

## Slow growth improves compensation ability: examining growth rate and starvation endurance in pit-building antlions from semi-arid and hyper-arid regions

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**Abstract** Different environments are expected to exert differential selective pressures, often generating distinct sets of traits in organisms inhabiting different geographic regions. Starvation endurance is an important trait for organisms in harsh (i.e., extreme climate and/or biotically poor) and unpredictable environments. This is especially true for sit-and-wait predators, such as antlions, which experience stronger fluctuations in prey arrivals than do actively searching predators. We conducted an experimental comparison of starvation endurance in pit-building antlions, originating from semi-arid and hyper-arid environments. We hypothesized that individuals from the climatically harsher and biotically poor environment (i.e., hyper-arid) should be better adapted to endure long starvation periods. Additionally, we posited that faster-growing individuals are expected to be more sensitive to starvation because of their need to sustain higher metabolic rates. We found that antlions originating from the semi-arid region maintained higher activity levels, which led to slightly higher mass loss rates during starvation, but enabled faster recovery when food supply was renewed. Conversely, antlions originating from the hyper-arid region had lower activity levels, consistent with their lower rate of mass loss during starvation, but this came at the expense of decreased response to prey and lower growth rate when food became available again. Each strategy holds its advantages for coping with long starvation periods, and we cannot say decisively which strategy is better. Results from both regions were consistent with the predictions of the growth compensation phenomenon: antlions that were fed less frequently pre-starvation grew at faster rates when food supply was renewed. Our study demonstrates that individuals originating from different environments adopt different strategies in order to endure starvation, exemplifying antlions' ability to compensate for mass lost during starvation.

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## Introduction

Different environments are expected to exert differential selective pressures, often generating distinct sets of traits in organisms inhabiting different geographic regions (Endler 1986, 1977; Hoffmann et al. 2005; Hoffmann and Watson 1993). To experimentally explore this assertion, common garden or reciprocal transplant experiments have been frequently conducted, during which a limited set of individual traits were quantified (e.g., Mousseau 2000; Read 1999; Reznick and Travis 2001). Such experiments have found differences in body size between latitudes within the same species (e.g., Atkinson 1994; Atkinson and Sibly 1997; Heinze et al. 2003), and have also generated the prediction that individuals originating from stressful environments should exhibit more phenotypic plasticity (or  $G \times E$  effect), because their habitat is characterized by a larger inter-annual variation (David et al. 2004; Maynard-Smith 1993; Petru et al. 2006; but see Scharf et al. 2008a).

Common garden and transplant experiments are very useful for studying genetic and phenotypic differences between populations originating from different geographic regions (Reznick and Travis 2001). However, inter-population variation in behavior or physiology often can be discerned only when the organism is exposed to environmental stress, shedding light on rarely-discussed aspects of local adaptation (Allan and Pannell 2009; Gilchrist et al. 2008; Hoffmann et al. 2005; Huey et al. 2002). For instance, when facing prey shortage, animals may reduce their metabolic rates to a minimum level possible and wait for some future improvement. Alternatively, they may keep their current metabolic rate (or even increase it) and search actively for a more prey-rich habitat (Gutman et al. 2007; Wang et al. 2006). These two strategies are definitely context-dependent: Reducing metabolic rate is possibly preferred under low food abundance or stochastic conditions, but increasing activity is preferred under rich or more predictable conditions (e.g., Scharf and Ovadia 2006), where prey shortage might be perceived as a localized event.

Body size is an important morphological trait, with implications for physiology, which in turn affects behavior, survival, mating success and fecundity (Blanckenhorn 2000; Fairbairn et al. 2009). Differences in body size between climatic regions may be a result of differences in relative growth rate or the length of the developmental period (e.g., Atkinson 1994; Atkinson and Sibly 1997; Heinze et al. 2003). Individual variation in relative growth rate should be strongly linked to starvation endurance (Gotthard et al. 1994; Scharf et al. 2009; Stoks et al. 2006). Specifically, faster-growing individuals are expected to be more sensitive to starvation because of their need to sustain higher metabolic rates (e.g., Scharf et al. 2009), although contrary examples do exist (Leggatt et al. 2003; Sundström and Devlin 2011).

Under natural conditions, differences in growth rate between individuals might arise due to sheer luck (e.g., Harwood et al. 2001), genetics (e.g., De Block et al. 2008b; Read 1999; Tracy 1999), or plastic responses to environmental conditions (Via et al. 1995). It has been traditionally assumed by life-history theoreticians that juvenile growth rates are maximized and that variation in this trait is due to the quality of the environment (Roff 1992; Stearns 1992). However, there is a large body of evidence showing that juvenile growth rates may vary adaptively both within and between populations (Gotthard 2000), implying that high

growth rates may be associated with costs, such as developmental instability (Dmitriew and Rowe 2005), reduced pupal size (Gotthard 1998), and increased risk of starvation during subsequent periods of food stress (Dmitriew and Rowe 2011).

