Time stress, predation risk and diurnal–nocturnal foraging trade-offs in larval prey

David Berger · Karl Gotthard

Abstract Insect larvae increase in size with several orders of magnitude throughout development making them more conspicuous to visually hunting predators. This change in predation pressure is likely to impose selection on larval anti-predator behaviour and since the risk of detection is likely to decrease in darkness, the night may offer safer foraging opportunities to large individuals. However, forsaking day foraging reduces development rate and could be extra costly if prey are subjected to seasonal time stress. Here we test if size-dependent risk and time constraints on feeding affect the foraging–predation risk trade-off expressed by the use of the diurnal–nocturnal period. We exposed larvae of one seasonal and one non-seasonal butterfly to different levels of seasonal time stress and time for diurnal–nocturnal feeding by rearing them in two photoperiods. In both species, diurnal foraging ceased at large sizes while nocturnal foraging remained constant or increased, thus larvae showed ontogenetic shifts in behaviour. Short night lengths forced small individuals to take higher risks and forage more during daytime, postponing the shift to strict night foraging to later on in development. In the non-seasonal species, seasonal time stress had a small effect on development and the diurnal–nocturnal foraging mode. In contrast, in the seasonal species, time for pupation and the timing of the foraging shift were strongly affected. We argue that a large part of the observed variation in larval diurnal–nocturnal activity and resulting growth rates is explained by changes in the cost/benefit ratio of foraging mediated by size-dependent predation and time stress.

Keywords Predation risk · Growth rate · Life history theory · Body size · Seasonal constraints

Introduction

The foraging decisions of prey are predicted to shift in unison with levels of predation risk and food abundance so that the behaviour serves to minimise the risk of mortality while at the same time reassuring efficient energy gain (Kozlowski 1992; Lima and Dill 1990; Werner and Gilliam 1984). Adaptive responses of prey to shifting levels of predation and food might involve the choice of at which rate (Abrams et al. 1996; Sibly et al. 1985) or time (Metcalfe et al. 1999; Werner and Anholt 1993) or in which habitat to forage (Gilliam and Fraser 1987; Werner and Gilliam 1984). Obviously, predation should select for cautious prey. However, being able to forage only in patches or during periods of low risk is a luxury that all prey may not afford. If low risk periods are few and far between, prey might be forced to feed during high levels of predator presence in order to avoid starvation (Clark 1994; Lima and Bednekoff 1999; Werner and Gilliam 1984). Seasonal stress might also limit the available options to the forager as certain rates of foraging are needed in order to finish development within a specific time frame (Gotthard 2001; Nylin and Gotthard 1998; Roff 2002) so the individual might not afford to practise a risk aversive strategy (Clark 1994; Ludwig and Rowe 1990).

   How important predictable fluctuation in predator presence will be for the shaping of prey foraging behaviour and patch use will depend on the absolute level of risk

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experienced (Lima and Bednekoff 1999; Sih et al. 2000). For example, the difference in mortality between high and low risk periods will be great for size classes of prey preferred by the predator but negligible for other size classes. As an individual progresses through ontogeny, its state changes; it attains a larger size, which, presumably exposes it to different predators or levels of predation risk (Werner and Gilliam 1984; Roff 2002) and attains a larger reproductive value which will alter the cost/benefit ratio of future foraging decisions (Clark 1994; Houston et al. 1988). Therefore, the optimal behavioural strategy and patch use in response to time stress and temporal variation in predation risk might change during juvenile development (Clark 1994; Houston et al. 1988; Ludwig and Rowe 1990; Werner and Gilliam 1984). In this study, we provide a rare empirical evaluation of these theoretical predictions which exemplifies how time stress and the perceived level of risk might affect the appearance and strength of ontogenetic niche shifts in temporal patch use.

Predation risk is usually high during daytime when both vertebrate and invertebrate predators are active (Kronfeld-Schor and Dayan 2003; Park 1940), and prey subjected to visually hunting predators might benefit from using daylight as a cue for increased predation risk, a pattern found in both fish (Bradford and Higgins 2001; Fraser et al. 2004; Imre and Boisclair 2004; Metcalfe et al. 1998), zooplankton (Lampert 1989) and aquatic insect larvae (Baker and Ball 1995; Culp and Scrimgeour 1993; Macchiusi and Baker 1992; Tikkanen et al. 1994). Visual predators are in fact believed to have driven prey species to a strict nocturnal lifestyle in a wide variety of taxa (Kronfeld-Schor and Dayan 2003), and in plant-feeding insects, high levels of daytime predation is held as one reason for instances of strict nocturnalism in the larval stage (Hassell and Southwood 1978; Heinrich 1993; Reavey 1993).

Visual predators that hunt for insect larvae during daytime (mainly birds and fish) are great threats to late instars while smaller larvae instead typically are preyed heavily upon by both diurnal and nocturnal arthropods (see examples: Atlegrim 1992; Buckner 1966; Feeny et al. 1985; Kristensen 1994; Zalucki et al. 2002). Thus, for small larvae in general, mortality risk is likely to show little variation over the 24-h period (Hassell and Southwood 1978; Zalucki et al. 2002), but as they grow bigger, their size may protect them from most nocturnal invertebrate predators while instead they grow into the window of daytime bird predation (Buckner 1966; Hassell and Southwood 1978). These conditions should create a size-dependent cost/benefit ratio associated with diurnal–nocturnal foraging, and thus, set the stage for the evolution of ontogenetic shifts in larval foraging behaviour.

