Biological Journal of the Linnean Society (1989), *38:* 155–171. With 8 figures

Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyrinae)

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Received 26 October 1988, accepted for publication 20 March 1989

Regulation of growth and development by photoperiod was studied in a population of the speckled wood butterfly, *Pararge aegeria* L. (Lepidoptera:Satyrinae), from southern Sweden. Individuals were reared in a range of photoperiodic regimes (9L to 22L) and temperatures (13°C to 21°C). Plasticity was found for important life-history traits—generation time, growth rate and final weight—and seasonal regulation of development in response to photoperiod was found to occur at two levels. *Pararge aegeria* hibernates as a third instar larva or in the pupal stage, entering one of four major developmental pathways in response to photoperiod: (1) direct development in both the larval and pupal stages, (2) pupal winter diapause with or (3) without a preceding larval summer diapause, or (4) larval winter diapause. In addition to this high-level regulation of individual development, larval growth rate and pupal development rate also appear to be finely regulated by photoperiod within each major pathway. As photoperiods decreased from 22 h to 17 h at 17°C, growth rate among directly developing larvae increased progressively, as was the case for larvae developing according to a univoltine life cycle from 17 h to 14 h. At two photoperiods, 13 h and 16 h (corresponding to shifts between major pathways), both larval and pupal development were extremely variable with the fastest individuals developing directly and the slowest developing with a diapause. This indicates a gradual nature of diapause itself, suggesting that the two levels may not be fundamentally different.

KEY WORDS:—Seasonality – diapause – life history – photoperiod – phenotypic plasticity.

CONTENTS

INTRODUCTION

The speckled wood butterfly, *Pararge aegeria*, has a life cycle which is unusually complex. It regularly hibernates either as a pupa or as a half-grown larva

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(Goddard, 1967; Robertson, 1980a, b; Shreeve, 1986). In addition, a summer diapause (aestivation) in the larval stage is known to occur in Sweden (Wiklund, Persson & Wickman, 1983). Each type of diapause is associated with a different duration of the larval or pupal stage, as well as with different growth rates at a given time of the year. Accordingly, individuals have to make a complex 'choice' between different diapause and developmental strategies, using environmental cues that signal the time of the year. There will be strong selection against any individuals that fail to correctly identify the time of the season and, as a result of this, develop according to a life cycle which is inappropriate at that time. Hence, only seasonal cues which can tell the date with great exactness can be expected to be used by *P. aegeria*.

Photoperiod (together with temperature) is known to be the most commonly used cue in insects in general (Danilevskii, 1965; Beck, 1980; Saunders, 1982). It constitutes a 'noise-free' signal that can act as a token of forthcoming conditions (Lees, 1955). In cases when photoperiod is a reliable cue to predict future conditions it can be expected to become coupled to seasonal variation in phenotype (Bradshaw, 1973; Shapiro, 1976). We here present results from a study on seasonal plasticity in *P. aegeria*. We show that individuals are able to regulate growth and development to an unexpected degree in response to photoperiod. The results may serve to point out the potential power of phenotypic plasticity as a means for an organism to adjust to a seasonally variable environment, as well as the importance of considering seasonality when modelling life histories.

MATERIAL AND METHODS

Gravid females of *P. aegeria* were collected at Ransvik in southern Sweden (56°N), a locality in which the butterfly is bivoltine and adults of the first generation fly in May–June and those of the second generation fly in August–September. After oviposition in the laboratory, offspring from all females was divided among different photoperiodic regimes.

Larvae were kept individually in transparent plastic jars in which the host plant *Poa annua* was cultured in ample supply. Four experimental series were run. (1) The effects of photoperiod on growth and development were tested by rearing larvae (originating from twenty-four females collected in 1986) in environmental chambers at a temperature of 17°C and in the following photoperiodic regimes (only cycles of 24 h L/D were used): 22L, 20L, 18L, 17L, 16L, 15L, 14L, 13L, 12L, 11L, 10L and 9L. 17°C was chosen as an approximation of mean temperatures in the field during larval development. The generation time of directly developing individuals bred in the laboratory at this temperature is similar to that in the field (50–60 days). (2) To investigate the shifts between development pathways more closely larvae were reared at 17°C in 17L, 16.5L, 16L, 15.5L, 15L, 14.5L, 14L and 13.5L. (3) In 16.5L at 17°C a portion of the larvae were moved to 20L and another portion to 15L in the third instar, to test how changes in photoperiod (from a value, 16.5L, which had earlier been found to be critical for diapause determination) affect development. (4) The effects of temperature were tested in all combinations of 13°C, 17°C and 21°C with the photoperiods 20L and 15L, made in two replicates. Experiments 3 and 4 were made with stock from ten females collected

in 1987, and experiment 2 with larvae originating from four females captured in 1988.

The duration of the larval and pupal stages were noted for each individual. On the day after pupation, pupae were sexed and weighed. To calculate growth rates and investigate how growth rates changed during individual development larvae were also individually weighed every seven days in 22L, 17L and 12L at 17°C (experiment 1) and every three days in experiment 2 and one replicate of the temperature experiment (4). Growth rates were calculated according to the formula:

$$\log r = (\log w_1 - \log w_0)/d$$

where r is the daily growth rate, w_0 and w_1 initial and final weights, respectively, in each time interval, and d the number of days between measurements.

GENERAL OBSERVATIONS

The durations of the larval and pupal stages were strongly dependent on photoperiod, as summarized in Figs 1 & 2. The duration of each stage varied between photoperiods in two ways: (a) large, qualitative shifts at certain daylengths that were critical for diapause determination and (b) smaller, quantitative shifts in between critical daylengths.

A large amount of individual variation showed up in the results (e.g. Fig. 1). Moreover, in some cases the variation was continuous, so that individuals could not easily be separated into different classes. This variation to some degree complicates interpretation but it is also an important characteristic of the results. The individual variation is due both to differences in genotype and to differences in the microhabitat experienced by the larvae. In Fig. 1 it is possible to compare the amount of such variation with the variation between experimental treatments. It can be concluded that most of the variation is due to the experimental conditions and thus is phenotypic rather than genotypic. When pupal duration is plotted against larval duration, as in Fig. 1, it can also be seen that individual variation in one of these traits is not random in respect to the other trait. Instead, they are correlated in ways which will be examined in more detail below.

