

# Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable?

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We investigated whether interpopulational variation in life-cycle regulation and life-history plasticity, in response to photoperiod, is predictable from considerations of what would be the adaptive life cycle and life history in a given environment. The investigation was performed on five populations of the speckled wood butterfly, *Pararge aegeria* (L.) (Lepidoptera: Nymphalidae), from central and south Sweden, England, Spain and Madeira. Insects from all five populations were reared at all daylengths from 10 h to 20 h at 17°C. Larval and pupal development times were noted. Predictions were met regarding the type of life-cycle regulation and the shape of reaction norms. Evidence for diapause (larval summer and winter diapause, pupal winter diapause) was found in the three northern populations (*P. a. tircis*) but not in the two southern populations (*P. a. aegeria*). Photoperiodic thresholds for diapause induction followed the predicted latitudinal patterns, and this was also the case regarding quantitative regulation of development time (by photoperiod) among directly developing individuals. Under direct development, development time was progressively shorter in shorter daylengths in the two Swedish populations, where this signals progressively later dates. This was not found in the English, Spanish and Madeiran populations where such a response is likely to be maladaptive, because one or more generations of larvae are present before summer solstice. There were also unexpected results, for which we propose preliminary adaptive explanations.

ADDITIONAL KEY WORDS:—Seasonality – reaction norms – photoperiod – diapause – growth – *Pararge aegeria* – Lepidoptera – Satyrinae.

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## INTRODUCTION

The subject of this investigation is interpopulational variation in life-cycle regulation, and in the seasonal plasticity of a key life history trait: development

time from hatchling to adult. In insects, the evolution of life histories should be intimately associated with the evolution of adaptations to seasonality in the environment. This is because most insects in temperate areas typically can diapause only in a specific developmental stage. There must have been strong selection for phenotypic plasticity in growth and development (using environmental cues which signal the season; Danilevski, 1965; Beck, 1980), favouring reaction norms which will ensure that each individual has a good possibility of reaching the overwintering stage before winter, or, if it belongs to an early generation, that its offspring does so. Besides diet, there are two important environmental parameters for such an insect: photoperiod (which signals the time of year) and temperature (which may affect growth- and developmental rates directly, or be used as an environmental cue, or both). Reaction norms describing which growth rates, development times and sizes are expressed in a range of photoperiods and temperatures have been studied in several species of butterflies (Nylin *et al.*, 1989; Nylin, 1992; Wiklund *et al.*, 1991; Nylin *et al.*, 1993). These studies show that butterflies possess complex reaction norms with a high degree of plastic responses to these environmental factors. In particular, rates of growth and development may vary according to photoperiod and result in a shorter development time when this is called for by time stress because of an approaching winter.

A population of the speckled wood butterfly, *Pararge aegeria* (L.), from southern Sweden was the subject of an earlier investigation on seasonal plasticity (Nylin *et al.*, 1989), where growth and development was found to be regulated by photoperiod at two levels; the qualitative choice of major developmental pathway (within the context of this paper, the word 'choice' refers to the facultative ontogeny of *P. aegeria*; where individuals follow one or the other developmental pathway in response to seasonal cues) and, within a given pathway, fine-tuned regulation in a quantitative response to photoperiod. Regulation of the life cycle was, in contrast, relatively independent of temperature. Here, this population is compared to populations from central Sweden, England, Spain and the island of Madeira, representing two subspecies, different degrees and types of seasonality in the environment and different numbers of generations per season. The questions addressed are the extent to which these populations differ in their life history response to photoperiod (reaction norms) and whether this variation can be predicted or at least be given an adaptive explanation. Predictions were as follows:

(1) Populations from more southern, less seasonal, areas should be characterized by lack of diapause or at least by less clear photoperiodic thresholds for diapause induction. In less seasonal areas photoperiod may not be a good predictor of future conditions. Other cues, such as temperature, can be expected to be more important.

(2) The 'critical' daylength for diapause induction should follow a latitudinal pattern reflecting the fact that days are longer at higher latitudes in the summer (Danilevski, 1965; Bradshaw, 1976). The critical daylength is the daylength that will induce diapause in 50% of the individuals (e.g. Danilevski, 1965).

(3) Reaction norms for photoperiodic responses should differ between populations in a way reflecting the fact that, in *P. aegeria*, short days always

correspond to late dates in northern, but not in southern, populations. Populations from more southern areas are more likely to have patterns of voltinism such that the earliest generation grows and develops before summer solstice. In northern areas the first generation occurs wholly or partly after summer solstice (cf. Fig. 8). Consequently, in the range of relatively long daylengths which induce direct development, we expected progressively shorter development times to be induced in progressively shorter daylengths (indicating a later date) in northern but not in southern populations.

#### MATERIAL AND METHODS

##### *Study organism*

Two subspecies of *P. aegeria*, are recognized in Europe; the northern *P. aegeria tircis* (north of the Alps and north of a zone through France and Greece) and the southern *P. aegeria aegeria* (south of this range, and including the Mediterranean islands and Northern Africa). Relatively recently (1970s; Higgins, 1977), *P. aegeria aegeria* colonized the Atlantic island of Madeira from an unknown Mediterranean source. A large population now coexists with the similar but larger-sized endemic *P. xiphia* (Owen *et al.*, 1986).

