

Karl Gotthard · Sören Nylin · Christer Wiklund

Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*

Received: 12 April 1994 / Accepted: 10 June 1994

Abstract An important assumption made in most life-history theory is that there is a trade-off between age and size at reproduction. This trade-off may, however, disappear if growth rate varies adaptively. The fact that individuals do not always grow at the maximum rate can only be understood if high growth rates carry a cost. This study investigates the presence and nature of such costs in *Pararge aegeria*. Five females from two populations with known differences in life history (south Sweden and Madeira) were allowed to oviposit in the laboratory and their offspring were reared in environmental chambers under conditions leading to direct development. We measured several aspects of life history, including development times, pupal and adult weights, growth rate, female fecundity, longevity and larval starvation endurance. In both populations there seemed to be genetic variation in growth rate. There was no evidence for a trade-off between age and size at pupation. As predicted, larvae with high growth rates also lost weight at a relatively higher rate during starvation. High weight-loss rates were furthermore associated with a lower probability of surviving when food became available again. This is apparently the first physiological trade-off with growth rate that has been experimentally demonstrated. In both populations there were significant differences in growth rate between the sexes, but the populations differed in which sex was growing at the highest rate. In Sweden males had higher growth rates than females, whereas the reverse was true for Madeira. These patterns most likely reflect differences in selection for protandry, in turn caused by differences in seasonality between Sweden and Madeira. Together with the finding that males had shorter average longevity than females in the Swedish, but not in the Madeira, population, this indicates that a lower adult quality also may be a cost of high growth rate. We argue that for the understanding of life history variation it is necessary to consider not only the two dimensions of age and size,

but also to take into full account the triangular nature of the relationship between size, time and growth rate.

Key words Physiological trade-off · Size and age at maturity · Starvation · Longevity · Satyrinae

Introduction

Life-history theory is an essential part of evolutionary biology because of the close relationship between life history traits and fitness, and a central theme in all theories about life history evolution is that there are trade-offs between different traits. If this was not the case we would expect all life history traits to be “driven to limits imposed by history and design” (Stearns 1989, 1992). The fact that many life history traits are maintained well within these limits suggests that trade-offs exist (Stearns 1989, 1992).

The existence of a trade-off between age and size at reproduction is an important assumption made in most life-history theory (Stearns and Koella 1986). These traits are of great importance because short development time or generation time leads to fast reproduction, which enhances fitness in growing populations, while body size often is positively correlated with fecundity and/or competitive capacity. Thus, short development times are thought to be associated with small size while a relatively larger body size can be achieved only by delaying reproduction in order to get a longer growth period. This assumption is, nevertheless, not always met. One explanation for this may be that an individual can reach the same size in a shorter time if it increases its growth rate (Nylin et al. 1993). However, life-history theory has traditionally assumed that growth rates are maximised and only vary in response to the quality of the environment (Ricklefs 1969, 1973; Roff 1980, 1983; Stearns and Koella 1986; Gebhardt and Stearns 1988; Perrin and Ruben 1990). The generality of this assumption has, nevertheless, been questioned (Case 1978; Conover and Present 1990; Reavey and Lawton 1991; Wiklund et al. 1991; Ny-

lin et al. 1993; P. Abrams, O. Leimar, S. Nylin, C. Wiklund submitted manuscript), and these authors argue that growth rate should instead be treated as a life-history trait in its own right, and as such a target for natural selection and not a parameter passively given by environmental factors such as temperature or food availability. There is empirical evidence for adaptive variation in growth rates in insects (Nylin et al. 1989, 1993; Reavey and Lawton 1991; Wiklund et al. 1991), spiders (Gunnarsson and Johnsson 1990), fish (Conover and Present 1990), molluscs (Crowl and Covich 1990), amphibians (Wilbur 1987; Skelly and Werner 1990), reptiles (Sinerovo 1990; Niewiarowski and Roosenburg 1993), and mammals (Negus and Berger 1992). The finding that growth rate often, even within populations, is not maximised but rather optimised strongly implies that high growth rates carry some kind of cost.

Costs of high growth rates that have been proposed in the literature can be divided into two categories: ecological or physiological costs. The ecological cost suggested is almost exclusively a higher susceptibility to predators and parasitoids (Werner 1986; Lima and Dill 1990; Skelly and Werner 1990; Reavey and Lawton, 1991; Fraser and Gilliam 1992; Rice et al. 1993; Werner and Anholt 1993). It is obvious that organisms with a high growth rate need more food per time unit and therefore are forced to adopt more "risk prone" foraging strategies. The notion that more active individuals encounter food at a higher rate but also are more vulnerable to predation has considerable empirical and theoretical support (Werner and Anholt 1993 and references therein). The physiological trade-offs that have been put forward as explanations for adaptive variation in growth rates mainly suggest that a high growth rate could be negatively correlated with survivorship under certain environmental conditions (Sibly and Calow 1986). Such conditions could for example be sub-optimal temperatures or periods of food shortage leading to starvation (Clutton-Brock et al. 1985; Conover and Present 1990; Wiklund et al. 1991). The mechanism proposed is that a high growth rate is associated with a high metabolic rate that would entail greater maintenance requirements and therefore higher mortality during, for example, periods of starvation (Conover and Present 1990; Wiklund et al. 1991). We wanted to test the prediction that there is a trade-off between growth rate and some other fitness correlate in *Pararge aegeria* L. (Nymphalidae, Satyrinae), and in this study we focused on possible physiological trade-offs.

