Growth Strategies and Optimal Body Size in Temperate Pararginii Butterflies[1]

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Synopsis. In temperate insects the evolution of growth strategies and the optimal age and size at maturity will depend strongly on seasonal variation in temperature and other resources. However, compared to photoperiod, temperature itself is a relatively poor predictor of seasonal change and timing decisions in insects are often most strongly influenced by the photoperiod. Here I review the evolution of seasonal growth strategies in the butterfly tribe Pararginii (Satyrinae: Nymphalidae) and relate it to life history theory. The results indicate that individual larvae may adjust their growth trajectories in relation to information on time horizons obtained from the photoperiod. The growth strategies can be characterized by a set of state-dependent decision rules that specify how an individual should respond to its internal state and external circumstances. These decision rules may also influence how individual growth change with a rise in temperature, showing that the standard expectation of increased growth rates with increasing temperatures may not always be true. With less time available individual larvae increase growth rates and thereby achieve shorter development times, most often without any effects on final sizes. One reason for the apparent optimization of growth rate seems to be that growing fast may incur costs that larvae developing under lower time limitations chose to avoid. The patterns of growth found in these and many other studies are difficult to reconcile with common assumptions of what typically determines optimal body size in insects. In particular it seems as if there should be some costs of a large body size that, so far, have been poorly documented.

INTRODUCTION

The optimal age and size at maturity is a frequently studied topic in life history theory and it is based on the fundamental trade-off between benefits of a large body size and costs of a long juvenile period (Roff, 1992; Stearns, 1992; Kingsolver *et al.*, 2004). A large adult size is often correlated with a high competitive ability as well as high fecundity, and life history models typically assume that fitness increases continuously with adult size. The most common argument for why we are not surrounded by gigantic organisms is that it takes time to grow large and a long juvenile period increases the risk of mortality before reproduction (Roff, 1992; Stearns, 1992; Blanckenhorn, 2000). These basic relationships suggest that natural selection should favor a maximization of juvenile growth rates that would allow organisms to become as large as possible in as short time as possible. However, an increasing number of studies have pointed to empirical patterns that cannot be explained by the simple trade-off between age and size at maturity and there are strong arguments that additional selective forces must often be present (Case, 1978; Conover and Present, 1990; Gotthard *et al.*, 1994; Abrams *et al.*, 1996; Leimar, 1996; Arendt, 1997; Nylin and Gotthard, 1998; Blanckenhorn, 2000; Gotthard, 2000). For example, most organisms do not maximize their juvenile growth effort and thus their growth rates unless they are forced to do so because of time or food limitations (Arendt, 1997). In insects it appears not uncommon that when individuals are facing a long growth season they "vol-untarily" reduce juvenile growth rates instead of trying to reach a larger final size. From the perspective of life history theory this pattern indicates that the optimal growth strategy of many insects is not growth maximization in all situations. In response to these results there is both empirical and theoretical work that investigate the conditions that would favor plasticity in insect growth in relation to variation in time constraints, temperature and resource levels (Masaki, 1978; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Nylin, 1994; Abrams *et al.*, 1996; Leimar, 1996; Arendt, 1997; Blanckenhorn, 1997, 1998; Nylin and Gotthard, 1998; Johansson and Rowe, 1999; Gotthard, 2001).

In the present paper I will briefly present some fundamentals of insect life cycle regulation, which will form the background of a review of the growth strategies of a group of temperate satyrinae butterflies. I will discuss these results in relation to some life history models and in particular how they relate to ideas of optimal size in insects.

Insect life cycle regulation

Seasonal variation in temperature strongly affects conditions for growth and development in temperate insects and it obviously constitutes a powerful selection pressure. Both the direct and indirect effects (lack of food) of low winter temperatures necessitate a mechanism for interrupting development and practically all temperate insects do this by entering a hormonally controlled diapause (Tauber *et al.*, 1986; Denlinger, 2001). This diapause can occur in any developmental stage (egg, larva, pupa, adult) but it is typically specific for each species. The diapause stage is phylogenetically quite conservative; *i.e.,* closely related species tend to have the same diapause stage but

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within a large group such as the butterflies there are examples of diapause in all developmental stages (Tauber *et al.*, 1986).

One important consequence of the species-specific diapause stage is that to have non-zero fitness, any individual must develop in such a manner that it, or its offspring, reach this stage before the onset of winter (and not continue development beyond it). Moreover, many temperate insects have alternative developmental pathways (Tauber *et al.*, 1986): diapause development, or direct development where the total development from oviposition to a new reproductive adult takes place in one season and there is no diapause. Hence, any individual can "choose" which pathway to follow and this decision typically depends on seasonal cues. Even though temperature variation is probably the main selective pressure that favors alternative developmental pathways, it is a relatively poor cue of seasonal progression compared to the photoperiod. Indeed, in most insects photoperiod is the most important cue for determining developmental pathway although variation in temperature typically augments the effect of photoperiod (Tauber *et al.*, 1986; Denlinger, 2001). The species-specific diapause stage tends to synchronize individual life cycles within populations. Moreover, seasonal occurrence of vital resources (*e.g.,* the presence of larval hosts) will also tend to synchronize the timing of the adult period. Finally, in insects with a short mating period (as is common in temperate butterflies) there is also strong selection for synchronization of male emergence with that of female emergence since reproductive success will depend heavily on the probability of finding mates (Wiklund and Fagerström, 1977; Fagerström and Wiklund, 1982).