The mechanisms behind and ultimate explanations for diurnal–nocturnal ontogenetic niche shifts have been poorly studied in insects, and the few rigorous studies found on the topic concern aquatic species (see Culp and Scrimgeour 1993; Tikkanen et al. 1994). Like other insect larvae, large lepidopteran larvae are heavily preyed upon by day active birds while different arthropod taxa usually are confirmed as main predators on small instars (reviewed in: Buckner 1966; Dempster 1984; Heinrich 1993; Montllor and Bernays 1993; Reavey 1993; Stamp and Wilkens 1993; Zalucki et al. 2002). We here test the hypothesis that Lepidopteran larvae economise their foraging throughout ontogeny in relation to the perceived level of risk and time stress on both the daily, as well as the seasonal scale. We measured the rates of diurnal and nocturnal growth rates throughout larval development in two butterflies showing clear differences in phenology: *Pararge xiphia*, occurring throughout the year without any clear response to seasonality, and *Hipparchia semele* with one clear flight period and a highly flexible growth trajectory responding to climatic conditions (Wickman et al. 1990). The larvae were exposed to two photoperiodic treatments in order to induce differences in (a) the length of the night (i.e. the time available for foraging in the dark) and (b) the perceived time of season. If predation risk is size dependent and traded off against growth rate, the following predictions can be made: (1) Both species should, at small sizes, maintain high growth rates by practising both night- and daytime foraging, but at larger more conspicuous sizes, shift to a strict nocturnal mode of foraging. (2) If there is a size-dependent shift, the strength of this shift to nocturnalism should be affected by the fact that the treatments differ in their time available for night foraging on the daily scale so that larvae in the treatment with short nights (short low risk periods) may be forced to utilise daytime (high risk periods) for feeding due to starvation risk. (3) Finally, if larvae show size-dependent shifts in their use of the diurnal–nocturnal cycle, we also predict that these shifts are affected by the perceived time of season so that larvae exposed to high levels of seasonal time stress must maintain higher growth rates and therefore be forced to use longer parts of the day for feeding than individuals exposed to lower levels of seasonal time stress. If so, a clear prediction would be that this effect will be present in the seasonal *H. semele* where delayed development should be associated with great fitness consequences but absent in the non-seasonal *P. xiphia*.

Materials and methods

Study species

P. xiphia is endemic to the island of Madeira where generations are continuous. The larvae do not diapause or show any clear growth response to naturally occurring day

lengths when reared in the laboratory (Gotthard, K., Berger, D. and Bergman, M., unpublished data). *H. semele* has one discrete generation per year all over Europe (Tolman 1997). The population used in the experiment originated from Sweden where the flight period extends from late July to early September (Eliasson et al. 2005). Thus, growth in *H. semele* should be governed by seasonal light regimes enabling timing of metamorphosis in a beneficial part of the season while no such response seems likely in *P. xiphia*. *H. semele* larvae have been reported as strict night active based on natural observations (Eliasson et al. 2005) while data on *P. xiphia* show that growth rate is relatively slow and development time is long in the last instar compared to the earlier instars (Berger et al. 2006), indicating size-specific foraging behaviour. Larvae of both species are cryptic and feed on grasses like other satyrines, but are relatively large compared to sympatric species of satyrines (Eliasson et al. 2005; Tolman 1997) and attain weights of 400–500 mg before pupation. Hence, these larvae spend long times at sizes that are potentially conspicuous to visual predators in spite of their cryptic coloration.

Growth experiment

The larvae used in the experiment were the offspring of 12 wildcaught females of *P. xiphia* and eight females of *H. semele*. The larvae of the Swedish populations of *H. semele* were reared outdoors over the winter months as this species naturally diapauses as second instar larvae through the winter and resumes growth in spring when temperatures again are warm. In the experiment, larval diapause was terminated by transferring larvae from outdoors to the experimental treatments. *P. xiphia* larvae were put into the treatment directly after hatching. The growth rates of the larvae were measured from the second instar at weights between 3 and 10 mg in *P. xiphia* and from the third instar between weights of 4 and 14 mg in *H. semele*. Larval growth rates were measured up until pupation, but in the statistical analysis, only measures taken when larvae weighed less than 300 mg were included. This was due to the fact that larval growth rates usually decrease prior to pupation (D'Amico et al. 2001; Esperk 2006). Sixty larvae of *P. xiphia* and 55 of *H. semele* were split by family and thereafter randomly assigned to one or the other of two photoperiodic treatments: the high-stress treatment with a 24-h cycle of 19 h light and 5 h dark (L:D 19:5), and the low-stress treatment with L:D 15:9. The photoperiod in the high-stress treatment is equivalent to Swedish summer solstice but never experienced on Madeira, while the photoperiod in the low-stress treatment is equivalent to Madeiran summer and Swedish spring conditions. The treatments render two important consequences: (1) The high-stress treatment has shorter nights, leaving fewer hours

