doi: 10.1111/j.1420-9101.2007.01453.x

A comparison between desert and Mediterranean antlion populations: differences in life history and morphology

I. SCHARF,* I. FILIN,* M. GOLAN,* M. BUCHSHTAV, A. SUBACH & O. OVADIA

Department of Life Sciences, Ben-Gurion University of the Negev, Beer Sheva, Israel

Keywords:
growth temperature;
Myrmeleontidae;
phenotypic plasticity;
reaction norms;
transplant experiment.

Abstract

We performed a transplant experiment to compare the life histories and morphologies of five geographically representative antlion *Myrmeleon hyalinus* populations along a sharp climatic gradient, from a Mediterranean climate in Israel's north to a desert climate in the south. Larvae were raised in two environmental chambers simulating Mediterranean and desert climates to investigate the extent to which the different populations exhibit phenotypic plasticity. Along the north-to-south climatic gradient, we observed a gradient in body mass prior to pupation and in pupation rate. Mediterranean populations suffered higher mortality rate when exposed to desert conditions, whereas the mortality rate of desert populations was consistent between Mediterranean and desert conditions. Our results regarding body mass, pupation rate and mortality rate suggest that Mediterranean populations had a more flexible response compared with desert populations. An analysis of digital photographs was used to measure population morphological differences, which were usually indicative of a decrease in trait size along the north-to-south gradient. We show how climatic gradients translate into phenotypic differences in an antlion population and provide a morphometric tool to distinguish between instar stages.

Introduction

Across habitats, populations of the same species can express large differences in morphology (Trussell, 2000; Langerhans *et al.*, 2003; Keeley *et al.*, 2007), life history (e.g. Augert & Joly, 1993; Niewiarowski & Roosenburg, 1993; Jonsson *et al.*, 2001), behaviour (McLaughlin & Grant, 1994; Bonte *et al.*, 2007) and genetic background (Roderick, 1996; Arnett & Gotelli, 1999a). Although such differences may result from genetic drift or spatially varying selection pressures, they may also be rooted in phenotypic plasticity. For example, the body size of chuckwallas in populations across southern USA and northern Mexico is positively correlated with the amount of annual rainfall, which, in turn, is positively correlated with habitat productivity, food availability and season length (Case, 1976; Tracy, 1990).

An important question in the study of life-history traits addresses the extent to which such inter-population differences are fixed (i.e. genetically determined), and whether they can exhibit any phenotypic flexibility that enables the animals to respond developmentally to varying conditions in the environment (e.g. Miaud *et al.*, 1999; Keeley *et al.*, 2007). The capacity of an organism to respond to changed conditions may itself vary during growth and development. For example, phenotypic plasticity in the face of a changing environment may be evident mainly during the early developmental stages, before canalization takes over (Schlichting & Pigliucci, 1998; p. 53). The goal of distinguishing the flexible from the fixed response is often achieved using common garden or transplant experiments, in which individuals of different populations are grown in controlled conditions in a laboratory or are reciprocally transplanted in the field (e.g. Tracy, 1990; Niewiarowski & Roosenburg, 1993; Arnett & Gotelli, 1999b; Trussell, 2000). Differences observed among individuals within the same species sharing identical environmental conditions may indicate that their growth, life history and morphological characters are genetically fixed.

Correspondence: Ofer Ovadia, Department of Life Sciences, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel.
Tel.: +972 8 6461359; fax: +972 8 6472648;
e-mail: oferovad@bgu.ac.il
*The first three authors contributed equally to this study.

The general principles underlying trait variation across geographical gradients were deduced from comparative experiments (e.g. Miaud *et al.*, 1999; David *et al.*, 2004). For example, Bergmann's rule describes the negative correlation between body size and temperature in natural environments (e.g. Ray, 1960; Ashton, 2004; Blanckenhorn & Demont, 2004), whereas the temperature–size rule, dictates that there is a negative correlation between adult body size and growth temperature in ectotherms raised in the laboratory (e.g. Sibly & Atkinson, 1994; Angilletta & Dunham, 2003; Walters & Hassall, 2006). Combining these two rules may help predict temperature-related developmental differences among populations and species.

A useful term in this type of research is the 'reaction norm', defined as the set of phenotypes a single genotype produces in a spectrum of different environments (Nylin & Gotthard, 1998; David *et al.*, 2004). Reaction norms enable comparisons between the levels of plasticity exhibited by different populations. For example, plasticity should be larger in populations experiencing higher variation or seasonal fluctuations (Van Buskirk, 2002; David *et al.*, 2004). Levels of plasticity may also depend on whether the variation is within or between seasons (e.g. Gilchrist, 1995).