The two Swedish populations studied are not arbitrarily defined, but distinct, geographically isolated, entities of different origin. The southern population reached Sweden via Denmark in the 1930s, while the central Swedish population probably is of Finnish origin (Nordström, 1955). The southern population has expanded northwards since the first capture in 1939, but few individuals are still seen in the transition zone between the two populations.

##### *Climate and phenology*

The five populations of *P. aegeria* sampled were from five latitudes: Stockholm (central Sweden, 59.5°N), Ransvik (south Sweden, 56°N), Oxford (England, 52°N), Madrid (Spain, 40°N) and Madeira (33°N).

The first three sites, inhabited by *P. aegeria tircis*, are characterized by similar oceanic temperate climates with strong seasonality. Summer is generally warm and wet and thus beneficial to growth and development of both butterflies and host plants (grasses) whereas the winter is too cold (especially in Sweden). One generation of all three populations consequently hibernates in a diapause, which can take place in either the pupal stage or as half-grown larvae (third instar; cf. e.g. Shreeve, 1986; Nylin *et al.*, 1989). There may also be a summer diapause in the third larval instar (Wiklund *et al.*, 1983; Nylin *et al.*, 1989). This makes for a complicated phenology south of central Sweden. In the univoltine central Swedish population there is a single adult peak in May–June (Wiklund, in prep.). Adults of the bi- to multivoltine populations of south Sweden and England fly in 4–5 peaks from about April to September (Goddard, 1967; Shreeve, 1986; Thomas, 1986). These flights are synchronized by diapause and by the reaction norms for control of development time (see Results), and are therefore relatively discrete.

The area of Madrid is characterized by a Mediterranean climate, with dry,

hot summers and relatively mild winters. *P. aegeria aegeria* flies from March to October, occurring continuously throughout summer in an unknown number of generations, but with a decline during the warm and dry midsummer.

Madeira has a mild oceanic climate with moderately warm temperatures all year round and seasonality is evident only in the lack of rain in July–August. All developmental stages of *P. aegeria* can be found simultaneously (Nylin & Wickman, personal observation), and adults of *P. aegeria aegeria* seem to fly more or less continuously all year round, at least at lower elevations (Higgins & Hargreaves, 1983; Owen *et al.*, 1986).

#### *Reaction norms*

In the five main experimental rearings, newly hatched larvae from 7–10 females (caught in the wild) of each population were used. They were pooled and divided among all photoperiods between 10 h light and 20 h light (with increments of one hour, using 24 h cycles in all cases). Twenty-five to thirty larvae were placed in each photoperiod, depending on availability, except for the experiment on the south Swedish population where larger sample sizes of 50 were used at some photoperiods. The experimental temperature used was 17°C. This is a typical daily mean field temperature during summer for the population from southern Sweden (laboratory generation time at this temperature is similar to that in the field), and was used in an earlier investigation on this population (Nylin *et al.*, 1989). To allow comparisons (some results of the earlier investigation are included here) the same temperature was used.

Larvae were reared in environmental cabinets with controlled photoperiod and temperature. They were kept individually in transparent plastic jars in which a host plant (*Poa annua*) was grown. The jars were rotated at intervals to avoid position effects within cabinets, and the duration of larval and pupal stages noted for each individual. On the day after pupation, pupae were sexed.

In all five populations, the duration of the larval stage was just over 30 days, and the pupal stage about 15 days, at long photoperiods (Figs 3–7). Hence, the total development time from newly hatched larva to adult was 45–50 days at these conditions (Fig. 1). Consequently, a development time similar to this was taken as an indication that an individual was developing directly. Individuals were judged as diapausing when they belonged to a more or less discrete category with longer development times. The distinction was generally clear, but not always, probably because of the quantitative nature of diapause in *P. aegeria* (Nylin *et al.*, 1989) and because some photoperiods are not experienced under natural conditions.

## RESULTS

### *Choice of developmental pathway*

#### *Total development time*

In the three northern populations the total development time of males was affected by photoperiod (Fig. 1), corresponding to conditions where diapause

