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Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength

Karl Gotthard, Sören Nylin and Christer Wiklund

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In this study we investigate how the need for seasonal timing of diapause and sexual maturation have selected for plasticity in life history traits in two butterfly species, *Lasionymata maera* and *Lopinga achine*. We test the general hypothesis that insects living in temperate areas should have shorter development times at progressively later dates of the growth season, and that they use daylength as a cue to determine the date. Both species have two different larval growth periods, the first in autumn and the second after termination of diapause in spring. Due to the difference in photoperiodic change in autumn and spring, we expected larvae to interpret daylengths qualitatively differently in the two growth periods. In other words, developmental decisions in response to daylength should depend on the seasonal state (autumn or spring) of larvae. In laboratory experiments we investigated the reaction norms relating larval development times to daylength. In both species the slopes of these reaction norms were different in autumn and in spring. The results of the experiment on *L. maera* supported specific predictions both in autumn and in spring. The same was true in autumn for *L. achine* but development time in spring seemed to be insensitive to daylength. In all cases, short development times were associated with high larval growth rates rather than with small final body sizes. Growth and development in these species can be described as state-dependent decision processes, where information about the external and internal environment is used at several points in development.

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The timing of life history events such as growth, maturation and reproduction in relation to the time of year are crucial aspects of the biology of any organism living in a seasonally changing environment. It is well documented that phenotypic plasticity in life history traits may represent an adaptation to environmental variation (Bradshaw 1965, Stearns 1992, Gotthard and Nylin 1995, Via et al. 1995, Nylin and Gotthard 1998). Variation in living conditions due to seasonality has been shown to promote the evolution of adaptive life history plasticity in many taxa (Bradshaw 1965, Brakefield and Larsen 1984, Conover and Present 1990, Negus and Berger 1992, Danks 1994, Nylin 1994, Gotthard and Nylin 1995, Leimar 1996, Nylin et al. 1996,

Nylin and Gotthard 1998). In temperate regions the evolution of insect life histories is obviously constrained by seasonality since a large part of the year is unsuitable for growth and reproduction. Typically, insects survive this period in a hormonally controlled diapause in a species-specific developmental stage. Hence, individuals must complete development up to the stage where diapause is possible before the onset of the unfavourable season (Reavey and Lawton 1991). The start of development and conditions for growth vary between individuals and between years. As a consequence, the time available for reaching the developmental stage appropriate for diapause will also vary between individuals. After winter the same individuals

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must break the diapause and continue development in accordance with the seasonal change so that they find mates, food and other resources needed for reproduction and offspring survival (Danks 1994).

The hypothesis that insects in general should have shorter development times later within a growth season has been proposed and empirically supported in several insect species (Lutz 1974, Masaki 1978, Nylin et al. 1989, 1996, Nylin 1992, Carrière et al. 1996, Leimar 1996, Gotthard 1998). More formal optimality models of life history evolution also suggest that plasticity in development time is likely to arise as an adaptation to seasonality (Abrams et al. 1996). This model (Abrams et al. 1996) explores the optimal responses of size, development time and growth rate to changes in the amount of time available for completion of the life cycle. It assumes that fitness is a function of adult size, juvenile mortality and the seasonal timing of reproduction or diapause. Moreover, the model assumes that individuals adaptively vary their growth rates by balancing it against juvenile mortality. Endogenous control of growth rate is a common phenomenon throughout the organic world (Case 1978, Arendt 1997) and costs of high growth rates can, for instance, be an increase in predation risk because of more risk prone foraging behaviour (Lima and Dill 1990, Werner and Anholt 1993) or direct physiological costs during periods of food shortage (Stockhoff 1991, Gotthard et al. 1994).

In insects, photoperiod is the most important source of information on the progression of season (Saunders 1981, Danks 1994, Nylin and Gotthard 1998). In this study we investigate how two closely related species of butterflies, *Lasiommata maera* and *Lopinga achine*, use such information to optimise development over the year. In Sweden, both species are univoltine and diapause during the winter as half grown larvae. Consequently they have two distinct larval growth periods, in late summer/autumn and spring/early summer, respectively. This means that they face two timing problems as larvae, to enter diapause at some optimal date in autumn and break diapause, grow and pupate in a way that allows them to emerge as adults at an appropriate time in summer. The specific prediction we wanted to test was whether these butterflies shorten larval development times in daylengths signalling relatively later dates, both in autumn and in spring. If this is the case, we expect individual larvae to interpret a given range of daylengths qualitatively differently in autumn and in spring. This is because in autumn daylengths are decreasing, and a relatively short daylength always signals a late date. In spring, on the other hand, daylengths are increasing and larvae should always interpret short daylengths as early dates of the growing season (Fig. 1). Hence, we expected that some aspect of internal state, that is different in autumn and spring, would alter the interpretation of what date a certain daylength indi-

cates. Such unknown aspects of internal state may for example be larval instar, hormone titers or other physiological effects of having spent several months in diapause. In the following we will for simplicity refer to individuals as being in different seasonal states in autumn and in spring, respectively. State-dependence of developmental decisions, as outlined here, would predict adaptive reaction norms, relating larval development time to photoperiod, to have a positive slope before diapause in autumn but a negative slope after diapause in spring (Fig. 1).

