

A trade-off between growth and starvation endurance in a pit-building antlion

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Abstract Trade-offs have a central role in evolutionary ecology and life-history theory. Here, we present evidence for the existence of a rarely studied trade-off between growth rate and starvation endurance in larvae of a pit-building antlion. We first manipulated antlions' feeding regime and obtained a spectrum of growth rates. Next, we starved the antlions and documented their rate of mass loss. Antlions growing faster during the feeding phase also lost mass faster during the successive starvation period, implying the existence of an induced trade-off between fast growth and starvation endurance. Finally, we fed all antlions with prey items of similar mass and measured both the giving-up prey mass (i.e. the remaining body mass of the prey that was not converted into predator body mass), and growth efficiency of antlions (i.e. proportion of prey consumed, negatively correlated with giving-up prey mass). The giving-up mass was negatively correlated with the growth rate of the antlions during the feeding phase, and positively correlated with their growth rate during the starvation phase (the opposite pattern was evident when

examining growth efficiency), incongruently with the common phenomenon of growth compensation (i.e. extracting more of the prey after a starvation period). We suggest that antlion larvae can adopt a physiological mode bounded by two extremes: one extreme is adapted to starvation, involving reduced metabolic rates but also reduced capability to exploit prey, while the other is adapted to fast growth, allowing an efficient exploitation of prey, but at the expense of lowered starvation endurance.

Keywords Feeding regime · Giving-up density · Growth rate · Myrmeleontidae · Sit-and-wait predators

Introduction

In a variety of insect species, there is a tight positive correlation between female size and fecundity (Honek 1993; Sokolovska et al. 2000). Larger size is also favoured by selection for increased life-span and by sexual selection (e.g. Sibly and Calow 1986, p 61; Blanckenhorn et al. 2007; Scharf et al. 2009). Therefore, it is expected that insects would be selected for increased body size, unless some opposing forces selecting for smaller size are also taken into consideration (e.g. Sibly and Calow 1986, p 92; Gotthard et al. 2007). Clearly, this is not the case in nature, since animals do not get larger over time, and there must be considerable costs for being too large. Nevertheless, while there is much evidence for the benefits of large size at maturity, there is only little empirical evidence for its costs (Blanckenhorn 2000, 2005; Thompson and Fincke 2002).

The most often-assumed cost in life-history theory is that increased size is achieved either by increased developmental time or by increased growth rate (Abrams et al. 1996; Metcalfe and Monaghan 2003)—both associated

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with increased predation risk (Gotthard 2000; Lewis 2001), meaning that the process of getting large may be risky. Another disadvantage of growing fast may emerge from physiological costs such as the expected negative effect of fast growth on maintenance efficiency and on repair of cellular damage, resulting in a shorter life-span, developmental instability and higher susceptibility to diseases (Arendt 1997; Metcalfe and Monaghan 2003). Additionally, sometimes being large, not only becoming large, has some costs, such as an increased predation risk (e.g. Mand et al. 2007).

A rarely observed cost of fast growth is the resistance to shortage in prey supply (i.e. low starvation endurance) as was illustrated in butterflies (Stockhoff 1991; Gotthard et al. 1994). A probable explanation is the induction of metabolic processes that demand energy and will deplete the stored reserves faster in a period of starvation (Gotthard 2001). Indeed, Stoks et al. (2006) have tested this explanation in a damselfly system, illustrating that fast-growing damselflies had a higher metabolic rate that was also associated with a faster depletion of their stored reserves (i.e. glycogen and triglycerides). In addition, Fischer et al. (2004) have shown that fast-growing butterflies lose more body mass during metamorphosis, possibly owing to higher respiration rate, supporting the idea that increased metabolic rate can be associated with a faster depletion of storage molecules.

