Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly

KARL GOTTHARD

Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden

Summary

1. Life history theoreticians have traditionally assumed that juvenile growth rates are maximized and that variation in this trait is due to the quality of the environment. In contrast to this assumption there is a large body of evidence showing that juvenile growth rates may vary adaptively both within and between populations. This adaptive variation implies that high growth rates may be associated with costs.

2. Here, I explicitly evaluate the often-proposed trade-off between growth rate and predation risk, in a study of the temperate butterfly, *Pararge aegeria* (L.).

3. By rearing larvae with a common genetic background in different photoperiods it was possible to experimentally manipulate larval growth rates, which vary in response to photoperiod. Predation risk was assessed by exposing larvae that were freely moving on their host plants to the predatory heteropteran, *Picromerus bidens* (L.).

4. The rate of predation was significantly higher in the fast-growing larvae. An approximately four times higher relative growth rate was associated with a 30% higher daily predation risk.

5. The main result demonstrates a trade-off between growth rate and predation risk, and there are reasons to believe that this trade-off is of general significance in free-living animals. The results also suggest that juvenile development of *P. aegeria* is governed by a strategic decision process within individuals.

Key-words: age and size at maturity, growth strategy, life history theory, predation risk, trade-off.

Journal of Animal Ecology (2000) **69**, 896–902

Introduction

Age and size at sexual maturity are fundamental life history traits and in most organisms they are closely related to fitness (Roff 1992; Stearns 1992). The possible combinations of age and size at maturity for a particular individual is constrained by its juvenile growth trajectory, of which growth rate is a key element. Most work investigating variation in age and size at maturity have, explicitly or implicitly, assumed that selection favours maximal juvenile growth rate (Roff 1992; Stearns 1992). The benefit of growing fast is obvious because, all other things equal, a shorter juvenile period will give a higher probability of surviving to reproduction (Roff 1992; Stearns 1992).

Despite these considerations, there is evidence that organisms often grow at a lower rate than they are physiologically capable of, and that genetic variation for growth rate is often present within and between populations (Arendt 1997). Thus, it appears that the optimal growth rate in a particular environment is not necessarily equal to the maximum possible. This observation predicts that high juvenile growth rates carry fitness costs, and that in certain circumstances it is beneficial for individuals to avoid these costs by growing more slowly. Hence, juvenile growth patterns would then the be the result of 'strategic decisions' where the costs and benefits of alternative growth trajectories are balanced against each other (Case 1978; Sibly & Calow 1986; Abrams *et al*. 1996; Arendt 1997; Nylin & Gotthard 1998; Gotthard 1999).

Explicit studies of the costs of high growth rates are rare and trade-offs with growth rate are poorly known (Arendt 1997). Some selection experiments with *Drosophila melanogaster* have found a genetic

Present address and correspondence: University of Neuchatel, Institute of Zoology, Rue Emile-Argand 11, CH-2007 Neuchatel, Switzerland, Fax: +41 32 7183001, E-mail: Karl.Gotthard@zool.unine.ch

correlation between larval growth rate and larval survival (Chippindale *et al.* 1997), while others did not (Zwaan, Bijlsma & Hoekstra 1995b). Two studies of butterflies report that fast-growing larvae have a lower starvation endurance (Stockhoff 1991; Gotthard, Nylin & Wiklund 1994), while in a third butterfly species this relationship could not be detected (Gotthard 1998). In *Drosophila* there is evidence that high juvenile growth rates are associated with a lower adult longevity (Sevenster & VanAlphen 1993; Chippindale *et al.* 1994) but again there is contrasting evidence (Zwaan *et al.* 1995a, b). It should be noted that not all of the above studies were directly designed to investigate costs of high growth rates and that there are methodological differences between them, which may explain some of the discrepancies. Moreover, physiological trade-offs are due to the allocation of limited resources to different demands within individuals. It is possible that the multitude of physiological demands within individuals create a large scope for variation in the set of optimal allocation rules. If so, it could be expected that the structure of physiological trade-offs will show relatively large variation across species and populations.