Materials and methods

Study organisms

L. maera is widely distributed across continental Europe up to 68°N (Higgins and Hargreaves 1983), and in

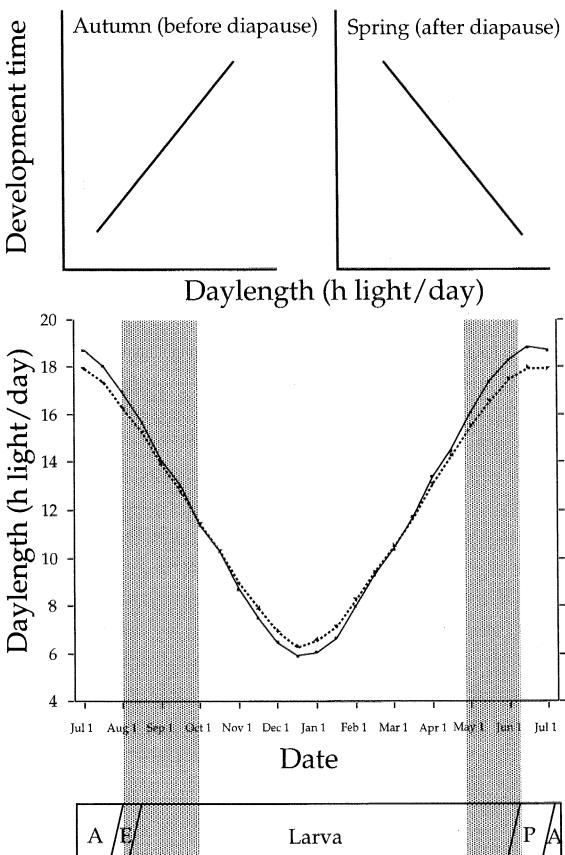


Fig. 1. (Bottom) Schematic phenology of *Lasiommata maera* and *Lopinga achine* in Sweden. A = Adult, E = Egg, P = Pupa. The phenology is mapped onto the year above. (Center) Yearly variation in daylengths at the latitudes of Stockholm (full drawn line) and Gotland (dotted line). The shaded areas extending from the phenology highlights the two periods of larval growth, before diapause in autumn and after diapause in spring. (Top) Predicted reaction norms before and after diapause, assuming shorter development times as the time available for growth decreases.

Sweden it is univoltine with adults flying from the end of June to the end of July. However, further south in Europe it has two generations per year. The females oviposit and the larvae feed on various grasses (Wiklund 1984). Also *L. achine* is univoltine in Sweden and adults are on the wing during July. We know of no reports of *L. achine* having more than one generation per year anywhere in its entire range. In Sweden the most preferred host plant is the sedge *Carex montana* but larvae also feed and survive well on a number of grasses (Wiklund 1984, K.-O. Bergman pers. comm.).

Experimental procedure

Two mated females of *L. maera* were caught in July 1995 in the Stockholm area (59.5°N) and they laid eggs on *Dactylis glomerata* in the laboratory. The newly hatched larvae were split among four climate cabinets with different photoperiods; 15L:9D (15 h daylength in the following), 16 h, 17 h and 18 h daylength. We placed five larvae from each female in each daylength treatment and the temperature was held at a constant 17°C . Larvae were reared individually in plastic jars where *D. glomerata* was cultured in ample supply. Two measurements of the timing of diapause were taken, the time of moulting into the third instar where winter diapause usually takes place, and the time when individual larvae stopped growing which is typical for the start of larval diapause. Larvae were checked several times a week and during the period of moulting into the third larval instar they were weighed every day. After this period larvae were weighed twice a week until day 72 when all larvae were moved outdoors to spend the winter in a shelter on the roof of the Department of Zoology building. In early spring (18 April) all larvae were moved back into the laboratory and then randomly split between the same photoperiods that had been used in autumn. We reared larvae as described above, weighed them twice a week and noted the time of pupation, the duration of the pupal stage, pupal weight and adult weight.

For *L. achine* we performed three separate experiments. The first was done in same way as the experiment on *L. maera* described above, except that we used *Carex montana* as food plant and the offspring of three wild caught females from Gotland (57.5°N). Age and weight at the moulting into the third larval instar were noted and between day 25 and 75 larvae were weighed twice a week. After this they were transferred outdoors. Because of high winter mortality the number of larvae were reduced and therefore we excluded the 19-h daylength when restarting the experiment in spring. The second experiment was started the next year (1996) using offspring from 10 wild caught females from Gotland. In this experiment we used a range of shorter daylengths; 12 h, 14 h, 16 h, in the autumn rearing, and

14.5 h, 16 h, 17.5 h in the rearing after diapause in spring. We did this to better match experimental daylengths with the natural daylengths on Gotland. The larvae were moved back to the laboratory approximately a month earlier than in the previous experiment (15 March) and were, furthermore, reared on a different food plant, *Festuca ovina*.