In different environments, distinct developmental strategies should be preferred (Roff 2002). Under harsh (i.e., extreme climate and/or biotically poor) or stochastic conditions it is better for an organism to reach its final size as quickly as possible, by increasing growth rate and/or shortening the developmental period, possibly resulting in a smaller final body size (Roff 1992; Stearns 1992). Furthermore, under acute food shortage, faster-growing animals, characterized by higher metabolism, are expected to lose mass faster and survive for shorter time periods than slow-growing animals. The safer route, which is expected to be preferred under richer and more stable conditions, should be a slower growth rate and a larger final body size (Roff 2002).

Individual variation in starvation endurance is strongly correlated with environmental conditions (Arnett and Gotelli 2003; Griffiths et al. 2005). This is especially true in sit-and-wait predators, which suffer from fluctuations in prey arrivals much more than do actively searching predators (Arnett and Gotelli 2003; Riechert 1992). Sit-and-wait predators are inherently constrained in their abilities to avoid stressful conditions (e.g., high temperatures and hunger) because of their low mobility levels. However, theory predicts that compared with widely foraging predators, sit-and-wait predators should better cope with stressful conditions (Huey and Pianka 1981; Perry and Pianka 1997).

When feeding resumes after an episode of starvation, a variety of species exhibit growth compensation (Metcalf and Monaghan 2001), or accelerated growth to compensate for the lack of growth during the starvation period (e.g., Dmitriew and Rowe 2005; Jespersen and Toft 2003; Jobling 2010; Stoks et al. 2006). Here, we use the term compensatory growth or growth compensation to indicate the relative growth rate when an animal is fed post-starvation, even if said growth rate is lower than the animal's growth rate when it is fed regularly.

In this research, we conducted an experimental comparison of the responses to starvation in pit-building antlions originating from semi-arid and hyper-arid climatic regions. These regions differ climatically, e.g., temperature, rainfall and relative humidity (Table 1). Furthermore, similar to other arid systems (e.g., Lightfoot and Whitford 1991; Whitford et al. 1995), the increase in annual precipitation from the hyper- to the semi-arid region of Israel is strongly associated with increased plant productivity (Abramsky 1988; Dall'Olmo and Karnieli 2002) and insect diversity (Sogavker 2004) (Table 1). To the best of our knowledge, our study is the first attempt to contrast the starvation endurance of individuals originating from semi-arid and hyper-arid environments, in animals in general, and insects in particular.

We tested for the existence of a trade-off between growth rate and starvation endurance in *Cueta lineosa* Rambur, 1842 (Neuroptera: Myrmeleontidae) larvae, and examined whether this trade-off differs between individuals originating from the semi and hyper-arid habitats. We thus treat growth rate as a proximate factor, which is expected to be strongly affected by prey encounter rate (i.e., feeding rate). Our working hypothesis was that there should be a trade-off between growth rate and starvation endurance, i.e., larvae exhibiting higher growth rates should lose more mass during a prolonged starvation period. However, this pattern of increased mass loss in fast-growing individuals should be less pronounced among individuals originating from hyper-arid habitats, which are better adapted to long starvation periods associated with low prey abundance, combined with the more stochastic prey arrival rate characterizing their habitat-of-origin.

**Table 1** Representative biotic and abiotic characteristics of the semi-arid (Be'er-Sheva) and hyper-arid (southern Arava) climatic regions

Region/ population	January temperature (°C)	August temperature (°C)	Annual precipitation (mm)	Annual precipitation C.V. (%)	Annual no. of rainy days (>0.1 mm)	Average humidity (%)	Normalized difference vegetation index (NDVI)*	Annual plant cover (%)**	Ant species richness***
Be'er-Sheva	11.2	25.7	204	30	41	60	0.10–0.11	30.3	9
Southern Arava	15.7	33.4	32	>40	10.6	35	0.00–0.07	6.2	5

Along the south-to-north gradient in Israel, there is a general decrease in the mean annual temperature, and an increase in the annual precipitation and relative humidity (Goldreich 2003). The increase in annual precipitation from the hyper- to the semi-arid region of Israel is strongly associated with increased plant productivity (Abramsky 1988; Dall'Omo and Karnieli 2002) and insect diversity (Sogavker 2004)

\* (NDVI: 0.00–0.07 vs. 0.10–0.11; Dall'Omo and Karnieli 2002); \*\* (6.2 vs. 30.3 %; Abramsky 1988); \*\*\* (5 vs. 9 species of ants; Sogavker 2004)

## Materials and methods

### Study species and habitats-of-origin

We collected *Cueta lineosa* Rambur, 1842 (Neuroptera: Myrmeleontidae), larvae from the loessial plains near Be'er-Sheva (N31°16', E34°50', semi-arid climate; Table 1) and from the southern Arava, near Samar (N29°49', E35°02', hyper-arid climate; Table 1) and brought them to the laboratory. Occurring mainly in the Israeli Negev desert, *C. lineosa* also exists in several small populations located in central and northern Israel, but is restricted to light soils, such as loess (Simon 1988). This species is a habitat specialist: its performance declines when placed in coarse-grained soils (Barkae et al. 2012). *Cueta lineosa* is mainly found in open microhabitats exposed to direct sunlight. The larvae develop through three instar stages, and emerge after pupation as short-lived, weak-flying adults, measuring up to 32 mm in length (Simon 1988).