In contrast, there may be a more fundamental trade-off between growth rate and predation risk since they are both functions of activity level in a wide range of organisms (see References in Lima & Dill 1990 and Werner & Anholt 1993). Typically, high growth rates necessitate high foraging activity, which in turn increases the exposure to predators. Here, I address the general question of what factors may be important for the evolution of optimal growth strategies, by explicitly testing if there is a positive relationship between growth rate and predation risk in a temperate butterfly, *Pararge aegeria* (Nymphalidae, Satyrinae).

Larval growth rates of *P. aegeria* and several of its closest relatives are highly plastic in relation to the daylength they experience during the larval period (Nylin, Wickman & Wiklund 1989, 1995; Nylin, Gotthard & Wiklund 1996; Gotthard 1998; Gotthard, Nylin & Wiklund 1999). The patterns of plasticity agree closely with adaptive predictions of life history models. As a consequence, larvae of these species do not grow at their physiologically maximal rates unless an apparent time limit forces them to do so. This pattern predicts that high larval growth rate in *P. aegeria* is associated with costs.

Materials and methods

THE PREY AND ITS LIFE HISTORY

The speckled wood butterfly, *P. aegeria*, is widely distributed throughout Europe, Asia and northern Africa. The larvae feed on grasses from several genera and have a green coloration that makes them cryptic on their food plants. The butterflies used in this study originate from a bi-voltine population in southern Sweden. In long daylengths ($\geqslant 17$ h light day^{-1}), corresponding to midsummer conditions, all individuals grow fast and develop directly to reproduction, while in slightly shorter daylengths (16–17 h light day^{-1}), corresponding to late summer conditions, larvae grow very slowly during the third instar and enter winter diapause in the pupa. In even shorter daylengths (14–16 h light day^{-1}) there is a gradual increase in growth rates with decreasing daylengths, and these individuals survive the winter in pupal diapause (Nylin *et al.* 1989). The interpretation of this pattern is that larvae in intermediate daylengths (16–17 h light day^{-1}) do not have time to complete an additional generation successfully, but compared to individuals in short daylengths (14–16 h) they have surplus time to reach the pupal stage before winter (Nylin *et al.* 1989).

THE PREDATOR

Picromerus bidens is a heteropteran bug in the family Pentatomidae and late instar nymphs and adults are generalist predators on insect larvae. Larvae of Lepidoptera and the beetle family Chrysomelidae are eaten most frequently but other insects are also caught (Southwood & Leston 1959; Stehlik 1987). It is a stalking predator and during the experiments no individual was observed to fly. They kill and feed on their prey by inserting the rostrum through the cuticle of larvae and sucking out the internal tissues, which may take several hours. The individuals that were used in the experiment were collected in the Stockholm area during early September.

EXPERIMENTAL PROCEDURE

Ten field-collected *P. aegeria* females were allowed to oviposit together in one cage in the laboratory. Over 10 days, eggs were collected on a daily basis and on the day of hatching larvae were put in pairs in plastic jars where the grass *Dactylis glomerata* was cultured. The jars were split between two daylength treatments, 16 h light: 8 h dark, or, 19 h light: 5 h dark, in incubators set a temperature of 17 °C (hereafter referred to as 16 h and 19 h daylengths). The 16 h daylength induces slow growth during the third instar while the 19 h daylength induces direct development and fast growth in all instars (Nylin *et al.* 1989 and this study). These two groups of larvae were used in the predator experiment. In addition, 10 individuals in each treatment were reared individually during the entire larval period to quan-

tify differences in growth rates. These larvae were weighed at days 0, 5 and 10 of development, and after day 10 they were weighed every day.

