Oviposition plant preference and offspring performance in the comma butterfly: correlations and conflicts

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Introduction

Thompson (1988) drew attention to the importance of studying correlations between the host-plant preferences of ovipositing female insect herbivores and performance of their offspring. The presence or absence of such correlations can reveal important features of insect-plant relationships and the evolution of such relationships. A strong positive correlation; i.e. a system where females prefer the plants on which offspring perform best, can be seen as evidence that 'internal' plant characteristics are important in shaping the preference hierarchy of females. In the context of this communication, internal characteristics are those whose effects on the immature insect can be measured in the laboratory, such as plant chemistry or morphology affecting larval growth.

Whereas the demonstration of a positive correlation can be easily explained, a weak or negative correlation is much harder to interpret. Of the several possibilities, the adaptive hypothesis (optimal female choice, offspring performance not measured correctly) has received the most attention, focusing on external plant properties (not easily measurable in the laboratory) that create a lack of positive preference-performance correlations. Thus the best host plants in the laboratory may be dangerous for the female to use in the field, because larvae on these hosts are prone to predation or parasitism (Bernays & Graham, 1988). Similarly, field variation in plant abundance or quality may also affect the female's choice, but cannot easily be incorporated into a laboratory experiment.

In addition to these considerations of 'external' plant properties, there are many aspects of offspring performance in the laboratory which are not always measured and which could explain the absence of positive correlations. Many of the reported weak or negative correlations have dealt with only one or two aspects of performance, such as larval survival, development time or final weight. Ideally, however, offspring performance should equal total offspring fitness, which necessitates consideration of the whole life cycle. Here, we will investigate simple models of offspring fitness, and relate them to our data on plant preferences and offspring performance in the nymphalid butterfly *Polygonia c-album* (L.). Our intention has been to discuss the models in a qualitative manner only, and to illustrate them with brief descriptions of our results.

Materials and methods

To complement earlier data we performed a rearing experiment in 1994. Three gravid females of *P. c-album* were caught in the Stockholm area of central Sweden in late April. After oviposition in the laboratory, newly hatched larvae were pooled and divided among the host plants *Urtica dioica* L. and *Salix caprea* L. on three different dates (20 larvae on each plant species in each cohort, or a total of 120 larvae) and reared individually in plastic jars in which cuttings of host plants could receive water from a lower jar. Plants were changed at frequent intervals and whenever they showed signs of senescence. The rearings were made in environmental chambers at 20 °C. The date of entry into the final instar was noted, and larvae were subsequently weighed daily until pupation, when they were sexed and weighed. A measure of mean relative growth rate (% weight

increase/day) was calculated from pupal weights, larval development times and a standard hatchling weight set at 0.25 mg (see Nylin, 1992).

Results

Growth of both sexes was consistently faster on *Urtica* in the present study (cf. Figure 1; the following results refer to the whole larval period: males: $42.8 \pm 0.8\%$/day on *Urtica* vs. $40.4 \pm 0.5\%$/day on *Salix*, $P<0.05$; females: 41.4 ± 0.8 day on *Urtica* vs. $38.6 \pm 0.8\%$/day on *Salix*, $P<0.05$), but this did not result in a high pupal weight (males: 328.3 ± 4.9 mg on *Urtica* vs. 361.3 ± 6.5 mg on *Salix*, $P<0.001$; females: 327.2 ± 4.4 mg on *Urtica* vs. 368.3 ± 7.1 mg on *Salix*, $P<0.001$). At present it is unclear why this should be so (except that it is a direct result of shorter development times on *U. dioica*; males: 20.3 ± 0.3 days on *Urtica* vs. 21.5 ± 0.2 days on *Salix*, $P<0.01$; females: 20.9 ± 0.3 days on *Urtica* vs. 22.5 ± 0.4 days on *Salix*, $P<0.001$; all statistics t-tests, N(males) = 54, N(females) = 55), and how common such patterns are in insects.

Discussion

Possible explanatory models. If an ovipositing female is behaving in an optimal manner her choices should be influenced by the effects of different host plants affecting *her own* fitness. This is given by the product of her realized fecundity and the mean fitness of her offspring or, more specifically, by the following formula:

$$mean\ oviposition\ rate\ \times\ days\ spent$$

$$ovipositing\ \times\ mean\ offspring\ fitness$$

Even this simple formula highlights the fact that a female's choice should not be determined solely by what happens to her offspring. Some instances of poor preference-performance correlations could result from a trade-off between the quantity and quality of offspring. Thus, abundant and safe (to the female) host plants could be used preferentially, even at some cost in terms of offspring fitness, because this would increase the oviposition rate and number of days spent ovipositing. For the same reason females can be predicted to include more than one plant species in the range of acceptable hosts, even though their offspring (if given

a choice) would all prefer to be on the very best host plant in terms of larval growth and survival.