Despite the strong synchronization of mating activities it is common that the total period of female oviposition stretches over a considerable time period and there are also differences in the start of development between years due to variation in weather. Hence, there is strong selection on timing of the life cycle (diapause, mating period) while there will always be variation among individuals within a given population in how much time they have available for development. In situations where time for development is in some way limited, such conditions predict the evolution of adaptations that allow individuals to estimate how much time is available for growth and development and to use this time efficiently. Intuitively, a likely response to a cue that indicates shorter time available would be to reduce development time to the diapausing or adult stage. Such a reduction can in principle be obtained by either finishing at a smaller size or by increasing growth rate, or a combination of the two. This problem has also been analyzed in more formal life history models that, despite some differences, all suggest that when there are seasonal time constraints the optimal development time and final size should vary with time horizons for juvenile growth and development (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Werner and Anholt, 1993; Abrams *et al.*,

1996). In particular the model of (Abrams *et al.*, 1996) has been guiding the research on growth strategies in butterflies that I will turn to in the next section.

GROWTH STRATEGIES OF PARARGINII BUTTERFLIES

The butterfly tribe Pararginii (Satyrinae: Nymphalidae) contains species that are common and widespread over most of Europe (*Pararge aegeria*, *Lasiommata megera*, *L. maera*) as well as species that are more patchily distributed (*L. petropolitana*, *Lopinga achine*) and island endemics (*P. xiphia* on Madeira and *P. xiphoides* on the Canary islands) (Fig. 1). Several of the species show strong latitudinal variation in voltinism (no. generations/year) where northern populations typically produce one generation per year, Mediterranean populations may have three or more generations per year and populations on subtropical islands (Madeira and the Canary islands) are continuously reproducing without winter diapause (Nylin *et al.*, 1995). The larval hosts of all species are various grasses and in the case of *Lo. achine* also sedges, but there are differences in habitat use ranging from forest living to more open habitats. Within the group there is unusually large variation in diapause stage. Preliminary phylogenetic evidence suggests that pupal diapause has evolved from the ancestral larval diapause one or two times in the group (Weingartner, Wahlberg, and Nylin, in preparation; Fig. 1). One species, *P. aegeria*, also has the very unusual capacity to enter winter diapause in either of two developmental stages (Fig. 1; Shreeve [1986]; Nylin *et al.* [1989, 1995]). The diapause decision is mainly based on the photoperiod, which is the primary cue used for timing "decisions."

Growth strategies and time horizons

The responses in larval growth and development to variation in photoperiod have been investigated in a series of laboratory experiments on several of these species (Wiklund *et al.*, 1983; Nylin *et al.*, 1989, 1993, 1994, 1995, 1996; Gotthard, 1998; Gotthard *et al.*, 1999, 2000). The experiments were all similar in design in that larvae were reared individually on the same host species in climate chambers where conditions could be controlled. The photoperiod is considered a seasonal cue but it is important to bear in mind that the information on seasonal time limitation that is provided by variation in photoperiod depends on whether it is experienced during spring or autumn. In spring before summer solstice short photoperiods indicate an early date and a low level of time limitation while in autumn after summer solstice the same short photoperiod indicates a late date and a high level of time limitation (Fig. 2).