In total, 10 days of predator experiments were conducted, and to reduce potentially confounding differences among larvae in traits other than growth rate (i.e. size) only third instar larvae were used in the predation trials. The day prior to an experiment, larvae from both daylength treatments were weighed and put singly on large tufts of *D. glomerata*. The grass tufts were cultured in pots and had been cut to be of approximately equal size (leaf length up to 30 cm). During the following night these larvae-containing plants were placed in incubators with daylength regimes corresponding to what the larvae had experienced earlier. This gave larvae approximately 16 h to find the preferred positions in the grass and reduced the stress levels due to handling. All larvae were located visually on the tuft in the next morning, and each plant was then placed in a separate cage (0·5 × 0·5 × 0·5 m). The plants were placed in the centre of the cages and were raised 20 cm above the cage floor. The experiment was started by introducing one *P. bidens* individual in each cage, and during the experimental day (6 h long) each cage was inspected every 30 min. Since *P. bidens* suck on a third instar larva for at least 30 min this procedure ensured that all successful predation attempts could be detected with a time resolution of 30 min. If a *P. bidens* female started to oviposit during the experiment it was replaced. At the end of each experimental day the surviving larvae were weighed, and if a larva was not found the trial was excluded from the results. The predators were removed from the cages and were kept individually in plastic cups until they were used in another experiment. During the experiments, 52 individuals of *P. bidens* were used. In a typical experimental day 10 larvae of each daylength treatment were run in parallel with two control larvae from each daylength. In all, 24 cages were used simultaneously and they were all standing in the same room where there was no natural daylight. Each cage was lit with a separate 75 W incandescent lamp. The lighting regime was chosen to minimize the risk of uncontrolled light sources biasing predator or prey movement in the cages. The temperature was measured every hour in three randomly chosen cages every day of experiments (mean ± 1 SD was 25·3 ± 1·4 °C). The controls were given the same treatment as the experimental larvae except that they were not subjected to a predator. The purpose of the controls was to investigate the average change in larval weight during an experimental day and to estimate daily mortality in the absence of predators. During 10 days of experiments a total of 95 larvae from each daylength regime was subjected to the predator treatment and from each daylength there were 16 controls.

DATA MANAGEMENT AND STATISTICAL TREATMENT

Butterfly larvae typically grow exponentially (Wickman, Wiklund & Karlsson 1990; Gotthard *et al.* 1994; Leimar 1996), and their growth trajectories can be approximated with the function, $W(t) = a\mathrm{e}^{bt}$, where W is the weight at time t, and b is the relative growth rate while a is the start weight. The relative growth rate (b) before and during the third larval instar was estimated by fitting this function to the individual growth trajectories of the 20 frequently weighed larvae. The relative change of weight ($\Delta \ln(W)$) of controls and surviving larvae in the predation experiment was calculated according to the formula, $\Delta \ln(W) = \ln(W_{end}) - \ln(W_{start})$. Since the time unit for the measurement is 1 day, $\Delta \ln(W) = b$ from the growth equation.

Differences between daylength treatments in predation risk were analysed first on the total material using a 2 × 2 table. Survival analysis was used to analyse further potential differences in predation rates. The statistical techniques of survival analysis allow the dataset to include both uncensored and censored observation (StatView 5·0, reference guide 1998). In this study all individuals that survived an entire experimental day were coded as right censored observations. Kaplan–Meier survival curves was estimated for each group and differences between categories in mortality pattern was investigated by a log-rank test. Experimental day was used as a stratification variable to correct for potential variation between days.

Results

GROWTH TRAJECTORIES

There were no significant differences between the daylength treatments in growth trajectories before they entered the third larval instar (Table 1). Thereafter, the 16 h larvae grew much slower than 19 h larvae. During the third instar the 19 h larvae grew 3·6 times faster than the 16 h larvae (Fig. 1, Table 1).

GROWTH AND MORTALITY OF CONTROLS

Two control larvae (one from each daylength treatment) started moulting during the day of experiment and were therefore excluded from the growth comparison. The weight gain of controls during 1 day in 'predator-free experiment conditions' indicated similar growth rate differences between 19 h and 16 h larvae, but did not attain statistical significance (means ± 1 SE for 19 h = 0·032 ± 0·016, and for 16 h = 0·008 ± 0·008, $N = 15$ in both cases, ANOVA: $F_{1,28} = 1·79$, $P = 0·19$). When the controls and the surviving larvae were pooled there was a significant difference between daylength treatments in weight gain during the day of experiment (means ± 1 SE

Table 1. Characteristics of the growth trajectories (mean ± 1 SE) before and after moulting to the third larval instar. The ANOVA results refer to differences between daylength treatments and $N = 10$ within each treatment