All required permits and approvals for this work were obtained from Israel's Nature and National Parks Protection Authority, permit no. 2010/37830. In compliance with all the relevant laws and regulations prevailing in Israel, self-regulation and accountability of local programs by an Institutional Animal Care and Use Committee (IACUC) are not applicable for the use of invertebrates in research (Israel's Animal Welfare Act 1984).

### Experimental procedures

We collected fresh antlions in the field and kept them separately in round plastic cups (10.5 cm diameter, 7 cm height) filled with 3 cm of loess. We fed the antlion larvae with mealworms twice a week until the beginning of the experiment (habituation period). Antlions' natural food consists of various arthropods, especially ants. However, mealworms are a viable substitute for natural prey, as is exemplified by antlions' ability to grow, develop and complete their life cycle within 1 year, as under natural field conditions, when fed with mealworms (Scharf et al. 2008a). Throughout the experiment, antlion larvae were kept in the lab at a room temperature of  $22 \pm 3$  °C (mean  $\pm$  1 SD) and a 12:12 h light:dark schedule. The experiment comprised three time periods: (1) Feeding: We randomly divided antlion larvae originating from each of the two climatic regions into three experimental groups ( $n = 30$  per group per climatic region, a total of 180 antlions) having similar body size distributions. The body mass of the antlions at this point was  $0.0039 \pm 0.0003$  and  $0.0092 \pm 0.0006$  g (mean  $\pm$  1 SE) for those originating from the hyper-arid and semi-arid regions, respectively. It is important to note that such differences in body mass are consistent with the expectations of the temperature-size rule (Atkinson and Sibly 1997). Indeed, two-fold differences in body mass between populations were also found in another pit-building antlion species, *Myrmeleon hyalinus* (Scharf et al. 2008a). Over 4 weeks, we fed the antlions in these three experimental groups at different frequencies (two mealworms per week, one mealworm per week or one mealworm per fortnight) in order to create a gradient of growth rates. All three feeding frequencies are below the maximum intake ability of the antlions, which can consume several mealworms a day when available, but all three frequencies enable positive growth rate and maintenance of a normal life cycle. (2) Starvation: We starved the larvae for 2 months. (3) Compensation: We fed the antlions three times over the course of 1 week.

A control group was regularly fed (one mealworm per week) throughout the whole experiment. We measured body mass and pit diameter periodically throughout the experiment. Pit diameter is regularly used in antlion studies as an indicator of foraging effort (reviewed in Scharf and Ovadia 2006). A larger pit is more likely to trap prey

(Farji-Brener 2003; Griffiths 1980; Wilson 1974), but maintaining a larger pit is costly (Lucas 1985), because the pit often has to be rebuilt due to wind and sand-throwing by nearby antlions (Barkae et al. 2010).

At the beginning of the experiment (before the separation into feeding treatments) and at the end of the starvation period, we fed one pre-weighed mealworm to each antlion in order to measure response time to prey (i.e., time from the placement of a mealworm inside the pit until the antlion made an attempt to subdue it) and growth efficiency (i.e., conversion of prey mass to predator mass). We measured growth efficiency by dividing the difference in antlion body mass before and after feeding by the prey body mass  $\left(\frac{\text{antlion\_mass}_{\text{after\_feeding}} - \text{antlion\_mass}_{\text{before\_feeding}}}{\text{prey\_mass}}\right)$  (Scharf et al. 2009). We measured response time to prey and growth efficiency for the first feeding in the compensation period, and weighed all the antlions again after the third feeding, to calculate relative growth rate over the entire compensation period. We also noted the percentage of antlions that responded to prey, as non-responsiveness indicates lower activity levels. An antlion that did not respond to prey within 60 s of its introduction was defined as “unresponsive”. Larvae were weighed throughout the experiments to  $\pm 0.1$  mg (CP224S, Sartorius AG, Goettingen, Germany). We calculated relative growth rate according to the common formula  $\left(\frac{\ln(Mass_{t2}) - \ln(Mass_{t1})}{\Delta t}\right)$  (e.g., Gotthard 2000; Gotthard et al. 1994). The time periods were: feeding (28 days), starvation (54 days), and compensation (8 days).