In the comma butterfly there is a clear hierarchy of host plants at the population level (Nylin, 1988; Nylin & Janz, 1993; Janz *et al.*, 1994). Ovipositing females prefer, on average, hosts in the order Urticales (*Urtica dioica* and *Ulmus glabra* Hudson) to *Salix caprea* and especially to *Betula pubescens* Ehrh. When we gave larvae the same choice (using cut-out pieces of leaves in Petri dishes; Nylin & Janz; in press) there was a difference in the results from females, as predicted. Females laid a relatively large proportion of their eggs on the less preferred *S. caprea* and *B. pubescens*, whereas larvae very rarely preferred *S. caprea* and never *B. pubescens*. Nevertheless, the basic hierarchy was very similar, suggesting that there are no strong conflicts between the interests of ovipositing females and their offspring in this system.

Thus, we might be justified in this case in ignoring the possible trade-off between quantity and quality of offspring and concentrate on the latter, offspring fitness:

$$offspring\ survival\ to\ reproduction\ \times\ offspring$$

$$reproductive\ success.$$

One further simplification that is often made is to ignore pupal and adult survival, because they should be less dependent on the host plant than on larval survival. Thus offspring fitness is:

$$larval\ survival \times fecundity\ of\ female\ offspring.$$

Survival through the larval stage is dependent on successful establishment and growth on the plant as measured in the laboratory, and may in addition be correlated with a short development time through the larval stage. If the insect is multivoltine, a short generation time also increases the chance that additional generations will be successful. Female fecundity is generally expected to be positively correlated with pupal weight. A high larval growth rate on a plant should thus be an especially good indicator of high fitness, because it permits a short development time and a relatively high pupal weight simultaneously. In contrast, it is probably true that, in general among herbivorous insects, poor host plants result in poor survival, slow growth, long development times and low pupal weights.

At the level of individual females there is actually considerable variation, with some females even preferring *S. caprea* (Janz *et al.*, 1994). Why does this preference variation persist? We believe that one answer
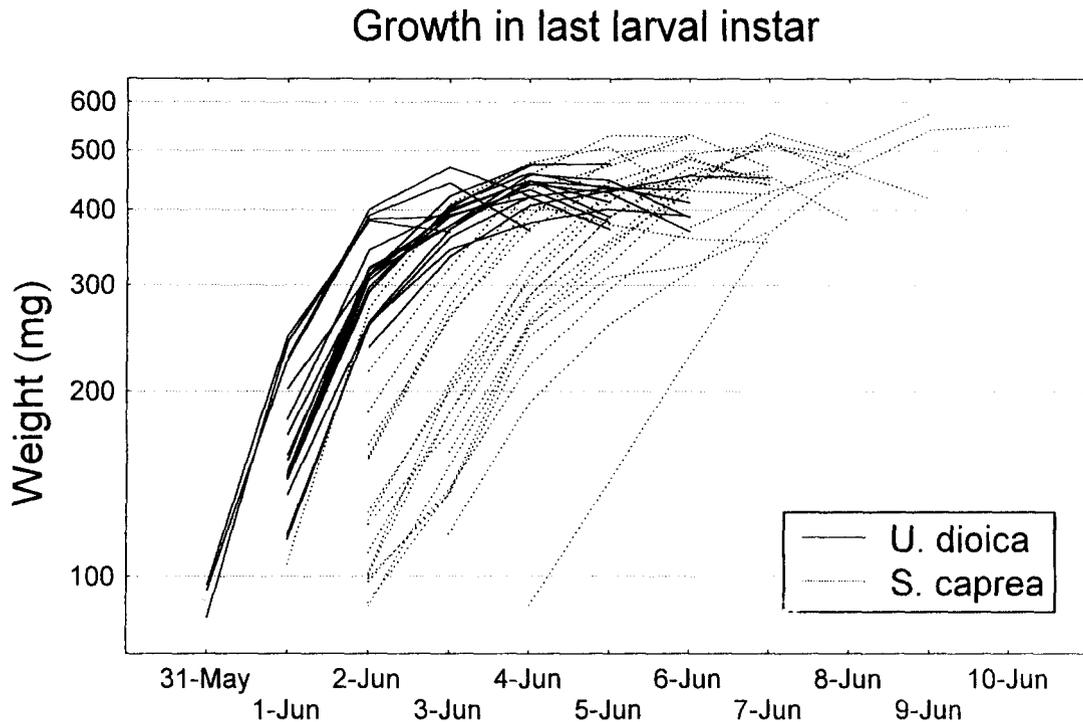
Growth in last larval instar