Possible adaptive variation in growth rate of *P. aegeria* has been identified on several levels of the biological hierarchy. (i) Larvae from less seasonal habitats such as the island of Madeira, typically grow at a slower rate compared to directly developing individuals from seasonal environments such as Sweden or England (Nylin et al. 1993 and this study). The Madeiran population always develops directly and never enters diapause (Nylin et al. 1993; S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript). The population difference in growth rate could be caused by the fact that the

Madeiran butterflies can reproduce all year around, and therefore are not stressed by having a limited amount of time available for growth and reproduction. (ii) In the northern populations, but not in the southern populations, the sexes differ considerably in growth rate in the directly developing generations (Nylin et al. 1993), most likely due to selection for males to emerge before females. However, when northern *P. aegeria* experience conditions leading to winter diapause the sexes grow at approximately the same rate. Instead, early male emergence is achieved by males breaking pupal diapause earlier than females (Nylin et al. 1993). The phenomenon of males emerging before females is found in the majority of insects with non-overlapping generations and it is known as protandry. It has been explained as a strategy by which males maximise the number of matings (Wiklund and Fagerström 1977). (iii) Directly developing *P. aegeria* larvae from Sweden and England display adaptive phenotypic plasticity in growth rates in response to variation in daylength. Larvae experiencing photoperiods that correspond to a late date in the season, and consequently indicating a short time available for growth before winter, grow faster than larvae that experience photoperiods signalling an early date of the season (Nylin et al. 1989; S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript). All the above examples show that larvae of *P. aegeria* do not grow at their maximum rate unless, for various reasons, they have to, and therefore we predict that a high growth rate is associated with some kind of cost.

In investigating the possible presence and nature of a trade-off between growth rate and some other life history trait in *P. aegeria*, we chose to work with two populations: one bi- to multi-voltine (southern Sweden) with little overlap between generations, and one multivoltine with total overlap of the generations (Madeira) (Nylin et al. 1989, 1993; S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript). We performed studies within populations as well as comparisons between the populations. We expected fast growing individuals, phenotypic classes (sexes) and populations to pay a cost for high growth rate.

Material and methods

Study organism

The speckled wood butterfly *P. aegeria* is widely distributed throughout Europe, Asia and northern Africa. Two subspecies are recognised, the northern *P. aegeria tircis* and the southern *P. aegeria aegeria*, and the border between them in Europe runs from east to west approximately at the same latitude as the Alps. Thus *P. a. aegeria* inhabits northern Africa and Mediterranean Europe, including southern France and the whole Iberian peninsula. In Europe the northern *P. a. tircis* ranges from the Alps to southern Sweden and Estonia. The two subspecies hybridise and intermediate forms are found where they meet in the field (Higgins and Hargreaves 1983). Relatively recently (1970s; Higgins 1977), *P. a. aegeria* colonised the Atlantic island of Madeira where it now co-exists with the endemic *Pararge xiphia* (Owen et al. 1986). Because of the mild oceanic climate on Madeira *P. a. aegeria* can

have approximately five generations per year. This suggests that since the colonisation of Madeira the population has gone through at least 100 generations, which means that it is possible that life history traits have become adapted to the new environment.

Life history comparisons

P. aegeria from a south Swedish population (56° N) and from the population on Madeira (33° N) were used in this study because of the known differences in life history adaptations (Nylin et al. 1993; S. Nylin, K. Gotthard, P.-O. Wickman, C. Wiklund submitted manuscript), most likely due to differences in seasonality at the two sites. Five wild caught females from each population were brought to the laboratory and were allowed to oviposit on the grass *Poa annua*, a host plant used at both locations (personal observation). Eggs from each female were kept separate, and at hatching larvae were placed individually in plastic jars where *Poa annua* was cultured. This individual control made it possible to investigate if there were any life history differences between offspring from different females. This would indicate genetic variation within populations for the trait in question. The offspring of one female are referred to as a "family" in the following. Larvae were reared in environmental chambers until the emergence of adults, under conditions similar to those experienced in the field under direct development which means that the temperature was held at 17° C in all experiments. Relevant field photoperiods leading to direct development differ between the two populations (S. Nylin, K. Gotthard, P.-O. Wickman, C. Wiklund submitted manuscript). Madeiran larvae and pupae were therefore held at a 12 h light: 12 h dark photoperiodic regime. In the case of the Swedish population we used a split brood design and larvae from all females were split between 17, 19 and 21 h light per day. This was done in order to induce a high degree of variation in growth rates due to phenotypic plasticity in response to daylength, known to exist in the Swedish population (Nylin et al. 1989; S. Nylin, K. Gotthard, P.-O. Wickman, C. Wiklund submitted manuscript). Such plasticity is not present in the Madeiran population (Nylin et al. 1993; S. Nylin, K. Gotthard, P.-O. Wickman, C. Wiklund submitted manuscript).