The third experiment (started 1996) was slightly different from the other two in that instead of using constant daylengths, we programmed the climate cabinets to follow the natural change in daylengths at the latitude of Gotland. In this experiment each daylength treatment mimicked a different date of egg hatch and consequently a different date for the start of larval development. This meant that larvae in an early experimental starting date in autumn began development in a longer daylength than larvae that were given a later starting date. Larvae in all treatments then experienced the natural decrease in daylength from their respective starting date. All cohorts were started simultaneously and consisted of five larvae from each of six wild caught females. In autumn, we used four experimental daylength regimes corresponding to four starting dates. The interval between starting dates was two weeks and the dates with corresponding daylengths were: 19 July (17.1 h), 2 August (16.2 h), 16 August (15.2 h) and 30 August (14.1 h). Also these larvae were monitored on a daily basis and weighed once a week until the entering of diapause, when they were moved outdoors for overwintering. Early in spring (14 March) we moved the diapausing larvae back to the laboratory and split them randomly among four daylength treatments. They corresponded to four starting dates in spring and followed the natural increase in daylength. As in the rearing before diapause, the dates for the start of development after diapause differed by two weeks: 15 April (14.3 h), 29 April (15.4 h), 13 May (16.4 h) and 27 May (17.3 h). Other than the differences mentioned we used the same experimental protocol in all rearings with *L. achine* as we did in the experiment on *L. maera*.

Butterfly growth rates can usually be well described as exponential (Nylin et al. 1989, 1996, Wickman et al. 1990, Leimar 1996). In all experiments, therefore, individual relative growth rates were approximated with the slope of the regression line for $\ln(\text{weight})$ on larval age (Gotthard et al. 1994). By using this approach we could estimate growth rate independently of larval development time and final size.

Statistical treatment

In all experiments we have used ANCOVA to test the effects on life history traits of daylength treatment, seasonal state (autumn or spring) and their interaction. Daylength was used as a covariate and seasonal state as a fixed factor. Means from each daylength treatment,

Table 1. Results of ANCOVAs on development time, growth rate and body size in the experiment with *Lasiommata maera*. Means of daylength treatments in autumn and in spring are used as independent observations. Significant *P*-values are in bold. Development in autumn is represented by the period from egg hatch to entering of the third larval instar. df for daylength, seasonal state, the interaction and error are 1, 1, 1, and 4 in all cases.

Dependent variable	Daylength	Seasonal state	Daylength × seasonal state	<i>r</i> ²
Development time (d)	<i>P</i> = 0.216	<i>P</i> = 0.015	<i>P</i> = 0.023	0.951
Relative growth rate	<i>P</i> = 0.482	<i>P</i> = 0.002	<i>P</i> = 0.003	0.954
Body size (mg)	<i>P</i> = 0.038	<i>P</i> = 0.128	<i>P</i> = 0.038	0.999

before and after diapause, were taken to be independent observations in these tests. In the analysis of *L. achine* in constant daylengths we pooled the means from both experiments. Of the two measurements on development before diapause that was collected, the different aspects of development to the third larval instar were generally best estimated. This is because of the higher resolution obtained by checking the time of larval moult daily as opposed to weighing once or twice a week to establish the time when larvae ceased to gain weight. Moreover, the moult to the third instar is a more unambiguous developmental event compared to the time of growth cessation. We have, therefore, used the data on development to the third instar in the analysis of state dependence, although we have done all analyses on both measurements. In some cases we have also investigated the effect of daylength within growth periods by linear regression on treatment means. In all experiments the effect of family was tested within each developmental period in an ANCOVA with daylength as a covariate and family as a fixed factor. In these tests individual values were used as independent observations. This two-step approach was taken to first test the effect of daylength and then the effect of family at reasonable levels of independence.

Results

Lasiommata maera

Daylength treatment had a significant effect on larval development time, growth rate and body size (Table 1, Fig. 2). The interaction between daylength and seasonal state was significant in all three cases showing that the same range of daylengths had different effects on development before and after diapause, respectively (Table 1). The correlation between larval development time and daylength was positive in autumn and negative in spring (Fig. 2a). Larval growth rate rather than body size seems to be the major determinant of the variation in larval development time (Fig. 2). In autumn, the treatments with the shortest development times and the highest growth rates (15 h and 16 h) were in fact slightly larger when entering the third larval instar compared to the other two treatments (17 h and 18 h, Fig. 2c, 3). The results on development time and

growth rate were the same when using the time to growth cessation as the measure of pre-diapause development. The effect of daylength treatment on body size was, however, not significant at that point in development. After diapause there were no significant differences between daylengths in pupal mass, nor was there an effect of daylength on the duration of the pupal stage. There were no significant differences between families, before or after diapause, in any of the traits measured.