of darkness left for safe foraging for both species, possibly imposing physiological constraints on feeding. (2) *H. semele* development might be under more severe seasonal time stress in the high-stress treatment since day lengths match late season conditions while the low-stress treatment is equivalent to early season conditions, still leaving plenty of time until the window for metamorphosis opens. Since *P. xiphia* has continuous generations, no response to photoperiodic cues is expected in this species. Each larva was placed in a 0.5 litre transparent plastic cup where its food plant was kept in water culture. *P. xiphia* was reared on *Dactylis glomerata* while *H. semele* was reared on *Festuca ovina*. The cups were randomised among four climate cabinets (two cabinets per treatment), with a constant temperature of 17°C. Growth rates during day and night were measured for each individual at several occasions throughout its development by weighing each individual at the start and end of the day period (start of the night period), and then again at the end of the night period during one 24-h cycle. This made it possible to calculate the relative size increase per hour during day and night. Since insect larval weight increase is close to proportional to the size of the individual, the calculations of relative growth rates were based on the formula: [Ln (end weight)− Ln (start weight)]/[time]*100 (see Nylin et al. 1989) yielding the increase in body mass per hour calculated as a percentage of the start weight. Since *H. semele* goes through five larval instars and *P. xiphia* goes through four, the growth rate measures were obtained once in the third and fourth instar and twice in the fifth instar (once at small size and once later at larger size) in *H. semele* while they were obtained once in the second and third instar and twice in the fourth instar in *P. xiphia*. In order to estimate treatment effects on development times, the starting day of the experiment and date of pupation were noted. In addition, 16 individuals of *H. semele* were reared outdoors under natural light and temperature conditions in order to assess the time of pupation under natural conditions.

Behaviour

To confirm that obtained growth rate differences between the diurnal–nocturnal periods also corresponded well with differences in the foraging behaviour of the larvae, behavioural observations were performed on the third and fourth (last) instar of *P. xiphia* and the fourth and fifth (last) instar of *H. semele* during light and dark periods. The observations were carried out on larvae exposed to a 19:5 L:D cycle in 17°C. For *P. xiphia*, individual larvae were put singly on pots of *D. glomerata*. Their movement and position were registered three times in both light and dark, respectively. Observations of behaviour were carried out once in the middle of the light and dark periods and 1 h

after the start and 1 h before the end of the respective period. A light and dark average was calculated for each individual. Movement was measured at each checkpoint by marking the placement of the larva with a sticker on the leaf and at the next checkpoint measuring how far it had moved with a ruler. The position of the larva was coded as either on top (individual on the upper half of the leaf), or at the bottom (lower half). For *H. semele*, three to five larvae were placed on tussocks of *F. ovina* and behavioural observations were carried out two times during the dark and light periods, respectively. Averages were then calculated for each tussock. Movement could not be measured as observations in the dark had to be carried out in low luminosity and very quickly as the larvae tried to hide by escaping down towards the bottom of the tussock as soon as the light was turned on. Instead, the placement of the larvae was recorded by measuring with a ruler the distance from the larva's head down to the bottom of the tussock at each checkpoint.

Statistics

Since repeated measurements of the same individual were taken over both the 24-h period (day and night) and throughout development (instars), it was necessary to convert one of these repeated measurements into a single variable. The growth rate measures taken from each larva throughout development were transformed to a single measure describing how growth changed with larval size. For each larva, we fitted a linear regression to the values of instantaneous growth rate on larval weight taken at the respective census points. The logarithmic value of larval size was used in order to make the relationship linear (see Fig. 2). Regressions were fitted to day and night data separately, so for each individual, two regressions were obtained, one describing the relationship between larval size and growth rate during daylight, and one describing it during nighttime. The slope coefficients of each regression were subsequently used to test for significant growth rate differences between the treatments and day and night periods. A positive slope coefficient means that the growth rate of the larva increased as it grew bigger while a negative coefficient means that it decreased as the larva increased in size. To improve criteria for parametric statistics, the Box–Cox family of transformations was used to search for the most appropriate transformation of the slope coefficients (see Quinn and Keough 2002 for further description of the method). The statistical analyses were performed on the transformed data, but we have chosen to show the raw data on slope coefficients in the figures in order to keep a higher level of clarity. Only larvae that were successfully measured throughout development were included in the statistical analysis. Out of the total 60 started *P. xiphia* larvae, 52

fulfilled the criteria for the growth rate analysis, while 37 out of 55 individuals did so in *H. semele*. Missing values were due to deaths, escapes or incidents where the observer failed to find small larvae. Treatment effects on size-dependent growth rates (the slope coefficients) during day and night were analysed with mixed model ANOVA by nesting the day/night repeated observations in each individual subject (larva) with photoperiodic treatment set as a fixed factor. Since the size-specific effect on growth rate is incorporated into the slope coefficients, a significant effect of [day/night] means that the pattern of how growth rates change with the size of the larva differs between day and night. In addition to the figure showing the slope coefficients (Fig. 3) on which the analyses were based, we also present a figure on the raw data from which the slope coefficients were calculated as we think this helps the interpretation of data (Fig. 2). In the text and in all figures, the variation around the means is given as ± two standard errors.

Treatment effects on the final sizes and development times were analysed with ANOVA except for the development time in *H. semele*, which, due to heterogeneous variances was tested with the non-parametric Mann–Whitney *U* test. Pupation of *H. semele*, both outdoors under natural conditions and in the main experiment, resulted in many failures and deaths; this is also the reason why the sample sizes between tests performed on *H. semele* pupae and larvae differ so much. This species buries into the soil prior to pupation (Eliasson et al. 2005), which was not possible in the plastic cups in the experiment; this is a likely explanation for the low success rate.