Trait	16 h daylength	19 h daylength	Result of ANOVA
Time to third instar (days)	15·9 ± 0·7	14·8 ± 0·5	$P = 0·19$
Weight at start of third instar (mg)	9·5 ± 0·6	9·2 ± 0·6	$P = 0·76$
Relative growth rate before third instar	0·226 ± 0·008	0·245 ± 0·008	$P = 0·12$
Relative growth rate during third instar	0·091 ± 0·008	0·330 ± 0·013	$P < 0·001$

for 19 h = $0·054 ± 0·013$, $N = 29$, and for 16 h = $0·006 ± 0·005$, $N = 46$, ANOVA: $F_{1,73} = 16·01$, $P < 0·001$). None of the 32 control larvae died during the experiment.

PREDATION RISK

After excluding missing larvae and larvae that started to moult to the fourth instar during the predation experiments there were in total 178 predation trials (91 from 16 h and 87 from 19 h). The average risk of predation during the experiment was significantly higher for the fast-growing larvae from the 19 h treatment compared to the slower-growing larvae from the 16 h treatment (Table 2).

Survival analysis showed that the predation rate was significantly higher in the faster-growing 19 h larvae than in the more slowly growing 16 h animals (Fig. 2, log-rank test for difference between the daylength categories stratified by experimental day, $\chi 2 = 8·53$, d.f. = 1, $P < 0·01$). Predation rates were more or less constant in both categories throughout the day (Fig. 2b, approximately linear relationships between cumulative predation rate and time), but in the 19 h treatment predation rates was consistently higher (steeper slope in Fig. 2b).
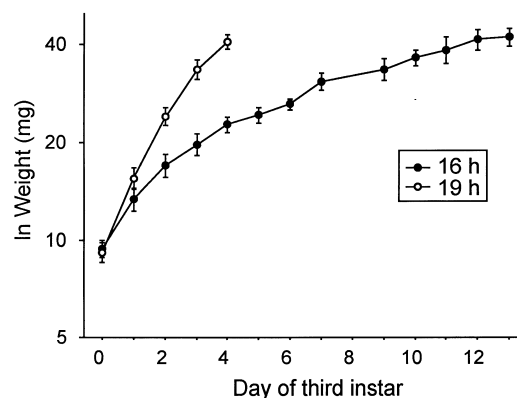
Fig. 1. Average growth trajectories of both daylength treatments during the third instar (daily means ± 1 SE). The trajectories end on the day the first individual in each treatment started to moult into the fourth instar.

There was a small but significant difference between daylength categories in the weight of larvae that were included in the predation experiment (mean ± 1 SE for 19 h = $21·5 ± 0·9$ mg, $N = 87$, and for 16 h = $24·5 ± 0·9$ mg, $N = 91$, ANOVA: $F_{1,176} = 5·30$, $P < 0·05$). However, there was no indication that larval weight influenced the risk of predation (mean ± 1 SE for survivors = $23·9 ± 1·4$ mg, $N = 44$, and for killed = $22·8 ± 0·8$ mg, $N = 134$, ANOVA: $F_{1,176} = 0·52$, $P = 0·47$).

Discussion

The results strongly suggests that there is a trade-off between juvenile growth rate and predation risk in *P. aegeria*. The faster-growing larvae from the 19 h treatment were more likely to be killed by a generalist predator compared to their more slowly growing siblings raised in a 16-h daylength (Table 2). The patterns of cumulative mortality rate indicate that the fast-growing 19 h larvae experienced higher predation rates, per unit time, throughout most of the day (Fig. 2b), and the daily predation risk was on average 30% higher in the 19 h animals (Table 2). There was no evidence that larger larvae were more susceptible to predation. However, the experimental design reduced variation in the size of larvae included in the predation experiment and larger differences in size might still be of importance for the risk of detection and predation by *P. bidens*.

During the third instar, larvae of *P. aegeria* from southern Sweden grew considerably faster in a 19-h daylength than when reared in a 16-h daylength (Fig. 1, Table 1). Although inclusion in the predation experiment reduced larval growth rates relative to the incubator environment, there was still a large difference between daylength treatments. Since the reduction in growth rates was evident both in the controls and in the surviving larvae it seems not to be related to the presence of predators. It is more likely to be due to the handling of larvae during the experiment, and to the difference in environmental conditions between the experimental cages and the climate chambers.