### Statistical analyses

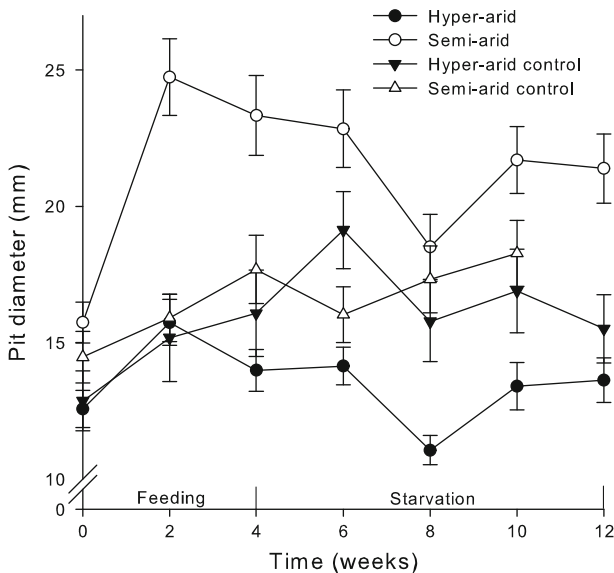
We analysed pit diameter and relative growth rate (or mass loss, with initial body mass as a covariate) using a two-way repeated measures ANCOVA with region and feeding treatment as between-subjects explanatory variables and initial body mass as a covariate. Similarly, the regularly-fed control group was analysed using a one-way repeated measures ANCOVA with region as a between-subjects explanatory variable and initial body mass as a covariate (feeding treatment is not applicable for this group). As mentioned above, growth efficiency was measured at the beginning of the experiment (before the separation into feeding groups) and at the end of the starvation period. Because feeding treatment is not applicable for the first measurement, we carried out two separate ANOVAs. Specifically, the first measurement was analysed using a one-way ANOVA with region as an explanatory variable, while the second was analysed using a two-way ANOVA with region and feeding treatment as explanatory variables. Growth efficiency of the regularly-fed control group was analysed using a one-way repeated measures ANOVA with region as a between-subjects explanatory variable. These analyses were conducted in STATISTICA, v8.0 (StatSoft, Ltd., Tulsa, OK, USA). To test for differences in survival and response times, we used the Cox proportional hazard model, i.e., time-to-event analysis (Kalbfleisch and Prentice 2002), with region, feeding treatment (except for the first response time measurement as well as for the analyses of the regularly-fed control group), initial body mass and the respective interaction terms as covariates. This statistical analysis was performed using S-PLUS 2000 (MathSoft, Inc., Cambridge, MA, USA).

### Results

Pit diameter of starved antlions originating from the semi-arid region was significantly larger than that of those originating from the hyper-arid region (Two-way repeated

measures ANCOVA using initial body mass as a covariate:  $F_{1,75} = 3.99$ ,  $P = 0.049$ ; Fig. 1). In addition, in both regions pit diameter increased with body mass, however, this pattern was more pronounced in the semi-arid region (Two-way repeated measures ANCOVA:  $F_{1,75} = 26.34$ ,  $P < 0.001$ ; Body mass  $\times$  Region interaction). Notably, throughout the entire range of overlapping body masses between the two regions, pit diameter of antlions from the semi-arid region was larger than that of those from the hyper-arid region. Antlions from the semi-arid region also showed a dramatic increase in pit diameter at the beginning of the feeding period (Two-way repeated measures ANCOVA:  $F_{6,450} = 3.022$ ,  $P = 0.007$ ; Time  $\times$  Region interaction). When examining the second month of the starvation period, antlions originating from the semi-arid region showed a marginally higher increase in pit diameter than those originating from the hyper-arid region (Two-way repeated measures ANCOVA:  $F_{1,111} = 3.86$ ,  $P = 0.052$ ; Time  $\times$  Region interaction). In the regularly-fed control group, initial pit sizes were similar for both regions. In antlions from the hyper-arid region, pit sizes increased dramatically in the first 2 weeks and decreased gradually in the remainder of the experiment, while in antlions from the semi-arid region, pit sizes increased gradually throughout the experiment. However, from week 4 until the end of the experiment, pit sizes were similar for both regions (One-way repeated measures ANCOVA:  $F_{5,80} = 6.11$ ,  $P < 0.001$ ; Time  $\times$  Region interaction; Fig. 1).

