

Adaptive Growth Decisions in Butterflies

KARL GOTTHARD

Caterpillars have a great capacity for rapid weight gain, but to reap the benefits of this capacity, larvae must be able to survive in a hostile environment and emerge as adults at the right time of year. In this article, I review examples of growth decisions in butterfly larvae that can be viewed as adaptations for optimized growth performance. These include sex-specific growth decisions that lead to protandry and sexual size dimorphism, fine-tuning of growth in response to photoperiod and temperature, development of alternative larval morphs that mimic the plant structures they feed on, and the peculiar growth patterns of lycaenid butterflies that manipulate ants and grow as “cuckoos” inside ant nests. I conclude that growth of an individual can be seen as the sum of several environmentally dependent decisions, which may influence the growth trajectory by changes in physiology, behavior, and morphology.

Keywords: growth strategy, age and size at maturity, growth decision, butterflies, plasticity

All multicellular organisms have some kind of juvenile growth period during which they accumulate resources and develop structures that are used for reproduction. In holometabolous insects such as butterflies, beetles, flies, and wasps, virtually all growth takes place in the larval stage, and it seems reasonable to assume that the holometabolous larva is primarily an adaptation for efficient growth. With respect to natural selection, an efficient growth trajectory is the combination of growth rate, survival, and timing of adult emergence that maximizes lifetime reproductive success (Abrams et al. 1996). For example, many insects may benefit from reaching a large adult size because doing so increases reproductive potential. Still, there is great variation in body size, and there may be a 20-fold difference in pupal size among species within a single family. A larger adult size can in principle be achieved by faster growth or a prolonged growth period. These changes in growth, however, are also expected to increase the risk of larval mortality because of a higher predation risk (Bernays 1997, Gotthard 2000). Because of such trade-offs, natural selection will favor genotypes that strike a strategic balance between fitness costs and benefits, which will lead to the evolution of adaptive growth strategies (Abrams et al. 1996, Nylin and Gotthard 1998).

Life history theory is widely used for analyzing and predicting optimal combinations of growth, survival, and reproduction (Stearns 1992). Life history theory views the scheduling of life events such as growth, sexual maturation, and reproduction as the result of strategic decisions over the life of an organism (McNamara and Houston 1996). The central idea presented in this article is that the growth trajectory of a larva is determined by a set of strategic developmental decisions. These decisions include when to start

growing, at what rate to grow, when to stop growing and pupate or enter diapause, and what larval morph to develop into. The word “decision” is used here and throughout this article not to imply cognitive processes, but rather to describe the presence of developmental switches that channel individuals through alternative developmental pathways depending both on their heredity and on the environment (West-Eberhart 2003).

Developmental decisions can be treated as adaptations resulting from natural selection for optimized development and growth performance. Natural selection can be expected to favor dissimilar trait values in different environments and in different classes of organisms, which leads to adaptive variation in growth decisions among genetic categories such as species, populations, and sexes. Moreover, the evolution of adaptive phenotypic plasticity may also be expected, whereby individual larvae make different growth decisions in response to changes in environmental conditions (Nylin and Gotthard 1998). The growth strategy of an individual can be seen as a sum of several environmentally dependent decisions, which may alter the growth trajectory through changes in physiological, behavioral, or morphological traits. Because this type of plasticity is a direct illustration of adaptive growth decisions, this article focuses particularly on such examples. Finally, this article is concerned with adaptive growth decisions of butterflies (and to some degree, moths), but the theoretical framework is general and has been applied to adaptive

Karl Gotthard (e-mail: karl.gotthard@zoologi.su.se) is with the Department of Zoology at Stockholm University in Sweden. © 2008 American Institute of Biological Sciences.

growth in many other organisms (Masaki 1978, Newman 1992, Arendt 1997, Metcalfe 1998, Gotthard 2001).

Butterfly growth

The larval stage of most holometabolous insects is morphologically and ecologically very different from the adult stage. For example, a majority of butterfly larvae feed on plant tissue, move relatively slowly, and have a limited capacity to disperse to new habitat (Stamp and Casey 1993). The caterpillars accumulate most of the nitrogen-rich resources that are necessary for reproduction in the adults (Karlsson 1998). Adults, on the other hand, are highly mobile and typically feed on nectar and other sugar-rich resources such as honeydew and decaying fruit. There are, however, some notable exceptions, such as the Neotropical genus *Heliconius*, in which the adults feed on nitrogen-rich pollen (Gilbert 1972).

During their larval growth period, caterpillars go through a varying number of instars. The physiological process that transfers larvae from one instar to another is called moult; during the moulting period, larvae build a new exoskeleton underneath the old one and do not grow (Esperk and Tammaru 2004). Butterfly larvae can grow very fast—indeed, one of the model species in lepidopteran growth physiology, the tobacco hornworm, *Manduca sexta* (Sphingidae), was given its scientific name on account of its large appetite (manduca means “the chewer” in Latin [Reynolds 1990]).