A closer inspection of the average growth trajectories suggests that before diapause there is a dichotomy in

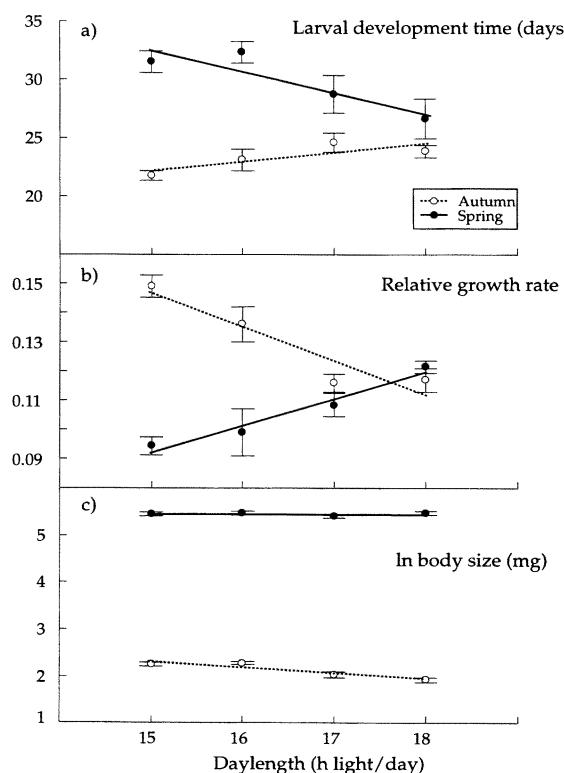


Fig. 2. The effect of daylength treatment on a) larval development time b) relative growth rate c) ln body size, in autumn and spring in *Lasiommata maera*. Development in autumn is represented by development to the third larval instar. Treatment means ± 1 SE in autumn (open) and in spring (filled) are shown. Sample sizes within each treatment are between 7 and 10 in autumn and between 4 and 6 in spring. The interaction between daylength and seasonal state was significant in all three cases (Table 1).

In weight (mg)

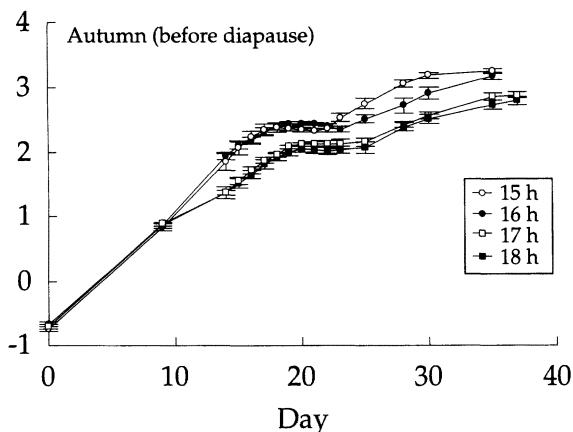


Fig. 3. Average growth trajectories of *Lasiommata maera* in four daylength treatments before diapause in autumn. Means ± 1 SE from days when all individuals could be weighed are shown. Sample sizes are between 7 and 10 within each treatment. The horizontal parts of the growth trajectories after approximately 20 d indicate the period of moulting into the third larval instar.

growth decisions made by the larvae; some time between 9 and 14 days of growth, larvae in the two shortest daylengths follow a steeper growth curve up to the third instar compared to larvae in the longer days (Fig. 3).

Lopinga achine – constant daylengths

All surviving individuals in both experiments with constant daylengths entered larval diapause. As in *L. maera* this typically happened in the third larval instar except in the shortest daylength (12 h), where a majority of larvae (9 of 14) stopped growing and instead entered winter diapause in the second instar. This complicated the analysis since the time of entering the third larval instar was better estimated than the time to growth cessation (see Materials and methods). We excluded the 12-h treatment when analysing development up to the third instar and report the results of both analyses if they produced different results, otherwise we give the results of development to the third instar only.

Larval development time (days)

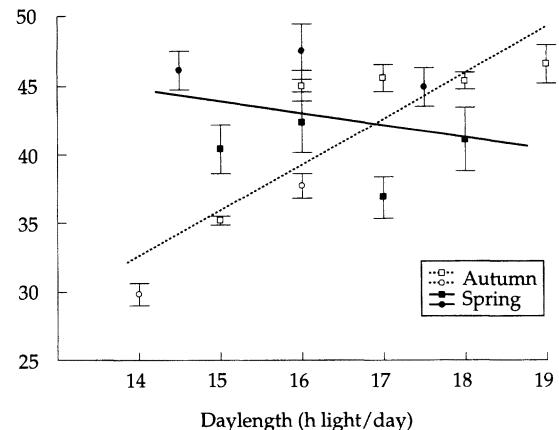


Fig. 4. The effect of daylength treatment on larval development time before and after diapause in *Lopinga achine*. Development in autumn is represented by development to the third larval instar. Open symbols are treatment means ± 1 SE in autumn and filled symbols represent means ± 1 SE in spring. The two different experiments are indicated by different symbols (95/96 = squares, 96/97 = circles). Sample sizes within each treatment are between 13 and 18 in autumn and between 9 and 15 in spring. The interaction between daylength and seasonal state is significant (Table 2). Note, that the slope of the reaction norm in spring is not significantly different from zero.