Estimates of natural predation risks of butterfly larvae are rare but Kristensen (1994) found an average daily predation risk of 0·14 during the total lar-

Table 2. Results of the predation experiment showing the difference between daylength treatments in absolute numbers and the average risk of predation during a 6 h day ($N = 10$ days)

| Daylength treatment	Total no. of killed vs. surviving larvae	Mean daily predation risk (± 1 SE)
16 h	60 vs. 31	0·66 ± 0·06
19 h	74 vs. 13	0·86 ± 0·05
Test for difference	$\chi^2 = 8\cdot74$, d.f. = 1, $P < 0\cdot01$	ANOVA†: $P < 0\cdot05$

†Analysis performed on arcsine transformed values.

val period of the cabbage butterfly, *Pieris brassicae* (my calculation based on data provided in the paper). A field study of *P. aegeria* in Sweden found that 54% of first instar larvae disappeared during 6 days after hatching from the egg (Bengt Karlsson, unpublished). Assuming that this was mainly due to predation it suggests a daily predation risk of 0·12 on average. The daily predation risk in the present experiment was 0·66 for the slow-growing larvae and 0·86 for the fast-growing larvae (a 30% increase in risk), indicating that larvae in the experiment were put in a very dangerous situation. Nevertheless, natural predation risks are bound to show a large temporal and spatial variation, and instantaneous predation rates close to those in the experiment are clearly conceivable in some natural situations.

Picromerus bidens is only one of many predatory species that may be of significance for the ecology and evolution of *P. aegeria*, and obviously the total level of predation constitutes the relevant selection pressure. Here, *P. bidens* was assumed to be a reasonable model for a generalist, invertebrate predator. This assumption is based on the fact that *P. bidens* feeds on a wide variety of insects from different orders including caterpillars (Stehlik 1987), and is unlikely to have specialized adaptations for detecting a particular prey species. More likely it relies on some combination of visual, tactile and olfactory cues for finding its prey (observations made during this study). This description is also true for a range of other invertebrate and vertebrate predators that may be potentially important for *P. aegeria*. There are no reports of specialist predators or parasitoids on *P. aegeria*. During the investigation of the present population, approximately 50 larvae of various sizes had been caught in the field and reared to pupation in the laboratory, and none had been parasitized (Christer Wiklund, personal communication).

The mechanistic link between growth rate and predation risk was not the prime target of this investigation and no systematic quantification of larval activity was undertaken. Other studies of Lepidoptera have shown that an increase in feeding activity may increase the risk of predation substantially. For example, Bernays (1997) compared the predation risks of Lepidopteran larvae in natural conditions when they were feeding and when they were resting, respectively. The result showed that feeding was
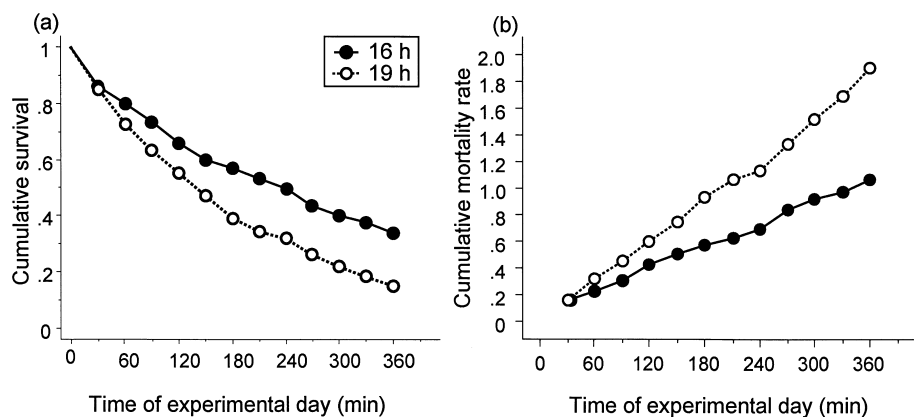
Fig. 2. Results of the predator experiment showing separately for both categories of larvae in (a) cumulative survival, and in (b) the corresponding cumulative mortality rate. Cumulative mortality rate may take values larger than 1, and a linear relationship indicates that the instantaneous mortality rate is constant over time. The difference in slopes indicates that the instantaneous mortality rate differs between treatments. Functions are averages over all experimental days.

