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Host plant utilization in the comma butterfly: sources of variation and evolutionary implications

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Abstract A major challenge in the study of insect-host plant interactions is to understand how the different aspects of offspring performance interact to produce a preference hierarchy in the ovipositing females. In this paper we investigate host plant preference of the polyphagous butterfly *Polygonia c-album* (Lepidoptera: Nymphalidae) and compare it with several aspects of the life history of its offspring (growth rate, development time, adult size, survival and female fecundity). Females and offspring were tested on four naturally used host plants (*Urtica dioica*, *Ulmus glabra*, *Salix caprea*, and *Betula pubescens*). There was substantial individual variation in host plant preference, including reversals in rank order, but the differences were largely confined to differences in the ranking of *Urtica dioica* and *S. caprea*. Different aspects of performance on these two plants gave conflicting and complementary results, implying a trade-off between short development time on *U. dioica*, and larger size and higher fecundity on *S. caprea*. As all performance components showed low individual variation the large variation in host plant preference was interpreted as due to alternative oviposition strategies on the basis of similar 'performance hierarchies'. This indicates that the larval performance component of host-plant utilization may be more conservative to evolutionary change than the preference of ovipositing females. Possible macro-evolutionary implications of this are discussed.

Key words Insect-host plant interactions · Life history Trade-offs · Seasonality · Plasticity

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Introduction

The reported strength of the correlation between oviposition preference and offspring performance in phytophagous insects has shown tremendous variation. Good correspondence has been reported in some instances (e.g. Rausher 1982; Rausher and Papaj 1983; Via 1986; Nylin 1988; Singer et al. 1988; Nylin and Janz 1993) but surprisingly often the correspondence has been relatively bad (e.g. Chew 1977; Rausher 1979; Courtney 1981, 1982; Williams 1983; Penz and Araújo 1990; Valladares and Lawton 1991). One necessary conclusion from this is that the relationship between female preference and offspring performance is more complicated than a simple correlation between oviposition preference and some aspect of performance, like development time or adult size. It is important to realize that oviposition preference should be correlated with total offspring fitness and not with just any performance measure. Ideally one should take all parts of the insect's life-cycle into account when trying to understand the host-plant choices of the females. A good host plant for the larva is not necessarily good for the egg or the pupa or the emerging adult butterfly (Reavey and Lawton 1991). Moreover, as Thompson (1988a) remarks, the different performance components affecting, for example, the larval stage need not be correlated among themselves.

To be able to understand the evolution of the relationship between preference and performance, studies on the individual level are necessary, since pooling the individuals will hide any within-population variation. Information on individual variation is needed to detect different host selection strategies and to understand the selection pressures that generate them. One problem with this approach is that if host plant preference is driven to optimization in a population, one would not expect to find much individual variation. For this reason it is important to be able to identify populations where conflicting selection pressures on host use can be expected.

Development time might perhaps be an important trait in temperate regions, since the length of the favourable season sets a limit on the time when larval growth is possible. However, the length of the season changes with latitude, and so does the possible number of generations the insects can fit into the season. As the length of the season is a continuous variable and generation time is a discrete variable, this will give rise to a latitudinal 'sawtooth-pattern'. At the latitudes where an extra generation sometimes becomes possible there will be a significant time stress on the developing larvae, and the females can be expected to restrict oviposition to the plants that give the shortest development times. On the other hand, in the areas that lie between these 'generation thresholds' there will never be enough time for an additional generation but still plenty of time for the number of generations that are possible. In these cases the correlation between female host choice and larval development time need not necessarily be very high, since the cost of ovipositing on 'suboptimal' plants (in relation to development time) will be reduced. Thus there will be more room for alternative oviposition strategies, especially in terms of specificity. This is the essence of a hypothesis of host specificity in seasonal environments first formulated by Nylin (1988) that was later independently described by Scriber and Lederhouse (1992) as the 'voltinism-suitability hypothesis'.