When we pooled the results from both experiments the interaction between daylength and seasonal state had a significant effect on development time (Table 2, Fig. 4). If we use the time to termination of growth as the measurement of pre-diapause development the trends are similar but the interaction is not significant ($P_{\text{daylength} \times \text{state}} = 0.17$). In autumn, there was a positive correlation between larval development time and daylength similar to what we found in *L. maera*. Contrary to our predictions and unlike the case of *L. maera*, the correlation between larval development time and daylength in spring was not significantly different from zero. This last result was also true for total post-diapause development time (larval + pupal development time).

There were no significant interactions between seasonal state and daylength in growth rate or body size (Table 2). As in the case with development time, there were no effects of daylength in spring in these other traits and therefore the results are not shown graphi-

Table 2. Results of ANCOVA:s on development time, growth rate and body size in the experiments with *Lopinga achine* in constant daylengths. Means of daylength treatments in autumn and in spring are used as independent observations and the two experiments are pooled. Significant P -values are in bold. Development in autumn is represented by the period from egg hatch to entering of the third larval instar. df for daylength, seasonal state, the interaction and error are 1, 1, 1, and 10 in all cases.

Dependent variable	Daylength	Seasonal state	Daylength × seasonal state	r^2
Development time (d)	$P = 0.122$	$P = 0.014$	$P = 0.016$	0.619
Relative growth rate	$P = 0.612$	$P = 0.167$	$P = 0.104$	0.635
Body size (mg)	$P = 0.034$	$P < 0.001$	$P = 0.780$	0.997

cally. In autumn, however, there were significant effects of daylength on growth rate and interesting trends in body size (Fig. 5). The results suggest a positive correlation between development time and daylength, a negative correlation between growth rate and daylength and a non-significant positive correlation between size and daylength. It seems, however, that these trends are largely induced by daylengths shorter than 17 h, whereas in longer daylengths the reaction norms become approximately flat (Fig. 5).

In the rearings after diapause in spring, we did not use daylengths as short as 12 h because of the possibil-

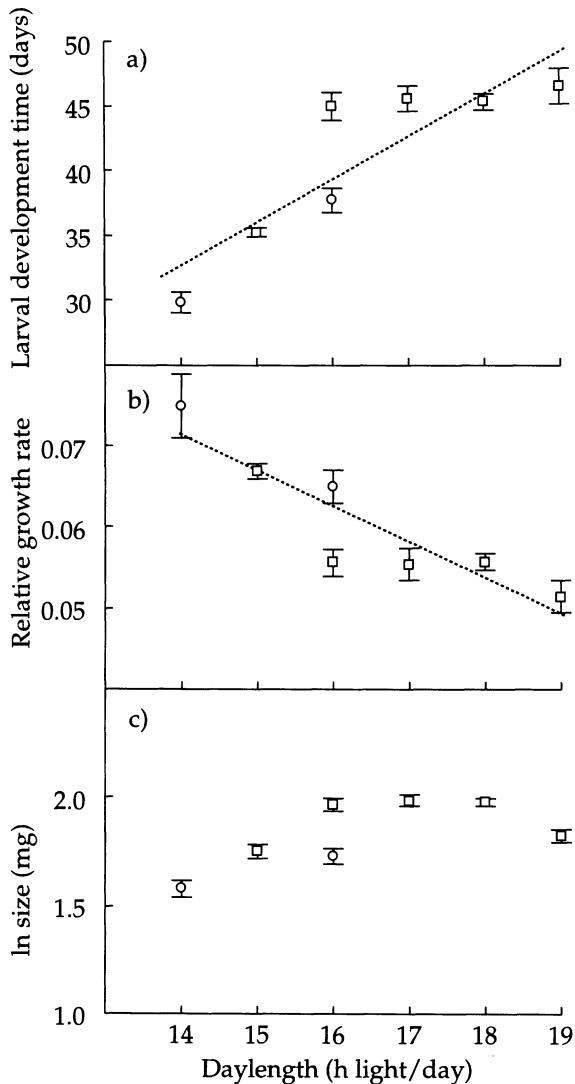


Fig. 5. The effect of daylength treatment in autumn on a) larval development time b) relative growth rate c) ln body size in *Lopinga achine*. The two different experiments are shown by different symbols representing means ± 1 SE (95/96 = squares, 96/97 = circles). Lines are significant linear regressions on treatment means from both experiments pooled ($P < 0.02$ in both cases). Sample sizes within each treatment are between 13 and 18 individuals.