Variation among ectotherm populations has been studied mostly in relation to three traits, size at maturity, time to maturity and growth rate, and most research revealed a trade-off between larger size and shorter developmental time (Roff, 2002; p. 211). The equilibrium point along this trade-off varies according to the environmental conditions. For example, although slow growth rates may be adaptive in poor environments (e.g. Arendt, 1997), they are sometimes fixed and do not change even when better conditions are provided (Niewiarowski & Roosenburg, 1993). Additionally, populations from less stressful environments and exhibiting higher growth rates sometimes show low survival rates under poorer conditions (Gotthard *et al.*, 1994; Arnett & Gotelli, 2003). Therefore, stressful environments should be discriminated according to the source of stress, i.e. lack of nutrients, high predation risk or short season length, to name a few. Environmental stress resulting from the impending end of the season, for example, can spur accelerated development, especially if some critical change in the habitat is expected (e.g. Rowe & Ludwig, 1991; De Block & Stoks, 2004). The magnitude of this trade-off depends on whether compensation for a small size at maturity is possible as an adult, i.e. whether the adult life span is long enough and whether the adult feeds (McPeek & Peckarsky, 1998). Other factors that were shown to affect growth rate, time to maturity and size at maturity are risk of predation and competition (Arendt, 1997; Nylin & Gotthard, 1998), both of which usually reduce growth rate, unless large size provides a refuge from predation or competition, i.e. the factors are size dependent (e.g. Arendt & Wilson, 1997).

In this research, we studied the morphology and life history of *Myrmeleon hyalinus* populations along geographical and ecological gradients in Israel. Characterized by a steep climatic gradient, Israel's weather varies from that of a mesic Mediterranean climate in the north to a xeric desert climate in the south, and its physical diversity supports a rich biotic diversity. As *M. hyalinus* adults are weak fliers and short lived (up to a week under laboratory conditions; I. Scharf, personal observations), we hypothesized that antlion populations are largely isolated, and differences among populations in morphology or life history should exist. Furthermore, because antlions are relatively immobile and spend the major part of their lives as larvae, we expect antlion larvae to exhibit high levels of phenotypic plasticity.

Antlion larvae collected for this research were raised in environmental chambers under controlled laboratory conditions, simulating either the Mediterranean or desert summer climate. This manipulation enables us to study the extent to which growth, morphology and other life-history traits vary across populations and whether they are genetically fixed or plastic. In addition, we investigated whether the observed fixed and plastic responses of *M. hyalinus* agree with the existing literature on the effects of temperature and other seasonal variations on life history and growth.

Methods

Natural history and study sites

In this study, we focused on the most abundant pit-building antlion species in Israel, *M. hyalinus* (Neuroptera: Myrmeleontidae), the larvae of which inhabit various sandy soil habitats usually located under trees or other shade providing cover (Simon, 1988). As it requires both suitable substrate and shade, the antlion is restricted to specific microhabitats or 'antlion zones' (Gotelli, 1993). Individual *M. hyalinus* spend most part of their lives as larvae that dig conical pits and ambush for small arthropod prey. After up to a year as a larva (I. Scharf, personal observations), a short-lived, weak-flying *M. hyalinus* adult emerges.

The antlion larvae collected for this study originated in five sandy regions ranging from northern to southern Israel: Caesarea, Rishon-LeZion, Nahal Secher, Holot Agur and Hatzeva (Fig. 1). These regions were classified into three climatic groups: Caesarea and Rishon-LeZion have a typical Mediterranean climate, Nahal Secher and Holot Agur have an arid climate, and Hatzeva has a hyper-arid climate (see Table S1 in the supplementary material; Goldreich, 2003; p. 13). In general, the north-to-south and west-to-east gradients in Israel are characterized by a decrease in annual precipitation rate, an increase in the rainfall coefficient of variation, an increase in temperature and a decrease in humidity (Goldreich, 2003; p. 56, 72, 99, 123).