For all individuals we recorded duration of larval and pupal development, pupal weight on the 2nd day after pupation and adult weight after the release of the meconium but before feeding or mating. Growth rate was measured either as the slope of the logarithmic growth curve obtained by weighing larvae every 3rd to 5th day during the larval period, or calculated according to the formula:

$$\text{Growth rate} = [\ln(\text{pupal weight}) - \ln(\text{hatchling weight})] / \text{Larval time}$$

In some cases individual hatchling weight was not recorded and in those cases we have used the average hatchling weight of the population. These two measurements of growth rate were highly correlated (regression: $n=108$, $r=0.914$, $P < 0.001$). Our conclusion is that calculating growth from larval time and pupal weight is a reasonable method for quantifying proportional growth rate when it is not possible to weigh larvae at frequent intervals. The measurements are estimates of the same parameter but they are never mixed in figures or analyses.

We calculated the proportionate weight loss between pupation and adult eclosion using the formula:

$$\text{Proportion weight lost} = 1 - (\text{adult weight} / \text{pupal weight})$$

We also measured adult longevity for all the Swedish individuals together with life-time fecundity for the Swedish females. Males were put in flying cages after pupation, while the females after mating were held separately in plastic jars with a tuft of *Poa annua* for egg laying. This made it possible to collect eggs from each female every day. In two other experiments directly compared adult longevity of the two populations by keeping individu-

als from both populations together in flying cages. All individuals had access to sugar water during all experiments.

Starvation

A lower capacity to endure starvation is one possible cost of a high growth rate suggested by several authors (Clutton-Brock et al. 1985; Conover and Present 1990; Wiklund et al. 1991). Therefore third instar larva from both populations that had reached a weight of 30 mg but not more than 47 mg, were starved for at least 6 days. We had no method to tell the sex of a living larvae of this size and therefore sexes are pooled in the analysis. During the starvation period we measured the daily weight loss. The natural logarithm of these weights were regressed on time and the slope of this "weight loss" function was used as a measurement of starvation endurance. To examine the relevance of this measure we allowed a proportion of the Swedish and all of the Madeiran larvae to feed again after 6 days without food, and recorded survival to the pupa.

Statistical analysis

All statistical analyses used the General Linear Model mode in SYSTAT for the Macintosh, version 5.2 (Wilkinson et al. 1992). In one of the Swedish families, no males developed in the shortest day length (17 h light) and therefore only four families are included in the analysis where we investigate how males are affected by photoperiod. To analyse how time spent in the larval stage, pupal weight and larval growth rate were related we regressed them against each other using sex as a factor in all cases (ANCOVA). This was done for the Swedish population only, because in this population we measured growth rate independently of larval time and pupal weight (i.e. the slope of the growth curve) for a majority of the individuals. Because growth rate was not independently measured for all individuals sample sizes are slightly different in the analyses where growth rate has been used. In the Madeiran population growth rates were calculated from pupal weight and larval time, and therefore there are necessarily autocorrelations between growth rate and the two other parameters. Thus, in the case of the Madeiran population we only calculated the correlation between development time and size.

Results

Growth rate

Individual larval growth in *P. aegeria* can be well described as logarithmic. When the natural logarithm of weight was regressed on time, r -values were never less than 0.9 for any individual.

Sources of variation

Growth rates differed significantly between sexes in both populations (Table 1). Interestingly, there was a difference between the populations in which sex grew at the highest rate (Fig. 1C and see below). There were furthermore significant differences between families in both the Madeiran and the Swedish population, indicating the presence of genetic variation (or alternatively, maternal effects) for growth rate within populations (Table 1). The

Table 1 Results of two-way analysis of variance of growth rate with sex and family as factors

Population	Source of variation	df	Mean square	F	P
S. Sweden	Sex	1	0.003	51.113	<0.001
	Family	4	0.0005	6.724	<0.001
	Sex × family	4	0.00025	2.466	0.050
	Error	99	6.1×10^5		
Madeira	Sex	1	0.004	19.231	<0.001
	Family	4	0.001	2.964	0.023
	Sex × family	4	0.0025	1.561	0.189
	Error	114	1.9×10^4		

Table 2 Analysis of variance for growth rate within the south Swedish population. Only directly developing individuals are included. Photoperiods were 17, 19 or 21 h light per day

Source of variation	df	Mean square	F	P
<i>Females:</i>				
Family	4	0.00022	0.688	0.604
Photoperiod	2	0.00026	0.789	0.461
Family × photoperiod	8	0.00018	0.546	0.814
Error	41	0.00033		
$r=0.241$				
<i>Males:</i>				
Family	3	0.00417	17.796	<0.001
Photoperiod	2	0.00146	6.225	0.005
Family × photoperiod	6	0.00060	2.550	0.039
Error	33	0.00023		
$r=0.842$				

significant sex × family interaction suggests that there is also genetic variation for the amount of protandry in the south Swedish population.

The Swedish population was further analysed in order to detect possible phenotypic plasticity in response to photoperiod. These results are discussed more thoroughly elsewhere (S. Nylin, K. Gotthard, P-O. Wickman, C.

Wiklund submitted manuscript) and will only be mentioned briefly here. Because of the differences between sexes we chose to analyse Swedish males and females separately when investigating the plasticity. As can be seen from Table 2, there were no significant effects of family or photoperiod on female growth rate. Growth rates of the males, however, were strongly affected by photoperiod. This effect did not depend on whether we treated photoperiod as a continuous or as a categorical factor (S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript), and here we only present the result of the analysis when photoperiod is treated as a categorical factor. Males from different families, furthermore, grew at significantly different rates, and there was also a significant family × photoperiod interaction, suggesting the presence of crossing reaction norms in the south Swedish population.