DIAPAUSE DETERMINATION

The results reported in the following two sections refer to the main experiment (1). Considering first long-day conditions at 17°C, no pupal diapause occurred in photoperiods between 22L and 17L (corresponding to early summer) as is shown by the short time spent in the pupal stage (10–20 days; Figs 1 & 2). Larvae also developed directly, without diapause, under long-day conditions (Figs 1 & 2). Hence, under long-day conditions in the field a second brood will be produced the same season (cf. Table 1).

However, in 17L there were two distinct classes of individuals. A proportion of the larvae (62%) did develop directly, but the remainder spent a considerably longer time in the larval stage (Figs 1 & 2). Accordingly, some half-grown larvae entered a summer diapause before completing their development.

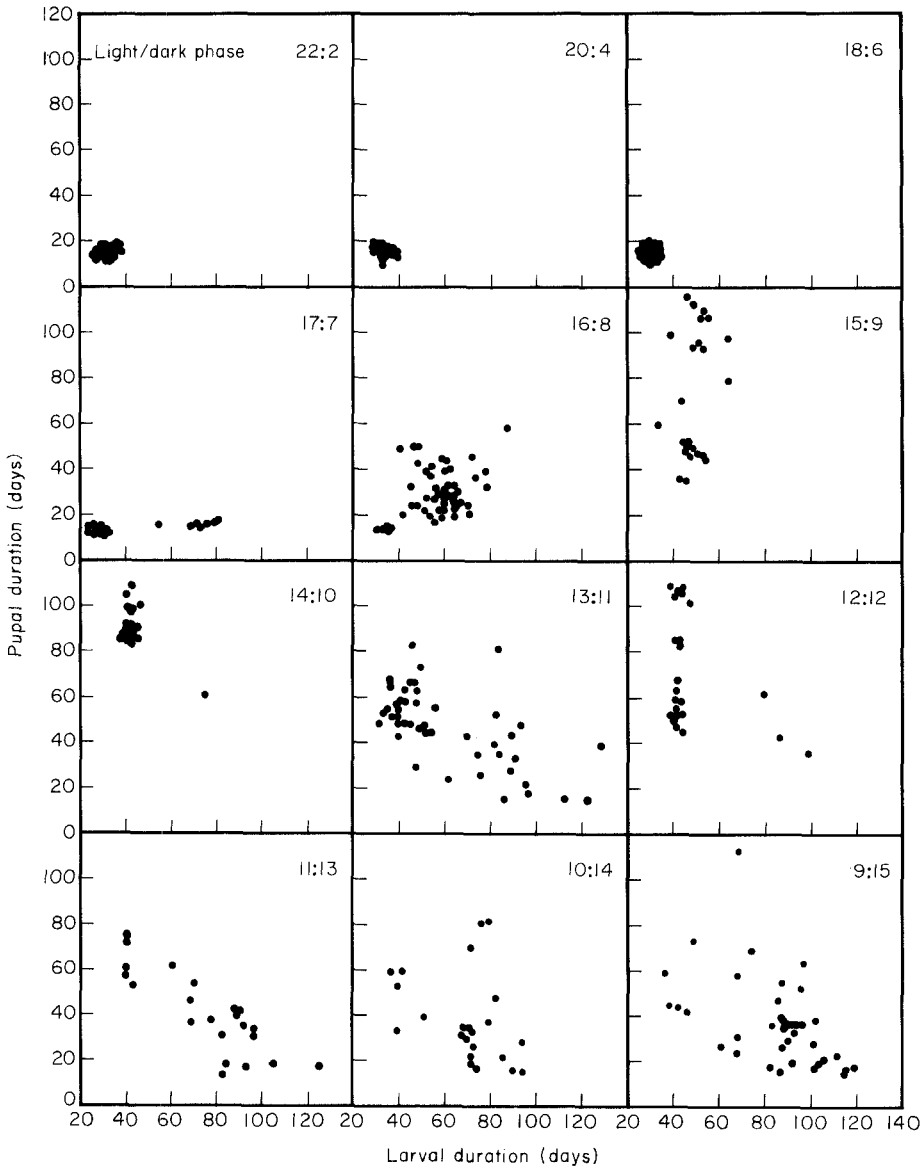

Figure 1. Duration of the larval stage *vs.* duration of the pupal stage for individuals of *Pararge aegeria* in a range of photoperiods at 17°C.

In shorter daylengths (<17L, corresponding to late summer or early autumn) pupal development was generally retarded, indicating pupal diapause (Figs 1 & 2). This was most pronounced in intermediate photoperiods, between 15L and 12L. The duration of the pupal stage varied greatly between individuals (Fig. 1), and only in 14L did all individuals show a strong retardation of pupal development. In 16L the tendency for pupal diapause was less evident, and the durations of both the larval and pupal stages were very variable (Fig. 1). However, there was a positive correlation between the durations of the larval and pupal stages (Fig. 1; $r=0.383$, $N=49$. $P<0.01$, sexes pooled), indicating a

