

Effects of larval host plant and sex on the propensity to enter diapause in the comma butterfly

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For polyphagous insects, the choice of host plants by ovipositing females may potentially have profound effects on the life histories and life cycles of their offspring. This is especially true for insects such as butterflies, that obtain most of the resources needed for adult maintenance and reproduction during the period of larval feeding. In this study we investigate the effect of larval host plant on the propensity to enter adult hibernation diapause (and pass through a univoltine life cycle) in the polyphagous comma butterfly, *Polygonia c-album* (Lepidoptera: Nymphalidae). Host plants resulting in slow larval growth rates (e.g. *Betula pubescens*) produced a larger proportion of individuals of the hibernating dark morph compared to larval host plants promoting a more rapid larval growth (e.g. *Urtica dioica*). Only the latter category of plants would support a bivoltine pathway in the field. The effect of host plant remained after controlling for growth rate, suggesting that the host plant may function as a “cue” for choice of life cycle, in combination with photoperiod and temperature. Males grew faster than females but had a higher propensity to enter diapause. There was also a steeper increase in frequency of diapause for males than for females at low temperatures and on poor host plants. This suggests that males which cannot achieve protandry under direct development, in situations when high growth rates are too costly, instead enter diapause.

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Life history theory (Cole 1954, Roff 1992, Stearns 1992) seeks to explain differences in developmental and reproductive traits, in insects often associated with seasonal adaptations such as diapause. The diet of animals has been documented to strongly influence both development and reproduction, and is thus important for our understanding of life history evolution (e.g. Boggs 1981, Behrens 1985, Tauber et al. 1986). For polyphagous insects, choice of larval host plants can potentially have drastic effects on the life histories of individuals. This is especially true for insects that obtain most of the resources needed for adult maintenance and reproduction during the period of larval feeding (Boggs 1981, 1990), and where the immature larvae cannot move readily from plant to plant. Many

butterflies fit this description and have therefore been described as “parasites” as opposed to “grazers” (Thompson 1982).

For such insects the female’s choice of larval host plant may have pronounced effects on the life histories of offspring, since host plants typically strongly influence the growth rates of juveniles (e.g. Scriber 1981, Nylin and Janz 1993, Stoyenoff et al. 1994), and growth rate affects two key life history traits: development time and/or final size (Abrams et al. 1996). Development time, in turn, can influence the fitness of males and females both directly (because a short development time reduces the risk of dying before reproduction) and indirectly, because it affects the timing of the adult insect. The outcome of these effects on fitness differs

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between the sexes and between the two possible main developmental pathways in temperate insects: direct development to sexual maturation, or with a hibernation diapause intruding in the life cycle before maturation.

Directly developing females have to eclose at a time when suitable host plants for egg laying are available, and directly developing males are often selected to eclose before the females in order to maximise their mating success, a phenomenon known as protandry (e.g. Wiklund and Fagerström 1977, Parker and Courtney 1983). Under selection for protandry, late emerging males will have fewer mating opportunities and may choose to enter a diapause route instead, resulting in more males than females entering early diapause (Wiklund et al. 1992).

The importance of a short development time also differs between the developmental pathways. Under direct development (bivoltinism), where a generation of offspring is produced the same season, a short development time in the first generation may be crucial for the survival of the second generation. If oviposition occurs too late in the season, there may not be enough time left for offspring to reach the hibernating developmental stage before winter. In contrast, if the first generation enters a diapause pathway (univoltinism) there is often surplus time for this single generation (Masaki 1978, Nylin et al. 1989, Nylin 1992) and a short development time is not crucial.

The costs of a short development time may be associated with a small final size or with having a high growth rate. Large size is typically important for female fecundity (Janz et al. 1994) but is also likely to be important for male fitness. The cost of having a high growth rate (thereby reaching a large size in a short time) may be that it necessitates increased feeding and therefore increased exposure to enemies, or that it results in a higher risk of death from starvation (Gotthard et al. 1994), or both.