The most general result from all studies is that individual larvae indeed reduce their development times in response to photoperiodic information about time limitation. For example in *L. petropolitana* we have investigated three populations; two from Sweden (Nylin *et al.*, 1996) and one from the French alps (Got-
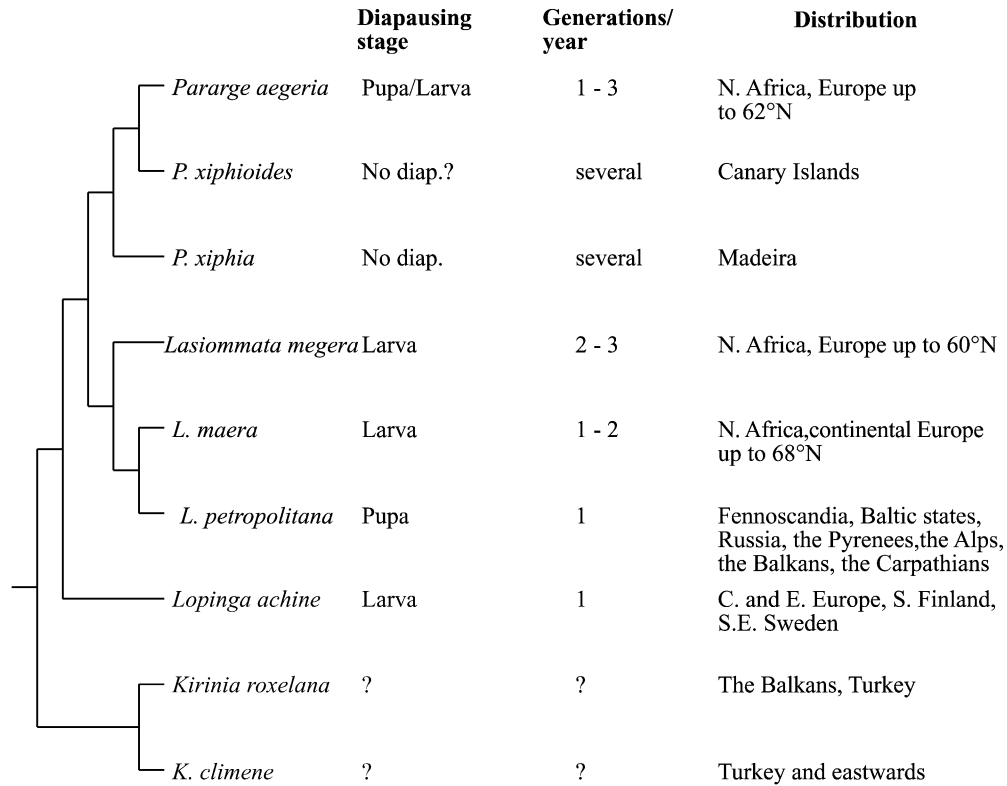
	Diapausing stage	Generations/ year	Distribution
Pararge aegeria	Pupa/Larva	1 - 3	N. Africa, Europe up to 62°N
P. xiphioides	No diap.?	several	Canary Islands
P. xiphia	No diap.	several	Madeira
Lasiommata megera	Larva	2 - 3	N. Africa, Europe up to 60°N
L. maera	Larva	1 - 2	N. Africa,continental Europe up to 68°N
L. petropolitana	Pupa	1	Fennoscandia, Baltic states, Russia, the Pyrenees,the Alps, the Balkans, the Carpathians
Lopinga achine	Larva	1	C. and E. Europe, S. Finland, S.E. Sweden
Kirinia roxelana	?	?	The Balkans, Turkey
K. climene	?	?	Turkey and eastwards

FIG. 1. A preliminary phylogeny of the European members of the butterfly tribe Pararginii. Mapped onto the tree are the life stages where winter diapause occurs (if they have one), reported number of generation produced throughout Europe, and approximate geographic distribution in Europe.

thard, 1998) that all are univoltine (one generation/ year). This species is a lowland forest species in Scandinavia and N.E. Europe while it is only found at high altitudes in southern Europe (the Alps, the Pyrenees,
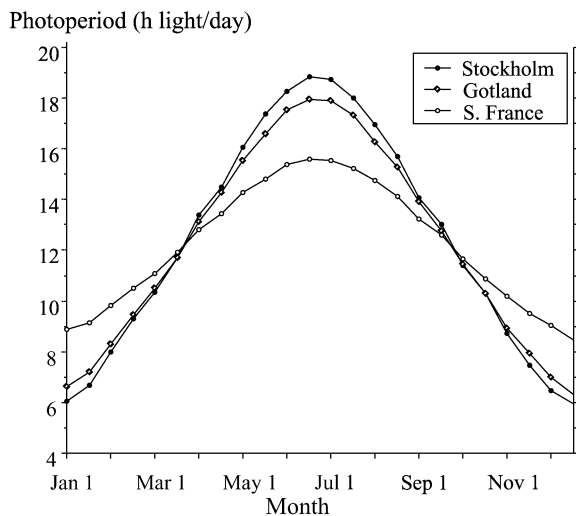

FIG. 2. The yearly variation in photoperiod, excluding civil twilight, at three sites where *Lasiommata petropolitana* has been sampled. It also illustrates the general pattern that a short photoperiod before summer solstice indicates an early date while after midsummer a short photoperiod should be interpreted as a late date in the season.

the Balkans) where summers are short and allow only one generation. In all these populations winter diapause is in the pupal stage, which means that larvae are primarily growing after summer solstice when a short photoperiod indicates a high level of time limitation. In line with this, larval development time decreased with decreasing photoperiod in all three populations (Figs. 3a, 4). This reduction in development time was always coupled with an increase in larval growth rates (Figs. 3b, 4), and in two of the populations (Stockholm and France) there were also associated decreases in pupal weight (Fig. 3c). It is also interesting to note that there seems to be a latitudinal trend in the reaction norms in that at a given photoperiod the more northern populations grow faster. This suggests that a given photoperiod represents a greater time limitation in more northern areas, which is well in line with the fact that when moving northwards, a given photoperiod indicates increasingly later dates (Fig. 2; a 15 hr daylength occurs in the French population on 24 July, on the island of Gotland on 17 August and in Stockholm on 22 August). The difference between the French and the two Swedish populations is likely to indicate local adaptation in relation to variation in photoperiodic regimes (Gotthard, 1998).