Specialized feeding strategies are much more common among plant-feeding insects than generalist strategies, and the reasons for the predominance of specialists over generalists have been the focus of much debate (Smiley 1978; Fox and Morrow 1981; Jermy 1984; Strong 1988; Bernays 1989; Jaenike 1990). Many butterfly species have a range of possible host plants suitable for larval growth that is wider than the range of plants actually used for oviposition. Wiklund (1975) argued that there should be selection for the larvae to be able to live on a wider range of host plants than are normally oviposited on, to maximize the probability of survival on the plant the females choose for them. This means that the females have specialized on a subset of the possible plants that for whatever reasons are the most suitable. Many species should then have a potential to evolve polyphagy (or oligophagy), given the right ecological circumstances. The zones with relaxed time-stress for the larvae described above could constitute such circumstances. When other performance components become more important in relation to short development time, it could pay to use low ranked plants to a greater extent and even to include additional plants in the oviposition hierarchy (cf. Nylin 1988; Scriber and Lederhouse 1992). This could perhaps even result in a new ranking of the plants, if other aspects of performance or host choice produce a different hierarchy.

The effect of relaxed time stress will most probably reveal itself as larger individual variation in host plant preference, rather than as a shift in the population mean. It will be more likely that some females will base their choices on other aspects of offspring performance than development time, which may result in a different ordering of the host plants by these females. The wider and/or reversed host plant hierarchy need not be reflected in the larval performance over the same plants. In herbivorous insects with parasitic lifestyles (Thompson 1982) larval specificity is really a population phenomenon and is a somewhat artificial character on an individual level, since it is never expressed. This is because in these species each individual larva is in effect monophagous on the plant species on which its mother laid this particular egg. Moreover, in general the larval hierarchy is probably more resistant to change than the choices of the adult females (e.g. Wasserman and Futuyma 1981; Futuyma et al. 1993).

The butterflies used in this study came from a population of the polyphagous *Polygonia c-album* that is forced to univoltinism by the length of the favourable season. We tested the hypothesis outlined above, that there should be a relatively large variation in the patterns of host plant preference in this population. We tried to outline the effects of four commonly used host plants on the offspring, in terms of larval growth rate, development time, pupal size, survival, and female fecundity, to be able to assess if the host plant choice of different females conforms to different aspects of performance.

Materials and methods

Study organism

Polygonia c-album, the comma butterfly, is a polyphagous butterfly feeding on a variety of plants from at least seven families in four orders: Urticaceae, Ulmaceae, and Cannabaceae (or Cannabidaceae) in Urticales, Salicaceae in Salicales, Betulaceae and Corylaceae in Fagales, and Saxifragaceae in Rosales. Of these plants it is considered to prefer the plants in Urticales, i.e. *Urtica dioica*, *Ulmus glabra*, and *Humulus lupulus* (Nylin 1988; Nylin and Janz 1993). This butterfly is potentially bi- or multivoltine, with a directly developing lighter morph being produced under favourable conditions, i.e. increasing daylength during the larval period (Nylin 1989). The population under study is univoltine, even if the light morph can be produced under laboratory conditions.

Host plant preference

Five females were wild caught just north of Stockholm at the very beginning of the flight season, between 4 and 14 May 1992. They were immediately put individually in cages (0.5 × 0.5 × 0.5 m) and were presented with a simultaneous choice trial with four natural host plants, *Urtica dioica*, *Ulmus glabra*, *S. caprea* and *B. pubescens*, cut to roughly the same size. The plants were standing in water, one in each corner of the cage at the same distance from the central light- and food sources, and were exchanged regularly so that the females always had fresh plants of all sorts to oviposit on.

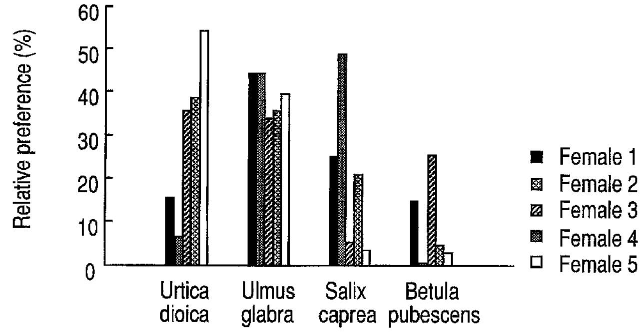

Fig. 1 Relative female preference for the four host plants *Urtica dioica*, *Ulmus glabra*, *Salix caprea* and *Betula pubescens* measured as the percentage of the total amount of eggs each female laid. *n* (number of eggs) for females 1–5 were 207, 234, 166, 191, and 323, respectively

Every 2nd day the eggs were counted and saved until eclosion. At every egg-counting occasion, the plants were moved about randomly between the positions in the cages. As this butterfly species typically lays eggs singly, and oviposition normally is preceded by a search-flight through the cage where the plants are evaluated in flight and sometimes landed on, each egg can be regarded as representing one oviposition decision. In a set-up of this kind the later pre-alighting phases together with the post-alighting phase affect the oviposition choice, but not the earlier large-scale decisions like choice of habitat. This, of course, is a shortcoming of all laboratory experiments on host plant preference.