The behavioural data were analysed with repeated measures ANOVA. We analysed differences in movement (centimetre per hour) and frequency on top of the grass leaves for *P. xiphia* and larval distance to soil (centimetre) for *H. semele* by using [light/dark] as the repeated measure nested in subject with [larval stage] set as a fixed factor. The sample size of *P. xiphia* was based on individual averages of three observations per individual in dark and light, respectively, while the sample size for the analysis on *H. semele* was based on averages for each tussock as several larvae were placed on the same tussock. In total, 25 third instar and 47 fourth instar *P. xiphia* larvae and 29 fourth instar and 21 fifth instar *H. semele* larvae were observed.

Results

Out of the 16 *H. semele* larvae kept outdoors, eight survived to pupation. These eight individuals all pupated between the 24th of June and the 9th of July. This indicates that the high-stress treatment (L:D 19:5) was accurately
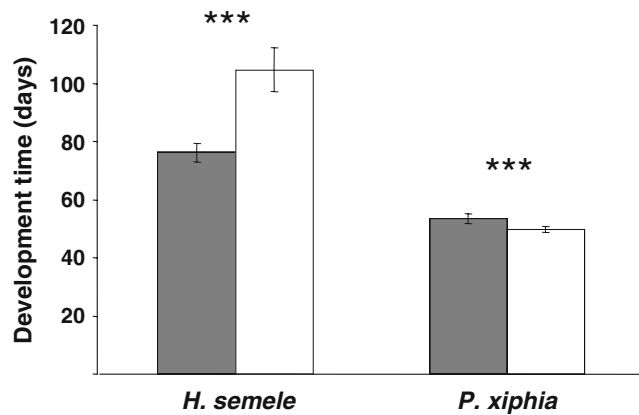
Fig. 1 Development times (means ± 2SE) of *H. semele* and *P. xiphia* in the high-stress treatment (*grey bars*) and low-stress treatment (*white bars*). *Stars* indicate $p<0.001$
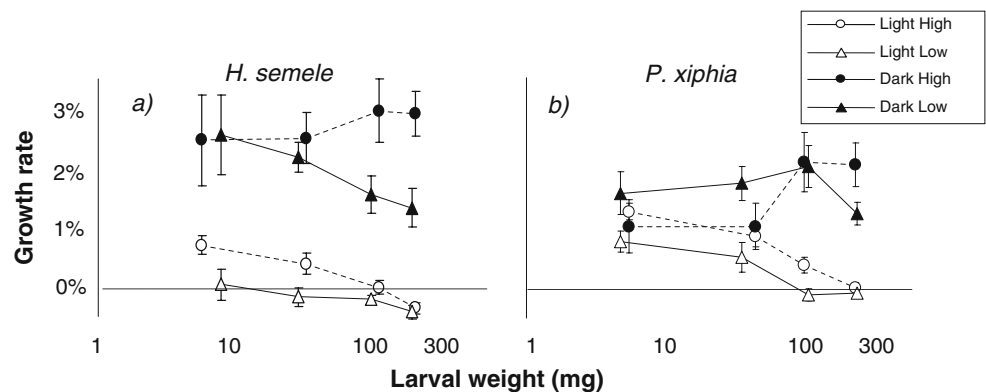
mimicking late season conditions since day lengths in Stockholm, Sweden in late June (midsummer) reach a maximum of 19 h.

Growth experiment

H. semele

There was no effect of treatment on pupal weight ($F_{1,21}$= 0.24, $p>0.6$, high: 315±35 mg, low: 330±49 mg), but a strong difference in development time between the photoperiodic treatments with a shorter development time in the high-stress treatment ($Z=-4.36$, N1=14, N2=20, $p<0.001$, Mann–Whitney U test; Fig. 1). The considerably shorter development times of the larvae in the high-stress treatment suggest that the treatments exposed larvae to substantial differences in the level of seasonal time stress. There was no general difference in how the diurnal–nocturnal feeding mode changed with larval size (day/night: $F_{1,35}$=0.25, $p=$ 0.62; Figs. 2a and 3a), but the size dependence of the foraging mode was affected by treatment (treatment × day/ night interaction: $F_{1,35}$=14.0, $p<0.001$). This was due to the fact that larvae in the low-stress treatment in essence never practised diurnal feeding and developed at slow pace

while small larvae in the high-stress treatment fed also during the day and developed faster. As larval size increased however, diurnal feeding finally ceased also in the high-stress treatment whereas nocturnal feeding increased at large sizes, allowing for sustained fast rates of development (Figs. 2a and 3a).

P. xiphia

There was no treatment effect on pupal weight ($F_{1,48}$=1.46, $p>0.2$, high: 272±10 mg, low: 263±11 mg), but development time in the high-stress treatment was, in contrast to *H. semele*, prolonged ($F_{1,48}$=11.9, $p<0.001$; Fig. 1). All larvae showed clear ontogenetic shifts in their feeding mode; there was a significant difference between day and night in how the foraging rates changed with the size of the larva (day/ night: $F_{1,50}$=52.5, $p<0.001$). As the size of the larva increased, nocturnal feeding became the exclusive foraging mode while diurnal feeding ceased regardless of photoperiodic treatment (Figs. 2b and 3b). The size dependence of the diurnal–nocturnal feeding mode was also affected by treatment (treatment × day/night interaction: $F_{1,50}$=4.07, $p=0.049$). In the high-stress treatment with fewer dark hours, diurnal feeding was more pronounced at small sizes and nocturnal feeding increased more strongly as larvae grew bigger in comparison to the low-stress treatment (Figs. 2b and 3b). We interpret this result as a consequence of the number of dark hours being limiting to the feeding physiology in the high-stress treatment, forcing individuals to practise diurnal foraging to a higher degree. At larger sizes, diurnal feeding was abandoned which explains the fact that larval development times were prolonged in the high-stress treatment (Fig. 1).

