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Author(s): Soren Nylin

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Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae)

Sören Nylin

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Larval performance and oviposition plant preferences on different natural host plants were studied in two populations of the polyphagous comma butterfly, *Polygonia c-album* L., from Sweden and England. Pupal weights and larval survival were similar on most hosts while larval development time differed. Ovipositing females discriminated strongly between hosts that are used by larvae in the field, in favour of hosts on which larval development was fast. Swedish females of the summer morph discriminated more strongly between hosts than those of the spring morph. English females of the summer morph discriminated more strongly than Swedish females of the summer morph. These results suggest that the degree of specialization is higher in females of generations and populations for which a fast larval development is relatively more important. Plants in the order Urticales were both most highly preferred by the females and the most suitable for the larvae. This may reflect ancestral specialization on Urticaceae in the tribe Nymphalini.

S. Nylin, Dept of Zoology, Univ. of Stockholm, S-106 91 Stockholm, Sweden.

Introduction

Most studies on host preferences in Lepidoptera are concerned with oligophagous species (e.g., Singer 1971, 1984, Chew 1977, Wiklund 1981, 1982, Courtney 1981, Stanton and Cook 1983), whereas studies on the host plant biology of polyphagous species are largely confined to studies on larval performance on different plants (cf. Scriber 1978, 1982, 1986, but see Cates 1981). Therefore, one aim of the present study was to investigate whether females of a polyphagous butterfly species, the comma butterfly, *Polygonia c-album* L., show any clear oviposition plant preferences. Since the differences in host plant quality can be expected to be particularly large for such species, they may provide good opportunities to study factors governing host plant choice by measuring important fitness parameters concerning larval performance on different hosts and how they correlate to female host plant choice.

There are several ecological factors that can be of importance for the degree of host plant specialization displayed by individuals, e.g. predation, competition

and plant abundance (for a review see Fox and Morrow 1981). Early pilot studies suggested that seasonality (not mentioned by Fox and Morrow) could be an important factor in the case of *P. c-album*. In a seasonal environment, the time available for larval development is limited. If a species has several possible hosts on which larval development time differ, the choice of host would be expected to be more specialized when a short larval development time is of greater relative importance.

The occurrence of two distinct seasonal morphs in *P. c-album* (cf. Frohawk 1924, Ford 1945, Higgins and Hargreaves 1983) makes this species a convenient subject for studies on the impact of seasonality on the degree of host plant specialization. One morph (the "spring morph") has wings with dark undersides. Individuals of this morph enter a reproductive diapause and hibernate in the adult stage before ovipositing in the spring. The other morph (the "summer morph") has wings with light undersides. Individuals of this morph rapidly mature sexually, oviposit in the summer, and give rise to a new generation of butterflies (of the dark, hibernating morph). The offspring of the dark morph in

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Tab. 1. Larval survival, development time (mean \pm S.E.) and pupal weight (mean \pm S.E.) for offspring of the Swedish spring morph on different host plants.

Host plant	No. of eggs	Larval survival n	%	Development time (d)	Pupal weight (mg)
<i>R. alpinum</i>	36	36	100	26.9 \pm 0.2	324.2 \pm 4.3
<i>B. verrucosa</i>	36	0	0	—	—
<i>C. avellana</i>	36	12*	>33*	31.7*	226.5 \pm 7.1
<i>C. avellana</i> [†]	10	6	60	42.8 \pm 2.1	222.6 \pm 10.5
<i>S. caprea</i>	36	35	97	27.9 \pm 0.5	304.3 \pm 6.4
<i>U. glabra</i>	36	33	92	21.0 \pm 0.2	301.2 \pm 4.3
<i>H. lupulus</i>	36	32	89	23.0 \pm 0.4	309.9 \pm 8.2
<i>U. dioica</i>	50	50	100	21.6 \pm 0.2	324.5 \pm 3.4

*) Since this experiment was interrupted the development time and larval survival refer to the 12 larvae that could be followed and represent minimum values. [†]) The second experiment was made in another year.

the spring can develop into either morph, and a given female may give rise to a mixed brood of both morphs (the ratio is regulated by photoperiod and temperature and can be artificially altered; Bailey 1984, Nylin, unpubl.). In the field, *P. c-album* is partially bivoltine in England, the summer morph constituting about 30–40% of the offspring from the hibernating generation (Frohawke 1924). In Sweden, the summer morph is rare, occurring only certain years in southern Sweden. Thus, the life cycle is generally univoltine in the Swedish population under study.