In weight (mg)

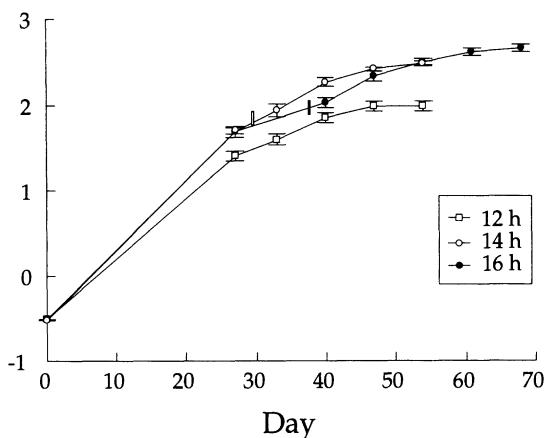


Fig. 6. Average growth trajectories of *Lopinga achine* in three daylength treatments before diapause in autumn. The results are from the 96/97 experiment, and only days when all individuals could be weighed are shown (mean ± 1 SE). Sample sizes within each treatment are between 14 and 18. The heavy bars plotted on the growth trajectories of the 14-h and the 16-h treatment indicate the average time of entering the third instar. Most of the larvae in the 12-h treatment did not enter the third larval instar.

ity that larvae would not break their diapause in such extreme short-day conditions. In the 14.5-h and 15-h treatments there were indeed a few larvae (4 of 27 in both treatments together) that had very long larval development times (over 80 d). They were excluded from the analysis since larval periods of that magnitude appear to be maladaptive and probably are due to the use of constant short daylengths.

The effect of family was tested separately within each experiment and was not significant for most traits. The only exception was found in growth rate and development time to growth termination in the first experiment with three families. In these cases the interaction between family and daylength treatment was also significant (Development time: $P_{\text{daylength}} = 0.671$, $P_{\text{family}} = 0.023$, $P_{\text{daylength} \times \text{family}} = 0.027$, $r^2 = 0.124$, Growth rate: $P_{\text{daylength}} = 0.012$, $P_{\text{family}} = 0.019$, $P_{\text{daylength} \times \text{family}} = 0.029$, $r^2 = 0.236$, df for daylength, family, interaction and error are 1, 2, 2 and 63 in both cases). In the second experiment with more families (10) there were no such effects.

For graphical clarity the average growth trajectories before diapause are shown from the second experiment only (Fig. 6). Some time before 27 d of growth in autumn, larvae in the 12 h treatment chose to follow a different trajectory compared to the larvae in the other two treatments. They stopped growing late in the second instar where a majority entered diapause. All larvae in the other treatments moulted into the third instar but after this the 14-h animals followed a steeper growth curve, compared to the larvae in 16 h, before

Table 3. Results of ANCOVA:s on development time, growth rate and body size in the experiments with *Lopinga achine* in naturally varying daylengths. Means of daylength treatments (start date) in autumn and in spring are used as independent observations. Significant *P*-values are in bold. Development in autumn is represented by the period from egg hatch to entering the third larval instar. df for daylength, seasonal state, the interaction and error are 1, 1, 1, and 4 in all cases.

Dependent variable	Daylength at start date	Seasonal state	Daylength × seasonal state	r^2
Development time (d)	$P = 0.029$	$P = 0.003$	$P = 0.008$	0.992
Relative growth rate	$P = 0.047$	$P = 0.007$	$P = 0.010$	0.946
Body size (mg)	$P = 0.547$	$P = 0.001$	$P = 0.242$	0.999

they stopped growing and entered diapause (Fig. 6). The growth trajectories of larvae in the other experiment fall approximately into the categories described by the two longer daylengths in Fig. 6. The 15-h treatment was very similar to 14 h and all other treatments were similar to the 16-h treatment.

Lopinga achine – “naturally varying” daylengths

In the last experiment all individuals were exposed to daylength regimes that mimicked naturally changing daylengths in climate chambers with a constant temperature of 17°C. The treatments only differed in what experimental dates larvae experienced in terms of daylength regime, from the day of hatching and thereafter. For comparison with the other experiments, however, we have used the daylength at the starting date as a measure of daylength treatment. The results of this experiment were similar to the experiments with constant daylengths. However, the variation in development time within daylength treatments was generally smaller than in the experiments with constant daylengths, and no individuals made obvious “developmental mistakes”. In autumn all larvae moulted into the third instar before they stopped growing and entered diapause. The interaction between daylength treatment and seasonal state had a significant effect on development time and growth rate (Table 3). As in the earlier experiment on *L. achine*, this was because daylength treatment had an effect on development in autumn but not in spring (Fig. 7). In autumn, later starting dates induced shorter development times and higher growth rates. The correlation with daylength was positive for development time and negative for growth rate. Moreover, larvae in later starting dates also showed a non-significant tendency to be smaller at the entry of the third instar. There were no significant differences between families in any of the traits. In conclusion, young larvae that found themselves in a daylength regime indicating a late date in autumn, shortened their development time by growing faster, and perhaps by moulting and entering diapause at a smaller size. After diapause in spring, however, the daylength regime did not alter any developmental decisions that we could measure.