Behaviour

H. semele larvae positioned themselves closer to the bottom of the tussock during the light period in comparison to the position in darkness ($F_{1:10}$=77.0, $p<0.001$). There was no difference between instars ($F_{1:10}$=0.97, $p=0.35$) and no

Fig. 2 Hourly growth rates (means ± 2SE) in the different treatments during day and night in *H. semele* (**a**) and *P. xiphia* (**b**). The average weights of the larvae at the time of the measurements are plotted on a logarithmic scale against the average rates of growth of the larvae. Each individual is represented up to eight times, at four different occasions throughout development, during both day and night
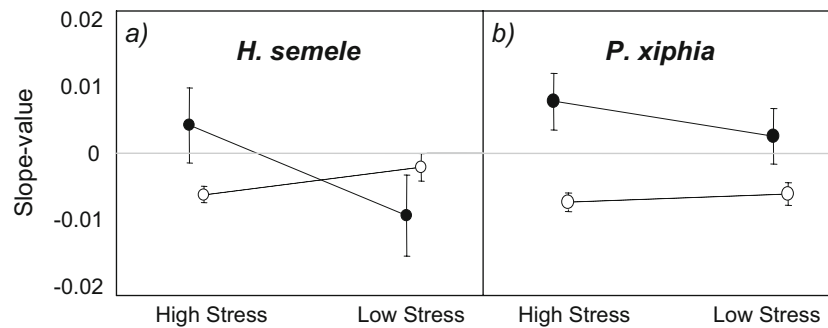
Fig. 3 Slope coefficients (means ± 2SE) based on the correlation between growth rate and the logarithm of larval weight for each individual of H. semele (**a**) and P. xiphia (**b**), during day (*open circles*) and night periods (*filled circles*) in the high- and low-stress treatment. Positive values indicate that growth rates increase with larval size while negative values indicate a growth decrease with size. The horizontal *grey line* is set at y=0, i.e. where the slope coefficients equal zero and there is no size dependence of growth

significant interaction effect ($F_{1:10}$, $p=1.77$, $p=0.21$; Fig. 4a). P. xiphia larvae moved significantly less in the light than in the dark ($F_{1:67}=43.9$, $p<0.001$). There was no main effect of instar on larval movement ($F_{1:67}=0.07$, $p=0.79$); however, the fourth instar larvae moved mostly during dark periods while the third instar larvae showed similar levels of movement during all periods of observation (interaction effect: $F_{1:67}=15.2$, $p<0.001$, third instar dark: 3.28±1.25 cm/h, light: 4.17±1.40 cm/h, fourth instar dark: 6.48±1.80 cm/h, light: 1.49±0.77 cm/h). Results on larval position on host plant were very consistent with the movement data: fourth instar larvae were found on top of the leaves during dark periods and in the bottom during light periods while third instar larvae positioned themselves more independently of the light conditions (light/dark: $F_{1:70}=43.9$, $p<0.001$; larval stage: $F_{1:70}=0.63$, $p=0.43$; interaction: $F_{1:70}=11.1$, $p=0.001$; Fig. 4b).

Discussion

Our assessments of foraging behaviour showed that large larvae seek refuge at the bottom of the plant or at the undersides of leaves in daylight conditions. The response pattern of behaviour between night and day and instars was very similar to the response of growth rate. Thus, even though a perfect correspondence between foraging behav-

iour, feeding and growth rate cannot always be expected (Arendt 1997); in these species, for the general questions asked here, we conclude that the growth rates obtained are good estimates of larval foraging and risk taking. The results show that, in general, daytime feeding decreased with larval size while nighttime feeding was practised at high levels in both species throughout their whole size span. Basing our conclusion on what is known about the key predators of Lepidopteran larvae (reviewed in: Buckner 1966; Dempster 1984; Heinrich 1993; Reavey 1993; Stamp and Wilkens 1993; Zalucki et al. 2002), we contend that the reason for this ontogenetic feeding shift is that levels of predation risk during daytime increase in relation to the risk at night as these larvae reach larger sizes.

Although the exact shape of how the terminal fitness changes with food consumption will be important for the optimal foraging strategy (Koops and Abrahams 1998; Krivan and Vrkoc 2000), prey should primarily utilise the period that renders the lowest risk of mortality per energy unit gained by foraging (the "minimise μ/g-rule", analytically derived for spatial patch use reviewed by Werner and Gilliam 1984) and only use suboptimal periods when forced to fulfil nutritional demands. Therefore, whenever food levels increase, or low risk periods become common enough to satiate the prey's hunger, high risk periods should be spent in refuge or at high vigilance (Lima and Bednekoff 1999; Metcalfe et al. 1999; Sih et al. 2000;