Time-to-event analysis (i.e., Cox proportional hazard model) indicated that at the beginning of the experiment, antlions originating from the semi-arid region responded to prey faster, and at higher percentages, than those originating from the hyper-arid region



**Fig. 1** Pit diameter (mean  $\pm$  1 SE) was larger in antlions (*C. lineosa*) originating from the semi-arid region (Two-way repeated measures ANCOVA using initial body mass as a covariate:  $F_{1,75} = 3.99$ ,  $P = 0.049$ ), which also showed a dramatic increase in pit diameter at the beginning of the feeding period ( $F_{6,450} = 3.022$ ,  $P = 0.007$ ; Time  $\times$  Region interaction). Pit diameter increased during the feeding period (weeks 1–4), and decreased during the first month of the starvation period (weeks 4–8). When examining the second month of the starvation period, antlions originating from the semi-arid region showed a marginally higher increase in pit diameter than those originating from the hyper-arid region ( $F_{1,111} = 3.86$ ,  $P = 0.052$ ; Time  $\times$  Region interaction). In the semi-arid control group, the last measurement is missing

( $Z = 4.86$ ,  $P < 0.001$ ; Fig. 2a). When fed for the first time after the starvation period, this difference between regions was still significant ( $Z = 6.22$ ,  $P < 0.001$ ; Fig. 2b). Additionally, antlions that were fed more frequently during the feeding period were less responsive to prey after starvation ( $Z = 2.81$ ,  $P = 0.005$ ; Fig. 2b) and this pattern was consistent between regions (non-significant Region  $\times$  Feeding treatment interaction;  $Z = 0.635$ ,  $P = 0.530$ ). In the control group, we found no significant differences in response time to prey between regions, neither at the beginning ( $Z = 1.04$ ,  $P = 0.3$ ) nor at the end ( $Z = 1.63$ ,  $P = 0.1$ ) of the experiment.

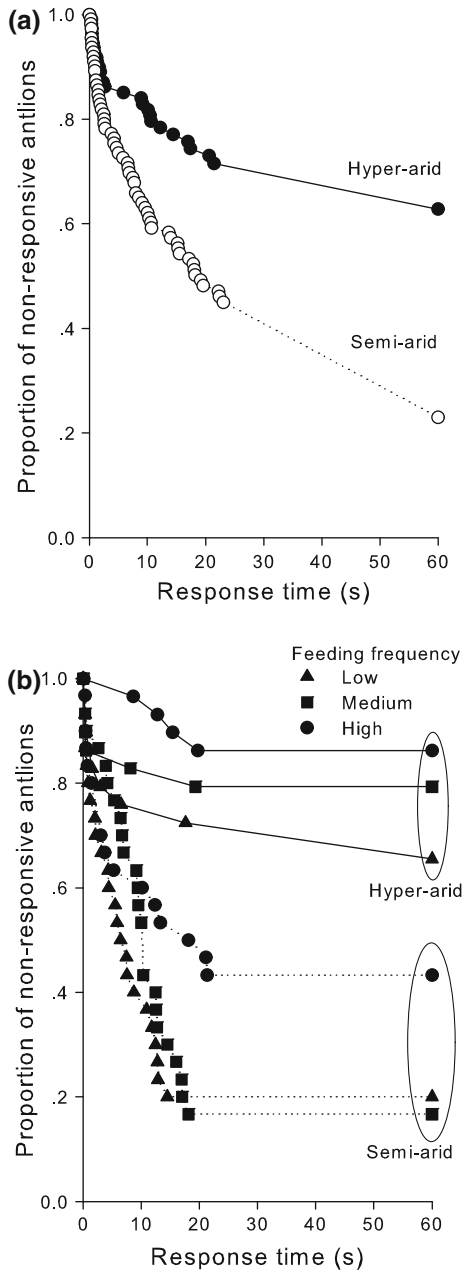
At the beginning of the experiment, there was no difference in growth efficiency between regions (One-way ANOVA:  $F_{1,171} = 0.32$ ,  $P = 0.572$ ; Fig. 3). When fed after the starvation period, growth efficiency was higher in antlions originating from the semi-arid region, compared to those originating from the hyper-arid region (Two-way ANOVA:  $F_{1,118} = 17.47$ ,  $P < 0.001$ ; Fig. 3). Antlions that were fed more frequently during the feeding period tended to have a lower growth efficiency when fed post-starvation, but this trend was only marginally significant (Two-way ANOVA:  $F_{2,118} = 2.81$ ,  $P = 0.064$ ). In addition, the interaction between region and feeding treatment was not significant (Two-way ANOVA:  $F_{2,118} = 0.14$ ,  $P = 0.874$ ). In the control group, no differences in growth efficiency were found at the beginning of the experiment, but at the end of the experiment, antlions originating from the semi-arid region showed higher growth efficiency than those originating from the hyper-arid region (One-way repeated measures ANOVA:  $F_{1,37} = 8.21$ ,  $P = 0.007$ ; Time  $\times$  Region interaction).