An example of a more complex growth strategy was evident in *L. maera* (a close relative of *L. petropolitana*), which is also univoltine in Sweden but can only

A) Larval development time (days)

B) Relative growth rate (%/mg*day)
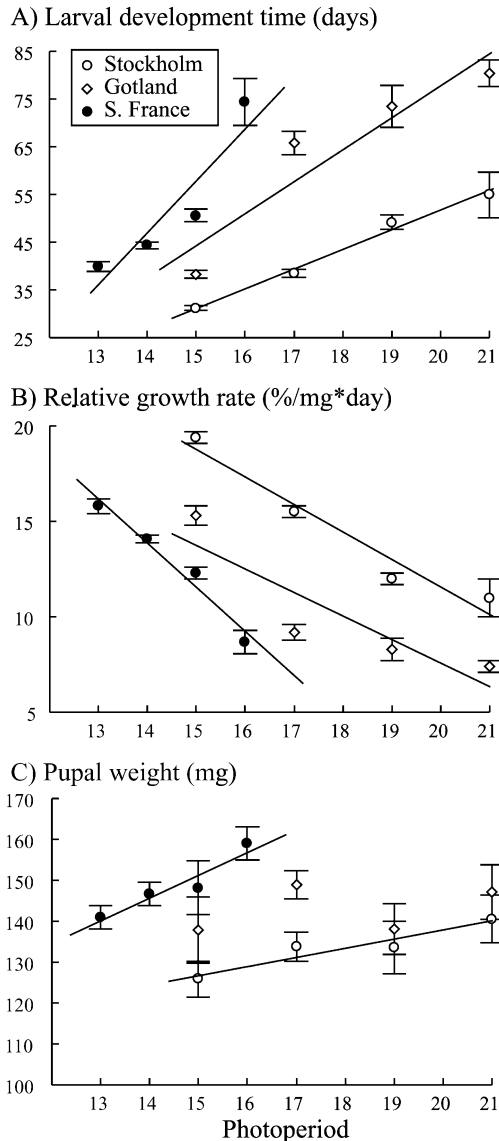

C) Pupal weight (mg)

FIG. 3. The responses in A) larval development time, B) growth rate and C) pupal weight to variation in the photoperiod experienced during development in three populations of *L. petropolitana* (means ± 1 SE). Only males are plotted but females behaved qualitatively similar. The effect of photoperiod was significant for all traits and populations except in the case of pupal weight in the population from Gotland (figures redrawn from Nylin *et al.*, 1996 and Gotthard, 1998).

enter winter diapause as a half grown larva (Gotthard *et al.*, 1999). This type of life cycle includes two separate growth periods: the first in late summer/autumn prior to diapause and the second in spring after diapause. Hence, all individuals face two different timing problems as larvae: first, to reach the third larval instar and enter diapause at some relevant date in autumn, and second, to break the diapause, grow and pupate in order to emerge as adults at an appropriate time in summer. If individual larvae in this species are selected to use the photoperiod for adjusting growth and development both in autumn and in spring, they must be
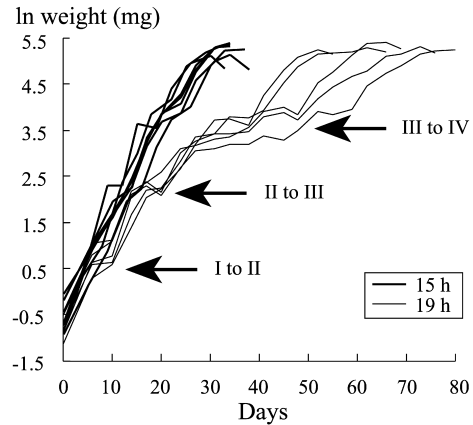
ln weight (mg)

FIG. 4. Example of individual growth trajectories of Pararginii butterflies, taken from an experiment on *L. petropolitana* from Gotland (Nylin *et al.*, 1996). For clarity only two photoperiods are shown and arrows indicate where the three moults occurred. A comparison between daylength treatments suggests that larvae made some decision of what growth trajectory they should follow before the second instar. Despite the difference in growth rates all individuals in both treatments followed the same general developmental pathway and entered diapause in the pupal stage.

able to interpret a given range of photoperiods differently during the two growth periods. The reaction norm relating larval development time to photoperiod before diapause (late summer/autumn growth period) was expected to have a positive slope since during this period shorter photoperiods indicate later dates and less time available, which should induce shorter development times (short photoperiod—short development time). However, after diapause in spring the same reaction norm should have a negative slope because photoperiods are increasing with time and a longer photoperiod indicates less time available and should induce a short development time (long photoperiod—short development time). A laboratory experiment where we followed a cohort of *L. maera* larvae during both growth periods did indeed show this pattern and that the slope of the reaction norm changed within individuals during their life (Fig. 5). The results suggest that the interpretation of photoperiod in this species is state-dependent, where the state variable may be something internal that gives information about growth period such as larval size, instar or just whether the individual has experienced diapause or not. The difference in response between the two growth periods also clearly shows that larvae are reacting on the information on seasonal progression that is given by the photoperiod and not the photoperiod itself. That is, although the response in relation to photoperiod was qualitatively different in the two growth periods (Fig. 5), they were indeed very similar in relation to the information on time horizon (less time available—faster development).