In the present study the host plant preferences of three categories of females (Swedish spring and summer morphs, English summer morph) and the performance of their offspring on different hosts were investigated. The prediction was tested that the degree of specialization should vary with the relative importance of a fast larval development and thus: 1) be higher in the partially bivoltine English population than in the Swedish univoltine population and 2) higher in the summer morph (which is invariably associated with a bivoltine life cycle) than in the spring morph.

Materials and methods

Polytonia c-album is polyphagous to a degree which is unusual in butterflies (cf. Higgins and Hargreaves 1983). Its larvae can be found on plants belonging to a whole range of families in four different orders (Rosales, Betulales, Salicales and Urticales; Seppänen 1970). They include herbs as well as bushes and trees.

Females were collected in early May in the vicinity of Stockholm, Sweden, and in April in Oxford, England, in both cases shortly after the emergence from hibernation and so in the beginning of the oviposition period for the species. However, all females collected had already mated in the wild. Seven Swedish females of the spring morph were used directly in the oviposition plant choice experiments. The summer morph was produced by keeping larvae originating from three wild-caught Swedish females and one English female in environmental

cabinets with increasing daylengths (12 h to 22 h) and high temperature (25°C). Seven females from each location were used in the oviposition plant choice experiments with the summer morph, which were made during June (English females) and July (Swedish females), with larval development during the following month, respectively.

The butterflies were kept solitarily in cages (about 0.5*0.5*0.5 m) and fed a solution of sugar in water. The animals were kept under these conditions for the whole oviposition period (about three weeks) and their host plant choices were recorded throughout this time (although about 75% of the eggs were laid during the first week of each experiment). The females were presented freshly cut foliage of different plant species which have been described as hosts for the larvae of *P. c-album*, representing all seven families listed by Seppänen (1970) and several orders (see Tab. 2). For practical reasons there were a few differences in the plant species used in the three experiments.

In the main experiments, the plants were presented two at a time, one of them in all cases being nettle, *Urtica dioica* (L.). From this was calculated a relative preference value for the host (No. of eggs laid on the species being tested/No. of eggs laid on *U. dioica*). All eggs were removed and counted daily, and the plant species were then changed in a random manner. *P. c-album* females lay their eggs singly, with an obligatory flight period in between, so each egg represents a unique choice of host.

As the larvae hatched, they were divided among the host plants and fed on a single species until pupation. They were kept two and two in transparent plastic jars in which the host plant was kept in ample supply (a lower jar contained water, plants were changed frequently and whenever they showed any signs of deterioration). The rearing took place in environmental cabinets at a temperature of 20°C and under a photoperiodic regime of L:D 21:3, producing 100% of the spring morph in Swedish animals and close to 100% of the summer morph in English animals.

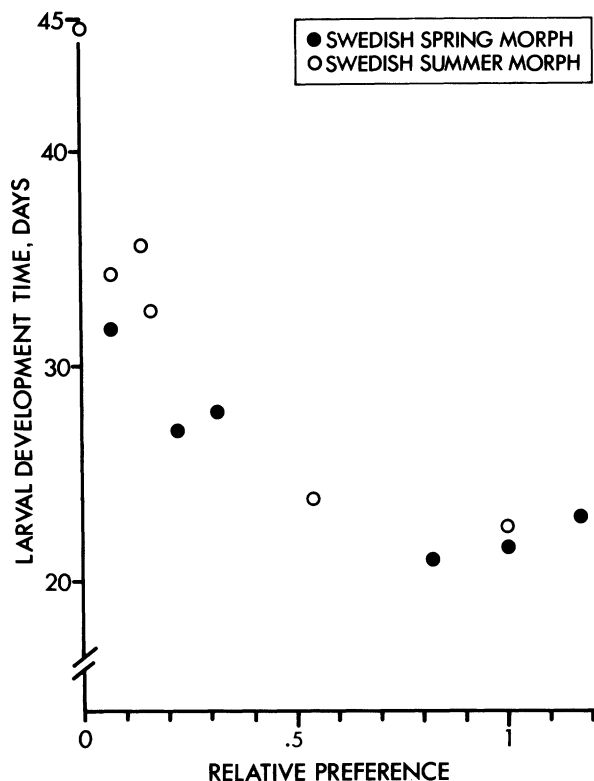


Fig. 1. Oviposition preferences (relative to *Urtica dioica*) and larval development time on a number of host plants for two categories of females of *Polygonia c-album*. Solid circles = Swedish spring morph. Open circles = Swedish summer morph. The correlations are significant ($p < 0.05$).