Despite being ectothermic, last-instar larvae of this species, when grown at 25 degrees Celsius, can gain fresh weight at a higher rate than similar-sized birds that are endothermic and regulate body temperatures at much higher levels (Reynolds 1990). The growth trajectories of butterfly larvae have often been described as being approximately exponential, but recent evidence suggests that they may often be better described as power functions (Tammaru and Esperk 2007). In any case, it is clear that the absolute increase in mass accelerates with development time (figure 1). For example, in *M. sexta*, approximately 88% of the increase in absolute size is due to growth during the final (fourth) instar (D’Amico et al. 2001). Although there is great variation among species in growth trajectories, it appears that this capacity for fast weight gain is present within a wide range of larval sizes. For example, among four species of satyrine butterflies that feed on the same host, some species stop growing at sizes at which other species continue growth at an undiminished rate (Wickman et al. 1990).

Closely related species with similar ecologies may evolve substantial differences in growth trajectories (figure 1). Moreover, a population of *M. sexta* that was kept for approximately 30 years (approximately 220 generations) in the laboratory evolved a 50% increase in pupal weight (D’Amico et al. 2001). This was due mainly to genetic changes in larval growth rate and the size at which the decision of metamorphosis induction was taken. The evolution of larval growth trajectories appears to be rarely limited by strong constraints such as a decrease in growth efficiency with increasing size. The reason natural selection does not typically

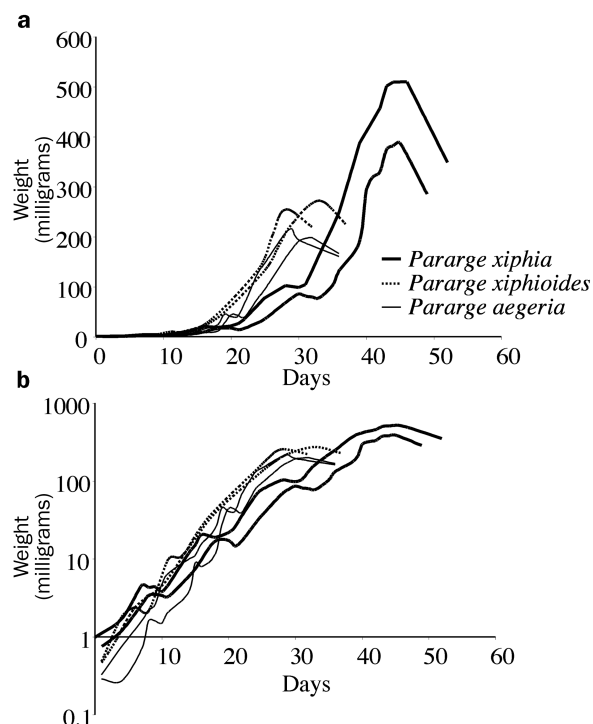


Figure 1. Growth trajectories of three closely related species of *Pararge* (Satyrinae) showing weight gain, in milligrams, with time on linear (a) and logarithmic scales (b). Approximately 10 individuals of the three species were grown on the same host plant (*Dactylus glomerata*) and with the same temperature regime (17–18 degrees Celsius), but for clarity only the two individual females that reached the largest and the smallest pupal size of each respective species are shown. The two largest species, *Pararge xiphioides* and *Pararge xiphia*, are island endemics native to the Canary Islands and Madeira, respectively. The third species *Pararge aegeria*, has a wide distribution throughout Europe and North Africa. In the 1970s the species colonized Madeira, most likely from North Africa (Weingartner et al. 2006). The *P. aegeria* individuals used here came from Madeira. These three closely related species show that growth trajectories may evolve relatively rapidly. The trajectories show the typical fast growth within larval instars and the lack of growth during moults (horizontal part of the trajectories in [b]), as well as the loss of mass before pupation. The growth trajectories in (a) also show the characteristic large increase in absolute size in the last part of the larval period. A linear relationship on the log scale in (b) would indicate that growth is exponential.

favor maximization of growth rates is most likely because there are also costs associated with growing fast (Stockhoff 1991, Gotthard et al. 1994, Bernays 1997, Gotthard 2000). If the cost-benefit structure changes, evolutionary changes in growth trajectories may be rapid.