The often-assumed benefits of being large for fecundity and mate choice have been lately questioned. For example, the strict positive association between body size and fecundity may disappear under natural field conditions, as female insects are often restricted by factors such as longevity, season and suitable places for oviposition rather than by the number of eggs they carry (Leather 1988; Gotthard et al. 2007). Thompson and Fincke (2002) even questioned the usually assumed benefits of larger body size, such as in sexual selection and clutch size, and claimed that evidence for the fitness benefits of a large size are too often taken for granted. Indeed, smaller males may be better competitors for females than larger males under certain conditions (e.g. colder temperatures, Moya-Larano et al. 2007). All of the above suggest that not only are there significant costs for being large but the expected benefit is not that obvious; indeed, expected benefit often depends on many other factors besides body size.

We used pit-building antlion larvae to test for a possible trade-off between growth rate and starvation endurance, and to evaluate the subsequent effects of starvation period on the ability of antlions to efficiently exploit prey items. Pit-building antlion larvae are especially appropriate animal models for such studies, since they are strict sit-and-wait predators, experiencing high fluctuations in their prey supply. They are exposed to long periods of starvation

and therefore should buffer those fluctuations in their habitat (Scharf and Ovadia 2006). Similarly to other sit-and-wait predators such as spiders, antlions are capable of dramatically reducing their metabolic rates (Lucas 1985; Matura and Murao 1994). Based on previous studies, demonstrating a trade-off between fast growth and starvation endurance (e.g. Gotthard et al. 1994), we predicted that fast-growing antlions should lose body mass at a faster rate during a successive starvation period compared to those initially exhibiting slower growth rates.

Previous studies have shown that fast-growing animals might exhibit reduced starvation endurance (e.g. Gotthard et al. 1994). We therefore also tested for differential reaction towards feeding after a starvation period. It is possible, for instance, that individuals exhibiting fast growth prior to starvation will be more efficient at exploiting prey when feeding is resumed. Similarly, individuals showing slow growth prior to starvation should resist starvation better at the expense of faster compensation for the starvation period. An alternative prediction, based on the often observed phenomenon of growth compensation, should also be considered: when access to food is resumed, starved individuals might grow faster than relatively more satiated individuals in order to compensate for the lost developmental time.

Our results point towards the existence of a physiological spectrum bounded by two extremes: one characterized by high starvation endurance (at the expense of prey exploitation efficiency) and the other by fast growth rate (at the expense of starvation endurance). Demonstrating the disadvantages of fast growth is important for understanding why animals often grow more slowly than the maximum rate physiologically possible (Arendt 1997; Metcalfe and Monaghan 2003).

Methods

Study species and habitat of origin

Myrmeleon hyalinus (Neuroptera: Myrmeleontidae) is the most abundant pit-building antlion in Israel. The larva attains a maximal length of about 10 mm and a body mass of up to 0.06 g before pupating. Similar to other sit-and-wait predators, antlion larvae are generalist predators that capture small arthropods (mainly ants) that fall into their pits. *M. hyalinus* larvae develop through three instar-stages (lasting ~1 year), enter pupation (lasting ~1 month), and then short-lived, weak-flying adults emerge (lasting ~1 week) (Scharf et al. 2009). *M. hyalinus* larvae are capable of inhabiting different types of sandy soils. They are found in high densities in shaded areas under trees, bushes, and rocks, named “antlion zones” by Gotelli

(1993). *M. hyalinus* larvae were collected under several tamarisk trees located in Nahal Secher (N 31°06', E 34°49'). This sandy area, 15 km south of the city of Beer-Sheva, Israel, is an extension of the sand belt of northern Sinai, and receives around 150 mm of rainfall per year.

Experimental procedure

We collected 106 antlion larvae and brought them to the laboratory. They were fed with small flour beetle larvae (of ~1 mg) for three consecutive days, and were then weighed (CP224S, Sartorius, Goettingen, Germany; accuracy of 0.1 mg) and divided into three treatment groups of feeding frequency characterised by similar initial body size distribution: three flour beetle larvae per week (hereafter, Feed₃, $n = 36$), one beetle larva per week (Feed₁, $n = 34$) and complete starvation (Feed₀, $n = 36$).