Survival of the larvae and development time in each stage was noted. Two days after pupation pupae were sexed, and weighed on a Cahn 28 automatic electrobalance.

Results

Larval growth abilities on the different hosts in offspring of the Swedish spring morph are given in Tab. 1. Since there were no significant differences in either development time or pupal weight between sexes or between offspring from individual females (ANOVA) all larvae, male and female, are treated together as a group. In the other two categories of larvae the number of individuals were too small to permit any certain conclusions, but some of the main differences are commented on below.

The majority of the larvae in all three categories survived to pupae on all tested host plants, with the exception of *Betula verrucosa* and English larvae on *Ribes alpinum* (38%, $N = 8$). Among the offspring of the Swedish spring morph none of the larvae survived the first instar on *B. verrucosa* (Tab. 1), and this was also the case with offspring of the summer morph ($N = 13$). This species was not tested with English animals.

Pupal weights were similar on different host plants in the offspring of the Swedish spring morph (Tab. 1), with the exception of larvae fed on *Corylus avellana*. These reached very low pupal weights resulting in small adults. The results from offspring of the Swedish summer morph were similar. Pupal weights were higher in English animals than in Swedish (t-test, $p < 0.001$, on all species except *C. avellana*: n.s.) but still similar on different plants, again excepting *C. avellana*.

Tab. 2. Oviposition preferences of three categories of females (Swedish spring morph, Swedish summer morph and English summer morph) measured as no. of eggs laid on tested plants over that laid on *U. dioica*. N (total number of eggs) in parentheses. Stars show statistical significance of results⁺.

Host plant	Female category			
	Sw. spr.		Sw. sum.	Eng. sum.
<i>Ribes alpinum</i>	0.22 (90) ***	n.s.	0.14 (398) ***	** 0.01 (76) ***
<i>Betula verrucosa</i>	0.00 (94) ***	**	0.09 (155) ***	** 0.00 (100) ***
<i>B. pubescens</i>	—		0.07 (174) ***	—
<i>Corylus avellana</i>	0.07 (144) ***	***	0.00 (255) ***	n.s. 0.00 (89) ***
<i>Salix caprea</i>	0.32 (141) ***	*	0.16 (258) ***	*** 0.01 (193) ***
<i>Ulmus glabra</i>	0.82 (226) n.s.	*	0.54 (329) ***	*** 0.19 (201) ***
<i>Humulus lupulus</i>	1.17 (178) n.s.		—	—
<i>Urtica dioica</i>	1		1	1

⁺ Stars show probability levels as determined by χ^2 -tests (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Stars below preference values indicate significance of difference between the tested plant and *U. dioica*. Stars between columns indicate significance of difference between the respective female categories.

