility is limited, relying on larval experience could conceivably be more efficient in some situations.

Another situation where HHSP might be worth looking for, is where conditions (especially host availability) are likely to vary greatly between patches. In such cases, local selection will also vary and larval feeding environment could provide a more accurate predictor of future host availability (cf. Davis & Stamps, 2004; Olsson *et al.*, 2006; Facknath & Wright, 2007). However, the outcome will be highly dependent on gene flow. A highly increased mobility will make larval cues less accurate, as the female may well oviposit in a different environment than her own larval feeding environment. Alternatively, a low mobility would again mean that the advantage of using an environmental cue rather than a genetic will diminish.

Thus, the conditions that should most likely favour HHSP are low variation in host quality among hosts, predictable and recurring temporal heterogeneity, high spatial heterogeneity (i.e. local host availability varies greatly between patches) and intermediate gene flow between spatial patches. Last, but not least, the cost of gathering information on host availability and suitability in the adult stage should be high. If these conditions are met, the environment may provide a more reliable and or/ more efficient source of information on future host availability than the genome, and the HHSP might be adaptive.

Our study species, *P. c-album*, has an unusually wide host range for a butterfly, and these hosts differ considerably in suitability for larval growth (Nylin, 1988; Nylin & Janz, 1993; Janz *et al.*, 1994). Spatial heterogeneity between habitats is arguably moderate, but is effectively further decreased by its high adult mobility and open population structure (Nylin *et al.*, 2005). The species occurs across a wide geographical range in seasonal environments, where there can be considerable stochastic variation between years. Taken together, and following the reasoning above, it is not surprising that no evidence for the HHSP was found in this species. Under these circumstances, the information that larval feeding environment can provide with regards to adult host availability and suitability, will hardly be an improvement on the information that is recorded in the genome.

Indeed, the circumstances required for HHSP to be adaptive are arguably so specific that it should not be invoked as a general hypothesis for host selection in plant-feeding insects. On the other hand, instead of ignoring it or invoking it as a general principle, we could focus on understanding when it should be adaptive to use juvenile cues early in development to induce changes later on in the life-cycle. Even if there are problems with such a time-lagged system (Padilla & Adolph, 1996), it is not unheard of. It is, for example, quite common that juvenile cues are used to choose developmental pathway in insects (Tauber *et al.*, 1986). Typically, these morphs require developmental adjustments, which rules out the use of cues later on in the life-cycle. This is not normally the case with host-plant selection, but again, it is not necessarily impossible. If a certain host preference is coupled with dispersal for example (Harrison, 1980), juvenile cues could be used to induce different developmental pathways that are correlated with host-plant selection.

It is interesting to note that the discussion on when and if HHSP should be evolutionarily realistic, bears many similarities to the discussion of host-specific 'gentes' in brood-parasitic cuckoos. As with the HHSP, these gentes have commonly been assumed to be maintained by host imprinting in juvenile cuckoos. Recent studies, however, have questioned this 'common knowledge' and have revealed genetic differences in host preference among gentes (Brooke & Davies, 1991; Gibbs *et al.*, 2000). Again as in phytophagous insects, host selection in cuckoos are likely to involve a multitude of genetic and environmental cues, and the relative importance of these cues will probably vary between species and habitats (Payne *et al.*, 2000; Honza *et al.*, 2001; Krüger & Davies, 2002).

We believe that further discussion on the applicability of HHSP, as well as of host imprinting in cuckoos, needs to explicitly consider the accuracy of the information which can be obtained from genetic versus environmental cues in any given case (cf. Leimar *et al.*, 2006). As a multitude of factors will potentially affect the relative accuracy of these cues, modelling should be the logical next step in order to yield predictions on whether and when juvenile imprinting should be expected to be a realistic evolutionary strategy.

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