Sex-specific growth decisions

Sexual differences in growth trajectories are common in insects and follow two broad patterns. First, females typically grow to be larger than males (Blanckenhorn et al. 2007). A likely explanation for this is that female fecundity increases with adult size, whereas male mating success is less dependent on size. Therefore, optimal adult size differs between the sexes. Second, in populations with nonoverlapping generations, the tendency is for males to emerge before females (Blanckenhorn et al. 2007). This pattern, known as protandry, has been explained as the result of sexual selection on males to maximize the expected number of matings (Wiklund and Fagerström 1977), or selection on females to minimize the period between adult emergence and mating (Fagerström and Wiklund 1982). Although it is reasonable to assume a direct causal relationship between the patterns of sexual size dimorphism and protandry (males smaller and have shorter development times), it has become increasingly clear that this causality is often broken by sex differences in larval growth rates (Blanckenhorn et al. 2007). For example, seasonal populations of the speckled wood butterfly (*Pararge aegeria*) are strongly protandrous, whereas less seasonal populations with overlapping generations show no protandry. Nonetheless, sexual size dimorphism is similar in both seasonal and nonseasonal populations (Nylin et al. 1993).

In seasonal populations, males achieve protandry by growing faster and by maturing at a lower weight than do females. In the nonseasonal populations, females grow faster, enabling them to reach a large size without having a longer developmental period than males (Gotthard et al. 1994). The green-veined white butterfly (*Pieris napi*) is an exception to the general rule of sexual size dimorphism, as males grow larger than females (most likely due to the females' high mating rate and to an associated strong sexual selection on male size). Most interestingly, the male *Pi. napi* does this without sacrificing protandry, and under direct development, males simply grow faster than females (Wiklund et al. 1991). However, males do not grow faster than females under development to pupal diapause when time constraints on larval growth are relaxed and there is no selection to achieve protandry by differential larval growth. In this generation, protandry is instead due to faster male pupal development in spring after winter diapause (Wiklund et al. 1991).

These two examples show that adaptive variation in growth decisions is present as genetic differences among populations (*P. aegeria*) and sexes (*P. aegeria* and *Pi. napi*), but also as plasticity in growth decisions of individuals that follow different developmental pathways (*Pi. napi* males following direct or diapause development).

Growth decisions and photoperiod

Organisms in seasonal environments perform different activities at different times of the year. For many butterflies, part of the year (in temperate areas, usually the winter) is unsuitable for growth and reproduction, and insects typically survive this period in a hormonally controlled diapause

(Tauber et al. 1986). A given species can typically enter diapause only in a specific developmental stage (e.g., in the egg, a given larval instar, the pupa, or the adult stage), which must be reached before the onset of unfavorable conditions. In addition, many butterfly species produce several consecutive generations per year (bivoltine or multivoltine), and individuals may enter direct development and reproduce within a single year or go into diapause and postpone reproduction until the next season. The choice of developmental pathway (direct or diapause development) is often made during larval growth and it is the best-studied adaptive developmental decision in insects (Bradshaw 1976, Tauber et al. 1986).

Seasonal cues such as photoperiod and temperature typically determine which pathway is followed. The exact seasonal timing of life history events such as larval growth, sexual maturation, and diapause will have a strong influence on fitness. We may therefore expect that individual larvae adjust their growth in response to information about the date in relation to the optimal time of adult emergence or diapause (Abrams et al. 1996). This type of reasoning has been the starting point for several life history models of optimal growth and development (Rowe and Ludwig 1991, Werner and Anholt 1993, Abrams et al. 1996). The models all assume a trade-off between juvenile growth and mortality rates, and converge on the quite intuitive prediction that with less time available, individuals should shorten their juvenile development times. In principle, this can be achieved by metamorphosing at a smaller size or speeding up the growth rate, or some combination of the two. In several species of temperate butterflies, larvae adjust their growth in response to the photoperiod, which is a reliable cue of time of year (e.g., figure 2). With less time available, larvae shorten their development time, mainly through an increased growth rate, but to a lesser extent by metamorphosing at a smaller size (Leimar 1996, Nylin et al. 1996, Gotthard 1998).

Studies on the satyrine tribe Parargini suggest adaptive variation in larval growth strategies among and within species (Nylin et al. 1996, Gotthard 2004). In some species in this group, individual larvae hatch during late summer, enter diapause as half-grown larvae in autumn, and then continue growing during spring and early summer. This sets the stage for an interesting situation in which photoperiod has to be interpreted differently during the two growth periods (Gotthard et al. 1999). This is because the photoperiod decreases with time during the first growth period in the autumn, and a shorter photoperiod means less time available for growth before the diapause; in contrast, the photoperiod increases during the second growth period in spring, and a shorter photoperiod now means more time available for growth before pupation. Individual larvae of *Lasiommata maera* and *Lopinga achine* make season-dependent interpretations (autumn or spring) of this cue, as they show qualitatively different growth responses to the same photoperiods when they are experienced before and after larval diapause (Gotthard et al. 1999). In autumn, larvae of both species develop faster to the diapausing larval stage under shorter photoperiods that