Larval performance

Immediately after eclosion, the larvae were weighed and placed individually in transparent plastic jars with fresh leaves from one of the four host plants tested in the preference test. The jars had a hole in the bottom and the plants stood in a lower jar filled with water. The plants were exchanged regularly and when showing any sign of senescence. Thirty larvae from each female were reared in this way on each plant, and were if necessary replaced with new larvae until establishment was successful. All larvae were reared under long-day conditions; 15 from each group were kept in about 20–22° C and the other 15 in 26–28° C. Data were collected on larval development time and pupal weight. Growth rates were then calculated from these data according to the formula:

$$\% \text{ weight increase} = [(m_p/m_h)^{1/t} - 1] \times 100$$

where m_p is pupal weight, m_h is hatchling weight, and t is larval development time. This formula produces a measure of percentage mean daily weight gain (or loss). Larval survival was measured as the fraction of the successfully established larvae that reached the adult stage.

To test the effect of host plant on female fecundity, 20 females that had been reared on the plants used in the preceding tests, five from each plant, were mated and kept individually in cages (two females, one from *S. caprea* and one from *B. pubescens*, did not produce fertilized eggs and were left out of the analysis). They were supplied with sugar and a host plant (*Urtica dioica*) for oviposition. The eggs were counted every 2nd day and the plants were exchanged for fresh ones when needed.

Table 1 Analysis of variance for female preference of *Urtica dioica*, *Ulmus glabra*, *Salix caprea*, and *Betula pubescens*; $n = 188$ (number of measurements), $r = 0.496$, $r^2 = 0.246$

Source	SS	*df*	MS	*F*	*P*
Plant	1163.661	3	387.887	5.696	0.001
Female	269.196	4	67.299	0.988	0.416
Plant × female	1920.652	12	160.054	2.350	0.008
Error	11440.663	168	68.099		

All statistics were calculated using SYSTAT (Wilkerson 1992).

Results

Host plant preference

On the population level *Ulmus glabra* were highest ranked (40% of the total number of eggs oviposited), followed by *Urtica dioica* (32%), *S. caprea* (20%) and *B. pubescens* (8%). This pattern conforms well to previous results (Nylin 1988). However, there were considerable differences in host plant selection on the individual level (Fig. 1, $P = 0.008$, ANOVA, see Table 1). Of the five females tested numbers 4 and 5 corresponded fairly well to the previously reported hierarchy, i.e. a preference for *Urtica* and/or *Ulmus*, followed by *Salix* and *Betula* in that order. Females 1 and 2 formed a second group with low rankings for *Urtica* and high rankings for *Ulmus* and *Salix*. In fact, *Urtica dioica* was the least preferred plant for female 1. Still, all but female 2 showed a preference for the plants in Urticales (*U. dioica* and *Ulmus glabra*) before *B. pubescens* and *S. caprea*. The higher preference of female 2 and to some extent female 1 and 3 for *Salix* and *Betula* at the expense of the plants in Urticales could indicate either a higher offspring efficiency on these plants or only a different host searching strategy.

In summary, all females laid a large proportion of their eggs on *Ulmus* and a relatively low proportion on *Betula*. On the other hand there was a considerable disagreement in the ranking of *Urtica* and *Salix*; most of the differences between the females are due to differential rankings of these two plants.

Larval performance and the correlation between preference and performance

As stated in the Introduction, different aspects of offspring performance can produce different results when compared to female preference. For this reason it is better to initially use a measure of performance that is as inclusive as possible, to get a measure of the overall correlation between preference and performance. Larval growth rate combines variation in pupal size and development time in one single measure and will therefore correlate with female preference regardless of whether the female is basing her choice on offspring size or development time. It will also give a more accurate figure if different plants are chosen for different reasons.