Antlions originating from the semi-arid region showed a higher relative growth rate during the feeding period, a faster rate of mass loss during the starvation period, and a higher relative growth rate during the compensation period (Two-way repeated measures ANCOVA using initial body mass as a covariate:  $F_{2,228} = 12.47$ ,  $P < 0.001$ ; Time  $\times$  Region interaction; Fig. 4). In addition, antlions that were fed more frequently during the feeding period had a lower relative growth rate during the compensation period (Two-way repeated measures ANCOVA:  $F_{4,228} = 7.63$ ,  $P < 0.001$ ; Time  $\times$  Feeding Frequency interaction; Fig. 5). We repeated the analysis for the starvation and compensation periods, using the body mass at the beginning of the starvation period as a covariate, but the results were qualitatively identical to the previous analysis. In the control group, growth rates were similar between regions during the regular feeding period, but higher in antlions from the semi-arid region during the compensation period (One-way repeated measures ANCOVA:  $F_{1,37} = 6.58$ ,  $P = 0.015$ ; Time  $\times$  Region interaction).

Time-to-event analysis (i.e., Cox proportional hazard model) indicated that the mortality rate of antlions originating from the semi-arid region tended to be lower than that of those originating from the hyper-arid region, but this trend was not significant ( $Z = -1.78$ ,  $P = 0.076$ ). When examining the number of surviving antlions at the end of the experiment compared to the number of antlions that were present at the beginning of the starvation period, the totals were 81/89 and 40/75 for the semi-arid and hyper-arid regions, respectively. This difference in survival is accounted for by the effect of initial body mass ( $Z = 5.42$ ,  $P < 0.001$ ). Specifically, every increase of 1 mg in the initial mass led, on average, to a decrease of 37.6 % in the mortality probability of individuals. As expected, each additional prey item consumed by antlions during the feeding phase led to a marginally non-significant decrease of 7 % in their mortality rate ( $Z = -1.67$ ,  $P = 0.094$ ). In the regularly-fed control group, no differences in survival were found between regions ( $Z = -0.05$ ,  $P = 0.960$ ). As in the starved groups, higher initial body mass improved survival rates ( $Z = -2.36$ ,  $P = 0.018$ ). Specifically, every increase of 1 mg in the initial mass led, on average, to a decrease of 47.7 % in the mortality probability of individuals.



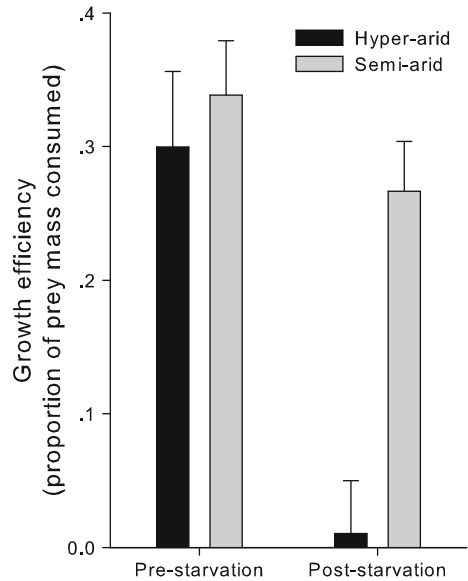
**Fig. 2** Response to prey at the beginning of the experiment (a) and after starvation (b). *Solid lines* indicate antlions originating from the hyper-arid region; *dotted lines* indicate antlions originating from the semi-arid region. Antlions originating from the semi-arid region were more responsive to prey in both measurements (beginning:  $Z = 4.86, P < 0.001$ ; after starvation:  $Z = 6.22, P < 0.001$ ). High pre-starvation feeding frequency led to decreased response to prey after the starvation period ( $Z = 2.81, P = 0.005$ )



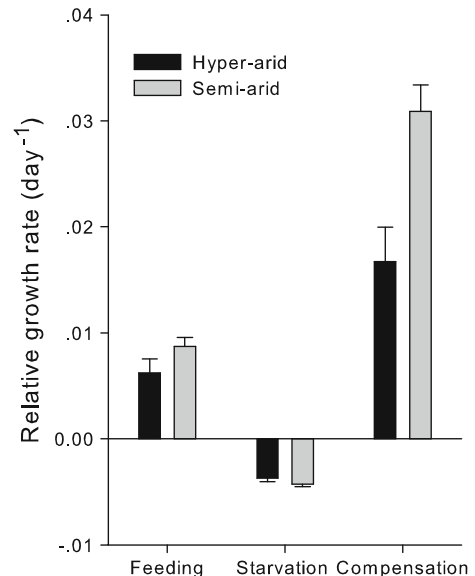
**Discussion**

Our study illustrates that antlions originating from different climatic regions vary in their behavior and life-history. Specifically, antlions originating from the semi-arid habitat maintained higher activity levels, as exemplified by their larger pit sizes. These higher activity levels enable faster recovery when food supply is renewed, as is evident from the