After a month, antlion larvae were weighed and the mean growth rate was calculated according to the common formula (e.g. Gotthard et al. 1994; Gotthard 2000) $\left(\frac{\ln(\text{Mass}_{t=30}) - \ln(\text{Mass}_{t=1})}{30}\right)$. Hereafter, we refer to this stage of the experiment as “feeding phase growth rate”. Next, antlions of the three feeding treatments were starved for an additional 2 weeks and then weighed. The mean growth rate for this period was calculated using the above formula but with $t = 14$. We refer to the change in mass during this second experimental period as “starvation phase growth rate” (note that it is always negative because antlions were starved and lost some weight). Finally, we provided the antlions with one prey item of known mass per individual. To reduce the possible effect of prey mass on the amount of prey consumed, we used only prey items (flour beetle larvae) of similar masses (mean mass ± 1 SD = 1.0 ± 0.3 mg, $n = 105$). On the following day we weighed the antlions once more and calculated the difference between prey mass (measured before the experiment) and the increase in body mass of the antlion larvae, i.e. the giving-up prey mass [prey mass – (antlion mass_{after feeding} – antlion mass_{before feeding})]. We documented both prey mass and the difference in the predator’s body mass for every feeding event individually. It would perhaps be more accurate to calculate the giving-up prey mass by weighing the prey before and after consumption; however, the remains of beetle larvae dry out quickly, and therefore it is not a good indicator for the amount of prey consumed. Additionally, prey remains were very light and were thus susceptible to a relatively large measurement error. Note that even weighing the antlions involved some measurement error, possibly related to the sand particles that are often attached to the larvae (though we brushed the antlion larvae before weighing). Clearly, this adds some noise to the data but it

should not alter the interpretation of the results. Owing to this measurement error, body masses were rounded to the maximal or minimal level possible. For instance, if the increase in an antlion body mass was larger than the mass of the provided prey, we assumed that there were no leftovers [i.e. a giving up mass (GUM) of zero] and that the antlion had a growth efficiency of 1. Similarly, when a negative growth rate was measured for an antlion that attacked the prey provided, we assumed that prey was not consumed (i.e. GUM equals prey mass), and that the antlion had a growth efficiency of 0. It is important to note that, because of this measurement error, even when there are no measurable leftovers, it does not necessarily mean that the prey was completely consumed and vice versa.

Giving-up mass is a surrogate of giving-up density (Brown 1988). Giving-up density has been used in various systems and is termed as the amount of resources left in a patch at the end of the foraging process (e.g. Brown 1988; Ziv and Kotler 2003). It reflects the value at which the forager can no longer forage profitably (Brown 1988). In our case, each flour beetle larva is considered as a patch, in a manner similar to studies of partial prey consumption, in which the decision to stop consuming one prey item and to move to the next one is compared to moving into a new patch (e.g. Pollard 1989; Samu 1993). Those studies show that consumption of prey is not fixed, especially in animals using external digestion, and is influenced by different factors, such as prey density (e.g., Griffiths 1982; Samu 1993). This measure enables comparison between the effects of different constraining factors on foraging behaviour. In order to illustrate that our results are robust, we also present the growth rate during the feeding and starvation phase against a similar measure [growth efficiency = (antlion mass_{after feeding} – antlion mass_{before feeding})/prey mass]. However, since growth efficiency is a proportion, we had to use an arcsine transformation (Sokal and Rohlf 1995, p 419). Transformed values were used in the statistical analysis while the growth efficiency prior to transformation was used in the figures for brevity. Only antlions that attacked the prey were included in the analysis ($n = 96$ when using GUM and $n = 93$ when using transformed growth efficiency; three outliers were removed). The environmental conditions were constant and uniform thorough the experiment. Therefore it is likely that differences in mass gain or prey consumption are a result of the antlions’ physiological condition, and are not related to behavioural differences. Antlion larvae are expected to show high growth efficiencies because of their low metabolic and respiration rate (Lucas 1985), as well as the fact that they dispose of faecal pellets only during the larva-pupa molt (Chapman 1998, p 38).