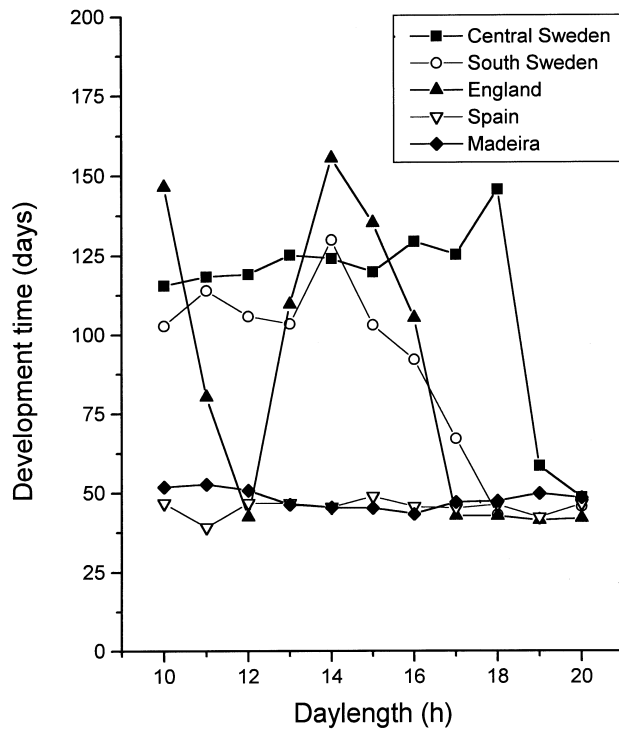


Figure 1. Mean total development time from hatching to adult at different daylengths and 17°C for the studied populations of *P. aegeria*. Results are shown for males, but were very similar for females.

(larval or pupal, summer or winter) or direct development, respectively, was induced. Under the experimental conditions there was no diapause in the two southern populations. Results for females were similar (Figs 3–7) and hence are not shown for total development time. There was very little mortality in all experiments (5% or less) except the one on the Spanish population, where about 20% of the larvae died, many from drowning late in development. This happened mostly in short photoperiods and could possibly show the presence of a diapause, if larvae were trying to get to a safer place for hibernation by crawling down to the base of the tufts of grass.

As predicted from latitudinal variation in daylengths, the critical photoperiod for induction of diapause or direct development was shifted towards shorter photoperiods in the more southern populations. Comparing the populations from central Sweden, southern Sweden and England, the constant photoperiod when larval summer diapause (in the field later followed by winter diapause in the pupa, see below and Fig. 2) first occurred in some individuals was, respectively, 19 h, 17 h and 16 h (cf. Fig. 1 and Figs 3–5).

#### *Life cycle regulation in P. a. tircis*

Results from the three northern populations are summarized in Fig. 2 and shown for both sexes in Figs 3–5. For the interpretation of results, it is important to realize that ‘choices’ between developmental pathways are made

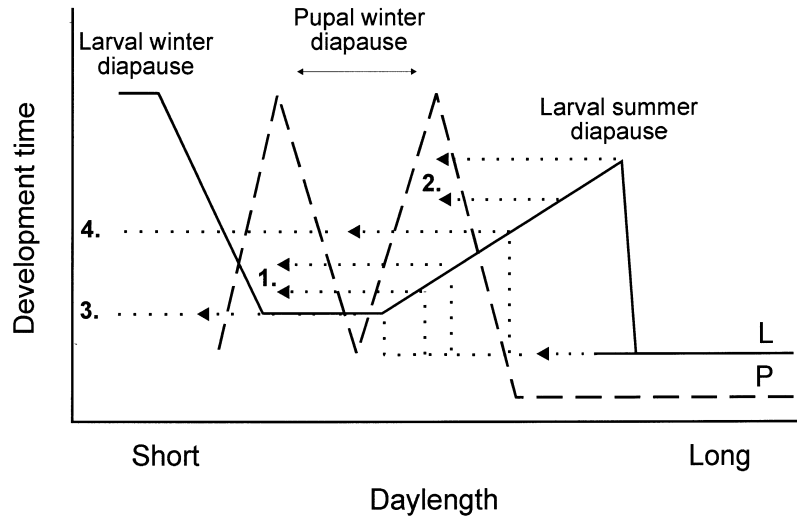


Figure 2. A schematic illustration of how we interpret life cycle regulation in *P. aegeria* and the reaction norms seen in Figs 3–5 for larval (L, solid line) and pupal (P, dashed line) development time in response to daylength. Dotted lines show some possible developmental pathways (1–4), with arrowheads indicating the late larval stages when the ‘decision’ is taken to enter pupal diapause or not. Individuals are constantly being ‘transported’ towards the left of the figure during development or summer diapause, because daylengths are decreasing in the field. Development is direct through both the larval and pupal stage in very long daylengths (short development times at the right). At a shorter daylength (signalling a late summer date) two categories of larvae are present. Larvae of the first category develop directly (lower path; pupal diapause averted by long daylengths) to produce a second generation. Pupal diapause is typically induced by the short-daylength peak in their offspring after a period of relatively slow larval growth (pathway 1; a bivoltine pathway). Larvae of the second category (upper path) enter a summer diapause of variable length (longer early in the season). This sloping reaction norm synchronizes the larvae, and pupal diapause is induced towards the end of the larval stage by the long-daylength peak (pathway 2; a univoltine pathway). Very late larvae (short daylengths experienced by young larvae) enter a larval winter diapause. They may be offspring of the first generation of adults (pathway 3;  $1-1\frac{1}{2}$  generations in a season depending on the stage used for hibernation by the first generation) or of the second generation (pathway 4;  $2-2\frac{1}{2}$  generations). Pathways 1 and 2 are probably typical for southern Sweden, pathways 1 and 3 for England.

by individuals at two developmental stages (Nylin *et al.*, 1989). First, photoperiods during the early larval stages determine whether larval diapause follows (summer or winter diapause). Second, photoperiods during late larval stages (arrowheads in Fig. 2) determine whether pupal winter diapause follows. In the following attempts to interpret the life-cycle regulation, particular attention is given to natural photoperiods when these larval stages occur in the field (cf. Fig. 8).