Correlations between female fecundity, size, time and growth rate

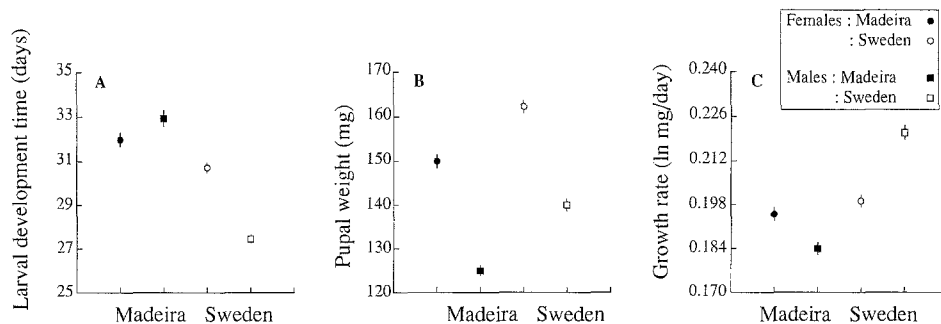
In none of the populations was there a significant correlation between larval time and pupal weight (Table 3), which shows that there are no simple trade-off between size and time. It is also obvious from Table 3 that sex but not growth rate (only tested in the Swedish population) is a significant factor in explaining variation in pupal

Table 3 The interrelationship between pupal weight, larval time and growth rate for the Swedish population and between pupal weight and larval time for the population from Madeira. Sex was

Population	Dependent variable	Source of variation	df	Mean square	F	P
S. Sweden	Pupal weight	Sex	1	10807.455	69.426	<0.001
		Larval time	1	203.158	1.205	0.255
		Error	160	155.668		
$r=0.622$						
S. Sweden	Pupal weight	Sex	1	7644.716	59.874	<0.001
		Growth rate	1	1.109	0.009	0.926
		Error	105	127.679		
$r=0.681$						
S. Sweden	Larval time	Sex	1	20.631	18.675	<0.001
		Growth rate	1	241.706	218.787	<0.001
		Sex × Gr.rate	1	15.649	14.165	<0.001
		Error	104	1.105		
$r=0.914$						
Madeira	Pupal weight	Sex	1	20536.233	194.749	<0.001
		Larval time	1	310.214	2.942	0.089
		Error	121	105.433		
$r=0.786$						

used as a factor in all analyses (ANCOVA) and if the interaction was non significant it was excluded from the analysis

Fig. 1A–C Comparison between sexes and populations of three life history traits (means \pm 1 SE). **A** Larval development time, **B** pupal weight, **C** growth rate. Sample sizes are between 59 and 83



weight. The same type of analysis of larval time in Sweden show that it is negatively correlated with growth rate but that this relationship differs between sexes (i.e. the interaction between sex and growth rate is significant, see Table 3). What differs between sexes is not the sign of the correlation but the slope of the regression line (females: larval time = $-95.9 \times$ growth rate + 53.1; males: larval time = $-57.0 \times$ growth rate + 42.3). In summary these patterns suggest that fast growing individuals of both sexes “use” their high growth rates to shorten the larval period rather than to reach a larger body size. The number of eggs that a Swedish female laid during its life time was not correlated with its larval growth rate (regression: $n=55$, $r=0.015$, $P=0.913$).

Differences between populations

Figure 1 illustrates population differences in larval time, pupal weight and growth rate as well as differences in sexual dimorphism of these traits. The Madeiran pupae are generally lighter (Fig. 1B), although the time they spend in the larval stage while reaching this weight is longer (Fig. 1A). Another pattern, obvious from Fig. 1A, is that the south Swedish population was strongly protandrous, whereas the Madeiran males actually had longer larval development times than the females on average (ANOVA; $F_{1,122}=28.138$, $r=0.186$, $P<0.001$). The similarity in sexual size dimorphism between the two populations supports earlier results concerning the weak relationship between sexual size dimorphism and protandry in *P. aegeria* (Nylin et al. 1993). The proximate explanation for the fact that the Madeiran butterflies are both smaller and have longer larval development times is that they have lower growth rates (Fig. 1C). The difference between the populations is, however, much greater for the males than for the females. It is obvious from these data that while males from Sweden grow faster than females the opposite relationship is true on Madeira. Thus, the Swedish males stand out as having the highest growth rate most likely as a result of selection for protandry. One straightforward prediction from these patterns of growth rate variation is that Swedish speckled woods “pay” some kind of cost compared to their Madeiran conspecifics, and this cost should be especially apparent in the Swedish males.

Costs of growth rate – starvation

As predicted, fast-growing larvae also lost weight at a relatively higher rate when starved. Within both populations there was a significant positive correlation between larval growth rate and the rate at which the larvae lost weight during starvation (regression: Madeira $n=78$, $r=0.249$, $P=0.028$; Sweden $n=52$, $r=0.314$, $P=0.023$). An even stronger support for this relationship was found when the data from both populations were pooled (Fig. 2). As mentioned above we could not distinguish between female and male larvae at this point of the larval development, which makes a comparison between the sexes impossible. It is, however possible to compare the populations, and contrary to our prediction there was no difference in weight loss rate between the populations. The population difference in growth rate at this early phase of the larval development is, however, very small (Fig. 2, mean \pm 1SE for: Madeira 0.293 ± 0.003 ln mg/day; Sweden 0.304 ± 0.004 ln mg/day). Larval weight at the start of the starvation experiment did not affect weight loss rate in either of the populations (regression: Madeira $n=78$, $r=0.058$, $P=0.615$; Sweden $n=52$, $r=0.226$, $P=0.108$).