Statistical analysis

First, we used one-way ANOVA to test for the effect of feeding regimes on the feeding phase growth rate. Next, we tested whether antlions that grew faster during the feeding phase lost more mass during the successive starvation phase compared to those that had lower growth rates during the feeding phase. When two successive measurements are taken on the same individuals, they tend, on average, to be closer to the mean on the second measurement, without any biological or statistical meaning. This effect or phenomenon, termed “regression toward the mean”, is caused by random error or random fluctuations in the same individual. Thus, extreme values are likely to be followed by values that are closer to the measurement “true” mean (Barnett et al. 2005). Consequently, it is necessary to detect whether there is a real change or “differential effect”, beyond that expected simply from the regression toward the mean. A differential effect should induce a change in variance between the first and second measurements (Kelly and Price 2005). Convergence to the mean and a corresponding reduction in variance are expected if individuals with high growth rates during the feeding phase lose mass at a faster rate than that expected by regression to the mean during the starvation period.

We compared the variances in growth rates between the feeding and starvation phases using Pitman’s test for the equality of variances in paired samples (see Kelly and Price 2005). Significantly distinct variances point to the existence of a differential effect in addition to the expected regression to the mean effect. Alternatively, if only the regression to the mean effect exists in this case, no change in variance between the first and second measurements should be observed. Another option is also possible: we would expect an increase in variance if individuals with higher growth rates during the feeding phase lost less mass during the starvation phase and individuals with lower growth rates lost more mass during the successive starvation period. To test if the correlation between growth rate and starvation endurance is robust, the above analysis was done twice. We first analysed the entire spectrum of growth rates generated during the feeding phase, including both positive and negative values, and next focussed on only a subset, including antlions having a positive growth rate. One might claim that using only those individuals having a positive growth rate during the feeding phase better distinguishes between the feeding and the successive starvation phases because it excludes the cases in which starvation continued throughout the experiment.

When plotting the growth rates of the feeding or starvation phases against the giving-up prey mass we noticed that the variance is not homogenous (i.e. it increases with the horizontal axis; Fig. 2). Therefore, one of the

assumptions of linear regression (i.e. homogeneity of the variance of the dependent variable) is violated (Cade and Noon 2003), and an alternative method should be used. Two plausible options are the least square regression on maximal values and quantile regression (Scharf et al. 1998). In the first method, observations are grouped into arbitrary number of equal size classes, and the uppermost values in each class are used to apply a least square regression model. Thus, the slope of the upper bound is estimated (Scharf et al. 1998). In the second method, it is possible to fit regression curves to other parts or quantiles (i.e. not necessarily the mean) of the distribution of the dependent variable (Cade and Noon 2003). If the upper limit is that of interest, it is possible to use only the upper values (such as only 30% of the uppermost values or even less). Quantile regression is less sensitive to extreme outlying values in the dependent variable and does not require an arbitrary division of the independent axis (Scharf et al. 1998). We used both methods described above to test for trends in our data set. Quantile regression was used over different quantiles of the results (upper 50, 30, 20 and 10% values). The difference of the quantile regression slopes from zero were tested using a quantile rank score test (Cade and Noon 2003). Least square regression was used on the uppermost values within each class, after grouping data into 12 clusters (of eight individuals). Only antlions that consumed a prey item were included in this analysis. Statistical analyses were performed using SYSTAT v. 11 and BLOSSOM Statistical Package.