**Fig. 3** Growth efficiency (mean  $\pm$  1 SE). At the beginning of the experiment, there was no difference in growth efficiency between regions ( $F_{1,171} = 0.32$ ,  $P = 0.572$ ). When fed after the starvation period, growth efficiency was higher in antlions originating from the semi-arid region, compared to those originating from the hyper-arid region ( $F_{1,118} = 17.47$ ,  $P < 0.001$ )

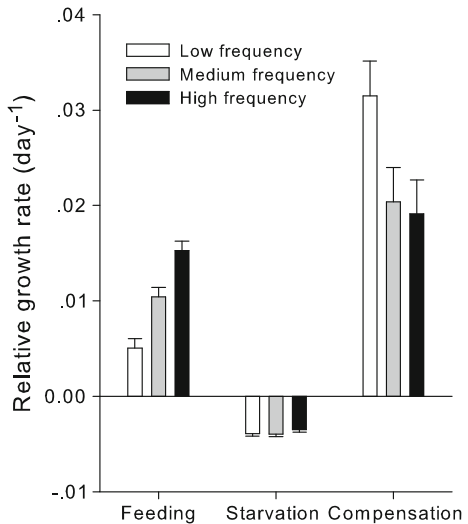


**Fig. 4** Relative growth rate by climatic region (mean  $\pm$  1 SE). During the feeding phase, relative growth rate was higher in antlions originating from the semi-arid region. During starvation, the rate of mass loss was higher in antlions originating from the semi-arid region, but they also gained mass at a higher rate during the compensation period (Two-way repeated measures ANCOVA using initial body mass as a covariate:  $F_{2,228} = 12.47$ ,  $P < 0.001$ ; Time  $\times$  Region interaction)



higher growth efficiency and faster relative growth rate of the semi-arid group after the starvation period. The control group from this region also utilized the increased prey supply during the compensation period better than the hyper-arid control group, as is evident from its higher relative growth rate. Antlions from the semi-arid region also increased their pit size after a prolonged starvation (before food supply was renewed), indicating an “optimistic” approach to the chances of future prey encounter. Antlions originating from hyper-arid habitats had lower activity levels (i.e., construct smaller pits). This lower activity level may be economic in terms of energy use and lower rate of mass

**Fig. 5** Relative growth rate by feeding frequency (mean  $\pm$  1 SE). Antlions that were fed more frequently before entering starvation had a lower relative growth rate during the compensation period (Two-way repeated measures ANCOVA using initial body mass as a covariate:  $F_{4,228} = 7.63$ ,  $P < 0.001$ ; Time  $\times$  feeding frequency interaction)



loss, but this comes at the expense of reduced response to prey, lower growth efficiency and lower growth rate when food is available again. In fact, their growth efficiency was near zero in their first prey encounter post-starvation, indicating perhaps some sort of starvation-induced torpor. A similar pattern of reduced growth efficiency was also found in antlions originating from the hyper-arid region, which were regularly fed throughout the experiment (i.e., control group). We interpret this to mean that these antlions were satiated, and thus unable to efficiently exploit large quantities of prey. However, starved antlions from the hyper-arid region did manage to return to higher activity levels as feeding continued and attain a positive growth rate. In addition, after the reduction in pit size brought about by starvation, pit sizes remained small, indicating a “pessimistic” forecast of future conditions. These antlions are adapted to more extreme temperatures and less abundant prey, and therefore they are expected to hold a strategy fit for the worst-case scenario. It is not a clear decision which strategy is better for prolonged starvation periods—the antlions from the hyper-arid region show more economic energy use (smaller pits and slower mass loss rate), but reduced ability to utilize prey resources when they become available, and lower survival due to their smaller body size. Therefore, our original hypothesis, predicting that antlions from the hyper-arid region would be better adapted to starvation, was somewhat refuted.

Our results agree with starvation studies on *Drosophila*, in which xeric species had lower metabolic rates than mesic species (Marron et al. 2003). However, it remains unclear to what extent geographical variation in starvation endurance, as detected in our study and in *Drosophila* studies, reflects differences in natural selection acting on this trait rather than correlated responses to selection on other traits (Rion and Kawecki 2007). Results from previous research raise an additional possibility of a trade-off between hunting ability and starvation endurance, as was found in the wolf spider *Pardosa pseudoannulata* (Iida 2005). A similar, albeit macro-evolutionary trade-off may be apparent when comparing *C. lineosa* and the closely-related pit-building species, *M. hyalinus* Olivier, 1811 (Neuroptera: Myrmeleontidae). The latter species was found to capture prey more efficiently, and this may come at the expense of reduced starvation endurance, compared to *C. lineosa* (Barkae et al. 2012; Rotkopf et al. 2012).