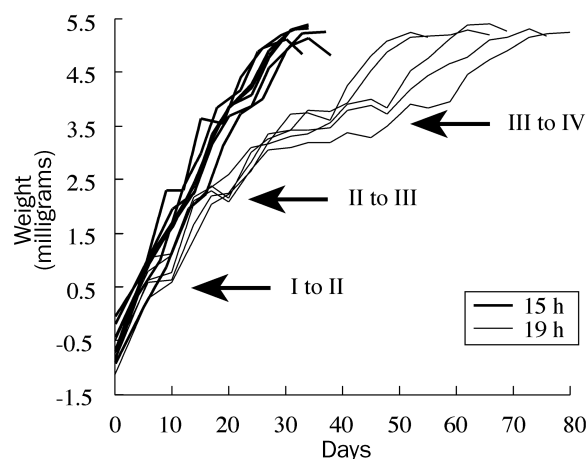


Figure 2. Example of seasonal growth strategies in the satyrine *Lasiommata petropolitana*. Because this species grows after midsummer, a shorter day length (15 hours of light) predicts less time available until the end of the season than a longer day length (19 hours). The arrows indicate moults. From the second instar onward, individuals with more predicted time for development “decided” to grow more slowly than their more time-stressed siblings. Despite these differences, all individuals followed the same general developmental pathway and entered winter diapause in the pupal stage.

predict a later date of the year (figures 3, 4). After diapause in spring, *L. maera* larvae develop faster in longer photoperiods, which during this time of year indeed signal a shorter time before adults has to be on the wing (figure 3). *Lopinga achine* shows no developmental response to photoperiod after diapause and seems not to use this information during development in spring (figure 4). Hence, in both species the growth decisions in response to photoperiod are dependent on the physiological state of individuals (i.e., before or after winter diapause). This state-dependency is most likely adaptive and shows that the strategic decisions are not ultimately dependent on photoperiod but rather on information about seasonal progression predicted by this environmental cue (Gotthard et al. 1999).

Growth decisions and temperature

The effect of ambient temperature on the growth of butterfly larvae has been the subject of research in physiology, ecology, and evolution (Kingsolver 2000, Fischer and Fiedler 2002, Davidowitz et al. 2004, Kingsolver et al. 2004). The thermal conditions that caterpillars experience often influence diapause decisions (Tauber et al. 1986) as well as the expression of seasonal morphs of the adult butterflies (Shapiro 1976). In the well-studied tropical genus *Bicyclus*, this mechanism is responsible for the development of wet- and dry-season morphs that show substantial adaptive differences in morphology and life history (Brakefield and Reitsma 1991). As ambient temperature has such strong, direct effects on

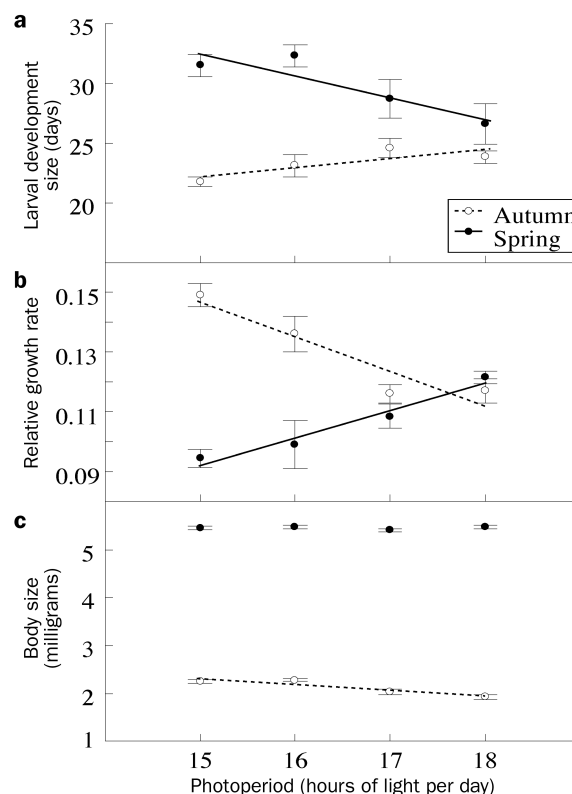


Figure 3. The effect of variation in photoperiod on (a) larval development time, (b) larval growth rate, and (c) final size (larval diapause and pupation, respectively) in autumn and in spring in the satyrine *Lasiommata maera*. A cohort of larvae, originating from six wild collected females, was divided among four different photoperiods in late summer/autumn and followed until all initiated larval diapause. After diapause in spring, the same larvae were again randomized over the same four photoperiods and followed to pupation.

growth in ectotherms, it is often difficult to disentangle direct effects on growth from strategic decisions based on the pattern of thermal variation. However, temperature influences larval growth decisions in *L. maera* (Gotthard et al. 2000). Larvae in a photoperiod indicating little time available for development grew significantly faster at a high temperature than at a low temperature; this response was much less pronounced when photoperiod instead indicated plenty of time for growth (figure 5). The larvae with plenty of time “decided” not to increase their growth rate in the higher temperatures, and this occurred during both growth periods of *L. maera* (autumn and spring).