Results

The feeding phase growth rate differed significantly between the three feeding treatments [ANOVA test $F_{2,103} = 83.13$, $P < 0.0001$; growth rates (mean \pm 1 SD): Feed₀: $-4.69 \times 10^{-3} \pm 2.26 \times 10^{-3}$, Feed₁: $-0.45 \times 10^{-3} \pm 3.33 \times 10^{-3}$, Feed₃: $7.89 \times 10^{-3} \pm 6.05 \times 10^{-3}$]. Therefore, we were able to induce different growth rates for the feeding phase of the experiment. Later, when analysing the starvation phase, we pooled together all feeding treatments, as the purpose of this feeding phase was solely to induce differential growth rates among individuals prior to starvation. Using Pitman’s test we found that the variance in growth rate decreased significantly from the feeding to the successive starvation phase ($t = 11.07$, $df = 103$, $P < 0.0001$), indicating that individuals were affected differently by starvation, depending on their feeding phase growth rates. Specifically, individuals that had higher growth rates during the feeding phase lost significantly more mass than that expected by regression to the mean during the successive starvation phase (Fig. 1). The same qualitative result was obtained when using only

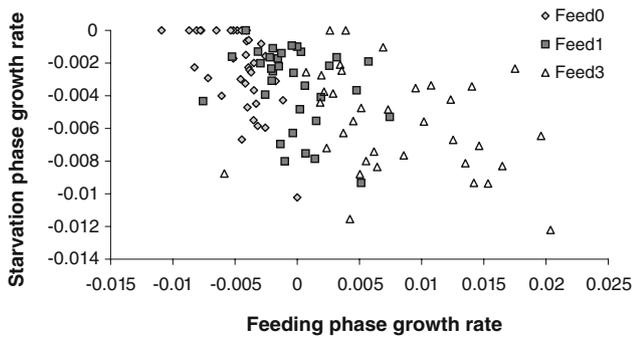


Fig. 1 Negative relationship between feeding phase and starvation phase growth rates. The three feeding treatments are also shown. Antlion larvae gaining more mass during the feeding phase lost more mass during the subsequent starvation phase. The significant ten-fold reduction in the variance between the feeding and starvation phases implies a strong differential effect in addition to the regression effect

those individuals that showed a positive growth rate during the feeding phase ($t = 4.83, df = 48, P < 0.0001$).

The slopes and significance tests of the quantile regression analyses over different quantiles are presented in Table 1. Overall, it is easy to see that the GUMs are negatively correlated with the feeding phase growth rates but positively correlated with starvation phase growth rate (Fig. 2a,b). The latter is true also when considering growth efficiency instead of GUM as the response variable (Fig. 2c,d), although to a somewhat lesser extent. But note that, since the proportion of prey consumed, i.e. growth efficiency, is negatively correlated with giving-up prey mass, the trend is in the opposite direction. As for the least square regression on uppermost values, similar results were obtained: a negative correlation between giving-up masses and feeding phase growth rates ($F_{1,10} = 5.44, P = 0.0418, R^2 = 0.353$) but a positive correlation with the starvation phase growth rates ($F_{1,10} = 6.25, P = 0.0314, R^2 = 0.385$). Results are qualitatively identical when using transformed growth efficiency rather than GUM (feeding phase growth rate vs transformed growth efficiency: $F_{1,10} = 5.74, P = 0.0376, R^2 = 0.301$; starvation phase growth rate vs transformed growth efficiency: $F_{1,10} = 6.97, P = 0.0247, R^2 = 0.352$).

Discussion

Body size has a vast importance for fitness, by means of sexual selection (e.g. Blanckenhorn 2005), intraspecific competition (e.g. Griffiths 1992), fecundity (Sibly and Calow 1986, p 123; Honek 1993; Sokolovska et al. 2000) and starvation endurance (e.g. Arnett and Gotelli 2003; Blanckenhorn et al. 2007). While the advantages of large body size are well known, there is little evidence for those

Table 1 Results of the quantile regression (see “Methods”) of the giving-up prey masses (GUM) and the transformed growth efficiency (Tr. Gr. Ef.) over the growth rate of antlion larvae during the feeding and starvation phases