In conclusion, it is likely that there are situations when a short development time would be very important under direct development, but cannot be achieved without large costs in terms of a small final size and/or a high growth rate. For instance, a poor host plant means that a high growth rate is likely to be very costly for a butterfly larva. In such situations it could be a better option to enter diapause development, i.e. use the diet as a cue for future conditions together with the more typical seasonal cues, photoperiod and temperature. Effects of diet on the incidence of diapause are relatively common in insects, and their importance has probably been underestimated (Behrens 1985, Tauber et al. 1986). The effects of diet and temperature should be stronger for males, since selection for protandry means that a short development time under direct development is even more important for males than for females. These hypotheses are natural extensions of

earlier results showing that male butterflies have a higher overall propensity to enter diapause (Nylin 1992, Wiklund et al. 1992).

In this study we investigate the effect of the female's choice of host plant on the propensity of her offspring to enter diapause. If host plants differ in their ability to support high larval growth rates, and the time available for growth of the following generation is limited by seasonality, we expect a higher frequency of diapausing individuals on poor host plants. Moreover, we expect a steeper increase in the diapause frequency on poorer host plants and at lower temperatures for males than for females.

Material and methods

The comma butterfly, *Polygonia c-album*, (Lepidoptera: Nymphalidae) is a polyphagous butterfly feeding on a range of host plants, including the stinging nettle (*Urtica dioica*), elm (*Ulmus glabra*), willow (*Salix caprea*) and birch (*Betula pubescens*), typically in this order of preference and offspring performance (Nylin 1988, Nylin and Janz 1993, Janz et al. 1994). The species hibernates in the adult stage. It is potentially bi- or multivoltine and shows seasonal polyphenism in the adult stage, with a directly developing lighter morph which is reproductively active soon after adult emergence and a darker morph which enters reproductive diapause and will not mate until the next year following adult hibernation (Nylin 1989, 1992).

In Sweden direct development is rare and normally only the dark morph is seen in autumn and in spring. The light morph is produced in the Swedish population under conditions of increasing daylengths throughout the larval period (i.e. corresponding to dates early in the season; Nylin 1989, 1992). In areas more to the south, such as England, direct development occurs at a higher frequency (Nylin 1989). Low temperatures increase the frequency of the hibernating morph (Nylin 1992). The comma butterfly has been shown to be protandrous, directly developing males having shorter development times than females (Nylin 1992, Wiklund et al. 1992).

Five gravid females were caught near Stockholm, Sweden, between 4 May and 14 May 1992, which corresponds to the beginning of the flight season after adult hibernation for the diapausing morph. Females were allowed to oviposit in the laboratory on their naturally occurring host plants and the eggs were removed. Following eclosion of the eggs, 120 larvae from each female were weighed and then reared individually on one of four different host plants (nettle, elm, willow or birch). There was some initial mortality, but dead larvae were replaced until a total of 30 larvae from each female were successfully established on each of the four

host plants. Rearings took place in plastic jars in which the cuttings of host plant could receive water from a jar below. Plants were exchanged for new ones taken from the field at frequent intervals whenever they showed signs of wilting. This procedure was followed, rather than using potted plants, in an attempt to mimic the natural changes in the plants' nutritional value over the season.

Fifteen larvae from each group were kept at 20–22°C (referred to as 20°C) and the other 15 at 26–28°C (referred to as 26°C). The temperature fluctuations were due to insufficient isolation of the climate rooms. Larvae were moved from 12 h to 22 h daylength when they had reached the third instar, to promote direct development. 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 developmental time in days. This formula produces a measure of percentage mean daily weight gain (or loss).

At emergence adult individuals were classified as being either directly developing or diapausing depending on their colour morph.

All statistics were calculated using SYSTAT (Wilkinson 1992). Results are presented as means \pm S.E. Since morph, the dependent variable, is not a continuous variable, it may not be appropriate to analyse the effects of sex, host plant, temperature and growth rate on the propensity to diapause by using a multiple ANOVA. We have therefore used a log-linear model, designed to detect significant effects of discrete factors on the frequencies of a discrete dependent factor.

The analysis was performed in two steps. In the first step the whole material was analysed together and only main factors inspected. In the second step the material was divided into the two experimental temperatures and analysed separately. This was done to reduce the large numbers of interactions between four main factors, to allow closer study of interactions between sex, host plant and growth rate.