Temperature may also determine the expression of color morphs of larvae, which affects the thermoregulation and growth of the caterpillars (Hazel 2002, Nice and Fordyce 2006). For example, in Texas, the pipevine swallowtail, *Battus philenor*, expresses a black larval morph in spring when it is relatively cold, and a red morph later in the summer when temperatures may reach harmfully high levels

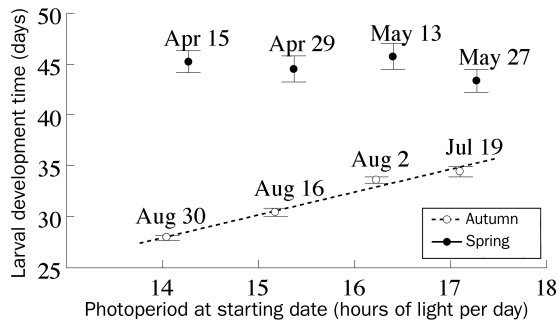


Figure 4. The effect of variation in photoperiod on larval development in late summer/autumn and spring in the satyrine *Lopinga achine*. Development times represent time to larval diapause in late summer/autumn and time to pupation in spring. To mimic the field situation, we used decreasing photoperiods in late summer/autumn and increasing photoperiods in spring.

(Nice and Fordyce 2006). This seasonal change in color is directly determined by temperature, and individuals may change morph between larval instars. When exposed to full sunlight, the red morph heats up more slowly and maintains a lower body temperature compared with the black morph. This morphological plasticity may be adaptive in allowing caterpillars to continue feeding and growing also at high summer temperatures (Nice and Fordyce 2006).

Growth decisions and larval host plants

The evolution and ecology of host plant utilization in butterflies and other insects has been the subject of many studies (Bernays and Chapman 1994). As with ambient temperature, it is clear that variation in larval host plant quality has such a profound direct effect on larval growth that it is difficult to detect potential strategic decisions. However, larvae of the polyphagous butterfly *Polygonia c-album* appear to use host-plant derived cues, in addition to the photoperiod, in decisions to diapause (Wedell et al. 1997). If a larva grows on a favorable host species in early summer (recognized by the photoperiod), it will be more likely than a larva growing on a less favorable plant to develop directly and produce a new brood before the end of the season. This is partly because the good host influences growth rate directly, but the results also suggest that larvae use the host as a cue of expected future conditions for successful direct development (Wedell et al. 1997). Similarly, larval host plants influence the diapause decisions in the Monarch (Goehring and Oberhauser 2002) and in the pierids *Leptidiana sinapis* and *Leptidiana reali* (Friberg et al. 2007).

Males of the green-veined white butterfly (*Pi. napi*) transfer nutritious “nuptial gifts” as a part of their ejaculate to females during mating (nuptial gifts are common in butterflies, and in insects in general). On average, the spermatophore, which contains the nuptial gift and sperm, makes up 15% of male body weight (Svärd and Wiklund 1989). Females

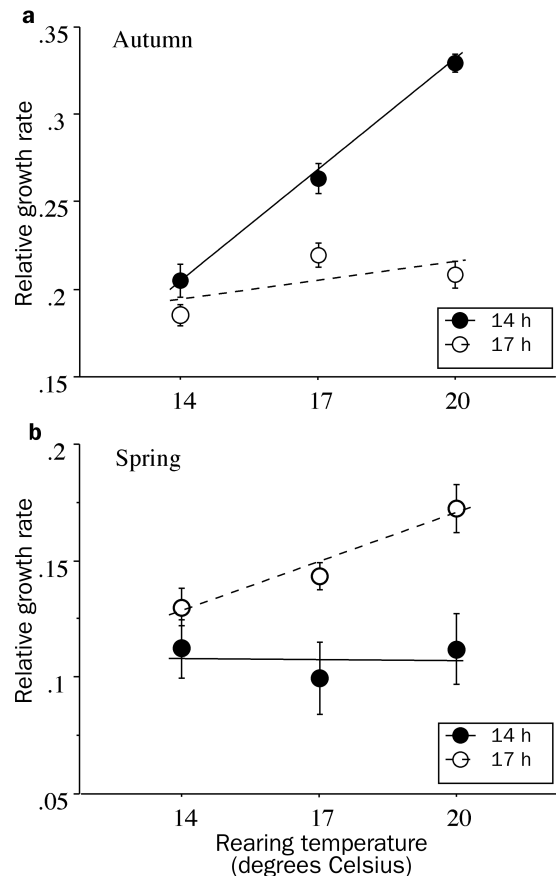


Figure 5. The effect of temperature on growth rate in *Lasiommata maera* larvae experiencing different photoperiods in (a) late summer/autumn or (b) spring. During both growth periods larvae that were “expecting” to need rapid development (14 hours of light in autumn, and 17 hours in spring) showed stronger increases in growth rate than larvae that were “expecting” plenty of time for growth. This indicates that the photoperiod-cued availability of time for development strongly influenced how individual larvae “decided” to react to temperature.