	Slope	Constant	P value
Feeding phase (GUM)			
Quantile = 0.5 (upper 50%)	0.00	0.20	0.1803
Quantile = 0.7 (upper 30%)	-13.21	0.43	0.1220
Quantile = 0.8 (upper 20%)	-16.85	0.54	0.0039
Quantile = 0.9 (upper 10%)	-14.81	0.69	0.0253
Starvation phase (GUM)			
Quantile = 0.5 (upper 50%)	14.15	0.30	0.0816
Quantile = 0.7 (upper 30%)	37.14	0.56	0.0176
Quantile = 0.8 (upper 20%)	41.66	0.70	0.0028
Quantile = 0.9 (upper 10%)	43.31	0.80	0.0005
Feeding phase (Tr. Gr. Ef.)			
Quantile = 0.5 (upper 50%)	5.23	1.02	0.0229
Quantile = 0.7 (upper 30%)	7.42	0.94	0.0803
Quantile = 0.8 (upper 20%)	12.47	0.83	0.1021
Quantile = 0.9 (upper 10%)	11.39	0.69	0.2910
Starvation phase (Tr. Gr. Ef.)			
Quantile = 0.5 (upper 50%)	-33.01	0.95	0.0146
Quantile = 0.7 (upper 30%)	-27.44	0.82	0.0064
Quantile = 0.8 (upper 20%)	-34.61	0.70	0.0203
Quantile = 0.9 (upper 10%)	-39.71	0.55	0.0328

When using GUM as the dependent variable, the total sample size is 96 (the actual sample size depends on the quantile used). When using the transformed growth efficiency, the sample size is 93 (three outliers were removed)

of smaller size (Blanckenhorn 2000, 2005). Similarly, animals were previously assumed to maximise growth rates (Stearns 1992, Chap. 6; Gotthard 2001), especially when their growing period is time limited (e.g. De Block and Stoks 2004). However, recent evidence shows that there are various costs associated with growing fast (e.g. Gotthard et al. 1994; Gotthard 2000; Lewis 2001; Metcalfe and Monaghan 2003; Stoks et al. 2006). Here, we provide evidence that fast-growing animals perform worse under some conditions: antlions that grew fast lost more weight during a successive period of starvation, thus showing reduced starvation endurance. Additionally, antlions that showed a small increase or even a decrease in mass during the feeding phase coped better with starvation and lost less mass, probably because their metabolic rate was already reduced. We also show that antlions that were starved for a long period exploited less of a provided prey item compared to those that were fed more frequently. This difference is probably due to a physiological response. Starved antlions are probably less efficient in extracting the fluid content of the prey or in converting it into body tissues (a physiological response). Yet, it is also possible that