In this context, growth rate was recoded as a discrete variable with four levels. The interpretation of the factor growth rate is somewhat problematic because growth rate could potentially be associated with developmental pathway both as cause and effect. Slow growth could increase the propensity for diapause, but it could also be the other way around; individuals destined for diapause could grow more slowly because they have surplus time (see Introduction). Here, we will deal with growth rate mainly as a potential causal factor (because this is necessary in order to separate its effects from those of other causal factors), but it should be kept in mind that the reverse interpretation is equally possible. Effects of growth rate variation which

remain after controlling for effects of experimental temperature, host plant species and sex may be due to microenvironmental variation (such as temperature gradients within cabinets and individual host plant quality within species), genetic differences in growth rate among butterfly individuals, or both.

Results

In total 545 individuals survived to adulthood: 267 at 20°C and 278 at 26°C. The increase in daylength was successful in promoting direct development: 384 individuals eclosed as directly developing adults, and 161 as the hibernating dark morph.

The log-linear model found that the propensity to enter diapause was strongly affected by all the main factors when the whole material was analysed together in the same model: temperature (likelihood Chi-square 390.7, $p = 0.0001$), larval host plant (661.6, $p = 0.0001$), sex (88.6, $p = 0.0001$) and growth rate (1688.2, $p = 0.0001$). Interactions were not analysed in this first step of the analysis, but in the second step the material was divided into the two experimental temperatures to allow inspection of two- and three-way interactions between the effects of larval host plant, sex and growth rate. Comparisons between temperatures regarding effects of these three factors also refer to the second step.

At the lower temperature more individuals chose the diapause route compared to the situation at high temperature (Fig. 1; likelihood Chi-square 390.7, $p = 0.0001$). The proportion of individuals entering diapause

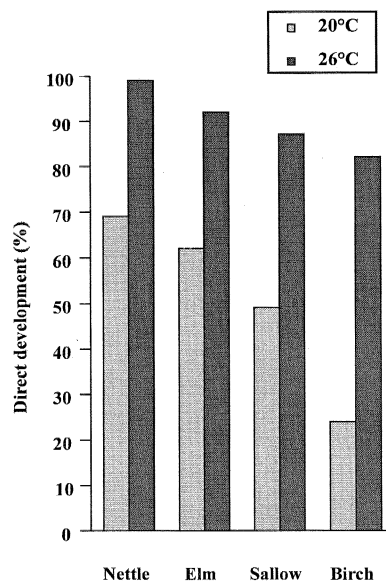


Fig. 1. Effects of larval host plant and temperature on the propensity to develop directly in *Polygonia c-album*. Sample sizes per plant and temperature range from 58 to 73 individuals.

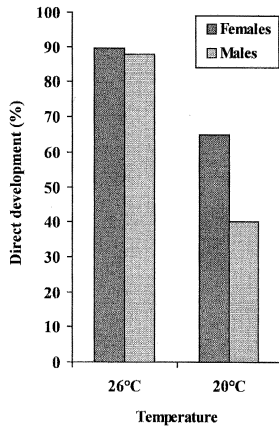


Fig. 2. Effects of sex and temperature on the propensity to develop directly in *Polygonia c-album*. Sample sizes per sex and temperature range from 125 to 146 individuals.

was 48.3% at the lower temperature regime and only 11.5% at the higher temperature.

The larval host plant was also found to affect the propensity to enter diapause (Fig. 1). There was a significant effect of larval host plant on the number of directly developing (light morph) individuals (likelihood Chi-square 661.6, $p = 0.0001$). A pattern of high frequencies of direct development on preferred host plants such as nettle, and low frequencies on less preferred plants such as birch, was found at the lower (192.5, $p = 0.0001$), as well as at the higher temperature regime (204.3, $p = 0.0001$, Fig. 1).

In total 103 males out of 288 (35.8%) entered the diapause pathway, compared to 58 females out of 257 (22.6%) (likelihood Chi-square 88.6, $p = 0.0001$). The separate analyses reveal that this effect was due to a difference at the lower temperature: significantly more males chose the diapause pathway at 20°C compared to females (45.1, $p = 0.0001$, Fig. 2). There was no effect of sex on the propensity to enter diapause at 26°C.

There was a significant effect of larval growth rate on the proportion of directly developing individuals, and/or vice versa, in the total material (1688.2, $p = 0.0001$) and at both experimental temperatures in the separate analyses: at 20°C (likelihood Chi-square 421.7, $p = 0.0001$) and at 26°C (426.1, $p = 0.0001$). Directly developing larvae grew faster, with an average of $46.8 \pm 0.36\%$ daily weight gain, corresponding to $43.8 \pm 0.76\%$ in individuals that eventually entered adult reproductive diapause.