In a third species, *Lo. achine*, with the same type of life cycle as described for *L. maera* we found a slightly different response (Gotthard *et al.*, 1999). Larval development was only regulated in response to
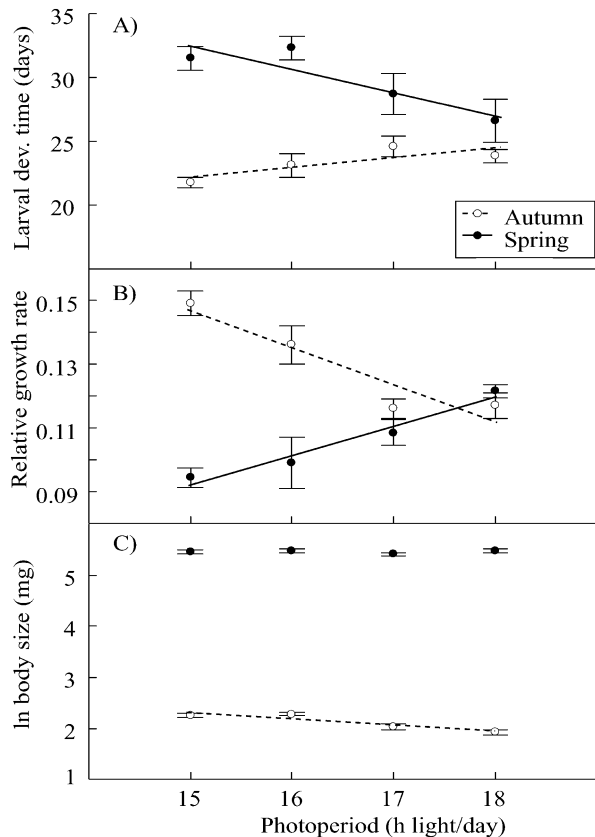
FIG. 5. The effect of photoperiod on A) larval development time, B) growth rate, C) ln final size (size at larval diapause and pupa, respectively), for the same cohort of *L. maera* grown first in autumn before diapause and then in spring after diapause (means ± 1 SE). The interaction between photoperiod and seasonal state (autumn or spring) was significant in all three cases, an indication that the interpretation of photoperiod was state-dependent (Gotthard *et al.*, 1999).
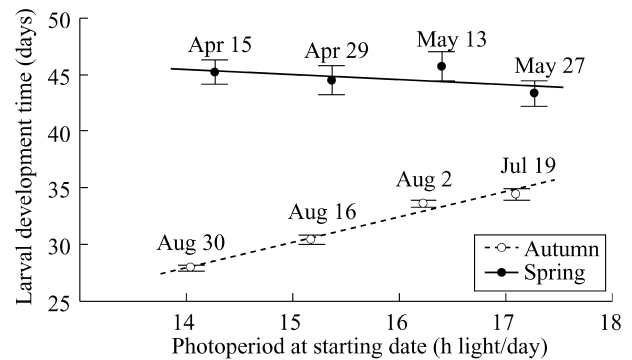

FIG. 6. The effect of photoperiod treatment on larval development time before and after larval diapause in *Lo. achine* (means ± 1 SE). To mimic the field situation, naturally changing photoperiods were used during both seasons in this experiment (decreasing in autumn and increasing in spring). The starting dates each treatment was programmed to simulate are given in the figure. The interaction between photoperiod and seasonal state was significant for larval development time and growth rate but not for final sizes. The slope of the reaction norm in spring was not significantly different from zero for any trait (Gotthard *et al.*, 1999).

photoperiod during the first growth period in autumn, whereas post-diapause larval development was insensitive to a large range of photoperiodic regimes (Fig. 6). In this species the slope of the development time–photoperiod reaction norm thus changed from positive to zero between seasons and larvae apparently do not use the information provided by photoperiod during spring growth.

One potential explanation for why there is a difference between *L. maera* and *Lo. achine* in how they react to photoperiod in the spring may be related to differences in patterns of voltinism. Further south in Europe *L. maera* typically has more than one generation per year and in a transition area where there is time for an additional generation in some years (partial bivoltinism) there may be a very high pay-off on the ability to use the available time efficiently these particular years. The type of reaction norm displayed by *L. maera* in spring would enhance this ability. It is likely that the largely univoltine populations of *L. maera* in Sweden have originated from partially bivoltine populations further south, and if given very long photoperiods during larval development also the Swedish

L. maera develops directly. In contrast, *Lo. achine* appears to be univoltine throughout its geographic range and the population investigated here never develops directly even in extreme laboratory conditions.