On the population level the growth rate was highest on *Urtica dioica* and *Ulmus glabra*, lowest on *B. pubescens* and intermediate on *S. caprea*. This hierarchy was relatively consistent on the individual level, with few

Table 2 Analysis of variance for larval growth rates in relation to temperature, host plant, and offspring family; $n = 545$, $r = 0.817$, $r^2 = 0.668$

Source	SS	*df*	MS	*F*	*P*
Temp	0.263	1	0.263	114.766	0.000
Plant	1.585	3	0.528	230.383	0.000
Family	0.170	4	0.043	18.536	0.000
Temp × Plant	0.020	3	0.007	2.865	0.036
Temp × Family	0.016	4	0.004	1.754	0.137
Plant × Family	0.115	12	0.010	4.172	0.000
Temp × Family × Plant	0.117	12	0.010	4.247	0.000
Error	1.158	505	0.002		

exceptions (Fig. 2). The growth rates of the offspring families showed less variation than the females' oviposition preferences. The analysis of variance (Table 2) shows that the effects of host plant species and temperature are responsible for the largest amount of variation in growth rate, while the effect of family is lower. The host plant × family interaction, i.e. the fact that the families respond differently to the four host plants, is significant but explains a relatively low amount of the variation. Growth rates differed significantly between all plants except between *Urtica dioica* and *Ulmus glabra* ($P < 0.001$ in all comparisons, Tukey HSD *post hoc* test). Interestingly, the plants also differed in the effect of temperature on growth rates (temperature × host plant interaction, see Table 2). On some plants growth rates were almost as high in the lower temperature as in the higher, while the difference due to temperature was large on other plants. To complicate the picture even more the plants that allowed unchanged growth rates over the two temperatures differed between the females (temperature × host plant × family interaction, see Table 2). For example, growth rates for the offspring changed very little between the temperatures on *Ulmus* and *Salix* for female 1, on *Betula* for female 3, on *Urtica* and *Salix* for female 4, and on *Urtica* for female 5 (Fig. 2).

Pearson correlation coefficients for female preference and larval growth rates show that there are large individual differences in the correlation between preference and performance (Table 3). The most remarkable result is perhaps the almost complete lack of correlation for female 3. The best mean correlation over the two temperatures was observed for female 4, followed by female 5, 1, 2, and 3 in that order. All correlations between female preference and family means for performance were significant, with the exception of family 3.

As mentioned above, females 1 and 2 had preference hierarchies that deviated from the expected, with a high preference for *S. caprea* at the expense of *U. dioica* (Fig. 1). The relatively low correlation with offspring growth rates suggests that this is caused by a different strategy of host choice. From Table 3 it is clear that females 1 and 2 had a lower preference for *U. dioica*, and that female 2 had a higher preference for *S. caprea*, than would be predicted from their offspring growth rates. Likewise, female 3 had a 'too high' preference for *B. pubescens* and female 5 a 'too low' preference for *S. caprea*.

When growth rates are decomposed into their components it is clear that in general the females are basing their oviposition choices on development time rather than on pupal weight (Table 3). Interestingly, female 1, who laid an unusually low proportion of her eggs on *U. dioica*, was the only female whose preference hierarchy correlated significantly with pupal weight. In fact, the second highest correlation between preference and pupal size (although not significant) was achieved by family 2, who also laid comparably few eggs on *Urtica*.

The separate experiment on female fecundity produced a somewhat different hierarchy than that based on growth rates (Fig. 3). However, only the difference between *U. dioica* and *S. caprea* was significant; females reared on *S. caprea* had a significantly higher reproductive output (total egg mass) than females that had grown on *U. dioica* ($P = 0.039$, Tukey HSD *post hoc* test on one-way ANOVA; $P = 0.012$, independent samples t-test with pooled variances). This implies a trade-off between fast development (*Urtica*) and high female fecundity (*Salix*). According to the predictions in the Introduction, females in an environment with relaxed time stress, such as the one under study, should be more prone to displace this trade-off towards higher fecun-

Table 3 Correlation coefficients (Bonferroni adjusted) for female preference and offspring growth rate, development time, and pupal weight