The relevance of weight loss rate as a measurement of starvation endurance was investigated by comparing the individuals that survived to pupation after 6 days of starvation with the ones that did not. Individuals that did not reach the pupal stage had higher weight-loss rates on average than those that pupated successfully (Table 4).

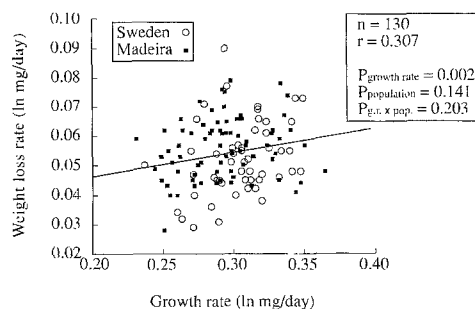


Fig. 2 The relationship between larval growth rate and weight loss rate during starvation. Statistics are given in the figure (ANCOVA). The populations are not significantly different and the regression line is for the pooled data

Table 4. Average weight loss rates (mean \pm 1 SE) for larvae that were allowed to feed after 6 days of starvation. Results are given for populations separately and for the pooled material (ANOVA)

	Survivors	Dead	
S. Sweden	0.045 \pm 0.003 <i>n</i> =12	0.063 \pm 0.006 <i>n</i> =4	<i>P</i> =0.019
Madeira	0.048 \pm 0.004 <i>n</i> =6	0.057 \pm 0.001 <i>n</i> =72	<i>P</i> =0.052
Pooled	0.048 \pm 0.003 <i>n</i> =18	0.060 \pm 0.003 <i>n</i> =76	<i>P</i> =0.001

The difference is significant in the Swedish population and nearly so in the Maderiran population. The most general test of the hypothesis is achieved by pooling all the data, in which case the difference is highly significant (Table 4).

In the starvation experiment with the Swedish population, four individuals had such low growth rates (mean \pm 1 SE: 0.194 \pm 0.012 ln mg/day) compared to the others (see above) that they were recorded as summer diapausing (aestivating) and were therefore excluded from the analysis above. Aestivation is a well known phenomena in *P. aegeria* and is thought to be a strategy for surviving bad conditions during the hottest part of the summer and/or as a way of spending surplus time in a preferred developmental stage (Wiklund et al. 1983; Nylin et al. 1989). These four individuals consequently had extremely low weight loss rates and if they are included in the analysis of the Swedish population the positive correlation becomes even stronger (regression: *n*=56, *r*=0.570, *P* < 0.001). This very low weight loss rate seemed also to be associated with an exceptional capacity to survive without any food. Two of these aestivating individuals received no food after the start of the starvation experiment but, nevertheless, they both survived for more than 20 days, which can be compared to the life span of the other individuals (non-aestivating) that were given the same treatment (mean \pm 1 SE: 9.02 \pm 0.17 days, *n*=36). The remaining two aestivating larvae were allowed to feed after 6 days of the no-food treatment and they both survived to pupation.

Costs of growth rate – adult longevity and weight loss in the pupae

In the analysis of the Swedish data two intriguing patterns emerged when we compared the sexes. First, average adult life span was shorter for the males than for the females (mean \pm 1 SE: females *n*=55, 18.9 \pm 0.8 days; males *n*=44, 12.2 \pm 0.9 days; ANOVA: *F*_{1, 97}=33.862, *r*=0.509, *P* < 0.001). Second, the proportion of mass lost during development to adult was much larger for males than for females (Table 5). This was not just an effect of differences in pupal development time, which was similar in both sexes (Table 5). The observation that Swedish males perform worse than females in these respects can

Table 5. Proportionate weight loss during development to adult and average pupal development times (mean \pm 1 SE for both variables). Probabilities refer to sexual differences (ANOVA)

		Proportionate weight loss	Pupal development time (days)
S. Sweden:	Females (<i>n</i> =83)	0.534 \pm 0.003	13.98 \pm 0.10
	Males (<i>n</i> =80)	0.604 \pm 0.003	14.21 \pm 0.10
		<i>P</i> <0.001	<i>P</i> =0.094
Madeira	Females (<i>n</i> =59)	0.529 \pm 0.004	12.76 \pm 0.10
	Males (<i>n</i> =65)	0.616 \pm 0.004	13.63 \pm 0.09
		<i>P</i> <0.001	<i>P</i> <0.001