In all three populations there was direct development through both the larval and pupal stages at the longest daylengths, down to the critical photoperiods (mentioned in the preceding section). This suggests that a long day is interpreted by both young and old larvae as indicating summer conditions, with time enough left of the season for an additional generation to reach the pupal stage or at least the third larval instar (larvae of other instars do not survive winter; Shreeve, 1986).

In a range of slightly shorter daylengths, long larval development times

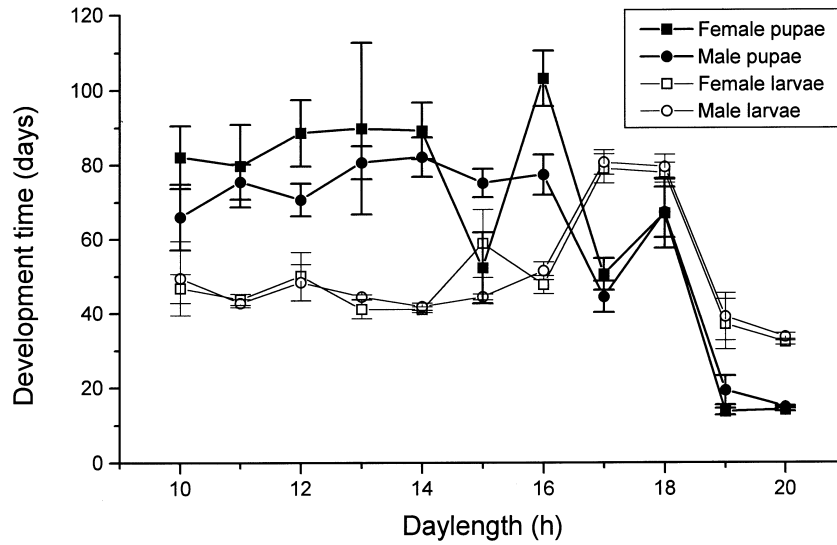


Figure 3. Larval and pupal development time (mean  $\pm$  SE) for the central Swedish population of *P. aegeria* at different daylengths and 17°C. Total  $n=236$ .

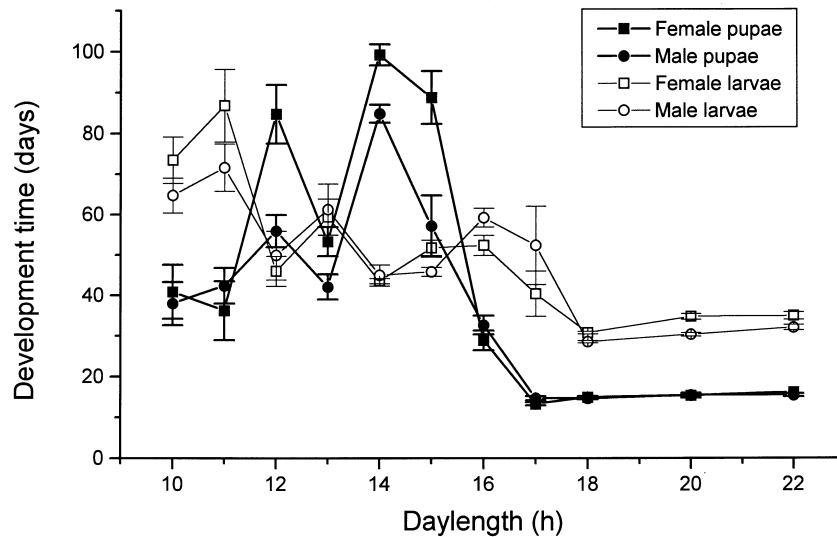


Figure 4. Larval and pupal development time (mean  $\pm$  SE) for the south Swedish population of *P. aegeria* at different daylengths and 17°C. Total  $n=308$ .

were shown by some individuals (Fig. 2). This corresponds to the increase in mean larval development times seen in Figures 3–5. We interpret this as a larval summer diapause, induced when there is ‘surplus’ time because additional generations are not possible. In Figures 3–5 only mean development time is shown, but the response to photoperiod was actually bimodal (Fig. 2), so that some individuals displayed long larval development times when others developed directly (Wiklund *et al.*, 1983; Nylin *et al.*, 1989). This was seen at 19 h daylength in the population from central Sweden, at 17 h