Fig. 4 Behaviour of last- and second to last instars of H. semele (**a**) and P. xiphia (**b**) in light (open circles) and dark (filled circles), (means ± 2SE). H. semele means were based on average positions of larvae per tussock. In total 29 fourth instar and 21 fifth instar larvae were observed, three to five larvae on each of 12 tussocks. P. xiphia means were based on individual averages from 25 third instar and 47 fourth instar larvae
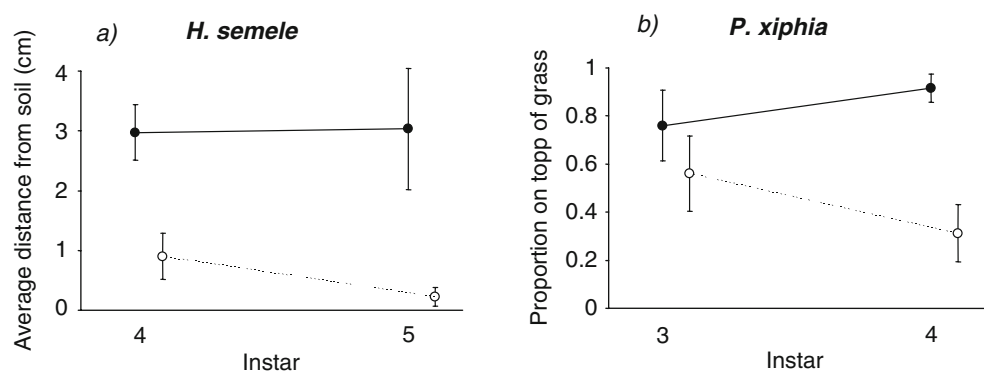
Werner and Gilliam 1984). In the low-stress treatment, with a 9-h night length, larvae showed low levels of day feeding, while in the high-stress treatment that limited the time available for safe foraging, daytime feeding was more pronounced (Fig. 2). Thus, the high-stress treatment made larvae accept greater risk in order to maintain growth rates which ultimately changed the timing and appearance of the ontogenetic shift. However, as larval size increased, daytime feeding finally ceased completely in both species also in the high-stress treatment. A likely explanation for this last result is that daytime predation risk at the largest larval sizes become so high as to shift the cost/benefit ratio of daytime foraging further towards complete nocturnalism. However, it cannot be ruled out that the complete abandonment of daytime feeding might have been caused by: (a) large larvae building up their reproductive value and thereby standing gradually more and more to lose by risky daytime feeding (see Clark 1994) or (b) a decreased cost of reduced growth if for example large larvae were in less of a hurry at the end of development (see Metcalfe et al. 1998). These processes are not exclusive and may all be at work.

In the seasonal H. semele, development time was shortened in the high-stress treatment (Fig. 1) and the feeding shift to strict nocturnalism was delayed to later in development (Figs. 2a and 3a). This was an expected response as the photoperiod of the treatment mimics late season conditions, and seasonal time stress sets limits to the minimum rate of development. Thus, seasonal time stress increased the costs associated with slow growth and a low risk foraging strategy, shifting the balance of the foraging–predation risk trade-off towards faster growth and acceptance of greater risk. In the non-seasonal P. xiphia, the high-stress treatment did not put seasonal constraints on development. Instead, the treatment seemed only to limit feeding by the time available for safe foraging during its short night length. This resulted in a small difference in the size dependence of foraging mode between the treatments (Figs. 2b and 3b), which, probably can be attributed to the feeding physiology of P. xiphia apparently not being adapted to strict nocturnalism in the night lengths of the high-stress treatment. This forced individuals to compensate by feeding during daytime. However, at large sizes larvae in the high-stress treatment also switched to strict nocturnalism which resulted in longer development times of individuals in this treatment (Fig. 1) further underlining the principally different response to the growth/predation risk trade-off in P. xiphia. Comparing the responses of one seasonal species with one non-seasonal species is not a rigorous test of any hypothesis concerning the combined effects of predation risk and time stress on optimal foraging behaviour. However, the two within-species comparisons between individual larvae belonging to the different treatments illustrate the trade-off between safe foraging and feeding constraints (seasonal and physiological), and these results correspond well to what would be predicted by foraging theory for seasonal and non-seasonal prey, respectively (Abrams et al. 1996; Johansson and Rowe 1999; Johansson et al. 2001; Lima and Dill 1990; Ludwig and Rowe 1990; Metcalfe et al. 1998). Thus, this study provides a rare example of how time stress might affect the appearance and strength of ontogenetic niche shifts in temporal patch use.

The optimal behavioural strategy will not only be determined by the relative risk associated with the foraging decision, but also by its energetic gains (Clark 1994; Gilliam and Fraser 1987; Werner and Gilliam 1984), so the prey's own foraging efficiency in a spatial or temporal patch will be of highest importance for the decision of whether to forage or not. For example, Metcalfe et al. (1999) showed that low risk nighttime foraging remained maximised as food concentrations were experimentally increased, while high risk daytime foraging drastically levelled off in juvenile Atlantic salmon enduring winter. The authors concluded that under low food concentrations the fish was forced to feed during daytime, during which, the prey's own foraging efficiency was high so only short bouts of compensatory feeding was needed. Even so, in high food concentrations fish became strictly nocturnal illustrating that not only changes in risk but also in prey foraging efficiency (i.e. food concentration, handling, finding and digestion) will be of importance for the optimal foraging decision. A shift to strict night activity will set new demands on prey physiology (Kronfeld-Schor and Dayan 2003; Park 1940). For larval insects, often living on their food plant, finding and handling the food do not seem to be a great problem in the dark. However, even though the temperature in this study was held constant in order to allow direct growth rate comparisons between dark and light periods, natural temperature variation between day and night is likely to be of great importance. The physiology of ectothermic organisms is more efficient in higher temperatures up until detrimental temperatures are reached (Angilletta et al. 2003; Atkinson and Sibly 1997). This also holds true for larval growth in insects (Casey 1993; Kingsolver et al. 2004; Kingsolver and Woods 1997; Slansky 1993). This implies that there are physiological limits to growth efficiency during nighttime when temperatures drop. Thus, even though predation risk may be lower at night, foraging during this period might have negative consequences for the butterfly larva if temperatures are limiting growth rates (Stamp and Wilkens 1993). This is one reasonable explanation as to why ontogenetic niche shifts to strict night foraging mostly have been observed in aquatic organisms (see Culp and Scrimgeour 1993; Tikkanen et al. 1994) which live in a medium showing less thermal variation. From this reasoning, it also becomes quite clear

that thermal adaptations to cold or varying temperatures might be expected in terrestrial animals that switch to nocturnalism at some point in development (Stamp and Bowers 1990).