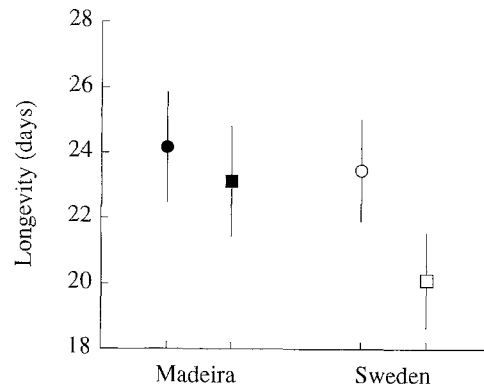


Fig. 3 Average longevity (mean \pm 1 SE) for populations and sexes respectively. Females are first in each pair and marked with circles, males are marked with squares. Means are calculated using the pooled data from two experiments (see Materials and methods) and sample sizes are for the Madeiran females = 32, Madeiran males = 31, Swedish females = 36 and Swedish males = 41

potentially be linked to the large sexual difference in growth rate present, with males growing faster than females. None of the parameters, however, showed a significant correlation with growth rate within sexes. It is nevertheless possible that adult longevity and/or weight loss during pupal development has been involved in trade-offs with growth rate in the past but that the genetic variation for such trade-offs has been exhausted, and therefore the allocation patterns are fixed within sexes today (cf. Stearns 1992 p. 75). If short longevity and large pupal weight loss represent such “historical” costs of high growth rates we would expect the Madeiran population to have a less pronounced or even reversed sexual difference in adult longevity and pupal weight loss, because of the reversed sexual dimorphism in growth rate (Fig. 1C).

Weight loss during development to adult showed a very similar pattern in the Madeiran case. Females from Madeira lost less weight than males and had only a slightly shorter duration of the pupal development (Table 5). Because females grew faster than males in this population, it is possible to conclude that sexual differences in weight loss during pupal development had very little, if anything, to do with sexual differences in larval growth

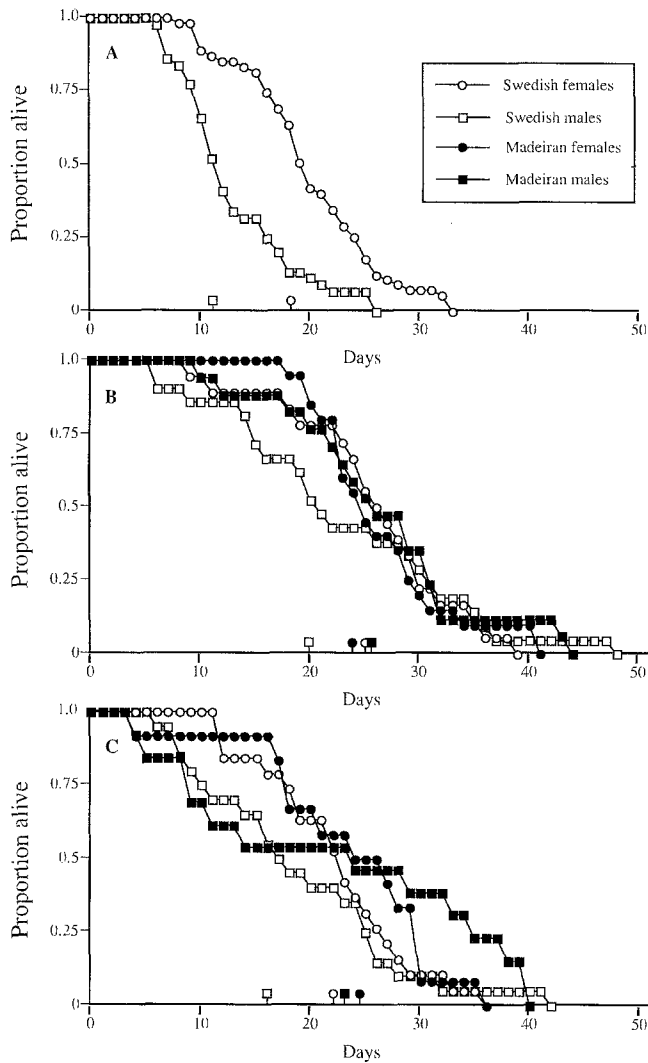


Fig. 4A–C The proportion of surviving butterflies by day in the laboratory, each graph describing a separate experiment. The median for each category is marked on the x axis with the symbol for each category respectively. The Swedish males (*open squares*) had the shortest median longevity in all three experiments. Sample sizes are for **A** females = 55, males = 44 only Swedish butterflies, **B** Madeiran females = 20, Madeiran males = 18, Swedish females = 17, Swedish males = 21 and for **C** Madeiran females = 12, Madeiran males = 13, Swedish females = 19, Swedish males = 20

rate. A quite different pattern emerged in the direct population comparison of adult longevity (Fig. 3), where we have pooled the results of two experiments to increase sample size. In the Madeiran population average adult longevity did not differ between males and females, and there was furthermore no significant difference between the two experiments (ANOVA: sex $F_{1,59}=0.195$, $P=0.661$; experiment $F_{1,59}=1.900$, $P=0.173$; interaction $F_{1,59}=0.010$, $P=0.921$). In these experiments the Swedish butterflies showed the same pattern as they did in the first one, with males having shorter lives than females on average. However, in this case the sexual difference in longevity was not significant (ANOVA: sex $F_{1,73}=2.546$, $P=0.115$; experiment $F_{1,73}=3.836$, $P=0.054$; interaction

$F_{1,73}=0.0004$, $P=0.985$). There was a nearly significant difference between the experiments but no interaction between sex and experiment. In other words, if the experiments differed this did not affect the relationship between the sexes. Figure 4 illustrates the rates at which the butterflies died in the three longevity experiments. In the first experiment, where there was only Swedish butterflies, males died faster than females, especially during the first 15 days (Fig. 4A). This pattern was also present for the Swedish butterflies in the two experiments with individuals from both populations (Fig. 4B, C). The males from Madeira had a death rate very similar to the females from both populations in one experiment (Fig. 4B) but were more similar to the Swedish males in the other (Fig. 4C). Note, however, that in all experiments the Swedish males were the category with the shortest median longevity (Fig. 4 A–C).