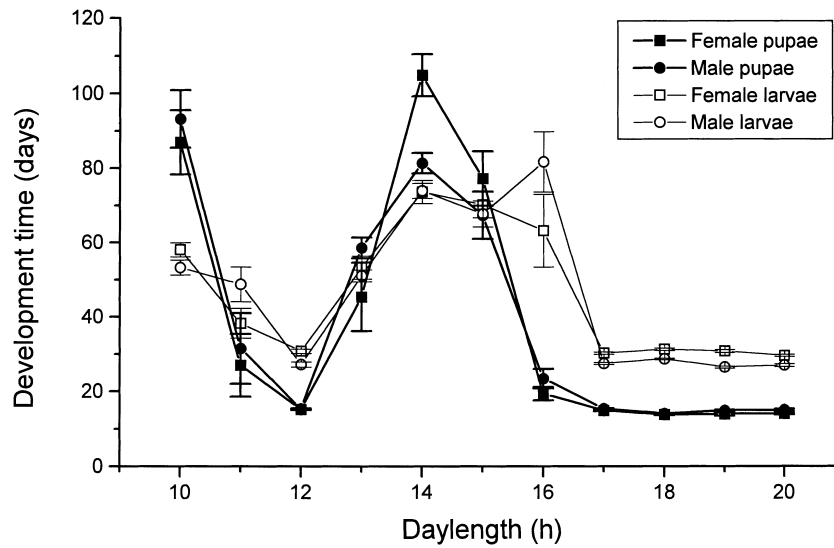


Figure 5. Larval and pupal development time (mean  $\pm$  SE) for the English population of *P. aegeria* at different daylengths and 17°C. Total  $n=277$ .

daylength in the population from south Sweden and at 16 h in the English population.

Evidently, larval summer diapause was present (in at least some individuals) at daylengths of 19–17 h in the central Swedish population (Fig. 3), at daylengths of 17–16 h in the south Swedish population (Fig. 4), and at daylengths of 16–13 h in the English population (Fig. 5). Pupal winter diapause was induced by a range of even shorter daylengths (Figs 2–5), and in all three populations there was evidence of larval winter diapause in the range of shortest daylengths (Fig. 2; not evident from Figs 3–5). Daylengths in this range are probably interpreted by larvae as dates late in the season. Individuals that would not have time enough to reach the pupal stage before winter may instead diapause as third instar larvae. This interpretation is supported by the fact that the same individuals invariably displayed the shortest pupal durations recorded at each daylength, an indication that pupal diapause was averted by a history of larval winter diapause (cf. Nylin *et al.*, 1989).

In central Sweden, induction of pupal diapause peaked at 18 h but also at 16 h and shorter daylengths (Fig. 3). In both sexes a decline in pupal development times was found at 17 h daylength, where pupal durations were intermediate between those displayed by directly developing and diapausing individuals, respectively (range: 29–78 days). A similar unexpected result from the English population was that in the laboratory using constant daylengths, direct development was induced by daylengths longer than 16 h but also by daylengths around 12 h (Fig. 5). Thus, there are again two induction peaks for pupal diapause (in this case discontinuous). In the south Swedish population we noted a lower mean pupal development time of 13 h daylength, compared to the flanking daylengths of 14 h and 12 h (Fig. 4; Nylin *et al.*, 1989). The similar patterns in the other two northern populations

suggest that the phenomenon should be given more attention. A probable explanation is that the unusual pattern of two induction peaks is related to an unusual aspect of the *P. aegeria* life cycle: the existence of two discrete categories of larvae in summer (directly developing and summer diapausing). Consideration of field phenology (for brevity not included here) suggests that the long-daylength peak may induce pupal diapause in offspring of larvae that have developed directly (pathway 1 in Fig. 2), whereas the short-day peak induces pupal diapause in individuals with a history of larval summer diapause, and fewer generations in the season (pathway 2 in Fig. 2).

The lack of strong pupal diapause at intermediate daylengths may have the function of permitting direct development in the pupa late in the season and hibernation by offspring as larvae (and an additional half generation; pathway 4 in Fig. 2).

The constant daylengths used in the experiments do not occur under natural conditions: this has three consequences. First, a given constant daylength may be ambiguous and correspond to a date before or after summer solstice, and this consideration is likely to be most important in more southern populations, where the first generation wholly or partly occurs before summer solstice. Second, young and old larvae are likely to differ in how they interpret and respond to a given constant daylength, because they occur at different dates in the season. Third, although larval and pupal development times are shown in the same graph (Figs 2–7), variation in larval development time among photoperiods is mostly a result of differences in growth and development induced in young larvae, whereas variation in pupal development time results from differences which are probably induced late in larval development. Consequently, a larval and a pupal development time which is induced by a given daylength should not be viewed as a correlated set of life history traits associated with this daylength: daylengths may have changed by several hours in the field before the late larval stages are reached when pupal development times are induced.

In the field, an individual which experiences a relatively long daylength as a young larva, and goes through a larval summer diapause in response to this daylength, is likely to go through pupal winter diapause as well, even though this long daylength averts pupal diapause in the laboratory. This is because by the time this individual reaches the late larval stages, natural daylengths have fallen to the range of short daylengths that induce pupal diapause (pathway 2 in Fig. 2).

#### *Quantitative regulation of development time*

##### *Central Sweden*

Earlier results from the south Swedish population (Nylin *et al.*, 1989) indicate that in addition to the qualitative 'choices' between pathways (i.e. to diapause or not in a given developmental stage and season) there is present in *P. aegeria* a lower-level life-cycle regulation where development times are fine-tuned in a quantitative response to photoperiod. Categories of regulation at these two levels merge with each other; at many photoperiods there are no sharply defined categories of diapausing or directly developing individuals.