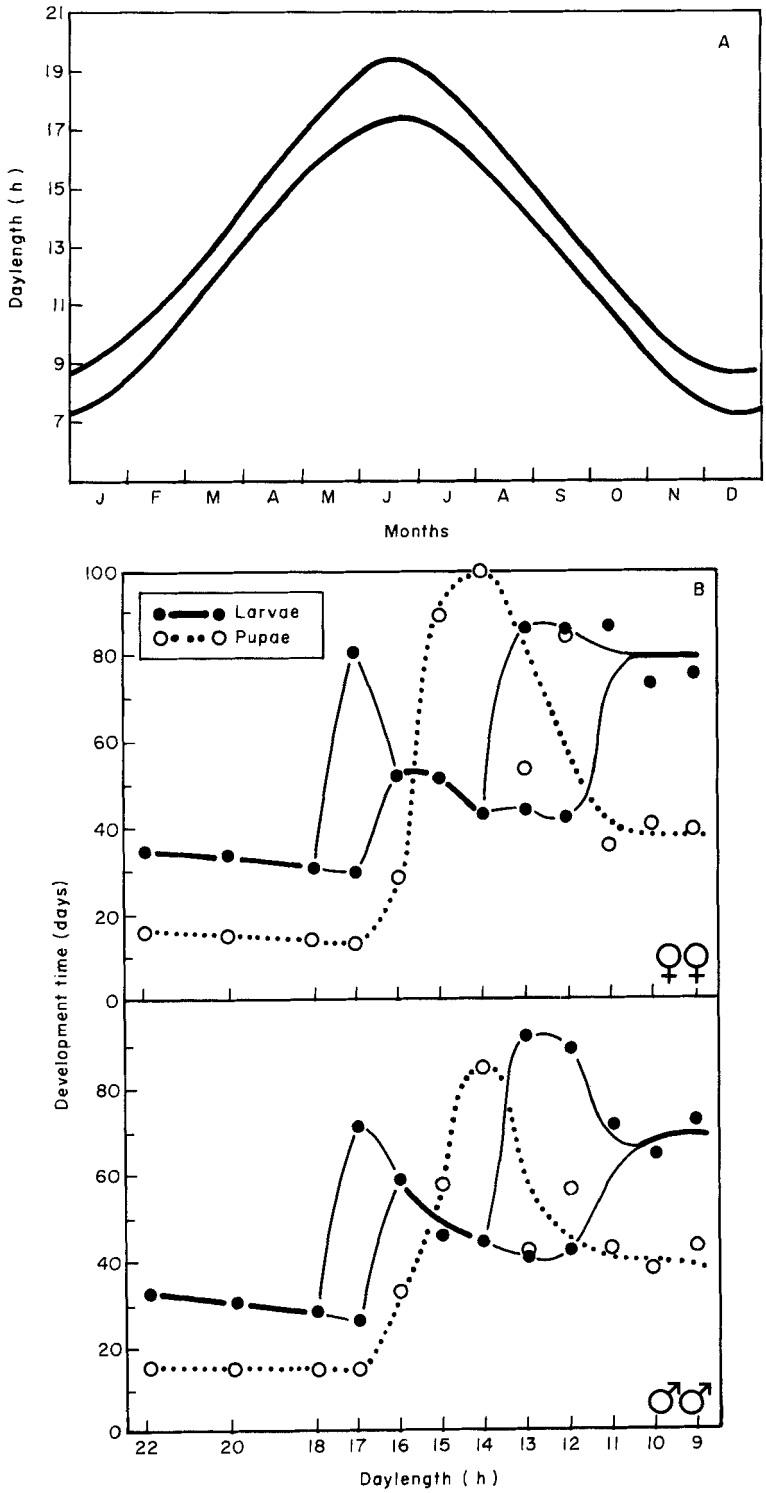

Figure 2. A, Annual variation in daylength (lower curve) and daylength plus civil twilight (upper curve) in southern Sweden (56°N). B, Larval and pupal durations of males and females of *Pararge aegeria* at 17°C and daylengths from 22L down to 9L. There are two critical daylengths for induction of larval diapause; 17L (for summer diapause) and 12–13L (for winter diapause). The critical daylength for pupal diapause is 15–16L, and at daylengths shorter than 12L the tendency for pupal diapause gradually disappears. Two classes of individuals are recognized in 17L (where larval summer diapause occurs) and in 12–13L (larval winter diapause). In the latter case the classes are not distinct.

TABLE 1. A schematic illustration of the four major developmental pathways of Swedish *Pararge aegeria* in response to time of season and daylength

		Development	
Daylength (h)	Season	Larva	Pupa
≥17	Early summer	Direct	Direct
16–17	Late summer	Diapause (summer)	Diapause (winter)
14–16	Early autumn	Direct	Diapause (winter)
≤13	Late autumn	Diapause (winter)	Direct

tendency for larvae that had diapaused in the summer also to enter pupal diapause. Conversely, directly developing larvae did not diapause in the pupal stage. However, most individuals spent intermediate times in both stages (Fig. 1). Thus, the typical larval duration times in 16L were intermediate between those recorded for the two classes of individuals (directly developing and aestivating) in 17L.

A new class of individuals with retarded larval development, presumably representing hibernation in the larval stage, first appeared in 13L. Under these conditions (in contrast to the situation in 16L) there was a negative correlation between the durations of the larval and pupal stages (Fig. 1; $r=-0.618$, $N=47$, $P<0.001$, sexes pooled). This shows that individual larvae developed comparatively fast with a following pupal diapause or slowly (larval hibernation diapause) without pupal diapause. No distinct classes of individuals could be distinguished, but rather a continuous variation in the duration of the larval and pupal stages (Fig. 1; in Fig. 2 an attempt has been made to distinguish between hibernating and non-hibernating larvae in photoperiods where the classes were most evident). However, the tendency for larval diapause increased in shorter daylengths, concomitantly with a decrease in the tendency for pupal diapause. Thus, the mean duration of the larval stage increased with shorter daylengths from 14L to 9L (Fig. 1; males: $r=-0.439$, $N=99$, $P<0.001$; females: $r=-0.613$, $N=74$, $P<0.001$), while the duration of the pupal stage decreased (Fig. 1; males: $r=0.453$, $N=99$, $P<0.001$; females: $r=0.551$, $N=74$, $P<0.001$).

QUANTITATIVE RESPONSES TO PHOTOPERIOD

Under long-day conditions (22L-17L) at 17°C, the duration of the larval stage in directly developing individuals was progressively shorter in shorter daylengths (Fig. 3; males: $r=0.655$, $N=54$, $P<0.001$; females: $r=0.711$, $N=50$, $P<0.001$). This can be interpreted to reflect the fact that progressively shorter daylengths (after summer solstice) indicate a later date and consequently less time in which to complete a bivoltine life cycle. A shorter duration of the larval stage could be achieved either by higher growth rates in shorter daylengths or by individuals ceasing to grow at a lower weight. The first mechanism is evidently most important, as is shown by the higher growth rates of directly developing larvae in 17L than in 22L (Table 2; t-test, $P<0.01$ for both males and females) and by the fact that in this range pupal weights were not significantly correlated with daylength (mean pupal weights were in fact similar over the whole range of daylengths).