	Temperature	Family 1	Family 2	Family 3	Family 4	Family 5	Mean
Growth rate	20–22°	0.625^{***}	0.444^{**}	-0.021^{ns}	0.716^{***}	0.579^{***}	0.466^{***}
	26–28°	0.324^{ns}	0.480^{***}	0.209^{ns}	0.763^{***}	0.474^{***}	0.417^{***}
	Mean	0.474	0.462	0.094	0.740	0.526	0.442
Dev. time	20–22°	-0.498^{***}	-0.446^{**}	-0.026^{ns}	-0.731^{***}	-0.548^{***}	-0.453^{***}
	26–28°	-0.274^{ns}	-0.505^{***}	-0.201^{ns}	-0.789^{***}	-0.491^{***}	-0.436^{***}
	Mean	−0.388	−0.478	−0.024	−0.760	−0.520	−0.444
Pupal weight	20–22°	0.377^{*}	0.215^{ns}	-0.262^{ns}	0.344^{ns}	0.084^{ns}	0.118^{ns}
	26–28°	0.481^{***}	0.131^{ns}	-0.226^{ns}	-0.053^{ns}	-0.008^{ns}	0.035^{ns}
	Mean	0.429	0.173	−0.244	0.145	0.038	0.076

$^{*}P \leqslant 0.05$, $^{**}P \leqslant 0.01$, $^{***}P \leqslant 0.001$, ns not significant