An alternative way of using photoperiod information during the two growth periods in autumn and in spring would be for larvae to be able to sense the direction of change in the photoperiod (increasing in spring, decreasing in autumn). In that case a state-dependent interpretation of photoperiod as was documented here would be unnecessary. There are indeed a number of insects where it has been shown that diapause induction/termination depends on the direction of change in the photoperiod (Tauber *et al.*, 1986; Nylin, 1989). However, in the experiments with *Lo. achine* we tested the effects of changing photoperiods and there was no qualitative difference between constant and naturally changing photoperiods (Gotthard *et al.*, 1999). The effect was instead that in the naturally changing photoperiods the variation within daylength treatments was generally smaller, possibly indicating that the developmental decisions were made with less error in these more natural conditions. This last observation suggest that in experiments as these the use of naturally changing photoperiod should be preferred, since the responses are likely to be more adequate in relation the natural situation and interpretation of results will be more unambiguous. The relative benefits of a state-dependent strategy and being able to sense the change in photoperiod are basically unexplored in a more general context. Further theoretical and empirical studies are needed to be able to predict when one strategy will be superior to the other.

Individual state and temperature dependence of growth

In a further study of the growth strategy of *L. maera* we investigated how variation in temperature during

growth could influence growth decisions of larvae (Gotthard *et al.*, 2000). The study was motivated by results showing that juvenile growth rates often increase faster with temperature in populations of ectotherms that experience high levels of seasonal time limitations than in populations that experience lower levels of time limitation (Conover and Schultz, 1995; Schultz *et al.*, 1996; Nylin and Gotthard, 1998). By applying a state-dependent approach (*cf.*, Houston and McNamara, 1992; McNamara and Houston, 1996) we investigated if variation in time limitation between individual larvae of *L. maera* could influence the relationship between growth rate and temperature in a manner analogous to what has been found in populations comparisons.

The results basically verified that the relationship between larval growth rate and temperature was state-dependent in *L. maera*. Individuals that experienced high levels of time limiation (manipulated by variation in photoperiod) showed a faster increase in growth rates with increasing temperatures than did individuals that experienced a lower level of time limiation (Fig. 7). This pattern was evident during both periods of larval growth and the experiments showed that the relevant state variable was indeed the information on time limitation given by the photoperiod and not photoperiod per se (Fig. 7, in autumn the faster increase in growth was found at the short photoperiod while in spring it was found at the longer photoperiod). The main mechanism behind these patterns appears to be that individuals that experienced little time limitation did not use the growth opportunity given by higher temperatures to its full potential and "chose" not to maximize growth (Fig. 7, large differences at high temperatures). On the other hand, individuals that experienced a shortage of time probably could not grow faster at the lower temperatures due to thermodynamic constraints (Fig. 7, small differences in low temperatures).

One general implication of these results relates to the use of degree-days in studies of developmental and growth processes. Degree-days are often used to express the developmental period as the cumulative sum of degrees above a critical low temperature threshold (where development is predicted to cease) that is needed to complete a given developmental stage. The use of degree-days to express developmental rates is motivated by the fact that temperature affects developmental processes and that degree-days may therefore be a better measurement of physiological time (Ratte, 1985; Blanckenhorn, 1997). If, however, adaptive state-dependent effects of the relationship between developmental rates and temperature are common, the use of degree-days may introduce new problems. This is because a given change in temperature will not produce the same developmental responses in individuals that differ in relevant state variables (Gotthard *et al.*, 2000).
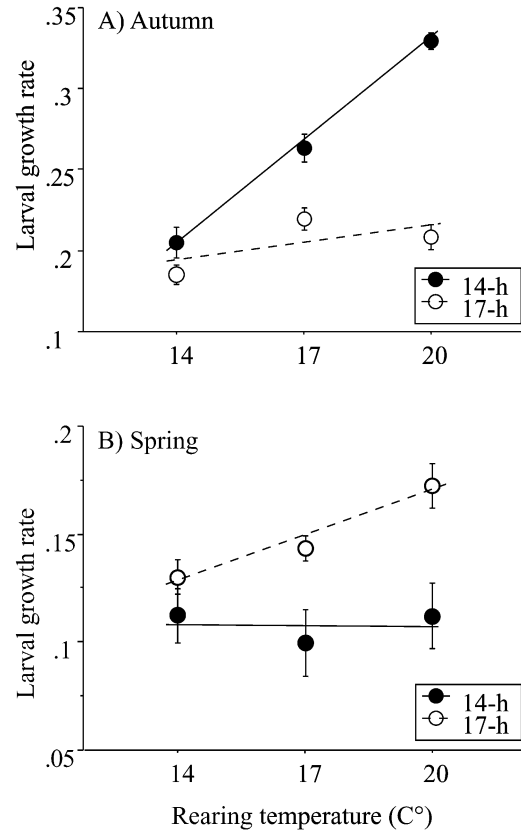

FIG. 7. The relationship between larval growth rates and temperature in *L. maera* that experience different degrees of seasonal time limitation (the photoperiod treatment) during autumn and spring growth, respectively. In autumn the shorter photoperiod (14 hr) indicates a high level of time limitation while in spring the same photoperiod indicates a low level of time limitation. The interaction between photoperiod and temperature was highly significant in autumn and close to significant in spring ($P = 0.07$). During both seasons larvae that experience a higher level of time limitation increased their growth rates faster with an increase in temperature. This indicates that the individual state of time limitation influences the relationship between larval growth and temperature (Gotthard *et al.*, 2000).