Mortality and changes in body size during winter

Mortality during the winter differed quite markedly between years, and both experiments that were started 1995 suffered from very high mortality. In the case of *L. maera*, 51% of the larvae died during the winter and the corresponding figure in *L. achine* was 38%. In both these experiments the mortality risk was significantly higher for individuals that were relatively small when they stopped growing (Table 4). In the two experiments with *L. achine* that were started in 1996 only 7% of the larvae died during the winter, presumably because they were brought back to the laboratory one month earlier. In this year there was no significant relationship between size at the start of diapause and mortality risk (Table 4). Interestingly, all larvae of *L. achine* from the constant 12-h treatment that entered diapause in the second instar survived the winter. In all experiments there was a significant positive correlation between the last measured weight in autumn and the weight early in spring (Table 4). Hence, a larva reaching a large size before the onset of winter was also relatively larger at the start of post-diapause development in spring.

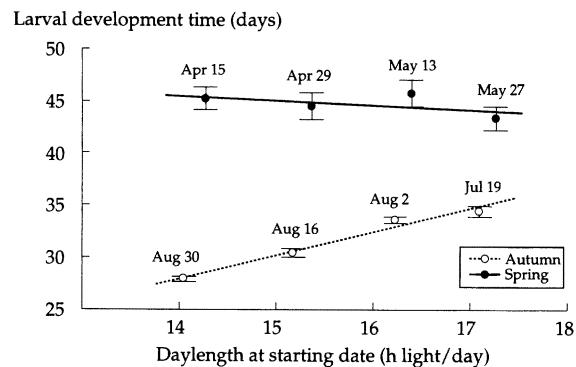


Fig. 7. Results of the experiment with *Lopinga achine* in naturally varying daylengths. Average larval development times ± 1 SE in autumn and in spring are plotted against the daylength at the start of development. Filled circles show development in autumn up to the third larval instar and open circles show development in spring. For each growth period the starting dates are indicated and the interval between starting dates are two weeks. Sample sizes within each daylength treatment in autumn are between 23 and 27 and in spring between 21 and 22. The slope of the reaction norm in spring is not significantly different from zero.

Table 4. The relationships between weight at diapause, winter mortality and weight at the start of post-diapause development in spring. Larval weights are means \pm 1 SE and stars indicate P -values of ANOVAs testing the difference in size between survivors and non-survivors. The last column shows correlation coefficients and significance levels of linear regressions of how the size after diapause early in spring depends on the size reached before diapause in autumn. * 0.05, ** 0.01, *** 0.001.

Experiment	Weight at diapause for survivors (mg)		Weight at diapause for non-survivors (mg)	Correlation coefficient Size _{spring} / Size _{autumn}
<i>L. maera</i> – 95/ 96	31.2 \pm 0.9 $N = 19$	**	26.0 \pm 0.9 $N = 20$	0.68 \pm 0.18 ** $N = 19$
<i>L. achine</i> – 95/ 96	15.2 \pm 0.4 $N = 43$	**	13.9 \pm 0.3 $N = 23$	1.02 \pm 0.3 ** $N = 43$
<i>L. achine</i> – 96/ 97	12.0 \pm 0.4 $N = 139$	n.s.	14.3 \pm 1.3 $N = 11$	0.77 \pm 0.02 *** $N = 139$

Discussion

It is well documented that many temperate insects use daylength to make the qualitative developmental decision whether to enter diapause or to develop directly to sexual maturity (Danilevskii 1965, Bradshaw 1976, Beck 1980, Saunders 1981, Tauber et al. 1986, Danks 1994). Both species investigated here, however, also use the information provided by daylength to make quantitative developmental decisions within a single developmental pathway. This pathway includes a growth period in late summer/autumn, diapause preferably in the third larval instar, a second growth period in spring/early summer and reproduction during July. The results presented here show that before diapause in autumn, the reaction norm that relates larval development time to daylength has a positive slope in both species (Figs 2, 5 and 7). Hence, the results regarding pre-diapause development in autumn support the predictions in both species. The growth trajectories before diapause also indicate that larvae make finely adjusted growth decisions, based on the daylength regime they experience. The behaviour of *L. achine* larvae in a constant daylength of 12 h provided an interesting observation, with a majority of larvae entering diapause in the second instar, which is one instar earlier than normal. This daylength corresponds to late September, and for *L. achine* in Sweden it is unrealistically short for the start of development, but still a photoperiod that larvae of this species may experience later in development before diapause. It is not known if diapause in the second instar ever occurs in the field but the observation, nevertheless, suggests that these larvae make developmental decisions which would be relevant under extreme time stress.