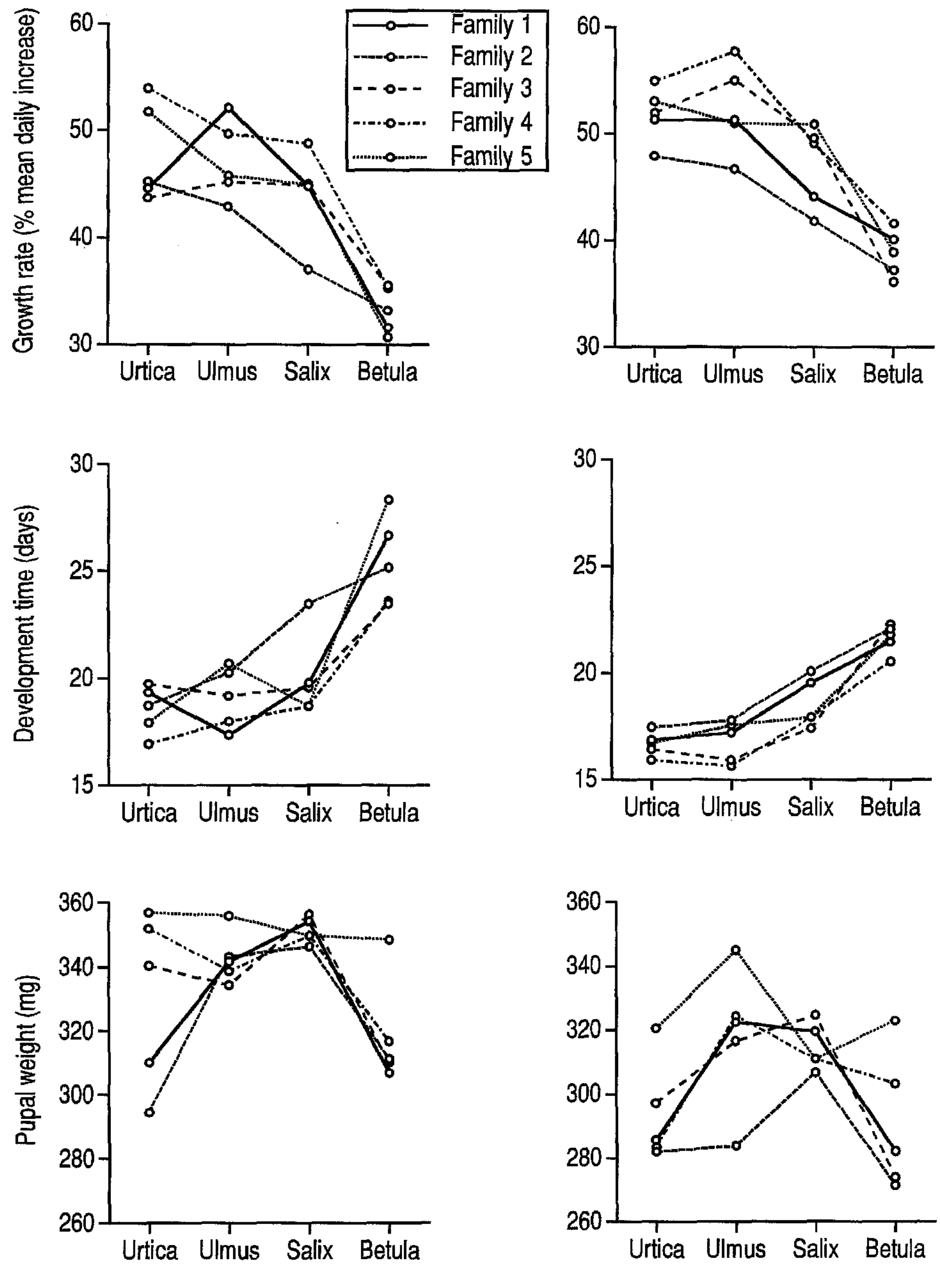

Fig. 2 Mean larval growth rate, development time, and pupal weight, on *Urtica dioica, Ulmus glabra, Salix caprea* and *Betula pubescens* in two temperature regimes (20–22°C to the *left* and 26–28°C to the *right*) for offspring family groups of the females used in the oviposition choice trail, sexes pooled. Measures of spread are omitted for clarity, but the largest SEs are ±3.3% for growth rates, ±1.13 days for development times, and ±11.0 mg for pupal weights

dity rather than fast growth, which is seen with female 2 and to some extent female 1.

Survival, perhaps the most clear-cut performance measure (however somewhat difficult to assess under laboratory conditions), gave rise to a hierarchy very similar to that produced by growth rate (Table 4), even if only the differences between *B. pubescens* and the two highest ranked plants (*U. dioica* and *Ulmus glabra*) were significant ($P < 0.001$, ANOVA and Tukey HSD *post hoc* test).

Discussion

Variation in host plant specificity within a similar rank order has been reported in several species of phy-

Table 4 Survival to the adult stage on the four host plants, means ± SE; *n* values represent the number of larvae that were successfully established on each plant

	Urtica dioica	*Ulmus glabra*	*Salix caprea*	*Betula pubescens*	Mean
Survival to adult stage	98.0 ± 0.8% (n = 149)	96.0 ± 2.0% (n = 149)	91.2 ± 2.6% (n = 149)	83.8 ± 4.7% (n = 149)	92.2 ± 1.8% (n = 596)

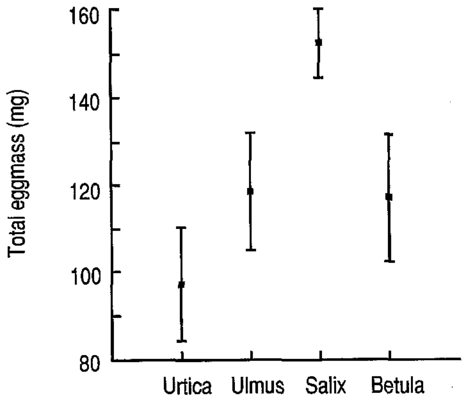

Fig. 3 Female lifetime reproductive output for offspring of the females used in the oviposition choice trail, reared on *Urtica dioica*, *Ulmus glabra*, *Salix caprea* and *Betula pubescens*. Means ± SE, *n* (number of females) = 18

tophagous insects (Tabashnik et al. 1981; Wiklund 1981, 1982; Singer et al. 1988; Thompson 1988b) but variation in the rank order itself has rarely been demonstrated (Jaenike 1990). This is to be expected, since wherever short development time is important it will constrain the possibilities available to the females to evolve a different rank order. Still, this study shows that there is substantial variation in female preference rank order within a single population of *Polygonia c-album* (Fig. 1), even though larval performance was very similar for the offspring families over the same plants (Fig. 2). Consequently there was a large variation in the correlation between preference and performance as well (Table 3). As the variation in larval performance is much smaller than the variation in preference over the same plants, the differences between the females cannot be a result of differences in offspring efficiency on the plants. The variation must be explained by different oviposition strategies, based on a similar underlying larval host plant hierarchy.

It is necessary to look upon the preference hierarchy of the ovipositing females as the result of a complex trade-off between a number of sometimes contradictory factors, including the chemical suitability of the host plants, plant abundance, predators and other enemies, and predicted time available for oviposition. There is probably no simple choice between good and bad host plants; plants that are favourable in some respects may be unfavourable in others. We should not expect one single life-history characteristic such as development time, pupal size, predator avoidance, or oviposition rate to be *the* factor all females are trying to optimize. The outcome of this trade-off could differ from population to population and from female to female due to local differences in the factors mentioned above, and due to different individual strategies (Fox and Morrow 1981; Singer 1983; Stanton and Cook 1983; Via 1984; Ng 1988; Ohsaki and Sato 1994). Relaxation of the importance of one factor will lead to a different oviposition pattern, by increasing the relative importance of the others.