Costs of growth rate

The presence of adaptive plasticity in juvenile growth rates suggests that there should be costs of growing fast, and there is empirical support for this notion in a wide range of animals (see reviews in Sibly and Calow, 1986; Lima and Dill, 1990; Werner and Anholt, 1993; Arendt, 1997; Nylin and Gotthard, 1998; Gotthard, 2001). In *P. aegeria* there is experimental evidence that a high larval growth rate may be costly in terms of lower starvation endurance (Gotthard *et al.*, 1994) and higher predation risk (Fig. 8, Gotthard, 2000). These types of costs of high growth rates have also been documented in other insects (Stockhoff, 1991; Chippindale *et al.*, 1996; Bernays, 1997; Blanckenhorn, 1998) as well as other ectotherms (Anholt and Werner, 1998; Munch and Conover, 2003, 2004).
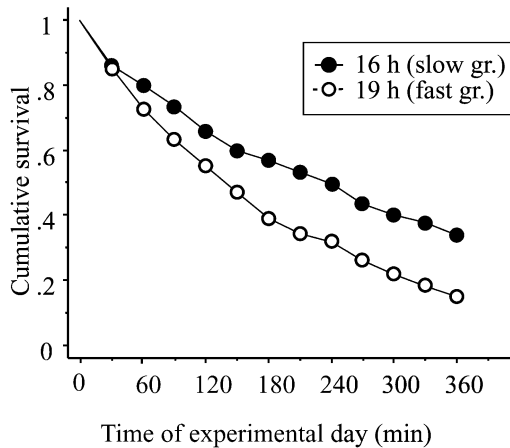
FIG. 8. Cumulative survival of third instar larvae of *P. aegeria* subjected to predation individually by the heteropteran bug, *Picromerus bidens*. Results are from a laboratory experiment testing the relationship between larval growth rate and predation risk (Gotthard, 2000). Larvae that previously had been reared in a 19 hr photoperiod (open circles) had approximately a four times higher growth rate than their siblings from a photoperiod of 16 hr. The fast growing larvae suffered an approximately 30% higher daily predation risk. The functions are averages of 10 experimental days including in total 178 predation trials.

LIFE HISTORY THEORY AND OPTIMAL BODY SIZE

In all experiments where development time decreased with increased time limitation there was always an associated increase in larval growth rate along the same axis, while the effects on final size were variable and mostly not significant. Hence, in all species of Pararginii investigated so far, shorter development times were achieved by increasing growth rates rather than by terminating development at smaller sizes. On the other hand, when there was a low level of time limitation individuals typically reduced their growth rates rather than trying to reach larger final sizes (*e.g.,* Figs. 3, 5).

There are some models of optimal age and size at maturity that specifically built in adaptive variation in juvenile growth by invoking a trade-off between growth and mortality (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Werner and Anholt, 1993; Abrams *et al.*, 1996). These models typically predict that growth rate should vary with the time horizon for growth, so that with less time available individuals should take greater risks to achieve higher growth rates. However, the predicted response in final size varies between models and also with specific assumptions of a particular model (*e.g.,* Abrams *et al.*, 1996). For example, the optimal solution will depend strongly on the relationship between adult size and fitness (linear, increasing in an accelerating fashion, decelerating) and on the growth trajectory the animal is following. Hence, to relate the results reviewed here to theory it is of some interest to evaluate what is known about these relationships in butterflies in general and the Pararginii in particular.