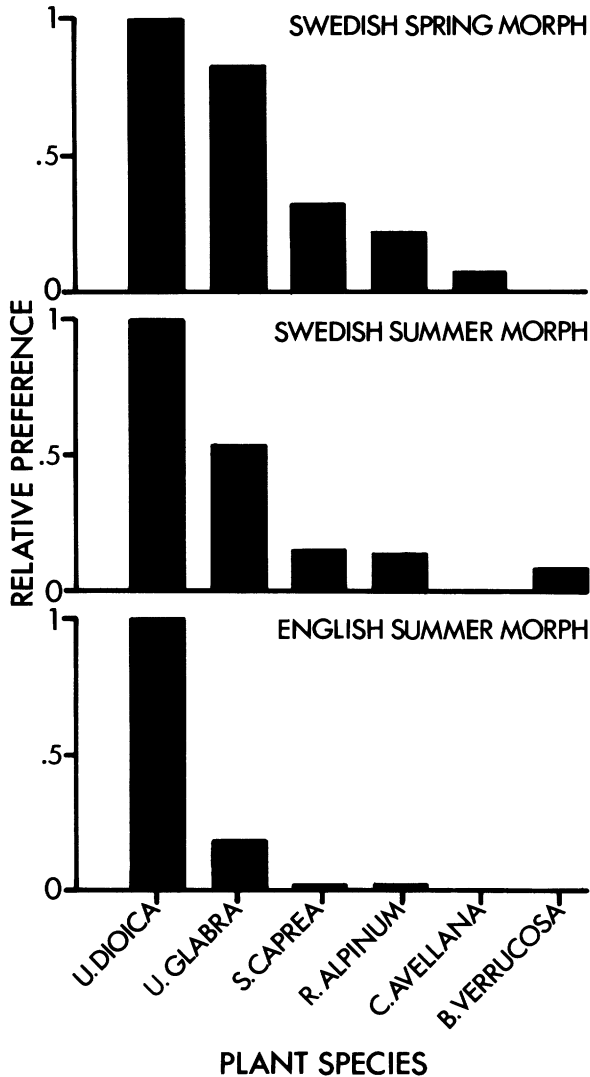


Fig. 2. Oviposition preferences (relative to *Urtica dioica*) of three categories of female *Polygonia c-album* for six host plant species that were tested with all three categories. The differences between the Swedish spring and summer morphs are significant (χ^2) in all cases except *R. alpinum*. The differences between the Swedish and English summer morphs are significant (χ^2) in all cases except *C. avellana*.

What did differ, however, was the time taken to complete larval development on different hosts (ANOVA on effect of host species: $p < 0.001$, Tab. 1, Fig. 1). Development times were about 100% longer on the plant species that was least favourable in this respect (*C. avellana* in the experiments with Swedish animals; *Ribes alpinum* when English animals were reared), than on the most favourable species (*U. dioica*, *Ulmus glabra* and *Humulus lupulus*).

In the host preference tests with females of the Swedish spring morph (Tab. 2, Figs 1 and 2) three host species, *H. lupulus*, *U. dioica* and *U. glabra*, had high relative preference values (relative preference for *U.*

dioica = 1). *Salix caprea* and *R. alpinum* had distinctly lower relative preference values while they were very low for *C. avellana*, and no eggs were laid on *B. verrucosa*. In the experiment with the Swedish summer morph the ranking of host plants, according to female oviposition preferences, were very similar (Tab. 2, Figs 1 and 2). Females of the English summer morph oviposited almost exclusively on the most preferred hosts (Tab. 2, Fig. 2).

The only significant correlations between larval performance and female oviposition preferences were those concerning larval development time (Fig. 1; Swedish spring morph: $r = -0.887$, $N = 6$, $p < 0.05$, Swedish summer morph: $r = -0.867$, $N = 6$, $p < 0.05$). This correlation was not significant in the experiment with the English summer morph ($r = -0.547$, $N = 5$). This is not surprising, considering that the relative preferences were very similar for most hosts.

Females of the Swedish summer morph seemed more specialized in their host plant choice than those of the spring morph (Tab. 2, Fig. 2). The relative preference values (relative to *U. dioica*) were lower in each case in the experiment with the summer morph than was the case with the spring morph, with the exception of *B. verrucosa*. The degree of specialization on *U. dioica* was highest in the experiment with English summer morph females, with relative preference values of zero or close to zero on all other species except *U. glabra* (Tab. 2, Fig. 2).

Discussion

It is known that relatively generalized species may be "local specialists", that is; oligophagous and polyphagous species may have more restricted diets in particular populations (Fox and Morrow 1981). The results of the present study show clearly that even highly polyphagous species like *P. c-album* may discriminate between hosts, thus reducing the effective degree of polyphagy. It should however be emphasized that the situation in the laboratory, where a preferred host (*U. dioica*) was always available, is artificial. In the field, even the most specialized category of females (English summer morph) would probably still be polyphagous.

The results that larval development time vary strongly between hosts and is correlated with the host plant preferences suggest that females of *P. c-album* discriminate between potential hosts mainly in favour of plant species on which larval development is fast. Survival and pupal weight vary little, except in the case of the least favourable hosts, and are not significantly correlated with the host plant preferences. Thus, these two components of fitness do not seem to be of great importance for the host plant choice of a female, beyond avoidance of the most unfavourable hosts.

These results were first obtained in an early pilot-study, and they suggested that host plant choice in *P. c-album* may be influenced by seasonality. This is be-

cause females may select host species on which development is fast to increase the probability that a second generation of offspring will be produced during the same season. Therefore, one aim of this study was to further examine the importance of this factor. If seasonality is a major factor governing the degree of specialization it could be predicted that females of generations and populations for which a fast larval development is of more critical importance should be more specialized. Two hypotheses were tested:

1) The summer morph in one area should be more specialized on hosts that permit rapid development than the spring morph. This is because the summer morph is always associated with a bivoltine life cycle and always oviposits later, when a smaller part of the favourable season remains for its offspring to complete development to adult. There will be strong selection in favour of mechanisms that will allow females of this morph to ensure rapid development of its offspring, since the alternative is that the larvae may be killed by frosts if they are "trapped" on a less favourable host. The spring morph, on the other hand, may or may not be associated with a bivoltine life cycle. Its offspring can also develop into the hibernating dark morph, in which case there will instead be surplus time. A high degree of specialization in this morph will not be as strongly selected for, since this would favour only those females that give rise to the summer morph, and since less specialized females can gain the benefits of generalization (e.g. shorter flights between oviposition events and spreading of risks).