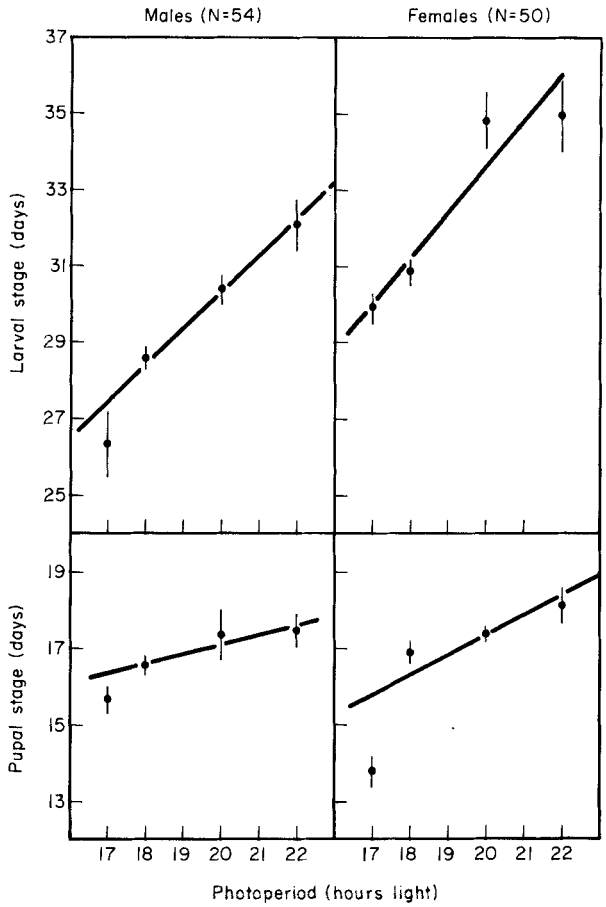

Figure 3. Duration of the larval and pupal stages of males and females of *Pararge aegeria* in response to photoperiods from 17L to 22L where development is direct (resulting in a bivoltine life cycle; in 17L only directly developing individuals are included). Vertical bars show S.E. on means. The regressions are significant in all cases ($P<0.001$, except male pupae; $P<0.05$).

Similarly, the duration of the pupal stage was progressively shorter in shorter daylengths in the same range of photoperiods (22L–17L; Fig. 3; males: $r=0.289$ $N=54$, $P<0.05$; females: $r=0.622$, $N=50$, $P<0.001$), which also is in accordance with the interpretation that short generation times in late individuals have been selected for in the population.

TABLE 2. Relative growth rates of larvae (±S.E.) in three photoperiods at 17°C. Only directly developing larvae are included

Light period (h)	Growth rate (mg/mg · day)			
	Males	N	Females	N
12	1.194±0.002	9	1.198±0.002	11
17	1.318±0.010	3	1.290±0.009	10
22	1.255±0.007	16	1.243±0.009	8

As mentioned above, in 17L a proportion of the larvae entered summer diapause. These individuals spent long times in the larval stage. Directly developing larvae at the same photoperiod, on the other hand, had the shortest recorded durations of the larval stage in any photoperiod and also the highest growth rates (Figs 1 & 2, Table 2). The pupae from these fast, directly developing, larvae were also lighter than those from aestivating individuals in 17L (males: 134.2 ± 4.4 mg, $N=3$ *vs.* 156.0 ± 4.4 mg, $N=4$, t-test: $P<0.05$; females: 163.6 ± 4.4 mg, $N=10$ *vs.* 179.7 ± 20.5 mg, $N=3$, n.s.), presumably representing a cost of fast development.

Following the longer mean durations of the larval stage in 17L and 16L due to summer diapause (Figs 1 & 2), the duration of the larval stage again was progressively shorter in shorter daylengths in most individuals in intermediate daylengths in the range 17L to 14L (Fig. 2; $r=0.427$, $N=91$, $P<0.001$, sexes pooled). Interestingly enough, in the same range of photoperiods, the duration of the pupal stage was instead progressively longer in shorter daylengths (Fig. 2; $r=-0.823$, $N=91$, $P<0.001$, sexes pooled), reflecting that the occurrence of pupal diapause was approaching its maximum at 14L. Thus, the duration of the larval stage, but not the pupal stage, was shorter at photoperiods corresponding to later dates. These results support the interpretation that development in this range of photoperiods in the field is according to a univoltine life cycle with pupal diapause.

Furthermore, in the range of photoperiods between 16L and 9L the duration of the larval stage was invariably longer than in the range 22L to 18L (Figs 1 & 2). As mean pupal weights were similar in all daylengths, this must be due to higher growth rates being induced in long days (where development is according to a bivoltine life cycle). This is also supported by a comparison of the recorded relative growth rates (Table 2). Directly developing larvae in 22L and 17L grew faster than directly developing larvae in 12L (t-test, $P<0.001$ for both males and females, both comparisons).

INDIVIDUAL GROWTH PATTERNS

A closer investigation of individual larval growth (using new stock) confirmed the results reported above and clarified how the shifts between developmental pathways are effectuated (Fig. 4). In this experiment the largest proportion of individuals aestivated in 16.5L, as can be seen from the fact that growth of most individuals was retarded in the third instar. In shorter daylengths growth was faster in the third instar but instead slow in the fourth. This seems to be the main reason why development times are longer in this range of daylengths than in long days. In very short days (13.5L) hibernating larvae occurred, and it can be seen that the diapausing stage again is the third instar, whereas the slow growth in the fourth instar gradually disappears in short days (Fig. 4).

RESPONSES TO CHANGES IN PHOTOPERIOD

The effects of moving larvae to another photoperiod in the third instar were striking. Individuals that developed in a constant photoperiod of 16.5L at 17°C