Butterfly larvae seem to be able to increase in size exponentially with time and a comparison between species indicates that this general capacity is true for a large range of sizes (Blau, 1981; Nylin *et al.*, 1989, 1996; Wickman *et al.*, 1990; Wiklund *et al.*, 1991; Nylin, 1992; Leimar, 1996; Gotthard *et al.*, 1999; D'Amico *et al.*, 2001; Davidowitz and Nijhout, 2004). Nevertheless, for a specific species of butterfly it often appears that the capacity for exponential growth is reduced at the end of a larval instar (Esperk and Tammaru, 2004). The cause of this pattern is still not well understood; in particular it is unclear to what degree it is due to adaptive growth decisions or to constraint on larval growth (Esperk and Tammaru, 2004). In any case it appears that relatively fast evolutionary changes in growth trajectories and final sizes are possible. For example, in a laboratory colony of the tobacco hornworm (*Manduca sexta*) the average body size increased by approximately 50% after 30 years of laboratory evolution (D'Amico *et al.*, 2001). This change in body size was largely explained by an increase in larval growth rate and by an increase in the critical weight in the last instar where metamorphosis is initiated (D'Amico *et al.*, 2001). Wickman *et al.* (1990) showed that at the size where one butterfly species stops growth and pupates, another related species might continue exponential growth even if they use the same host plant. Likewise, among the three species of the genus *Pararge* (Fig. 1) there is an approximately two-fold difference in adult size (*P. aegeria* smallest and *P. xiphia* largest, K. Gotthard, unpublished) and larval growth is exponential also in the last instar of the largest species. These examples indicate that evolution towards substantially larger sizes, by changes in growth trajectories, may often be possible in relatively short evolutionary time scales.

Laboratory estimates of lifetime fecundity in butterflies indicate that it may increase by a positive allometric relationship with female body size (a power function with an exponent larger than 1, Blau, 1981; Jones *et al.*, 1982; Karlsson and Wickman, 1990) and this appears often to be the case in other ectotherms (reviewed in Roff, 1992). The study of Karlsson and Wickman (1990) was performed on *P. aegeria* suggesting that such a relationship is likely to be present also in the Pararginii (exponent = 3.6). Hence, the present knowledge indicates that butterflies (and many other insects) may increase in size exponentially (or at least at a substantial rate) also beyond their typical size range, and that female fecundity increases by a positive allometric relationship with final size. This situation makes it hard to understand why individual larvae of the Pararginii and several other butterfly species seem not to use "extra time" to increase in final size (Abrams *et al.*, 1996; Leimar, 1996). The characteristic response is instead what has been documented here: "extra time" is used to reduce larval growth rate.

Leimar (1996) discussed some circumstances that could explain the lack of variation in size when the time horizon for larval growth increases. For instance, larval mortality may be strongly size dependent so that

above a certain size, foraging becomes increasingly dangerous. Larvae that continue growth well above the ''normal'' size for the species may, for example, quickly become more conspicuous on the structures they feed on and may therefore suffer substantially higher rates of predation than larvae that are within the ''normal'' size range. The empirical support for this mechanism is weak so far and rates of natural mortality appear not to be necessarily higher in later larval instars (*e.g.,* Kristensen, 1994). However, a really stringent test would require an estimation of the predation risk of larvae that are somehow manipulated to become considerably larger than the normal size range.

Another potential explanation could be that laboratory estimates of the relationship between potential lifetime fecundity and female body size are poor in predicting the fecundity that females typically can realize in the field (Leather, 1988). The estimation of the fecundity-size relationship is usually done in conditions that are designed to allow females to fully realize their potential fecundity. A big discrepancy between potential and realized fecundity seems not unlikely since it is reasonable to assume that natural conditions are more demanding than the standard laboratory environment and that life-time expectancy is lower in the field than in the laboratory (Leather, 1988). If so, it is possible that the relationship between realized fecundity and female size typically follows some decelerating relationship whereby a continuously larger size has diminishing returns in terms of fecundity. However, in a field study of the fecundity-size relationship in the lymantriid moth genus *Orgyia* Tammaru *et al.* (2002) showed that fecundity increased linearly with size also at natural conditions and there was no sign of diminishing returns. It should be noted that the life history of this genus is somewhat extreme; females are wingless and remain on their cocoons during their short adult lives and all eggs are typically deposited on the cocoon. It can indeed be expected that the link between potential and realized fecundity should be particularly strong in extreme capital breeders such as *Orgyia*. However, along the continuum from capital to income breeding the link between potential and realized fecundity is expected to become weaker as a number of adult activities is likely to obscure this correlation (Tammaru and Haukioja, 1996). For example, many of the factors that could improve the relative performance of small butterfly females may be flight related: *e.g.,* agility, predator avoidance and a lower thermal threshold for activity allowing oviposition and feeding. Preliminary data on the size-fecundity relationship in *P. aegeria* suggest that a more demanding temperature environment may produce a diminishing returns pattern (K. Gotthard and D. Berger, unpublished data). With the assumption of a decelerating relationship between fitness and size, some life history models can indeed predict adaptive plasticity in size, development time and juvenile growth rate in response to variation in time horizons that is similar to the empirical patterns found in the Pararginii and some other butterflies (Abrams *et al.*, 1996).

In a review of body size evolution (Blanckenhorn, 2000) identified the central question as ''what keeps organisms small?'' and concluded that despite of theoretical arguments and several suggested costs of a large adult size there is a substantial lack of empirical evidence for the various mechanisms suggested in the literature. At present there is some evidence for costs of *becoming big* (mortality costs of a long juvenile period and high growth rates), but both theory and empirical patterns suggest that there may also be costs of *being big*. To demonstrate these costs empirically will be an important task in insect life history biology.

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