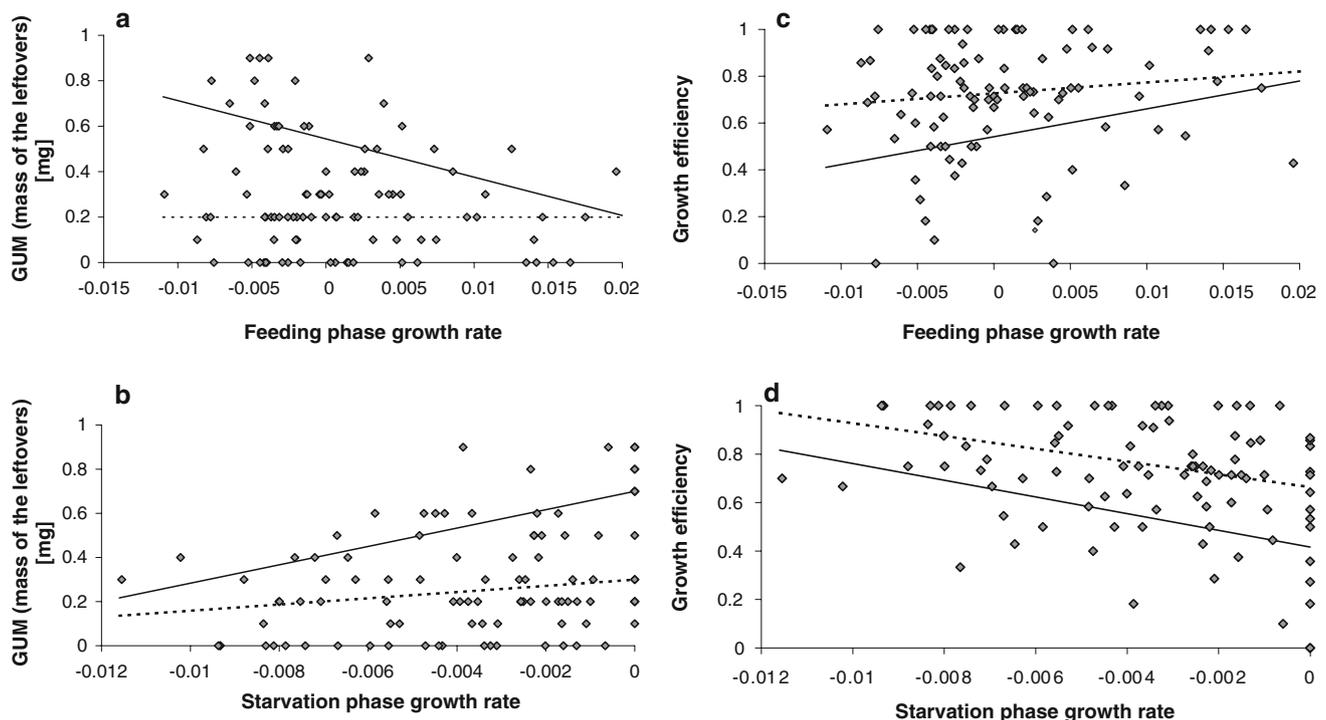


Fig. 2 The relationship between the giving-up prey mass and the growth rate of antlion larvae during the **a** feeding and **b** starvation phases using giving-up mass (*GUM*) as the dependent variable. The growth rate during the **c** feeding and **d** starvation phases against the growth efficiency are also presented. *GUM* was negatively correlated with the growth rate of antlions during the feeding phase but

positively correlated with their growth during the starvation phase. Slopes and constants were estimated using quantile regressions. Quantiles = 0.5 (*dashed line*) and 0.8 (*continuous line*) are presented. Growth efficiencies are presented in the figure, but arcsine-transformed values were used in the statistical analysis

since antlions cannot exploit more from the prey item without excessive costs, they “decide” to leave it sooner (a mixed behavioural–physiological response). Thus, we suggest that antlion physiological mode is bounded by two extremes: one extreme is adapted for starvation and involves reduced metabolic rates but also reduced capability to exploit prey items, while the other is adapted to fast growth and capable of exploiting the most out of prey items encountered, but at the expense of starvation endurance.

It is worthwhile clarifying at this point the difference between inherent and induced trade-offs. For example, some individuals perform better in conditions of high food abundance and can show a high growth rate, but this comes at the expense of resisting starvation when food abundance is low (i.e. an inherent trade-off). An induced trade-off means that after growing fast, animals will face starvation less well than after growing more slowly, irrespective of their innate capabilities. In the latter case, the cost of growth is direct while in the former it is indirect. We thus suggest that the trade-off presented in the current paper is an induced trade-off, although we cannot really distinguish between those two trade-off types in the current setting. In other words, the negative correlation between the growth

rates in the feeding and starvation phases is probably a direct consequence of feeding (i.e. an induced trade-off); however, individual different feeding strategies cannot be ruled out (i.e. an inherent trade-off).