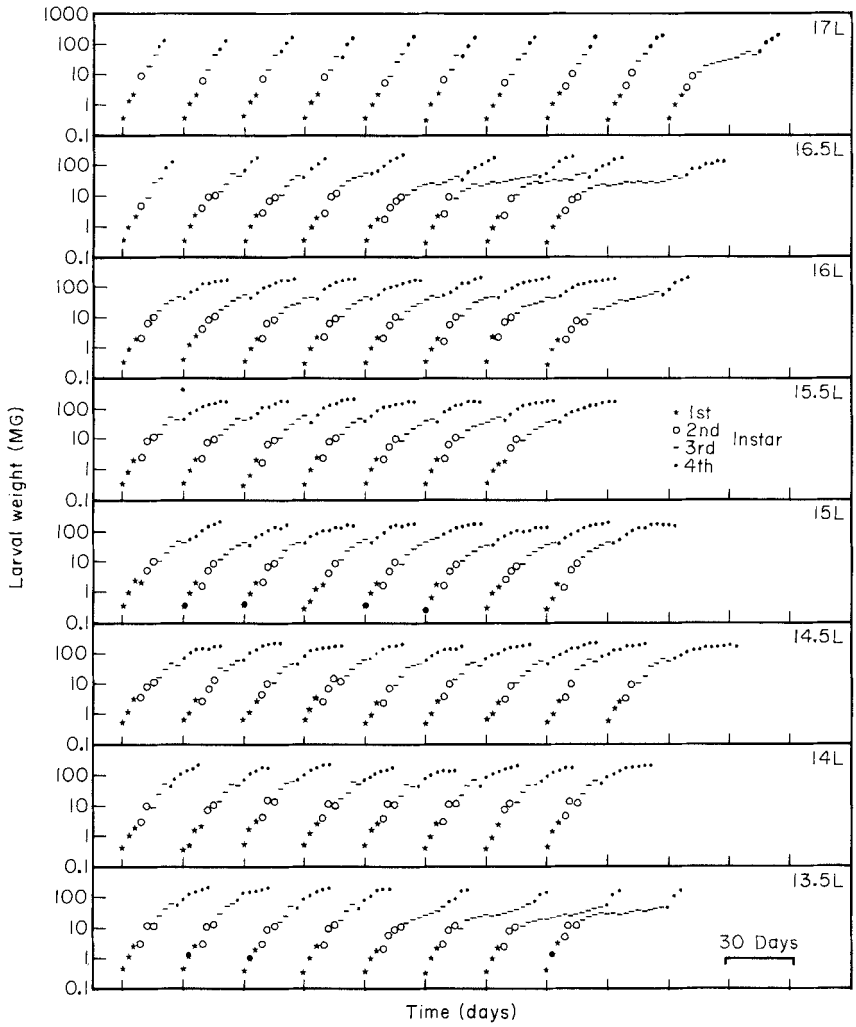

Figure 4. Growth of individual larvae of *Pararge aegeria* at 17°C in response to photoperiod. Different larval instars are shown with symbols.

exhibited a very variable response, similar to the result in 16L in the main experiment even though new stock was used (Fig. 5A, cf. Fig. 1). When growth of individual larvae is investigated, it can be seen that growth in the slower larvae levels off in the third instar (Fig. 6) which indicates that they were aestivating (cf. Fig. 4). Transferring larvae to either 15L or 20L had a strong synchronizing effect (Fig. 5A). However, larval and pupal development times centred around very different values depending on the photoperiod during the late instars. When larvae were moved to a photoperiod of 15L they continued to develop relatively slowly in the final larval stages (Fig. 5B) and thereafter spent long times in the pupal stage (Fig. 5A), a situation similar to that in stationary daylengths of 15L (Figs 1 & 4). When transfer was to 20L larval development was fast in the late instars and pupae also developed directly (Fig. 5A, B).

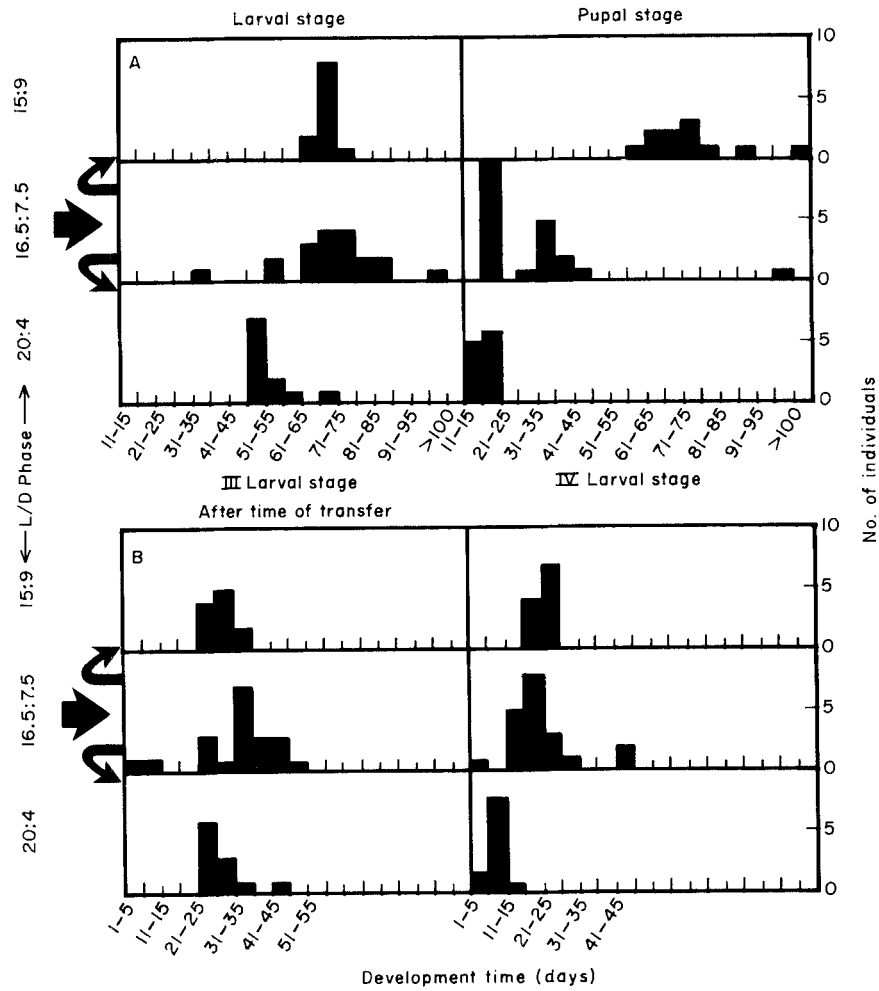

Figure 5. A, Durations of the larval and pupal stages of *Pararge aegeria* in 17°C when larvae were kept in 16.5L during their whole development (middle diagram) or transferred in the third instar from this photoperiod to either 15L or 20L. B, The durations of the third (from the day of transfer) and fourth larval instars, respectively, in the same experiment.