A shift to strict nighttime foraging might also generate changes in life history. Most obvious is the prediction that development times are likely to be longer since strict night activity will reduce opportunities for feeding, and low night temperatures will reduce growth rates. Also, evolution of a larger size at maturity might be expected if predation pressure on large individuals is relaxed, decreasing size-dependent costs associated with prolonged growth. These initial changes might then drive selection on correlated life history characters. A study by Takeda (2005) on two sympatric populations of Hyphantria moths provides a good example. In one of the populations, individuals are univoltine and the larvae feed mainly at night, whereas larvae of the bivoltine population utilise both day and night to feed. The populations also differ in larval development times and the critical day length for induction of pupal diapause. The author speculates that the univoltine population is not able to complete a second generation due to low temperatures during night feeding but instead gains the advantage of lower mortality from predation in comparison to the bivoltine population, although this remains to be demonstrated.

We have not been able to assess predation risk in the field during day- and nighttime to different size classes of the investigated species. Instead, we have based our underlying assumptions of this study upon the data for the Lepidoptera as a group, thus, not on the particular species investigated. Apart from the effects from predation and time constraints, other factors may also influence the evolution of size-dependent foraging strategies during the diurnal–nocturnal cycle. If for instance temperatures reach harmful levels during the day, larvae might be restricted to shade at the bottom of the host plant or to undersides of leaves (Casey 1993; Reavey 1993; Slansky 1993). This explanation, although applicable to other cases in which temperatures get hotter at the end of the growth season when larvae have reached large sizes, does not seem probable in the species described here. Firstly, even though temperature was held constant in the experiment, both species showed clear ontogenetic shifts in their feeding. Secondly, small *H. semele* larvae occurring naturally in spring when day temperatures seldom are high also seem mostly night active and engaged in daytime feeding only when time stressed. Thirdly, in *P. xiphia*, larvae of all instars are present throughout the year as generations are continuous on Madeira, but only fourth instar larvae practise strict nighttime foraging. Another reason could be that larvae actively feed during the night and use the whole day for basking in order to increase the rates of digestion (Casey

1993). However, observations of behaviour show that the larvae of these species do not bask but rather hide away from light when they have reached large sizes. Thus, we contend that changes in predation risk ratios between the day- and nighttime is the most plausible explanation for the growth patterns observed in these species. Nevertheless, since the thermal conditions experienced during night and day will influence the benefits associated with this type of ontogenetic shift, it seems quite clear that the feeding mode will be dependent on species phenology and biogeography. As a consequence, changes in foraging mode are also likely to drive selection on thermal adaptations and on correlated life history traits such as development time and size at maturity. Thus, incorporating foraging theory and "the ontogenetic niche shift" into the classic life history framework is likely to broaden our understanding of the observed variation in physiology and life history among and within different ectotherms.

References

Abrams PA, Leimar O, Nylin S, Wiklund C (1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. Am Nat 147:381–395

Angilletta MJ, Wilson RS, Navas CA, James RS (2003) Tradeoffs and the evolution of thermal reaction norms. Tree 18:234–240

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72:149–177

Atkinson D, Sibly RM (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Tree 12:235–239

Atlegrim O (1992) Mechanisms regulating bird predation on a herbivorous larva guild in boreal coniferous forests. Ecography 15:19–24

Baker RL, Ball SL (1995) Microhabitat selection by larval *Chironomus tentans* (Diptera, Chironomidae)—effects of predators, food, cover and light. Freshw Biol 34:101–106

Berger D, Walters R, Gotthard K (2006) What keeps insects small?—size dependent predation on two species of butterfly larvae. Evol Ecol 20:575–589

Bradford MJ, Higgins PS (2001) Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Can J Fish Aquat Sci 58:365–374

Buckner CH (1966) The role of vertebrate predators in the biological control of forest insects. Ann Rev Entomol 11:449–470

Casey TM (1993) Effects of temperature on foraging of caterpillars. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 1. Chapman & Hall, New York, pp 5–28

Clark CW (1994) Antipredator behavior and the asset-protection principle. Behav Ecol 5:159–170

Culp JM, Scrimgeour GJ (1993) Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish. Oikos 68:242–250

D'Amico LJ, Davidowitz G, Nijhout HF (2001) The development and physiological basis of body size evolution in an insect. Proc R Soc Lond B 268:1589–1593

Dempster JP (1984) The natural enemies of butterflies. In: Vane-Wright RI, Ackery PR (eds) The Biology of Butterflies. Academic, London, pp 97–104

Eliasson CU, Ryrholm N, Holmer M, Jilg K, Gärdenfors U (2005) Nationalnyckeln till Sveriges flora och fauna. Fjärilar: Dagfjärilar. Hesperiidae–Nymphalidae. Reuter Media Group, ArtDatabanken, SLU, Uppsala. Laholm, Sweden