three times more dangerous in one species (*Manducta sexta*), while it increased the risk of predation 100 times in another species (*Uresiphita reversalis*). There is empirical evidence that many animals lower their activity levels, and thus their growth rates, when the risk of predation is higher (cf. Lima & Dill 1990; Werner & Anholt 1993). Moreover, an experimental study of larval wood frogs, *Rana sylvatica*, indicated a causal link between decreased activity levels (due to increased food abundance) and a decrease in mortality due to predation (Anholt & Werner 1998). In the present study the instantaneous predation rate was higher for the fast-growing larvae throughout the experimental day, which indirectly complies with the notion that general activity level may be the link between growth and mortality rates.

The fast-growing larvae in this experiment were not forced to their high growth rates by some deterioration of living conditions. More likely, they choose to grow fast because there is a high fitness pay-off on producing an additional generation before the onset of winter. Moreover, fast growth and direct development reduce the total larval period considerably compared with the larvae destined for pupal diapause. A shorter larval period will decrease the risk of mortality during the larval stage *per se* and, in fact, this is the most commonly assumed cost of juvenile development in life history theory (cf. Stearns 1992). The total larval mortality risk (m_{tot}) can be expressed as a function of the average daily survival rate (s) and the larval development time in days (t), so that $m_{tot} = 1 - s^t$. This expression shows that, although the fast-growing larvae in the present experiment are subjected to a high instantaneous mortality risk (s), they may still suffer a lower total larval mortality risk because of their shorter larval development time (t). With respect to the situation of *P. aegeria*, however, it is important to realize that once an individual has chosen diapause development, it has a fixed time period that it has to survive (next reproductive opportunity is in early summer next year). In such a situation it will be especially important to adjust development so that the mortality per unit time ($1-s$) is minimized. Moreover, this type of threshold in time horizons is likely to be commonly occurring in organisms living in seasonal environments.

When high juvenile growth rates are costly, organisms may benefit from being able to vary their growth rates in relation to environmental conditions. Several theoretical investigations suggest that adaptive plasticity in growth rate is likely to arise (Sibly & Calow 1986; Werner & Anholt 1993; Abrams & Rowe 1996; Abrams *et al.* 1996), and there is ample empirical evidence that it is common (Case 1978; Arendt 1997; Nylin & Gotthard 1998). It has been pointed out that to obtain reliable predictions from these models, more has to be known about the relationship between juvenile growth rate and juvenile mortality (Abrams & Rowe 1996; Abrams *et al.* 1996). Since there are reasons to believe that all free-living animals are potentially affected by a trade-off between growth rate and predation risk (references in Lima & Dill 1990 and Werner & Anholt 1993), it is important to explicitly demonstrate and quantify this relationship. When individuals adjust development adaptively, juvenile growth is likely to be governed by some strategic decision process at the level of individual genotypes. The target of selection will be the decision rules that define the growth strategy (Houston & McNamara 1992; McNamara & Houston 1996). The optimal growth strategy will depend on factors such as timing requirements, the relationship between fitness and adult size, and the relationship between growth rate and juvenile mortality. The results presented here support the notion that juvenile development of *P. aegeria* is governed by this type of strategic decision process.

Acknowledgements

References

Abrams, P.A., Leimar, O., Nylin, S. & Wiklund, C. (1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist*, **147**, 381–395.

Abrams, P.A. & Rowe, L. (1996) The effects of predation on the age and size of maturity of prey. *Evolution*, **50**, 1052–1061.

Anholt, B.R. & Werner, E.E. (1998) Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evolutionary Ecology*, **12**, 729–738.

Arendt, J.D. (1997) Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology*, **72**, 149–177.

Bernays, E.A. (1997) Feeding by lepidopteran larvae is dangerous. *Ecological Entomology*, **22**, 121–123.

Case, T.J. (1978) On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology*, **53**, 243–282.