EFFECTS OF TEMPERATURE

The effects of temperature were tested at photoperiods 15L and 20L. At 15L the response in the main experiment at 17°C was a very variable pupal development time and a much less variable larval development time (Fig. 1). This outcome was repeated at 13°C, 17°C and 21°C (Fig. 7). In other words, the differences in temperature did not affect the main developmental pathway taken by individuals. Even at 21°C no individuals developed directly in the pupal stage (as was the case at 17°C with stationary photoperiods of 16L; Fig. 1) and even at 13°C only a single individual exhibited the larval hibernation diapause seen at 17°C in 13L and shorter daylengths (Fig. 7, cf. Figs 1, 2 & 4).

Moreover, the increase in temperature shortened the time spent in the pupal stage (Fig. 7; $r = -0.848$, $N = 122$, $P < 0.001$, sexes pooled) but did not

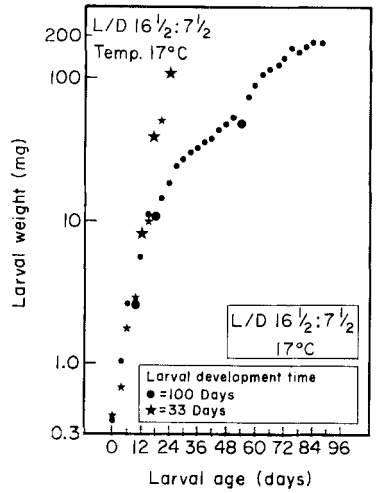

Figure 6. Growth of the fastest (stars) and slowest (dots) individuals of *Pararge aegeria* at a photoperiod of 16.5L in 17°C. Larger symbols show moltings to new instars.

significantly change larval development time (Fig. 7; $r = -0.084$, sexes pooled). A closer analysis of this phenomenon shows that growth was indeed somewhat faster at higher temperatures in the early larval instars, but this was fully compensated for by slower growth in later instars (Fig. 8). Growth at low temperatures resulted in heavier pupae among females ($r = -0.629$, $N = 51$, $P < 0.001$), and perhaps in males ($r = -0.177$, $N = 70$, n.s.).

A photoperiod of 20L resulted in direct development in both the larval and pupal stages at 17°C (Figs 1 & 2), a result that was repeated at 13°C, 17°C and 21°C (Fig. 7). Larval development times were shorter at higher temperatures ($r = -0.944$, $N = 132$, $P < 0.001$, sexes pooled), as were pupal development times ($r = -0.929$, $N = 132$, $P < 0.001$, sexes pooled). The shorter development times

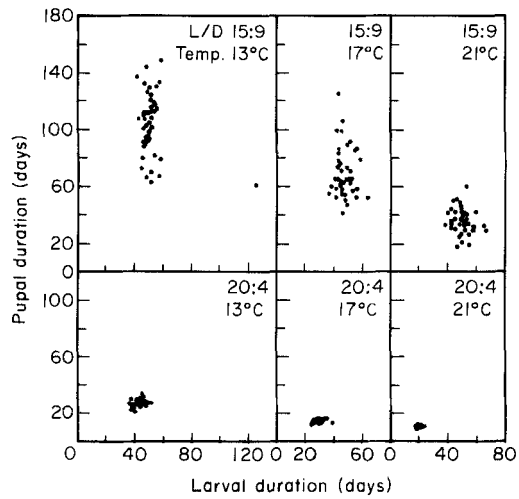

Figure 7. Duration of the larval stage *vs.* duration of the pupal stage for individuals of *Pararge aegeria* in combinations of two photoperiods and three temperatures.

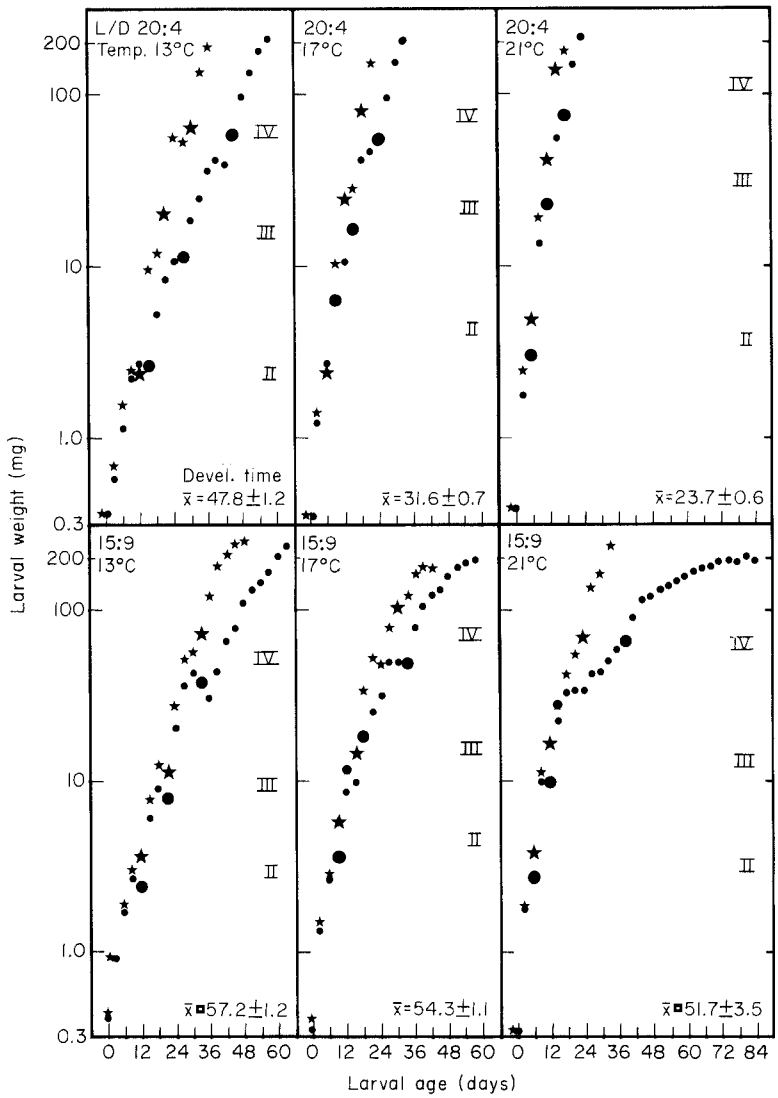

Figure 8. Growth of the fastest (stars) and slowest (dots) larvae of *Pararge aegeria* in combinations of two photoperiods and three temperatures. Larger symbols show moltings to new instars. Mean development times (±S.E.) are shown in the lower right corner of each diagram.

were partly due to lower weights in higher temperatures (males: $r=-0.182$, $N=67$, n.s; females: $r=-0.403$, $N=65$, $P<0.001$) and partly to faster development (Fig. 8).