This study reveals a strong correlation between female preference and larval growth rate at the population level, which suggests that growth rate is an important life-history trait in this population. However, this hides high individual variation. The correlations between individual females and their offspring range from very high (family 4) to no correlation at all (family 3). This result highlights the importance of doing correlation analyses on the individual or family level, rather than just pooling all females in the study into a single measure. In principle, variation in female age or egg-load could contribute to the variation in oviposition preference, but we saw no trends over time during the experiment consistent with such an explanation. As in all studies using wild-caught females one cannot control for the effect of learning or conditioning on the females' oviposition choices. All females were caught in a very restricted area with uniform vegetation, but early conditioning could still be a possible factor causing the large variation in preference in this study. In any case, females that showed low correlation with larval growth rate were obviously basing their host plant choices neither on development time nor on pupal size. But host plant chemistry can influence larval performance in more subtle ways than just affecting mean growth rates.

It is difficult to interpret the meaning of the unchanged growth rates over the two temperatures for certain plants (Fig. 2, Table 2), but the fact that these plants correspond relatively well to the plants the females preferred (cf. Fig. 1) is intriguing. In any case this result implies that larval 'performance hierarchies' that are generated by rearing the larvae in only one temperature must be interpreted with caution, as these hierarchies could be temperature-dependent.

When growth rates are decomposed into size and development time (Fig. 2) some interesting patterns emerge. The classic trade-off between size and development time appears in general to be less strict in butterflies than in some other animals due to plasticity in growth rate (e.g. Nylin et al. 1989; Wiklund et al. 1991; Nylin 1992). Accordingly, in this experiment larvae reared on *Ulmus* grew larger in a short time while larvae reared on *Betula* remained smaller in spite of a long development time (Fig. 2). This conforms very well with the oviposition preference of the females, all females showed a high preference for *Ulmus* and a low preference for *Betula*. On the other hand, for larvae reared on *Urtica* and *Salix* there seems to be a trade-off that has produced quite different results on the two plants. Offspring reared on *Urtica* had short development times but 'paid' for this with low pupal weights, while larvae reared on *Salix* used long development times to reach high pupal weights. The higher pupal weight of larvae reared on *S. caprea* compared to larvae reared on *U. dioica* ($P < 0.001$, ANOVA and Tukey HSD *post hoc* test) also resulted in a higher fecundity (Fig. 3). The fact that the outcome of this larval trade-off differs between these two plants means that the egg-laying females are faced with a trade-off where they can choose between short development times and large size/high fecundity for their offspring by choosing host plant. The outcome depends on the predation risk in the larval and adult stages respectively (cf. Reavey and Lawton 1991) and on the chances of succeeding in producing a second generation during the favourable season.

No data on stage-specific mortality rates are available for this species. However, as these butterflies hibernate as adults it might be reasonable to assume that, since they are adapted to spend large amounts of time in this stage, it is probably 'safer' than the larval stage. This would, in general, favour oviposition on the 'faster plants', i.e. *Urtica* and *Ulmus*. The chances of succeeding in producing an additional generation depend on the length of the favourable season. The study area is located approximately half-way between the northern limit of the geographical range of *Polygonia c-album* and the latitude where it becomes bivoltine. In this area there is plenty of time for one generation but not enough time for two generations, consequently there will be a smaller advantage in concentrating on the 'fastest' plant. All other things being equal, this will cause the result of the trade-off mentioned above to more often favour higher offspring fecundity (i.e. *S. caprea*) at the expense of a short development time (i.e. *U. dioica*). This is reflected in the preference hierarchies of female 1 and 2 who laid a comparably large amount of eggs on *Salix* at the expense of *Urtica*. Moreover, the offspring of the females that instead did lay a large proportion of their eggs on *Urtica* showed the smallest difference in pupal weight between *Urtica* and *Salix*, especially in the ecologically more relevant lower temperature (Fig. 2).