Esperk T (2006) Larval instar as a key element of insect growth schedules. PhD thesis, Tartu University, Tartu, Estonia

Feeny P, Blau WS, Kareiva PM (1985) Larval growth and survivorship of the black swallowtail butterfly in central New York. Ecol Monogr 55:167–187

Fraser DF, Gilliam JF, Akkara JT, Albanese BW, Snider SB (2004) Night feeding by guppies under predator release: effects on growth and daytime courtship. Ecology 85:312–319

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard—test of a model with foraging minnows. Ecology 68:1856–1862

Gotthard K (2001) Growth strategies of ectothermic animals in temperate environments. In: Atkinson D, Thorndyke M (eds) Animal developmental ecology. BIOS Scientific, Oxford

Hassell MP, Southwood TRE (1978) Foraging strategies of insects. Ann Rev Ecolog Syst 9:75–98

Heinrich B (1993) How avian predators constrain caterpillar foraging. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 7. Chapman & Hall, New York, pp 224–247

Houston A, Clark C, McNamara J, Mangel M (1988) Dynamic models in behavioral and evolutionary ecology. Nature 332:29–34

Imre I, Boisclair D (2004) Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year. J Fish Biol 64:1731–1736

Johansson F, Rowe L (1999) Life history and behavioral responses to time constraints in a damselfly. Ecology 80:1242–1252

Johansson F, Stoks R, Rowe L, De Block M (2001) Life history plasticity in a damselfly: effects of combined time and biotic constraints. Ecology 82:1857–1869

Kingsolver JG, Ragland GJ, Shlichta JG (2004) Quantitative genetics of continuous reaction norms: thermal sensitivity of caterpillar growth rates. Evolution 58:1521–1529

Kingsolver JG, Woods HA (1997) Thermal sensitivity of growth and feeding in Manduca sexta caterpillars. Physiol Biochem Zool 70:631–638

Koops MA, Abrahams MV (1998) Life history and the fitness consequences of imperfect information. Evol Ecol 12:601–613

Kozlowski J (1992) Optimal allocation of resources to growth and reproduction—implications for age and size at maturity. Tree 7:15–19

Kristensen CO (1994) Investigations on the natural mortality of eggs and larvae of the large white Pieris brassicae (Lep-Pieridae). J Appl Entomol 117:92–98

Krivan V, Vrkoc I (2000) Patch choice under predation hazard. Theor Popul Biol 58:329–340

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Ann Rev Ecol Evol Syst 34:153–181

Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. Func Ecol 3:21–27

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation—a review and prospectus. Can J Zool 68:619–640

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153:549–659

Ludwig D, Rowe L (1990) Life-history strategies for energy gain and predator avoidance under time constraints. Am Nat 135:686–707

Macchiusi F, Baker RL (1992) Effects of predators and food availability on activity and growth of Chironomus tentans (Chironomidae, Diptera). Freshw Biol 28:207–216

Metcalfe NB, Fraser NHC, Burns MD (1998) State-dependent shifts between nocturnal and diurnal activity in salmon. Proc R Soc Lond B 265:1503–1507

Metcalfe NB, Fraser NHC, Burns MD (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. J Anim Ecol 68:371–381

Montllor CB, Bernays EA (1993) Invertebrate predators and caterpillar foraging. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 5. Chapman & Hall, New York, pp 170–203

Nylin S, Gotthard K (1998) Plasticity in life-history traits. Ann Rev Entomol 43:63–83

Nylin S, Wickman PO, Wiklund C (1989) Seasonal plasticity in growth and development of the speckled wood butterfly, Pararge aegeria (Satyrinae). Biol J Linn Soc 38:155–171

Park O (1940) Nocturnalism—the development of a problem. Ecol Monogr 10:485–536

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge, Cambridge University Press

Reavey D (1993) Why body size matters to caterpillars. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 8. Chapman & Hall, New York, pp 248–282

Roff DA (2002) Life history evolution. Sinnauer, Sunderland, USA

Sibly RM, Calow P, Nichols N (1985) Are patterns of growth adaptive? J Theor Biol 112:553–574

Sih A, Ziemba R, Harding KC (2000) New insights on how temporal variation in predation risk shapes prey behavior. Tree 15:3–4

Slansky F (1993) Nutritional ecology: the fundamental quest for nutrients. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 2. Chapman & Hall, New York, pp 29–92

Stamp NE, Bowers D (1990) Variation in food quality and temperature constrain foraging of gregarious caterpillars. Ecology 71:1031–1039

Stamp NE, Wilkens RT (1993) On the cryptic side of life: being unapparent to enemies and the consequences for foraging and growth in caterpillars. In: Stamp NE, Casey TM (eds) Caterpillars—ecological and evolutionary constraints on foraging, chapter 9. Chapman & Hall, New York, pp 283–331

Takeda M (2005) Differentiation in life cycle of sympatric populations of two forms of Hypantria moth in central Missouri. Entomol Sci 8:211–218

Tikkanen P, Muotka T, Huhta A (1994) Predator detection and avoidance by lotic mayfly nymphs of different size. Oecologia 99:252–259

Tolman T (1997) Butterflies of Europe. Princeton University Press, Princeton

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

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Ann Rev Ecolog Syst 15:393–425

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

Zalucki MP, Clarke AR, Malcolm SB (2002) Ecology and behaviour of first instar larval Lepidoptera. Ann Rev Entomol 47:361–393