Discussion

The results presented here support the conclusions of other studies concerning the lack of a simple trade-off between development time and body size, and the presence of adaptive variation in growth rate in *P. aegeria* (Nylin et al. 1989, 1993; S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript). The latter becomes especially evident when we compare the two populations in terms of sexual dimorphism in growth rate. The strong seasonality in southern Sweden leads to non-overlapping generations and selection for protandry. This forces the Swedish males to grow at a rate far exceeding that of the females. On Madeira protandry is apparently not selected for, probably because generations overlap (Singer 1982). Consequently in this population the sexual difference in growth rate is not as large and males are actually growing more slowly than females (Fig. 1, Nylin et al. 1993). Furthermore, in both populations there seems to be genetically based variation in growth rate (Table 1). Fast-growing individuals do not become heavier than individuals that grow more slowly but instead shorten their growth period. This indicates that there is strong selection for being the “right” size as well as having a short development time and that it sometimes is worth taking the cost of growing faster.

The main aim of this work was to investigate if there is a trade-off between growth rate and any other life history characteristic. The most interesting result in this respect is perhaps the presence of a significant correlation between growth rate and the rate of weight loss during starvation. As predicted, individuals with high growth rates lose weight faster than individuals with more moderate rates of growth, and the same pattern seems to be present in both populations. Moreover, individuals that lose weight fast during starvation also have higher mortality when they are allowed to feed again, implying that a high growth rate is costly in terms of fitness during periods of food shortage. Although a trade-off between

growth rate and starvation endurance has been suggested several times (Clutton-Brock et al. 1985; Conover and Present 1990; Wiklund et al. 1991), this seems to be the first time that it has been experimentally demonstrated. As far as we know, it also the first demonstration that high growth rate carries a physiological cost, and means that growth rate should be considered as a life-history variable in its own right. Physiological trade-offs are present when two or more processes compete for the limited amount of resources within a individual (Stearns 1992). The studied trade-off can be thought of as a trade-off between growth and maintenance. All else being equal, allocating more resources to growth, and therefore having a higher metabolic rate, will result in a lower capacity for maintaining or storing resources that can be used when no food is available.

As mentioned above, *P. aegeria* larvae feed on various grasses. In the laboratory, one tuft of *Poa annua* is not enough food for an individual to reach the pupal stage. This is likely to reflect the situation in the field which means that an individual has to change host plant during its larval period. The main habitat of *P. aegeria* is open forests, where tufts of grass are often distributed in patches. It seems reasonable to assume that larvae at times face a situation where they have to move around and search for suitable host plants, while being under food stress.

The investigation of the south Swedish population suggested two other potential costs of high growth rate, a large proportion of weight lost in the pupal stage during development to adult and reduced longevity. This was due to the fact that the fast growing Swedish males lost more weight between pupation and adult eclosion and had significantly shorter lives than the females. None of these parameters were significantly related to growth rate within sexes. However, growth rate varies less within than between sexes, which may make it hard to find effects on pupal weight loss and longevity within these phenotypic categories. Another possibility is that the patterns we see today are a result of historical trade-offs for which there is no genetic variation today (Stearns 1992). Because of the reversed sexual dimorphism in growth rate in the Madeiran population (females faster than males) it was possible, by comparing the two populations, to test whether any of these traits are or have at some point been involved in a trade-off with growth rate. Interestingly, weight loss between pupation and adult eclosion was very much the same in the Madeiran population as in the Swedish population (contrary to our predictions), whereas the sexual difference in longevity, on the other hand, was less pronounced if present at all (as predicted). This suggests that pupal weight loss during development to adult is not influenced by larval growth rate and that the differences between sexes is not due to differences in metabolic rate in this case. They may, however, be the result of some other sexual difference, resulting in a male phenotype being more costly to produce in terms of energy. If there is no such difference between the sexes it is hard to understand why males

lose so much weight during this phase of development; females are the living proof that it is possible to do better. Although not conclusive, the results of the longevity study indicate that a shorter life span may represent a cost of high growth rates, at least when sexes are compared. We draw this conclusion from the fact that the fast growing Swedish males in three experiments had shorter average life spans than females from the same location, a pattern not seen in the Madeiran population. Adult longevity in laboratory conditions can be seen as measuring an aspect of adult quality, and differences in that respect may be less pronounced because of the good living conditions experienced in the laboratory. An alternative explanation is that the population differences in average longevity is a result of different selection pressures on life span itself. It seems likely that a long life is not as profitable for a male in Sweden compared to a male on Madeira in terms of mating opportunities. This is because the strong seasonality in Sweden synchronises adult eclosion and creates characteristic, short term peaks of abundance of both males and females. On Madeira, however, virgin females are emerging throughout the whole year and the probability of meeting an unmated female is perhaps to a higher degree dependent on the longevity of a male.