Results from central Sweden (Figs 3, 8) show some similarities in these respects. Going from daylengths of 20 h to 19 h, directly developing males displayed shorter larval and pupal durations in response to the shorter daylength (Fig. 8;  $n = 22$ ; larvae:  $33.0 \pm 0.8$  days vs.  $25.6 \pm 0.6$  days;  $t$ -test,  $P < 0.001$ ; pupae:  $15.2 \pm 0.2$  days vs.  $13.9 \pm 0.3$  days;  $t$ -test,  $P < 0.001$ ). These tendencies were also present in female larvae, but not in pupae (Fig. 8;  $n = 17$ ; larvae:  $32.3 \pm 0.8$  days vs.  $27.9 \pm 0.6$  days;  $t$ -test,  $P < 0.001$ ; pupae:  $14.1 \pm 0.4$  days vs.  $14.1 \pm 0.2$  days,  $P = 0.97$ ). The statistical significance of these results is dependent on the criterion used to judge whether an individual diapaused or not (individuals with larval durations in excess of 40 days were judged to be diapausing, and excluded from comparisons of both larval and pupal development times) and they should be treated with caution.

No other graded responses are evident from the results, except possibly for a gradual decrease in larval development time going from 18 h to 14 h, representing progressively later dates and less 'surplus' time for the single generation (Fig. 3).

#### *South Sweden*

This population has been described earlier (Nylin *et al.*, 1989) and here we point out some features similar to the results from central Sweden. In the range of long daylengths where individuals developed directly, there is a decrease in both larval and pupal development times in response to shorter daylengths (Fig. 8; this pattern is not as clear from Fig. 4, where larvae which entered summer diapause at 17 h were included in the means). The decreases in larval and pupal durations are statistically significant for both sexes and both developmental stages (Nylin *et al.*, 1989).

In a range of shorter daylengths, a gradual decrease in mean larval development times (of individuals which were presumably headed for pupal winter diapause) was found in progressively shorter daylengths from 17 h (where they first occurred) to 14 h daylength (Fig. 4). For both patterns we suggest the interpretation that shorter daylengths indicate later dates and less time remaining of the favourable season.

#### *England*

Interestingly enough, the reaction norm of the English population is different to that of the two Swedish populations, in the range of long daylengths where direct development occur (Figs 5, 8). Instead of a decrease in larval and pupal durations in shorter daylengths, durations tend to increase going from 20 h to 17 h (male larvae:  $P < 0.05$ ; female larvae:  $P < 0.05$ ; male pupae:  $P = 0.69$ , n.s.; female pupae:  $P < 0.05$ ; males,  $n = 55$ ; females,  $n = 44$ ; all regressions negative). It seems probable that this is because to larvae of this population a long daylength does not necessarily indicate an early date. With directly developing individuals in a range of relatively long daylengths, the opposite relationship or, alternatively, no relationship between photoperiod and date in the season appears to be closer to the truth (cf. Fig. 8). Offspring of the first flight experience increasing daylengths as larvae, and offspring of the second flight experience photoperiods at and immediately

after summer solstice, when daylengths are at their maximum and slowly decreasing.

A second gradual response is the gradual decline in mean larval development time in the range 16 h–12 h (Fig. 5). This quantitative pattern is probably analogous to the similar patterns in the central and south Swedish populations, namely, a way of spending 'surplus' time in the larval stage. In this short-daylength range, a relatively shorter day indicates a relatively later date and less time left to develop all the way to a stage suitable for hibernation. The depression in pupal diapause induction at daylengths of about 12 h can be given the adaptive explanation suggested above, i.e. avoidance of pupal diapause when an additional half generation is possible. There is a progression of such points representing low intensity of pupal diapause, going from the high-latitude central Swedish population, where spring is late and daylengths long, over the south Swedish and English populations to even the Spanish: 17 h, 13 h, 12 h and 11 h (Figs 3–6).

The sloping reaction norms described above also seem to synchronize larvae so they experience relevant daylengths at the time of the second pathway 'decision' (Fig. 2). In the English population, longer larval development times are induced by longer daylengths in the range 12–14 h (Fig. 5), which means that early and late individuals in a given generation may all avert pupal diapause in a similar way via the depression in pupal diapause induction or, for offspring from other flights, enter pupal diapause via the short-day peak. This function is related to the earlier interpretation (Nylin *et al.*, 1989) of larval summer diapause as an adaptation to spend 'surplus' time in a developmental stage well adapted for this purpose.

#### *Spain and Madeira*

As noted above, there is no indication of diapause in butterflies from Spain or Madeira under the investigated conditions (Figs 1, 6, 7). In the Madrid area of Spain actual daylengths vary from about 10.5 h to 16 h, including civil twilight, and on Madeira from about 11 h to 15.5 h. In other words, the daylengths used in the investigations include all that could be relevant for diapause induction in the field. Possibly, however, short daylengths could induce winter diapause in at least Spanish individuals, when combined with lower temperatures.