INTERPRETATION OF THE LIFE CYCLE

Pararge aegeria hibernates either in the pupa or as a half-grown larva (third instar, Shreeve, 1986). A summer diapause also occurs in the larval stage (Wiklund *et al.*, 1983). The life cycle of the population in southern Sweden is summarized in Table 1 and Fig. 2 and the following explanation is proposed.

(1) Very long daylengths (>17L) indicate early summer conditions. No diapause occurs in either the larval or the pupal stage. Development is fast, and a second brood will be produced the same season. Growth rates are dependent on temperature.

(2) Shorter daylengths within the range 22L–17L correspond to a later date. Faster development is therefore induced in shorter daylengths in both the larval and the pupal stages making the second brood possible. In this range, any selective disadvantage associated with faster development is balanced by a greater chance of completing the second brood before winter. These disadvantages include a lower final weight for directly developing larvae in 17L (found also by Wiklund *et al.*, 1983) and at high temperatures in 20L.

(3) When the first brood is late, a sufficient number of days (or daydegrees) may not always remain for completing a second brood. Accordingly, intermediate and short daylengths (<16L) induce a pupal diapause in some, or all, of the individuals.

(4) A pronounced summer diapause in the larval stage is induced in some individuals by intermediate daylengths (17L–16L) resulting in univoltine development. Individuals that develop according to a univoltine life cycle, at daylengths in which many siblings develop according to a bivoltine life cycle, will have considerable surplus time. At 17L all individuals that aestivate do so as larvae, none as pupae. This is in accordance with the interpretation that Swedish satyrines, of which 17 out of 20 species overwinter as larvae, have life-history adaptations for spending long periods in this stage. In the field, individuals that aestivate as larvae hibernate in the pupal stage, but at a constant daylength of 17L in the laboratory none of the aestivating larvae entered pupal diapause. This indicates that the sensitive period for determination of pupal diapause occurs in almost full grown larvae, and accordingly that larvae of *P. aegeria* have *two* sensitive periods for diapause determination; one in young larvae that determines larval (summer or winter) diapause, and one in almost full grown larvae that determines pupal diapause. In the field individuals that enter summer diapause at a daylength of 17L will later experience shorter daylengths as almost full grown larvae (cf. Fig. 2), and will accordingly also enter pupal diapause. Further evidence for the existence of two separate sensitive stages (or perhaps continuous sensitivity) is given by the results of moving third instar larvae from 16.5L to other daylengths (Fig. 5A, B): individuals grew slowly and entered pupal diapause when moved to 15L, but grew fast and developed directly in the pupal stage when moved to 20L.

At 16.5L or 16L development is variable, with some individuals developing directly (i.e. resulting in a bivoltine life cycle), and some individuals entering diapause (resulting in a univoltine life cycle). Most individuals, however, exhibit intermediate development times. The probable explanation is that these daylengths represent a shift between three very different developmental pathways; direct development, or pupal diapause with or without a preceding aestivation in the third instar. The synchronizing effect of moving larvae to other photoperiods (Fig. 5A, B) should be seen in this light. Photoperiods are not stationary in nature and at least in this range of photoperiods an individual seems to need a sequence of two different photoperiods to follow a relevant developmental pathway.

It is interesting to note that there is a positive correlation between larval and

pupal diapause at 16L, so that the strongest tendency for pupal diapause is found in individuals that have exhibited summer diapause in the larval stage. In the field, individuals that have aestivated would have the least time available in which to complete a bivoltine life cycle.

(5) When comparing development times for larvae from 17L to 14L (excluding directly developing individuals at 17L), it again becomes obvious that larvae developing along the same major pathway also have finely tuned adaptations on a lower level, enabling them to respond adaptively to daylength by speeding up their larval development with the progression of autumn. Shorter daylengths indicate that there is a decreasing length of time available for the remaining period of larval development before winter. Larval development accordingly becomes faster, from a pronounced aestivation at 17L–16.5L down to almost direct development at 14L and shorter daylengths. The shortest development times in this range are found at daylengths shorter than 15L, that is at photoperiodic regimes when larval winter diapause is first induced in some other individuals (cf. Figs 2 & 4). This suggests that it is a better option to hibernate as a larva than to incur the costs associated with an even faster development, necessary for completing larval development and pupating before winter. The change in duration of the pupal stage is in accordance with this view, as it increases progressively from direct development at 17L to the most pronounced diapause at 14L, and then decreases again at even shorter daylengths when larval hibernation becomes the major pathway entered by most individuals.

At 15L larval development times are only slightly affected by differences in temperature from 13°C to 21°C. This surprising phenomenon (typical growth rates in insects are correlated with temperature and, as a rule of thumb, double for every 10°C increase; Wigglesworth, 1972) further indicates that larvae have surplus time when they develop through a univoltine life cycle, since it is a result of larvae at high temperatures growing extraordinarily slowly in the final instars. It also shows that photoperiod is used as the principal key to indicate the time of the season and hence to determine diapause response, whereas temperature does not seem to influence diapause response in any way.

(6) Larvae of the second brood will always experience daylengths shorter than 16L, and so these individuals will always diapause in the field. However, there may not always be time for the second brood to reach the pupal stage before winter. Accordingly, very short daylengths ($<$13L) will induce a larval diapause. A pupal diapause will not be expected to occur in nature under these conditions. This should be the reason why the duration of the pupal stage in this range of daylengths (14L–9L) is shorter in shorter daylengths. There is a negative correlation between the durations of the larval and pupal stages in this range, which suggests the possibility that some mechanism causes hibernation diapause to occur in only one of the two possible stages in a given individual. This is contrary to the situation concerning aestivation and pupal diapause, which on the above reasoning would be expected to be coupled; this indeed seems to be the case.