typically mate repeatedly and use the male-derived nutrients to boost egg production and longevity (Wiklund et al. 1993). Large *Pi. napi* males typically produce large spermatophores (Wiklund and Kaitala 1995) and have greater chances of fertilizing a given female’s eggs (Bissoondath and Wiklund 1997). This form of sexual selection may explain why *Pi. napi* is one of relatively few butterfly species in which males are similar to or larger than females (Wiklund and Forsberg 1991). In this species, the value of reaching a large body size may be more important for males than for females, which should influence sex-specific growth decisions in relation to the quality of larval food (Leimar et al. 1994). When larvae of *Pi. napi* were reared on low-quality food, the reduction in size was more pronounced in females than in males (figure 6a), which suggests that when male and female larvae are faced with low-quality food, they make different growth decisions. This demon-

strates the general principle that individuals should obtain resources at the lowest possible cost. For a *P. napi* female reared on low-quality larval food, it may be more costly to acquire resources in the larval stage than to rely on male-derived nuptial gifts. Male reproduction is highly dependent on adult size, but males have no means of acquiring the relevant resources during the adult stage. Therefore, males are likely to accept a higher acquisition cost when food conditions are constrained during larval growth (Leimar et al. 1994).

In the speckled wood butterfly (*P. aegeria*), the same general principle predicts a reversed pattern of sex-specific growth decisions, compared with *Pi. napi* (Karlsson et al. 1997). Males of *P. aegeria* are smaller than females and they produce very small spermatophores (on average 1.4% of male body weight), and females rarely remate (on average 1.04 matings per female in the field). In this situation, adult size influences female fecundity more strongly than it influences male mating success. Without substantial nuptial gifts, females have only the option of acquiring resources in the larval stage. Females of *P. aegeria* did show a smaller reduction in final size than did males when they were given low-quality food, which suggests that in this species, females were accepting the highest acquisition cost during larval growth (figure 6b). To further test their hypothesis, researchers (Leimar et al. 1994, Karlsson et al. 1997) also performed comparative analyses using 16 species of satyrids and pierids. For each species, they estimated the degree of natural variability in female size in samples collected within in a given locality and year. A high level of size variation was seen as an indication of a high degree of strategic growth in relation to food quality. The comparative analyses supported the hypothesis: the variability in female size was higher in species in which males produce relatively larger spermatophores (a cue of male investment; Leimar et al. 1994), and in species in which females mate many times (a female strategy to obtain resources from males; Karlsson et al. 1997).

Adaptive larval dimorphism and host plant

Host-plant cues may also influence the development of alternative larval morphs that display different growth patterns. A spectacular example is the larval morphs of the emerald moth *Nemoria arizonaria* (Geometridae) in North America (southwestern United States and northern Mexico). The species is bioltine, and larvae of the first spring brood feed on staminate flowers (catkins) of several species of oaks. The second, summer generation feeds on leaves of the same oaks (all catkins are gone at this time of year). At hatching, the larvae of the two generations look the same, but the catkin-feeding, spring-generation larvae develop into remarkable mimics of the catkins on which they feed, while the second-generation larvae develop into mimics of first-year oak twigs. A series of field surveys and laboratory experiments established that it is indeed the food (catkins or leaves) that determines the morph, rather than photoperiod, temperature, or wavelength of light (Greene 1989, 1996). The catkin diet is superior to the leaf diet—larvae develop faster and pupate