Figure 1. Individual growth trajectories (log weight *versus* time) of a cohort of larvae of *Polygonia c-album* in the final (fifth) instar, when reared on *Urtica dioica* and *Salix caprea* . Growth trajectories end on the day before the prepupal stage and thus exclude the loss in weight at pupation. Larvae on *U. dioica* entered the final instar earlier, and subsequently grew faster initially (steeper slopes of growth trajectories). For clarity, sexes are not distinguished, as differences between sexes were smaller than between host plants.

lies in the second half of the model above. Female (and male) pupal weight is consistently higher, on average, on *S. caprea* than on *U. dioica* (Nylin, 1988; Janz *et al.*, 1994) and so is the fecundity of resulting females (Janz *et al.*, 1994). We have suggested that use of *S. caprea* may be favoured in areas where two generations in one season do not occur, but where there is ample time for a single generation, since this diminishes the fitness advantages associated with a short development time (Janz *et al.*, 1994). This is related to the observed pattern (Nylin, 1988) that the preference for *U. dioica* is more accentuated in England (a partially bivoltine population where short development times means that a second generation is possible) than in Sweden (a univoltine population).

The differences between *S. caprea* and *U. dioica* as hosts for *P. c-album*, reported here and elsewhere, do not conform to the generalisations concerning how host plants typically affect insect life histories. If they turn out to be common, it will be necessary to abandon the notion of plants ranked on a single 'growth rate-axis', in favour of more dynamic models of the relative

fitness advantages associated with short development times and high pupal weights in different situations.

So far, we have considered only the female part of reproductive success as a component of 'offspring fitness'. However, *P. c-album* is a strongly polyandrous species, where males produce large spermatophores that are likely to be important in both sperm competition and as paternal investments (Svärd & Wiklund, 1989). A new model created to specifically include the male component of offspring fitness would be much more complex:

$$larval\ survival \times (female\ fecundity +$$

$$(number\ of\ mates \times mean\ fecundity$$

$$of\ mates \times mean\ proportion\ of\ paternity))$$

In other words, the male contribution to offspring reproductive success is determined not only by how many mates a male can get and by their fecundity but (in a polyandrous species) also by the likelihood that his sperm will fertilise the eggs of his mates. In *P. c-album* there are indications that none

of these components can be ignored. Females mated more rapidly with males reared on *U. dioica* than with males reared on *S. caprea* in a no-choice experiment (N. Wedell, unpubl.). Males reared on this species produce spermatophores which are more rich in protein (N. Wedell, N. Janz & S. Nylin, unpubl.) and labelling with radioactive isotopes shows that nitrogen from spermatophores are used to produce eggs (N. Wedell, unpubl.). Females that have mated with *'Urtica'* males can spend less of their own nitrogen resources in egg production and also live longer (N. Wedell, unpubl.). Although not evident in the laboratory (where females were mated only once), under natural conditions this could translate to higher fecundity for females mated with *Urtica* males, and hence to higher reproductive success for *Urtica* males.

In conclusion, the concept of 'performance' is not as straightforward as it might first seem, even if 'external' plant characteristics and trade-offs between quantity and quality of offspring can be disregarded (as may be the case in *P. c-album*). It may not be feasible to measure every aspect of parent and offspring fitness in detail, but it is necessary to at least examine them superficially before deciding what aspects can safely be ignored in a given species. Concerning *P. c-album*, we have some evidence that survival to the adult stage, development time, female fecundity and male reproductive success are all dependent on the larval host plant and may affect the host-plant preferences of ovipositing females, but we are not yet at the point where we can incorporate all the factors into a complete model of offspring fitness. We hope to have demonstrated, however, the value of explicit models of fitness in studies on preference-performance correlations. They show that alternative adaptive hypotheses are possible; it may not always be necessary to invoke constraint explanations for poor preference-performance correlations.

References

Bernays, E. A. & M. Graham, 1988. On the evolution of host specificity in phytophagous arthropods. Ecology, 69: 886–892.

Janz, N., S. Nylin & N. Wedell, 1994. Host plant utilization in the comma butterfly: Sources of variation and evolutionary implications. Oecologia, 99: 132–140.

Nylin, S., 1988. Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae). Oikos 53: 381–386.

Nylin, S., 1992. Seasonal plasticity in life history traits: growth and development in *Polygonia c-album* (Lepidoptera: Nymphalidae). Biological Journal of the Linnean Society 47: 301–323.

Nylin, S. & N. Janz, 1993. Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae) – The choice between bad and worse. Ecological Entomology 18: 394–398.

Nylin, S. & N. Janz. Host plant preferences in the comma butterfly (*Polygonia c-album*): do parents and offspring agree? Ecoscience, in press.

Svärd, L. & C. Wiklund, 1989. Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies. Behavioural Ecology and Sociobiology 24: 395–402.

Thompson, J. N., 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomologia Experimentalis et Applicata 47: 3–14.