Chippindale, A.K., Alipaz, J.A., Chen, H.-W. & Rose, M.R. (1997) Experimental evolution of accelerated development in *Drosophila melanogaster*. 1. Developmental speed and larval survival. *Evolution*, **51**, 1536–1551.

Chippindale, A.K., Hoang, D.T., Service, P.M. & Rose, M.R. (1994) The evolution of development in *Drosophila melanogaster* selected for postponed senescence. *Evolution*, **48**, 1880–1899.

Gotthard, K. (1998) Life history plasticity in the satyrine butterfly *Lasiommata petropolitana*: investigating an

adaptive reaction norm. *Journal of Evolutionary Biology*, **11**, 21–39.

Gotthard, K. (1999) Life history analysis of growth strategies in temperate butterflies. PhD Thesis, Stockholm University.

Gotthard, K., Nylin, S. & Wiklund, C. (1994) Adaptive variation in growth rate – life history costs and consequences in the speckled wood butterfly, *Pararge aegeria. Oecologia*, **99**, 281–289.

Gotthard, K., Nylin, S. & Wiklund, C. (1999) Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. *Oikos*, **84**, 453–462.

Houston, A.I. & McNamara, J.M. (1992) Phenotypic plasticity as a state-dependent life-history decision. *Evolutionary Ecology*, **6**, 243–253.

Kristensen, C.O. (1994) Investigations on the natural mortality of eggs and larvae of the large white *Pieris brassicae* (L.) (Lep. Pieridae). *Journal of Applied Entomology*, **117**, 92–98.

Leimar, O. (1996) Life history plasticity: influence of photoperiod on growth and development in the common blue butterfly. *Oikos*, **76**, 228–234.

Lima, S. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.

Nylin, S. & Gotthard, K. (1998) Plasticity in life history traits. *Annual Review of Entomology*, **43**, 63–83.

Nylin, S., Gotthard, K. & Wiklund, C. (1996) Reaction norms for age and size at maturity in *Lasiommata* butterflies: predictions and tests. *Evolution*, **50**, 1351–1358.

Nylin, S., Wickman, P.-O. & Wiklund, C. (1989) Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyrinae). *Biological Journal of the Linnean Society*, **38**, 155–171.

Nylin, S., Wickman, P.O. & Wiklund, C. (1995) Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable? *Biological Journal of the Linnean Society*, **55**, 143–157.

Roff, D.A. (1992). *The Evolution of Life Histories*. Chapman & Hall. New York.

Sevenster, J.G. & VanAlphen, J.J.M. (1993) A life history trade-off in *Drosophila* species and community structure in variable environments. *Journal of Animal Ecology*, **62**, 720–736.

Sibly, R.M. & Calow, P. (1986). *Physiological Ecology of Animals: an Evolutionary Approach*. Blackwell Scientific Publications. Oxford.

Southwood, T.R.E. & Leston, D. (1959). *Land and Water Bugs of the British Isles*. Frederick Warne, London.

Stearns, S.C. (1992). *The Evolution of Life Histories*, 1st edn. Oxford University Press, Oxford.

Stehlik, J.L. (1987) Results of the investigations on hemiptera in Moravia made by the Moravian museum (Pentatomoidea VI.). *Acta Musei Moraviae Scientiae Naturales*, **72**, 183–201.

Stockhoff, B.A. (1991) Starvation resistance of gypsy moth, *Lymantria dispar* (L.) (Leipidoptera: Lymantriidae): trade-offs among growth, body size, and survival. *Oecologia*, **88**, 422–429.

Werner, E.E. & Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*, **142**, 242–272.

Wickman, P.-O., Wiklund, C. & Karlsson, B. (1990) Comparative phenology of four satyrine butterflies inhabiting dry grasslands in Sweden. *Holarctic Ecology*, **13**, 238–346.

Zwaan, B., Bijlsma, R. & Hoekstra, H. (1995a) Direct selection on life span in *Drosophila melanogaster*. *Evolution*, **49**, 649–659.

Zwaan, B., Bijlsma, R. & Hoekstra, R.F. (1995b) Artificial selection for developmental time in *Drosophila melanogaster* in relation to the evolution of ageing: direct and correlated responses. *Evolution*, **49**, 635–648.