The observed critical daylengths for the induction of larval summer diapause (about 16–17L), pupal diapause (about 15–16L) and larval winter diapause (about 11–13L) agree well with those that (following the above interpretation of the life cycle) can be predicted from natural variation in daylength in southern

Sweden (Fig. 2A) and with the fact that the population under study is normally bivoltine and generally hibernates in the pupal stage, whereas larval aestivation and hibernation is unusual but does occur (Wiklund, unpublished). The maximum daylength at this latitude is about 19L, including civil twilight. The early instars of first brood larvae typically occur close to these maximum daylengths and so neither aestivation nor larval diapause will be induced. The late instars occur in July–August when daylengths are decreasing but are still between 16–18L. Hence, no pupal diapause will normally be induced in the first brood.

The early instars of the second brood can usually be expected to occur in September, when daylengths are about 13–14L. The late instars will occur in October, corresponding to a daylength of about 12L. Thus, most individuals diapause in the pupal stage, larval diapause being uncommon except in cool years.

According to our results, aestivation is induced by daylengths of 16–17L during early larval instars. If solar day plus civil twilight is the correct measure of daylength as experienced by *P. aegeria,* this would mean that aestivation is induced only in very late larvae of the first brood; for example, from the latest eggs laid in a cool year or from eggs laid by females that have hibernated in the larval stage. Pupal diapause and a univoltine life cycle would then inevitably follow in these individuals, as in the univoltine population further to the north, where aestivation typically occurs (Wiklund *et al.,* 1983).

DISCUSSION

The results must be interpreted as a flexible response to local seasonal variation, where photoperiod is used as a cue to signal future conditions. The complex regulation of growth and development in *P. aegeria* can be understood if the phenotypic plasticity displayed is regarded on two different levels.

(a) As an effect of daylengths over or under certain critical values, individuals diapause (pupal diapause, larval winter or summer diapause) or develop directly. This high-level 'decision' has to be taken by each individual in the majority of temperate insect species. Therefore, effective hormonal control of this decision has evolved and individuals diapause or not in response to seasonal cues. For instance, in 'long-day' or type 1 diapause (Danilevskii, 1965; Beck, 1980) all individuals diapause at daylengths under certain critical value, whereas at longer daylengths none diapause. The larval winter diapause of *P. aegeria* may fit this category. Larval aestivation and pupal diapause is displayed only in a certain range of daylengths, which has been termed type 3 diapause (Beck, 1980). The prevailing view of the nature of diapause has been that even at the critical daylength a given individual will typically either diapause completely or not at all. Thus, the diapause decision is usually considered an 'all-or-none' process, where a certain developmental pathway is taken by an individual during stages sensitive to photoperiod (cf. Lees, 1955). Considering the basic nature of this choice, for example, between a univoltine or a bivoltine life cycle, it is not surprising that this should generally be true under natural conditions. However, it is known that photoperiod and temperature experienced by prediapause stages may influence the intensity of diapause (Beck, 1980) and in the present study it is interesting to note the apparent break-down of the 'all-or-

none' view of diapause at, for example, photoperiods 16L and 13L where both larval and pupal durations appear to be normally distributed about a mean.

(b) Given a certain developmental pathway, the results presented here and by others (e.g. Masaki, 1967, 1978; Tanaka, 1978; Fuzeau-Braesch & Ismail, 1976; Kamm, 1972; Ahkmedov & Abdinbekova, 1977; Saunders, 1983) show that photoperiod can also be used to regulate growth and development on a lower level, in order to adjust development according to the season. In *P. aegeria* low level regulation seems to be at work at least in the following cases: (1) larval and pupal development time is progressively shorter at shorter daylengths within a range of long days where no diapause will be induced, and (2) the same is true for larval development time in intermediate daylengths, where a pupal diapause will follow larval development. The first of these cases differs in one important respect from the other studies cited above. They all concern pre-diapause regulation of growth, whereas *P. aegeria* apparently regulates growth by photoperiod also in individuals that do not diapause. To our knowledge, a graded response to photoperiod in regulation of growth rates, not coupled to diapause, has not been documented before in an insect (cf. Beck, 1980; Saunders, 1982; Tauber, Tauber & Masaki, 1986).

The mechanism for these finer adjustments may differ from the diapause induction, since they can be observed as graded responses to the actual photoperiod. On the other hand, the sometimes gradual nature of diapause itself displayed in the present study indicates that the two levels may not be fundamentally different.

The comparison between development in long ($>$17L) and short ($<$17L) days, respectively, is interesting. Larval development time is always shorter in long days (where development to adult follows directly) than in shorter days (where diapause follows). Thus, larvae appear to regulate growth according to whether diapause will follow or not. Similarly, high temperatures on long days (20L) result in even shorter development times, partly at the expense of lower final weights, and partly due to faster growth, whereas in shorter days (15L) the development times are not affected. Moreover, pupae have lower final weights in high temperatures also at this photoperiod, so in 15L mean growth rates are, in fact, slower at high temperatures. Clearly, the selective premium on a fast development in long days (a generation of offspring during the same season) is higher than in short days (earlier pupation), especially considering that *P. aegeria* (like the majority of temperate satyrines) seems to be well adapted for spending long periods in the larval stage.

It is probable that these larger differences in larval development times are induced during those larval stages that are sensitive to diapause-inducing photoperiods and form part of the diapause decision. Seasonal polyphenism is often intimately coupled to diapause (Shapiro, 1976) but has most often been studied in relation to visual phenotypic differences that show up after or during diapause. This may be an example of pre-diapause polyphenism coupled to diapause, and thus be a part of the high-level regulation.

Temperature seems to play a secondary role in this system, in contrast to the case in some other insects where temperature has a large direct effect on the incidence of diapause (e.g. *Pieris brassicae*; Danilevskii, 1965). In the field, low temperatures may however have the effect of delaying the stages sensitive to photoperiod until after a critical daylength has been passed. Thus, in cool

summers a greater proportion of individuals probably diapause as larvae rather than pupae (cf. Shreeve, 1986).

Finally, the results of the present study emphasize the importance of considering seasonality when life histories are modelled. Key life-history traits like growth rate, generation time and final weight may be greatly affected by phenotypic plasticity in these traits in response to the time of the year. Attempts have been made to incorporate phenotypic plasticity in models of life histories (Stearns & Koella, 1986) but the effects of seasonal plasticity in the character traits have not been considered. Such considerations can be expected to be most important for animals with generation times similar to the period of seasonal fluctuations, for example, insects.

ACKNOWLEDGEMENTS

We thank Birgitta Tullberg for critical reading of the manuscript and many valuable suggestions.

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