In the Spanish population, mean larval and pupal durations vary only slightly between daylengths, and there are no trends (Fig. 6). Possibly, the short pupal development time in 11 h is related to the declines in pupal diapause induction found in the northern populations.

The reaction norm of the Madeiran population (Fig. 7) shows differences to that of the Spanish population (Fig. 6). Both larval and pupal development times increase slightly with decreasing daylengths in the range of daylengths relevant in the field (11 h–16 h), but the significance of this pattern, if any, is beyond interpretation at present. Possibly, there has not been time enough for selection to adapt the Madeiran population to local conditions since the colonization in the 1970s. However, the population has passed through 80–100 generations in this time, which means that local adaptation is at least possible for life history traits, since they are often strongly related to fitness (see Nylin *et al.*, 1993, for an example).

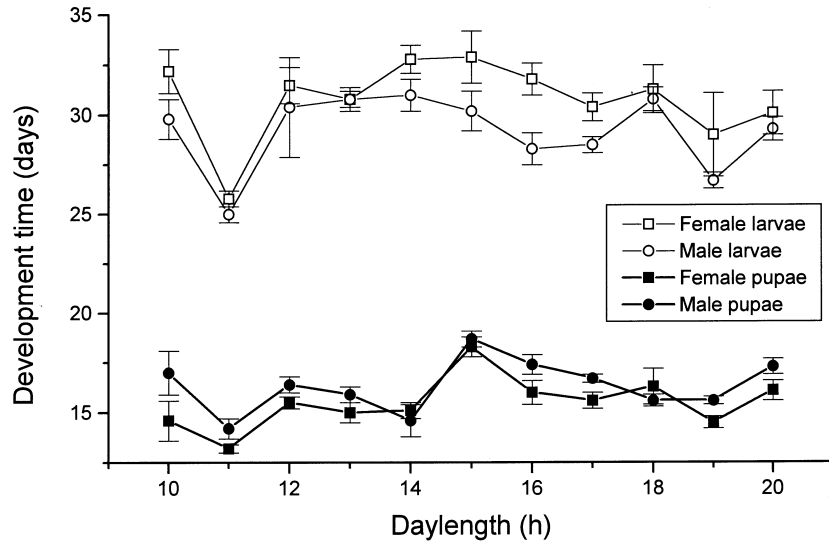


Figure 6. Larval and pupal development time (mean  $\pm$  SE) for the Spanish population of *P. aegeria* at different daylengths and 17°C. Total  $n=188$ .

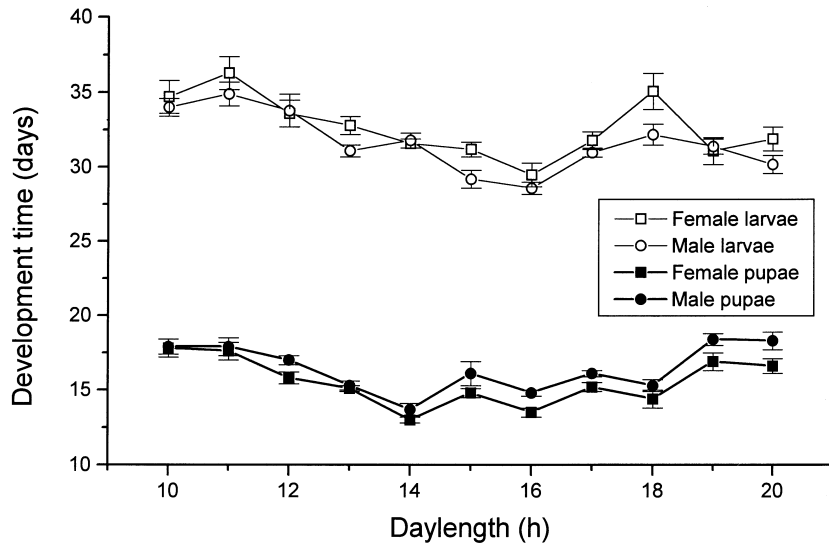


Figure 7. Larval and pupal development time (mean  $\pm$  SE) for the Madeiran population of *P. aegeria* at different daylengths and 17°C. Total  $n=238$ .

## DISCUSSION

Our results confirm that it is possible to predict reaction norms for how individuals of different populations should respond to photoperiodic information. This is true for both life cycle regulation and life history plasticity. In the Introduction, we outlined three predictions which were all met:

(1) The lack of sharp diapause thresholds in the two southern populations was as predicted, but the total lack of diapause nevertheless was unexpected. Possibly, lower temperatures in combination with short daylengths are necessary to induce complete diapause. As mentioned above, the mortality seen in the experiment on the Spanish population could also possibly represent evidence of diapause.

(2) The critical daylength for diapause induction evidently does follow a pattern reflecting the longer days in the north (cf. e.g. Danilevski, 1965; Bradshaw, 1976). There is a similar latitudinal trend in low points for pupal diapause, presumably reflecting a mechanism to prevent pupal diapause when an additional half generation is possible.