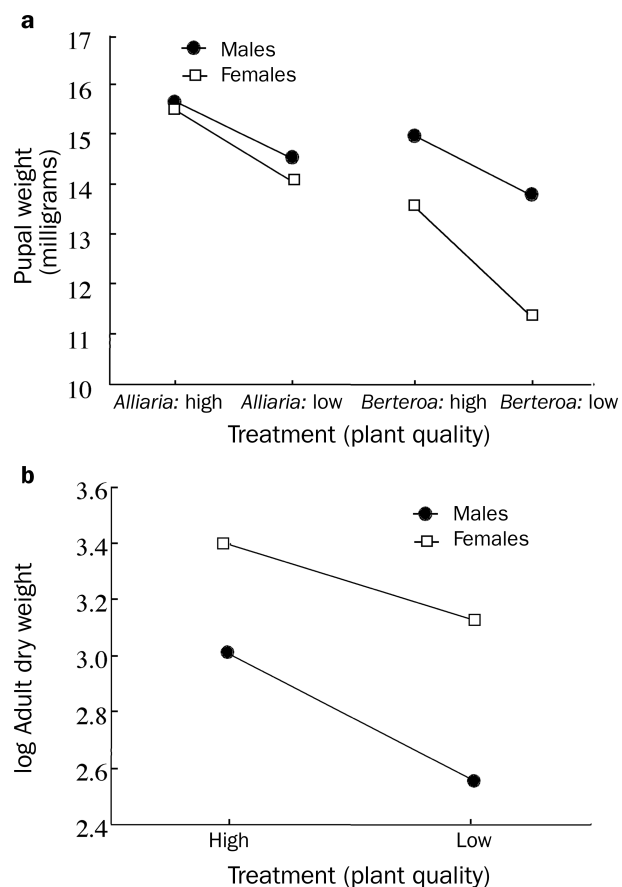


Figure 6. Results showing strategic growth decisions, depending on variation host plant quality in (a) *Pieris napi* (Pieridae) and (b) *Pararge aegeria* (Satyridae). In both panels, host plant quality decreases along the x-axis. Larvae of *P. napi* were reared on high- and low-quality plants of two host species that differ in suitability (*Alliaria petiolata* is superior to *Berteroa incana*), whereas *Pa. aegeria* larvae were reared on high- and low-quality plants of one host species (*Poa annua*) (Leimar et al. 1994, Karlsson et al. 1997).

at larger sizes when fed catkins. Nevertheless, producing an additional summer generation that feeds on oak leaves gives a big fitness advantage compared with the alternative univoltine strategy of postponing reproduction until next year's oak catkins are available. This demographic advantage, in combination with strong selection for crypsis as a defense against visually hunting predators, appears to have led to the evolution of a seasonal morph polyphenism in the larval stage of *N. arizonaria*.

Growth decisions of lycaenid butterflies living inside ant nests

Most lycaenid butterflies are ecologically associated with ants. These fascinating associations vary in strength from facultative to obligate, and range from mutualism to parasitism (Pierce et al. 2002). Larvae and pupae of the Lycaenidae

possess chemical, physiological, and behavioral adaptations that allow them to manipulate ants. For example, late-instar larvae of the butterfly genus *Maculinea* live as predators or as social parasites inside nests of *Myrmica* ants (Elmes et al. 2001). During the first three instars, these larvae feed on appropriate host plants, but then they drop to the ground and mimic ant larvae, and are transported by workers to the ant nest. Larvae of some *Maculinea* species prey on ant larvae in the nest, whereas larvae of other species are directly fed by the ants as if they were ant larvae (cuckoo species; Elmes et al. 2001). The integration of such cuckoo larvae into the ant colony may be so strong that the ants treat the caterpillars in preference to their own brood (Thomas et al. 1998). The fourth-instar caterpillars spend the winter inside the nest, but they grow only during late summer and early autumn and in spring (during winter, larvae lose weight).

The switch from herbivory to social parasitism is accompanied by a remarkable change in growth pattern. During the first three herbivorous instars, larvae show a two- to five-fold increase in mass (newly moulted fourth-instar larvae weigh between 1.5 and 2.5 milligrams [mg]), whereas larvae increase 50- to 60-fold during the fourth instar inside the ant nest and pupal weights vary between 75 and 125 mg. This massive increase in weight during the last instar in *Maculinea* and in some other genera that also are social parasites appears to be atypical in the Lycaenidae, including other predacious species.

Three types of selection may explain the evolution of this peculiar growth strategy (Elmes et al. 2001). First, to be adopted by ant workers, a larva may have to be small to mimic ant larvae, and small enough to be carried to the nest by a single worker. Second, social parasites may have evolved from smaller than average ancestors, and the transition to social parasitism could have allowed them to evolve larger body sizes. Third, since larvae of the ant host (*Myrmica*) also show amplified growth in the last instar, this growth strategy inside ant nests may have some unknown adaptive value.

In addition, *Maculinea* larvae display different growth strategies within populations (Thomas et al. 1998). Larvae of all the European species investigated so far either complete their development in a single year, spending ten months in the ant nest, or follow a two-year cycle and therefore spend 22 months inside the ant nest. Both categories start growing in late summer, but often diverge in size by the first winter, which is about 25 weeks before one-year larvae finish their growth before pupation (Thomas et al. 1998, Schonrogge et al. 2000). To what degree this is due to a genetic polymorphism or phenotypic plasticity is not clear, but when larvae are reared in similar conditions in the laboratory (i.e., similar sized host colonies of ants), both strategies are found (Thomas et al. 1998, Schonrogge et al. 2000). This suggests that there is a strong genetic component to the propensity to follow a given growth strategy.