At these latitudes oviposition rate will also become increasingly important compared with larval development time (Courtney 1984). The females should thus be more willing to accept additional but 'suboptimal' host plants to increase the oviposition rate. Both *S. caprea* and *B. pubescens* are probably more common plants than *Ulmus glabra* and *Urtica dioica*, at least from a historical point of view, even though both *Urtica dioica* and *Ulmus glabra* (as well as *Humulus lupulus*) have increased in abundance due to human activities. The advantage of using these more abundant host plants may be counterbalanced by a somewhat higher mortality (at least on *Betula* compared with *Urtica* and *Ulmus*). Still, there should be lower selection against the more abundant lower quality host plants in an univoltine population such as the one studied. In a population that is partially bivoltine, e.g. in southern England, the situation is different. Here one would expect a greater tendency towards specialization on the plants that give the shortest development times, as indeed seems to be the case (Nylin 1988).

There is a latitudinal trend at the species level among papilionid butterflies of an increasing percentage of polyphagous species with increasing latitude (Scriber 1973). If this is a general trend, it leads to the interesting possibility that the temperate regions could act as a generator of polyphagous populations, by relaxing the selection pressure for fast growth and short development times and thus reducing the cost of ovipositing on 'slower' plants. Other factors, the ones mentioned above as well as predation risk, competition, and other 'ecological' factors will become increasingly important in shaping the oviposition preference hierarchy. In time the larval hierarchy may be adjusted in favour of whatever new plant the females prefer, which in turn can lead to subsequent host shifts if the host range at a later time decreases again (cf. Courtney et al. 1989).

The fact that the variation in female preference is larger than variation in the growth rates of their offspring (Figs. 1 and 2) leads to another related point. It suggests that the host-plant hierarchy of the larvae is more conservative and more difficult to change than that of the ovipositing females. Wasserman and Futuyma (1981) showed that it was possible to change the oviposition preference hierarchy of the southern cowpea weevil *Callosobruchus maculatus* by artificial selection in just a few generations, but that larval development time and survival was not changed at all in 11 generations. As the larval host range is often wider than the range of plants actually used for oviposition this larval conservatism suggests that, at least in some degree, the wider host plant range of the larvae could reflect the ancestral host plants used in the evolutionary past. This can be tested by a combination of phylogenetic and experimental methods using establishment tests. Such tests have been performed and are being prepared for publication (S. Nylin and N. Janz, in preparation). The hypothesis that the larvae should be able to feed on ancestral host plants after host shifts or increased specialization (cf. Ronquist and Nylin 1990) rests on the assumption that no severe trade-off exists between feeding efficiency and diet width. Attempts to reveal such a trade-off has not led to any conclusive results and in most cases it was not demonstrated (e.g. Scriber and Feeny 1979; Futuyma and Wasserman 1981; Scriber 1984; Moran 1986; Futuyma and Philippi 1987), although it has been found in a few cases (e.g. Via 1991). Furthermore, it is not necessary that the excluded plant should remain *suitable* for larval growth, only that growth and survival on the plant are still possible for at least some larvae. In a recent study on the host plant affiliations of a group of chrysomelid beetles Futuyma et al. (1993) found that 'preadaptive' genetically variable capacities to feed on a plant may persist for extended evolutionary time. This would allow us to detect ancestral host plant species by larval establishment tests and it would make it easier for the butterfly species to recolonize the plant at a later time as the larvae are literally preadapted for it. Host shifts should therefore be expected to predominantly involve such ancestral host plants, which could partly account for the conservatism of host plant utilization among groups of related butterflies that has often been pointed out (Ehrlich and Raven 1964; Berenbaum 1983; Feeny et al. 1983; Futuyma 1983; Feeny 1991; Mitter et al. 1991).

Lability of host plant utilization has been pointed out as an important factor in host range evolution (e.g. Bernays and Graham 1988), but we believe this needs some clarification. The oviposition preferences may be labile, but the larval host range is probably not. Lability of host use is therefore constrained within fairly narrow host plant limits. The examples of rapid host shifts that have been examined in more detail show that the genetic potential to feed on the new plant already existed in the population, so the shift only involved a behavioural change in host plant preference (Tabashnik 1983; Thomas et al. 1987). It has been argued that in general behavioural plasticity (such as oviposition preference) should be more evolutionarily labile than morphological or physiological plasticity (such as larval growth on different plants), and that for this reason the more labile trait will be more likely to be an initiator of new directions in evolution (West-Eberhard 1989). It should therefore be the ovipositing females that take the leading role in the evolution of host-plant utilization. There is room for female opportunism, but somehow the constraint of the larval performance hierarchy must be relaxed. We believe that the lowered selection for short development time in parts of the temperate zone can accomplish this, allowing more rapid host range evolution.

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