(3) Moreover, reaction norms for life-history plasticity *within* developmental pathways also seem to follow predictable patterns. Among directly developing individuals, development time is shorter in shorter daylengths in the two Swedish populations, where this is a reasonably good indicator that it is becoming late in the season. There is no such pattern in the English population or in the two populations of the southern subspecies. Figure 8 reveals that even in the south Swedish population, photoperiodic information may be ambiguous. This could be the reason why there seems to be genetic (or possibly maternal) variation in the shape of reaction norms in this population (K. Gotthard, S. Nylin and C. Wiklund, unpublished data). There may be no single optimal reaction norm for this population but rather an evolutionarily stable mix of reaction norms with equal fitness. Alternatively, the current mix is not stable but rather under selection varying from year to year, resulting in a proportion of individuals with suboptimal reaction norms.

There were also unexpected results, such as the two peaks for induction of pupal diapause which are apparently present. We think it possible to give plausible adaptive *post hoc* explanation for these features of life-cycle regulation and life-history plasticity. For a full understanding, replicates and detailed investigations on each population are necessary, especially concerning phenology and the potentially very important effects of interactions with temperature. The life cycle of *P. aegeria* is unusually complex, and the fact that successful predictions or at least an adaptive understanding seem possible even in this case is encouraging.

## ACKNOWLEDGEMENTS

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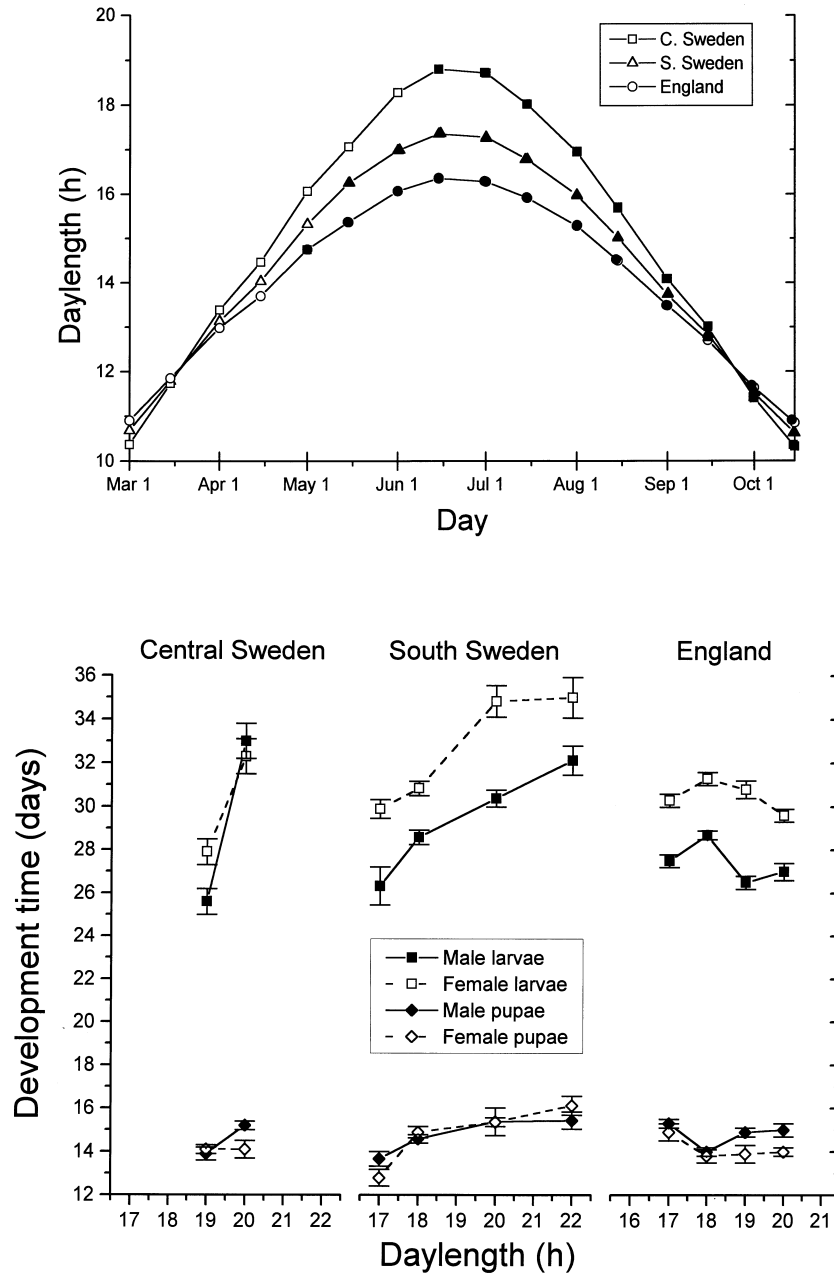


Figure 8. (Top) Natural variation in daylength (excluding twilight) at the source areas for the three studied populations of the northern subspecies, *P. aegeria tircis*. Solid symbols show the part of the summer when the stages sensitive to photoperiod (larvae) are likely to be present. (Bottom) Larval and pupal development time (mean  $\pm$  SE) in response to photoperiod (17°C) in the three populations. Only directly developing individuals included.

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