The developmental response to daylength changed after diapause in both species in accordance with the general prediction. It was, however, only the results from *L. maera* that supported the more specific prediction regarding growth in spring. In this species the development time-daylength reaction norm had the expected negative slope in spring, but because of high winter mortality the sample size of the rearing after diapause was quite small. The reaction norm of *L.*

maera in spring has, however, been investigated in an earlier experiment (Nylin et al. 1996) and a comparison of the two experiments show that the reaction norms found are almost identical (ANCOVA on daylength treatment means; $P_{\text{daylength}} = 0.004$, $P_{\text{experiment}} = 0.393$, $P_{\text{dayl.} \times \text{exp.}} = 0.381$, $N = 8$, $r^2 = 0.935$). Hence, the available evidence suggests that in *L. maera* the sign of the reaction norm changes from positive in autumn to negative in spring, within individual larvae. The experiments on *L. achine* all suggest that daylength regime in spring do not affect any developmental decisions that we could measure. Thus, in this species the slope of the reaction norm changes from positive in autumn to zero in spring, within individuals.

The difference between species in their plastic responses in spring was unexpected. It may, however, be related to a difference between the species in their latitudinal patterns of voltinism. In central and southern Europe *L. maera* typically have more than one generation per year. In a transition area where there is time for an additional generation only in some years, there may be a high pay-off for the ability to utilise the available growth season maximally these particular years. The type of reaction norm that *L. maera* have in spring would enhance this ability. The capacity to develop directly, and not enter diapause, is present in *L. maera* from Sweden, and direct development can be induced by very long daylengths in the laboratory. It is likely that the univoltine populations of *L. maera* in Sweden have originated from partially bivoltine populations. The reaction norm in spring may now be maintained by much weaker selection in the population investigated here or by gene flow from more southern populations. In contrast, there are no reports of *L. achine* having more than one generation a year throughout its entire distribution and it never develops directly in extreme long day conditions in the laboratory.

The experiment on *L. achine* with naturally varying photoperiods confirmed the results from the rearings with constant photoperiods. Naturally changing daylengths seemed to be easier for the larvae to interpret correctly. For example, before diapause in autumn the variation within treatments was generally smaller in the

experiment with natural daylengths compared to the experiments with constant daylengths. This suggests that developmental decisions are made more than once within this growth period. In constant photoperiods this could be a problem, since a certain daylength in the first larval instar could indicate a shortage of time before winter while experiencing it three weeks later would tell a larva that it has plenty of time for growth. Hence, it is possible that in some constant daylength treatments the results, to a degree, are the product of an unnatural mixture of developmental decisions.

The results are in quite good agreement with the expectations from the model of Abrams et al. (1996). According to the model, the most likely effects of decreasing the time available for development are a shorter development time, higher (or unchanged) growth rate and a smaller (or unchanged) final size. In all rearings where development times decreased with the perceived time available for development, growth rates indeed increased along the same axis (Figs 2 and 5, Table 3). The effect on final weight, however, was more variable and not significant. Thus, the association between development time and growth rate was typically stronger than the association between development time and final size. In all the experiments with *L. achine* there was, nevertheless, a tendency also for size to decrease when the time available for development in autumn became shorter (Fig. 5, Table 3). In these cases it seems as if the increase in growth rate was not big enough to fully compensate for the necessity of a short development time. In the model of Abrams et al. (1996) final size should be unchanged when the growing season is shortened, if the relationship between growth rate and mortality is linear. If this relationship is accelerating, however, final size should decrease when the time available for growth decreases. Such exact knowledge of the trade-off between growth rate and mortality is not available, but the results presented here suggest that the function may be more accelerating in *L. achine* than in *L. maera*. One further indication in this direction is that the growth rates of *L. achine* in general are only 50% of the growth rates found in *L. maera* (Fig. 2b, 5b). Possible mechanisms may be differences in predation pressure or host plant phenology that penalises high growth rates more in *L. achine*.

The size a larva reached in autumn before entering diapause is likely to have effects on fitness. In both experiments with high winter mortality larger individuals survived better, and in all experiments a large size before diapause carried over to a relatively larger size at the start of development in spring (Table 4). Thus, reaching a large size before entering diapause may give the advantage of having to grow less during spring which means a less constrained time budget. Alternatively it may give a better chance to reach a large adult size.

State-dependent life history theory defines a strategy as a decision rule that specifies how an organism should respond to its internal state and its environment. If the response varies with these parameters the strategy is plastic, and this theoretical framework has been proposed as a natural setting for discussing adaptive plasticity (Houston and McNamara 1992, McNamara and Houston 1996). Typically, empirical work on life history plasticity has studied the environmental dependence of phenotypic expression when organisms on average are in the same internal state. The most interesting result of the present study, however, was that a change in internal state of individuals altered the environmental dependence (Tables 1–3). Our explanation is that to make use of the photoperiodic information both in autumn and in spring, an individual larva must change the interpretation of what date a certain daylength signals. If this change is not an evolutionary option, the organism should only use the photoperiodic information during one of the seasons and perhaps use some other source of relevant information during the other. In conclusion, we believe that the concept of state-dependence highlights an important mechanism for how reaction norms like these come about. Growth and development are dynamic decision processes, where individuals make decisions based on information about the external as well as the internal environment at several points in development. Life history reaction norms like the ones described here are the sum of all these decisions.

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