Matsura and Murao (1994) reported different antlion strategies to cope with starvation: some species sharply reduce respiration rates followed by an overall decrease in activity (i.e. relocation rate), while others show a more moderate decrease in respiration rates but do not reduce activity. Additionally, starvation endurance and the rate of mass loss were tightly correlated with respiration rates (e.g. Stoks et al. 2006). Moreover, many previous studies have shown that, in response to low prey abundance, insects reduce their metabolic rate and thus are able to resist starvation better and to reduce the rate of mass loss (e.g. Harshman and Schmid 1998). This reduced metabolic rate may also explain why prey was less efficiently exploited by antlions when feeding after the second phase of the experiment was resumed. This is parallel evidence that fast growers may pay some cost, or at least do worse when the environmental conditions change. Our study provides complementary data by pointing at possible trade-offs between starvation endurance and intense feeding in one antlion species. In a previous study, we compared

life-history traits of desert versus Mediterranean populations of a pit-building antlion species (Scharf et al. 2008). We showed that desert antlions reach smaller final masses, exhibit a shorter developmental period but have a similar growth rate compared with that of Mediterranean antlions. The results of the current study may explain why desert antlions do not compensate for their shorter developmental period by increasing growth rate: it may interfere with their ability to resist starvation, which might be common also in desert environments, meaning that their growth rate is possibly optimised but surely not maximised (Abrams et al. 1996; Arendt 1997; Metcalfe and Monaghan 2001).

Similarly to antlions, many other animal species trade-off high growth rate in rich environments with their ability to resist starvation in poor environments. Tessier et al. (2000) have shown that *Daphnia* occurring in freshwater lakes trade-off growth rates in rich versus poor resource conditions, a phenomenon existing within and also across species. Several other examples for possible costs of high growth rate are presented by Reznick et al. (2000), who also arrived at the conclusion that “super phenotypes” (i.e. individuals having a high growth rate) are beneficial only under certain environmental conditions (e.g. high abundance of food). When examining the variance in growth rate among individuals, it is possible to separate between genetic effects and external effects, such as food availability, temperature or photoperiod. In the current study, we focussed on growth variation induced by different levels of feeding (i.e. an external factor). Still, pure genetic differences are also important and can interact with the external factors. For instance, Engqvist (2007) has highlighted the strong interaction between genetic and environmental factors on growth rate of scorpionfly larvae. Specifically, in conditions of high food availability there was a positive correlation between developmental time and final body mass, while the opposite was true in low food availability. This supports the previous claim that growth rate should be evaluated under different conditions in order to detect possible trade-offs (Reznick et al. 2000).

Growth compensation is a common phenomenon occurring when individuals deprived of prey renew their access to resources and then show accelerated growth (Metcalfe and Monaghan 2001). Our results are not in accord with this observed pattern: antlions losing more mass (i.e. belonging to the physiological mode adapted to starvation endurance) exploited less of the prey when their access to prey is renewed, compared to those that previously gained more mass and were experiencing only a short-term starvation (i.e. the successive 2-week starvation period). This result is to some extent counterintuitive, because we expected antlions that were deprived of prey for a longer period to exploit the most possible from the prey provided. However, antlions that experienced a longer

starvation period exploited less of the prey than those that had experienced shorter starvation periods. Notably, in our experiment antlions were not starved or exhausted to the extent that they could not handle the prey item. This is evident from the high proportion of antlions attacking and consuming at least some of the prey (about 91%). It may point towards possible costs associated with growth compensation, and should not occur if the costs associated are larger than the possible benefits (Metcalfe and Monaghan 2001). Trade-offs (i.e. the negative association between two traits) are the keystone of life history theory (Stearns 1992, Chap. 6; Gotthard 2001), and it is important to study them in various model systems and under different conditions in order to either support or refute assumptions of life history models. It will be interesting to test the same trade-off in different sub-populations of the same species, experiencing different climatic conditions. It is possible that individuals from more fluctuating, unpredictable or harsh environments will show lower growth rates when prey is provided ad libitum compared with an expected higher growth rate of individuals from more stable or rich environments, which are not adapted for resisting long periods of shortage in prey. A similar pattern was suggested by Iwasa (1991): plants growing in harsh conditions are not thought to increase growth rate even when exposed to better conditions. However, Iwasa’s predictions still remain to be more thoroughly tested.

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