It is becoming increasingly clear that growth rates may vary adaptively and not only as a consequence of the quality of the environment (Case 1978; Wilbur 1987; Nylin et al. 1989, 1993; Conover and Present 1990; Reavey and Lawton, 1991; Wiklund et al. 1991; Negus and Berger 1992; S. Nylin, K. Gotthard, P-O. Wickman, C. Wiklund submitted manuscript). When this is the case, the expected trade-off between time and size is not necessarily seen, unless growth rate is driven to a point where the cost of increasing it further is higher than the cost of decreasing size or increasing development time. Thus, a crucial parameter in understanding the relationship between time, size and growth rate is the cost of growth rate. This is also one of the conclusions of a recent model (P. Abrams, O. Leimar, S. Nylin, C. Wiklund submitted manuscript), that explores the effects of flexible growth rates on optimal sizes and development times. There is no doubt that growth rate is the least studied of these three major determinants of life histories, and trade-offs with growth rate has hardly ever been studied. Our results show that there may be genetic variation for growth rate within and between populations, and support the notion that high growth rates carry a cost. We do, furthermore, argue that for the understanding of life history variation it is necessary to take into full account the three-dimensional relationship between size, time and growth rate.

Acknowledgements We thank N. Janz and N. Wedell for help with the experiments. This research was supported by grants from Wallenbergs Jubileumsfond and Kinanders fond to KG and from the Swedish Natural Research Council to SN and CW.

References

- Case TJ (1978) On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Q Rev Biol* 53: 243–282
- Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313: 131–133
- Conover DO, Present TMC (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83: 316–324
- Crowl TA, Covich AP (1990) Predator-induced life-history shifts in a freshwater snail. *Science* 247: 949–951
- Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73: 959–970
- Gebhardt MD, Stearns SC (1988) Reaction norms for development time and weight at eclosion in *Drosophila mercatorum*. *J Evol Biol* 1: 335–354
- Gunnarsson B, Johnsson J (1990) Protandry and moulting in the spider *Pityohyphantes phrygianus*. *Oikos* 59: 205–212
- Higgins LG (1977) The speckled wood (*Pararge aegeria* L.) in Madeira. *Entomol Rec J Var* 89: 22–23
- Higgins LG, Hargreaves B (1983) The butterflies of Britain and Europe. Collins, London
- Lima S, Dill LM (1990) Behavioral decision made under the risk of predation: a review and prospectus. *Can J Zool* 68: 619–640
- Negus NC, Berger PJ (1992) Phenotypic plasticity of the montane vole (*Microtus montanus*) in unpredictable environments. *Can J Zool* 70: 2121–2124
- Niewiarowski PH, Roosenburg W (1993) Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* 74: 1992–2002
- Nylin S, Wickman P-O, Wiklund C (1989) Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyridae). *Biol J Linn Soc* 38: 155–171
- Nylin S, Wiklund C, Wickman P-O, Garcia-Barros E (1993) Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology* 74: 1414–1427
- Owen DF, Shreeve TG, Smith AG (1986) Colonization of Madeira by the speckled wood butterfly, *Pararge aegeria* (Satyridae), and its impact on the endemic *Pararge xiphia*. *Ecol Entomol* 11: 349–352
- Perrin N, Rubin JF (1990) On dome-shaped norms of reaction for size-to-age at maturity in fishes. *Funct Ecol* 4: 53–57
- Reavey D, Lawton JH (1991) Larval contribution to fitness in leaf-eating insects. In: Bailey WJ, Ridsdill-Smith J (eds) Reproductive behaviour of insects. Chapman and Hall, London, pp 293–329
- Rice JA, Miller TJ, Rose KA, Crowder LB, Marschall EA, Trebitz AS, Deangelis DL (1993) Growth rate variation and larval survival- inferences from an individual-based size-dependent predation model. *Can J Fish Aqu Sci* 50: 133–142
- Ricklefs RE (1969) Preliminary models for growth rates in birds. *Ecology* 50: 1031–1039
- Ricklefs RE (1973) Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 177–210
- Roff DA (1980) Optimizing development time in a seasonal environment: the “ups and downs” of clinal variation. *Oecologia* 45: 202–208
- Roff DA (1983) Phenological adaptation in a seasonal environment: A theoretical perspective. In: Brown VK, Hodek I (eds) Diapause and life cycle strategies in insects. Junk, The Hague pp 253–270
- Sibly RM, Calow P (1986) Physiological ecology of animals: an evolutionary approach. Blackwell Scientific Oxford.
- Sinervo B (1990) Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia* 83: 228–237
- Singer MC (1982) Sexual selection for small size in male butterflies. *Am Nat* 119: 337–365
- Skelly DK, Werner EE (1990) Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71: 2313–2322
- Stearns SC (1989) Trade-offs in life-history evolution. *Funct Ecol* 3: 259–268
- Stearns SC (1992) The evolution of life histories (1st edn). Oxford University Press, Oxford
- Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893–913
- Werner EE (1986) Amphibian metamorphosis: growth rates, predation risk and the optimal size at transformation. *Am Nat* 128: 319–341
- Werner EE, Anholt BR (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am Nat*, 142: 242–272
- Wiklund C, Fagerström T (1977) Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* 31: 153–158
- Wiklund C, Persson A, Wickman P-O (1983) Larval aestivation and direct development as alternative strategies in the speckled wood butterfly, *Pararge aegeria*, in Sweden. *Ecol Entomol* 8: 233–238
- Wiklund C, Nylin S, Forsberg J (1991) Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, *Pieris napi*. *Oikos* 60: 241–250
- Wilbur HM (1987) Regulation of structure in complex systems; experimental temporary pond communities. *Ecology* 68: 1437–1452
- Wilkinson L, Hill M, Miceli S, Howe P, Vang E (1992) SYSTAT. 5.2. Systat, Evanston, Illinois.