In any case, the stable presence of this pattern among populations and species suggest that it has some adaptive value. The size and quality of *Myrmica* nests vary greatly, which could be seen as a highly unpredictable resource for

Maculinea larvae (Witek et al. 2006). Caterpillars that end up in a large ant nest with few other conspecific competitors may have enough resources to complete development in one year. Larvae adopted into small nests or into nests with many other *Maculinea* larvae, where the access to food is lower, may benefit by slower growth over an extra season, so they can reach a large enough pupal weight. In most other cases this would not be beneficial, as a longer development time increases the risk of juvenile mortality. Because *Maculinea* larvae within ant nests are well protected, two-year larvae experience low additional juvenile mortality (Thomas et al. 1998).

Because the quality of ant nest in which the larva arrives is unpredictable, it has been suggested that dimorphic growth represents a bet-hedging strategy whereby individual females produce offspring of both types, either through genetic polymorphism or through phenotypic plasticity (Thomas et al. 1998, Witek et al. 2006). However, in the best-studied case of *Maculinea rebeli*, approximately 75% of larvae follow a two-year cycle, and detailed modeling of this species implies that bet hedging cannot explain why more than 50% of larvae postpone growth (Hovestadt et al. 2007). In *M. rebeli* other fitness benefits—for example, increased fecundity, lower rates of parasitism, and earlier emergence of adults in the season—may also contribute to evolution-delayed development.

Growth strategies and the evolution of body size

Large final body size often correlates with a high reproductive capacity, so the decision of when to stop growing and metamorphose into a reproductive adult is clearly important. This decision directly links growth strategies to life history analysis of age and size at maturity (Stearns 1992, Roff 2002). The growth strategies discussed above show that butterflies have a remarkable capacity for rapid growth, but also that they typically do not grow at physiologically maximal rates. For example, when larvae have plenty of time to grow, they often reduce growth rates instead of using this time to become considerably larger (Leimar 1996, Gotthard 2004). This suggests that the cost of growing at the physiological maximum is greater than the reproductive benefit of reaching a larger size. Nevertheless, laboratory studies show that female fecundity may increase rapidly with body size. In combination with most butterflies' high capacity for rapid weight gain, it is difficult to see how realistic levels of larval mortality can outweigh the fecundity benefit of faster growth or, for that matter, continued growth for a few extra days. In fact, it is generally unclear what does keep butterflies and many other insects small (Blanckenhorn 2000).

A potential explanation is that predation risk may increase with larval size, and above a certain size, foraging is simply too dangerous (Leimar 1996, Berger et al. 2006, Mänd et al. 2007). Larvae that grow far larger than the "normal" size for a given species may become conspicuous on the structures they feed on and thereby attract more predators. Positive size-dependent predation risks of this kind have been found, and may lead to a reduction in optimal size (Berger et al. 2006, but

see Mänd et al. 2007). Another explanation has been suggested by researchers who question whether the potential fecundity benefit of large size can be realized in nature (Springer and Boggs 1986, Leather 1988, Gotthard et al. 2007). Field conditions typically limit the amount of time females can be active and lay eggs, which may dampen the fecundity benefit of larger females (Gotthard et al. 2007). Hence, an important explanation could be that the fecundity benefit of continued larval growth is in fact relatively limited under natural conditions.

Conclusions

It seems likely that the larval stage of holometabolous insects is primarily an adaptation for efficient growth. Butterfly larvae can grow very fast, but usually they do not seem to grow at maximal rates, most likely because high growth rates are associated with extra mortality costs. This illustrates the important point that natural selection will favor the combination of growth rate, survival, and sexual maturation that maximizes long-term reproductive success. The growth trajectory of a caterpillar is governed by growth decisions that are adaptations for optimized growth. These decision rules vary adaptively among categories such as sex, population, and species, which suggests that they have a genetic basis and have evolved by natural selection.

Moreover, individual larvae show adaptive phenotypic plasticity in growth decisions, and they adjust growth in relation to the environment they encounter. To do this, larvae must have adaptations for retrieving and interpreting information that predicts future conditions. Studies of how photoperiod, food quality, temperature, and sex influence growth decisions show that such adaptations do exist. Adaptive variation in growth decisions have been described in many other insects (Masaki 1978, Tauber et al. 1986, Nylin and Gotthard 1998, Blanckenhorn et al. 2007) as well as in vertebrates such as amphibians and fish (Newman 1992, Arendt 1997, Metcalfe 1998, Gotthard 2001), and it is a phenomenon of general importance for life history evolution. Most likely, growth decisions arise from developmental switch mechanisms that integrate genetic and environmental effects on phenotypes during development (West-Eberhart 2003). Such switch mechanisms underlie heritable variation in developmental plasticity. Because phenotypic evolution often is synonymous with evolution of development, it appears likely that natural selection on developmental switches is a major route for evolutionary change in general (West-Eberhart 2003).

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