Growth compensation is a common phenomenon occurring when individuals deprived of prey renew their access to resources and then show accelerated growth (Metcalf and Monaghan 2001; Stoks et al. 2006). For example, damselflies (genus *Lestes*) after a transient period of starvation as larvae, showed full compensation in body mass at emergence, although this sometimes came at the expense of a reduced investment in immune response and energy storage (De Block et al. 2008a). Our results are consistent with the predictions of the growth compensation (i.e., animals that experience low food abundance have the potential for accelerated growth when abundant food is encountered) phenomenon: in antlions from both climatic regions, the relative growth rate during the compensation period is negatively correlated with the amount of food encountered prior to starvation. Notably, this pattern of increased growth rate during the compensation period was also evident among antlions from the semi-arid region that were regularly fed throughout the experiment (i.e., control group). These findings suggest that there are genetic differences in growth compensation potential between antlions from these two climatic regions. It is also possible that these differences in potential growth rate are affected by the antlions' prey encounter rate during their early life stages (in the field), setting higher potential growth rates for antlions from the semi-arid region due to experience, as well as genetics. Furthermore, our results may have much broader implications for understanding individual variation in a key fitness component, namely body size. Specifically, the rarely-explored trade-off between growth rate before starvation and compensation ability post-starvation, investigated in this study, is important in determining an organism's final body size, especially when food supply is unpredictable.

It has been long accepted that animals are selected to maximise growth rates (Gotthard 2001; Stearns 1992), 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 (Gotthard 2000; Gotthard et al. 1994; Lewis 2001; Metcalfe and Monaghan 2003; Stoks et al. 2006). Here, we provide evidence that fast-growing animals perform worse under some conditions. Indeed, starvation endurance did not seem to be affected by growth rate, as antlions in the three feeding treatments lost mass at the same rate during starvation, but in the compensation period there was a significant advantage for the slow-growing group, which compensated best. These results are inconsistent with a similar experiment conducted with another antlion species, *M. hyalinus* (Scharf et al. 2009), in which antlions that were fed more frequently lost more mass during starvation, but exploited prey better when feeding was renewed. *M. hyalinus* and *C. lineosa* co-occur over large areas in Israel's Negev and Arava deserts, but they differ in their habitat and micro-habitats preferences. Specifically, *C. lineosa* is restricted to fine-grained soils (e.g., loess) and is found in open microhabitats, exposed to direct sunlight (Simon 1988). *M. hyalinus*, on the other hand, is more abundant in the coarse-grained soils, which are known to be more productive in the southern part of Israel, in accordance with the inverse texture hypothesis (Noy-Meir 1973). Furthermore, *M. hyalinus* is found only in the shade, under trees or large bushes (Scharf et al. 2008b; Simon 1988). In arid habitats, temperature and relative humidity are dramatically affected by shade (Buxton 1924). Areas exposed to direct sunlight are characterized by both high temperature and low relative humidity, while shaded areas, albeit in desert climates, experience lower temperatures and higher relative humidity (Lucas 1989). The temperature tolerance of an organism, through behavioral or physiological responses, is expected to be a crucial factor in its habitat and microhabitat choices, and also affect its mechanism of response to starvation (Chown and Gaston 1999; Sisodia and Singh 2010). To this end, both the habitat and microhabitat preference of *M. hyalinus* imply that this species is adapted to relatively benign conditions and higher prey

abundance. Conversely, *C. lineosa* likely experiences higher temperatures and lower prey abundance, and thus can benefit from adopting a strategy enabling it to endure starvation and still exploit prey efficiently when it becomes available.

In conclusion, our study demonstrates that individuals originating from different climatic regions adopt different strategies in order to endure starvation. Such differences may be the result of either fixed genetic differences (e.g., Futuyma and Peterson 1985) or developmental events occurring early in the life-cycle as a response to local environmental conditions (Applebaum and Heifetz 1999; Bateson et al. 2004; Mousseau and Dingle 1991). Previous studies have shown that starvation endurance and the rate of mass loss are tightly correlated with respiration rates (e.g., Stoks et al. 2006). Specifically, 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). We suggest that this reduced metabolic rate is reversible, and that the best strategy for starvation endurance is to reduce metabolic rate during starvation, but still retain the ability to increase metabolic rate and utilize prey efficiently when it becomes available. Antlions are unique in their extremely low metabolic rates, compared to other insects, and even when compared to other sit-and-wait predators, such as spiders. This strategy may not be applicable for insects with higher metabolic rates, which will not be able to survive such long periods of starvation. Future directions for this research should include an exploration of the physiological and molecular mechanisms underlying *C. lineosa*'s starvation endurance, and examine differences in these mechanisms between several populations originating from different regions along a climatic gradient. These mechanisms could include cuticle lipid composition and permeability to water loss (Gibbs 1998, 2002), differences in metabolic rates and metabolic fuel utilization (e.g., Kalra and Gefen 2012), and different expression levels of genes involved in distinct physiological pathways mediating sugar and fat metabolism, and cell growth (Zinke et al. 2002).

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