Furthermore, significant interactions between the main factors were found. There was a significant interaction between larval host plant and growth rate on the number of the two morphs produced at both 20°C (likelihood Chi-square 208.5, $p = 0.0001$) and 26°C (366.8, $p = 0.0001$), indicating that growth rate affected diapause propensity differently on different host plants (or vice versa). Although we do not want to make too

much out of this result without replicates, it is interesting to note that low growth rates were associated with diapause on the poorest host plant but not on the best (Fig. 3). This pattern was similar at both temperatures.

At the lower temperature the propensity for diapause increased more on poor host plants in males than in females (interaction between sex and host plant; 10.8, $p = 0.030$). This pattern was not found at the higher temperature. Similarly, there was no significant interaction between sex and growth rate on the propensity to enter diapause at the higher temperature. However, at 20°C when more males chose the diapausing route, directly developing males had a higher growth rate compared to directly developing females, on average $45.6 \pm 0.74\%$ versus $43.6 \pm 0.70\%$ (14.2, $p = 0.002$).

There was also a significant three-way interaction between sex, larval host plant and growth rate (7.6, $p = 0.006$) on the proportion of individuals entering diapause. The combination of factors that resulted in the highest proportion of diapausing individuals was males growing at a low growth rate on birch at a low temperature, and the highest frequency of direct development resulted from females growing at a high rate on nettle at a high temperature.

Discussion

The larval host plant of the comma butterfly was found to affect strongly the propensity to enter diapause. Diet has been found to influence the propensity for diapause in several insects (see Behrens 1985, Tauber et al. 1986 for references), but to our knowledge this has not been previously documented for a butterfly. The effects on diapause propensity were consistent with the preference and performance hierarchies that have been found earlier (Nylin 1988, Nylin and Janz 1993, Janz et al. 1994), i.e. a larger proportion of individuals entered diapause when growing on less preferred, and poorer, host

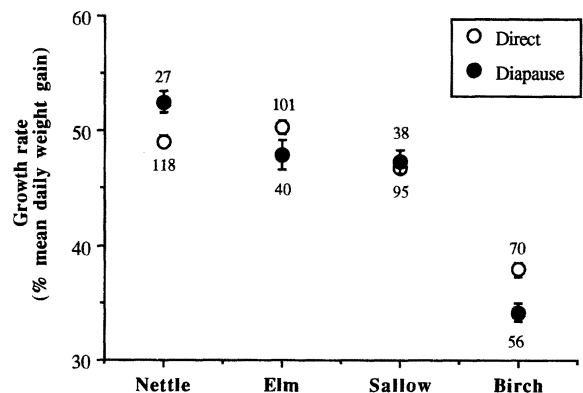


Fig. 3. Interactions between larval host plant, growth rate and developmental pathway in *Polygonia c-album*. Circles represent means \pm SE; sample sizes can be seen from frequencies above and below each circle.

plants. The present results further confirm the performance hierarchy in that the growth rates of larvae also differed depending on their larval host plant (cf. Fig. 3). Host plants resulting in slow larval growth rates (e.g. birch) produced a larger number of diapausing individuals compared to larval host plants promoting a more rapid larval growth (e.g. nettle). It is therefore likely that the "choice" of developmental route is mediated partly through the larval growth rate which the host plant can support.

Nevertheless, we suggest that the finding that larval host plant affects the incidence of diapause cannot be explained only as a simple effect of growth rate itself. A highly significant effect of larval host plant on the propensity for diapause was found also when growth rate was included in the model as a potential causal factor. Also, low growth rates of individuals were associated with a high propensity to enter diapause on the poorest plant but not on the best plant. Although this is hard to document rigorously, we believe that the results indicate that larvae make use of some sort of "plant cue", besides growth rate, for their choice of developmental pathway. This is speculative, but feeding on a high quality host plant such as nettle could for the larvae mean that this plant is able to support rapid growth not only at present, but also in the future (up to pupation), i.e. a short development time is possible and therefore a generation of offspring in the same season (direct development is a feasible option).