2) Populations from areas where the life cycle is partially bivoltine should be more specialized than populations from areas where a univoltine life cycle (involving only the spring morph) is the rule. This is because in the first case a fast larval development is critical for the completion of both broods during the favourable season. In England most of the population (60–70%) develop according to a univoltine life cycle (Frohawke 1924). Because of the great selective premium on a second generation of offspring during the same season, this implies that the possible benefit is balanced by a great risk of not being able to complete development to adult in time before winter. Although the selection pressure for fast development should be strongest on the summer morph, a comparatively fast development of the offspring is important also for the spring morph if it increases the chances of giving rise to a second generation (as would be more likely in England than in Sweden).

Females of the Swedish spring morph choose preferentially hosts on which larval development is fast, and this pattern is more pronounced in Swedish females of the summer morph. English females of the summer morph discriminate even more strongly between hosts than Swedish females of the same morph. This is in accordance with what could be expected if the degree of specialization is in part governed by seasonality. Al-

though potentially very important in temperate species with generation times similar to the period of seasonal fluctuations in the environment, e.g. most insects, seasonality to my knowledge has not been considered in previous studies of host plant choice. The results presented here suggest that this factor should be further studied.

Regarding the difference between the spring and the summer morph another factor, seasonal changes in host plant quality, may however also be of importance, namely if the less preferred hosts (bushes and trees) deteriorate relatively more from spring to summer than the preferred hosts (mainly herbs). This seems possible, and so these two causes cannot be separated in the present study.

I am aware of only one other study documenting a difference between generations of insects in the degree of specialization on host plants. Stanton and Cook (1983) documented a higher post-landing oviposition likelihood in second brood females of *Colias philodice eriphyle* (oligophagous on Leguminosae).

If a difference between the morphs of *P. c-album* exists, which is due to changes inherent in the butterflies and not to changes in the environment (e.g. in the quality of the host plants), there are two possible mechanisms: 1) genetic differentiation and 2) developmental differences between broods (cf. Stanton and Cook 1983). The striking visual phenotypic difference between the two morphs of *P. c-album*, which is induced by photoperiod and temperature during the larval stage (Bailey 1984, Nylin, unpubl.), do suggest a potential for differences also in oviposition behaviour which could be induced during development.

The fact that adult oviposition preferences and larval growth abilities are in such good general agreement strongly implies that plant chemistry is of great importance in enforcing the degree of host specificity that *P. c-album* displays. This conclusion is supported by the fact that the group of three hosts that are preferred by ovipositing females as well as most suitable for the larvae (*U. dioica*, *H. lupulus* and *U. glabra*) all belong to the order Urticales, while the three hosts in the order Betulales (*B. verrucosa*, *B. pubescens* and *C. avellana*) are the least preferred as well as the least suitable. Water content of the leaves is one important component of plant chemistry (Schriber 1977), and may explain some of the results, e.g. the fact that larvae survived on *B. pubescens* but not on *B. verrucosa*. The leaves of the latter species seem to have lower water content than those of *B. pubescens* (Nylin, unpubl.). Some other aspect of plant chemistry, more specific for groups of related host plants, is however probably also of importance for the suitability of (and the preference for) plants belonging to the order Urticales. There is a possibility that specialization on Urticaceae may be ancestral to the tribe Nymphalini. This would explain why *Polygonia* still retains relatively strong ties with Urticales. Support for this hypothesis is given by the fact that most

of the species in the genera *Aglais*, *Vanessa* and *Inachis* in the tribe as well as *Araschnia levana* in the related tribe Araschnini are monophagous on *U. dioica* or oligophagous on Urticaceae. On the other hand species in the genus *Nymphalis*, which is considered closely related to *Polygonia* (Niculescu 1985), use exclusively trees and bushes. It is interesting to note that many of the trees used as hosts by various *Nymphalis* spp. are among those used by *P. c-album*. The genus *Nymphalis* may have performed a full switch to trees and bushes as hosts while the switch is only partial in most species of *Polygonia*. In the absence of a reliable phylogeny for the tribes and genera in Nymphalinae this can however at present only be speculation.

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