It is clear that the choice of developmental pathway is not just a side effect of a rapid or slow growth up until a point where the individual larva makes the "decision" to enter a diapause pathway or to develop directly. Rather, the decision seems to be influenced by at least four additional factors: photoperiod, temperature, host plant and sex. Photoperiod is the main seasonal cue which tells the individual how much time remains of the favourable season (Danilevskii 1965, Beck 1980, Tauber et al. 1986, Nylin 1989). In this experiment all individuals experienced increasing day-lengths, which indicates a date early in the season. Temperature may also act as a seasonal cue of this type, since high temperatures suggest summer conditions (Behrens 1985, Tauber et al. 1986), but may also indicate to the larva something of the cost of having a high growth rate. At low temperatures, high growth rates are likely to be more costly for metabolic reasons, from which follows that short development times and therefore direct development are less feasible options. The effect of host plant (or the often found effects of diet in general on diapause frequency in insects; Tauber et al. 1986) on the propensity to enter diapause could be similar, in that a poor host plant indicates that high future growth rates are likely to be costly.

The fourth factor, sex, is not an environmental cue, but affects the choice of pathway because it affects the functions linking the key life history traits of develop-

ment time, growth rate and final size to fitness (Abrams et al. 1996). Males tended to enter diapause to a greater extent than females. This was especially true on poor host plants and at the lower temperature regime. A sex difference in the propensity to enter diapause development has previously been shown for several butterfly species, and has been interpreted as a consequence of simultaneous selection for protandry and large male size (Wiklund et al. 1992, Nylin et al. 1995). Selection for protandry means that a short development time is more important for a male than for a female under direct development, which means that a male should be more prone to enter diapause when a short development time can only be achieved through high growth rates (because large final size is also important for fitness) and when such high growth rates are likely to be very costly (because of low temperatures and/or poor host plants). Possibly, the significant interactions between sex and the environmental factors should be seen in this light.

Larger males have higher reproductive success in several insects (e.g. Sigurjónsdóttir and Parker 1981, Partridge et al. 1987). One reason for this is that large size covaries with spermatophore size (e.g. Svärd and Wiklund 1989, Wedell 1993), and that spermatophore size in turn affects fertilisation success (e.g. Dickinson 1988, Wedell 1991). In some butterflies males also transfer nutrients in the spermatophore at mating, which results in increased reproductive output of these females (Boggs and Gilbert 1979, Wiklund et al. 1993). Radiolabelling studies have shown that males of the comma butterfly transfer substances during mating that are being incorporated into developing eggs (Wedell 1996). Females of this species mate several times, and it is therefore likely that large body size is reproductively beneficial for males. Finally, males defend territories, hence it is conceivable that a large size may also be advantageous in territorial disputes.

The present results, showing that the host plant may act as a cue for the choice of developmental pathway, could help explain some anomalies in earlier results from the comma butterfly. The general pattern in phytophagous insects is that the preferred host plants are those which can support high growth rates, and therefore result in both short development times and large final sizes. In general this is true for the comma butterfly as well; female preference is correlated with high growth rates and short development times (Nylin 1988, Nylin and Janz 1993, Janz et al. 1994). However, the anomaly is that final size does not follow the typical pattern. Size is in fact larger on *sallow* than on *nettle*, although growth rates are lower, and this results in higher female fecundity (Janz et al. 1994, Nylin et al. 1996). Proximally, this difference is caused by larvae leaving the exponential part of their growth trajectories earlier on *nettle* (Nylin et al. 1996). Females are very variable in their preferences for these two plants, and

we have suggested that this may be because of varying outcomes of the trade-off between the advantages of a short development time and a large final size.

Choosing a host plant which can support a short development time and therefore bivoltinism should be relatively more important in populations (such as the English one) where a second generation is probable, than in populations (such as the Swedish one) where univoltinism is the rule, and direct development is rare. There does seem to exist a pattern of higher specialisation on the “faster” plants in England than in Sweden (Nylin 1988) as predicted by this “voltinism-suitability hypothesis” (independently suggested by Scriber and Lederhouse 1992). Possibly, the anomaly of a relatively small final size on nettle can be explained at least partly if this plant acts as a cue suggesting to the developing larva that a second generation may be feasible. This increases the fitness gains associated with a short development time relative to those associated with a large final size, perhaps to the point that growth should stop early to leave more time for the second generation (which is only barely possible to fit into the season). The reverse situation applies to sallow: this plant can probably never support growth rates high enough for a second generation in the field, and it follows that growth should continue, to take full advantage of a long development time and a large final size.

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