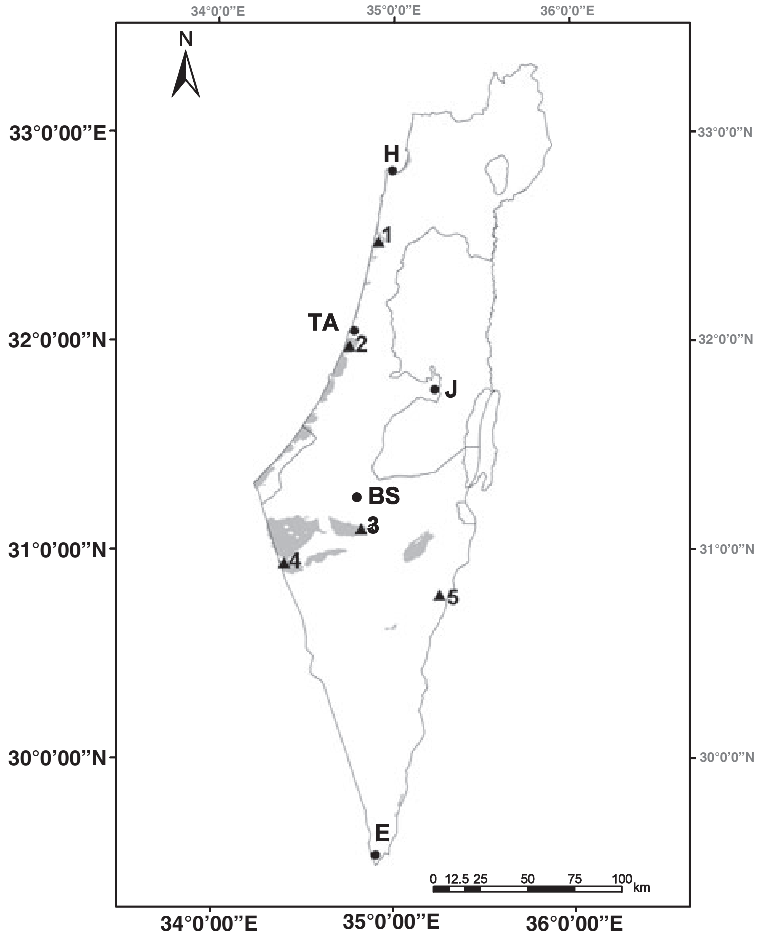

Fig. 1 Sites (▲) from which antlion larvae were collected: Caesarea (1), Rishon Le-Zion (2), Nahal Secher (3), Holot Agur (4) and Hatzeva (5). Major cities are marked with circles: Haifa (H), Tel Aviv (TA), Jerusalem (J), Beer Sheva (BS) and Eilat (E). Sandy areas are marked in grey.

In statistical analyses (see below), the antlions were coded 1–5 according to their respective origins: Hatzeva, Holot Agur, Nahal Secher, Rishon-LeZion and Caesarea, in that order. Additionally, they were also classified according to three climatic regions: hyper-arid (Hatzeva; region code 0), arid (Holot Agur and Nahal Secher; region code 1) and Mediterranean (Rishon-LeZion and Caesarea; region code 2). Note that in all statistical analyses, the effect of 'Population' and not 'Region' was tested, except for the analysis of mortality rate in which 'Region' was used instead.

Collection and experimental design

During June and July 2006, we collected 473 antlion larvae from under trees or bushes in the five regions described above. In the laboratory, individual larvae were randomly assigned to either a Mediterranean climate treatment (temperature and humidity of July–September in Tel Aviv), or to a desert climate treatment (temperature and humidity of July–September in Eilat; see Table S1 in the Supplementary material). In the statistical analyses (see below), the climate treatments were coded either 1 or 2 for Mediterranean or desert respectively.

Antlion larvae were grown separately in round, plastic cups (5 cm diameter) filled with sand (2 cm), and they were weighed every 3 weeks. Each larva was fed flour beetle larvae (mean beetle larva mass: ~0.006 g) twice a week. The experiment started immediately after collection (June–July 2006) and lasted up to 290 days (until early April 2007), during which most antlions (93%) completed their life cycles or died. Pupation and mortality events were recorded throughout the entire experimental duration. Individual larvae (257 individuals) were photographed between late August and early September 2007 using a digital camera (Micropublisher 5.0, QImaging, Surrey, BC, Canada) connected to a Nikon stereoscope (SMZ 800, Nikon, Kawaski, Japan).

Larval morphology

On each of the 257 antlion larva photos, we measured 12 different larval body features: distance between mandibles (DBM), mandible length (ML), curved mandible length (CML), mandible width (MW), head length

(HL), head width (HW), distance between mandible first and third tooth (T13), distance between mandible second and third tooth (T23), thorax length (TL), thorax width (TW), abdomen length (AL) and abdomen width (AW) (Fig. 2a). We used both uni- and multivariate analyses to test for differences across both populations and instars. We also used principal component analysis (PCA) and canonical discriminant function analysis (e.g. Zelditch *et al.*, 2004; ch. 7) to describe the differences among populations and among instars. Analyses were performed using MATLAB v. 6.5 (Mathworks, Natick, MA, USA), S-PLUS 2000 (Mathsoft, Needham, MA, USA) and SYSTAT v. 11 (SYSTAT Software, San Jose, CA, USA).

Larval body mass and growth trajectory

Using nonlinear regression (NLINFIT in MATLAB), we fitted the following logistic growth equation,

$$\mathrm{Mass}_t = \frac{\mathrm{MaxMass}}{1 + [(\mathrm{MaxMass} - \mathrm{Mass}_{t=0})/\mathrm{Mass}_{t=0}]\mathrm{e}^{-rt}},$$

to the body mass data of all individuals with more than three recorded body mass measurements, whereas an exponential growth equation was assigned to individuals with fewer than three body mass measurements. The logistic growth equation, a special case of the generic balance equation of growth, is a common method for describing increases in body mass (Karkach, 2006). We

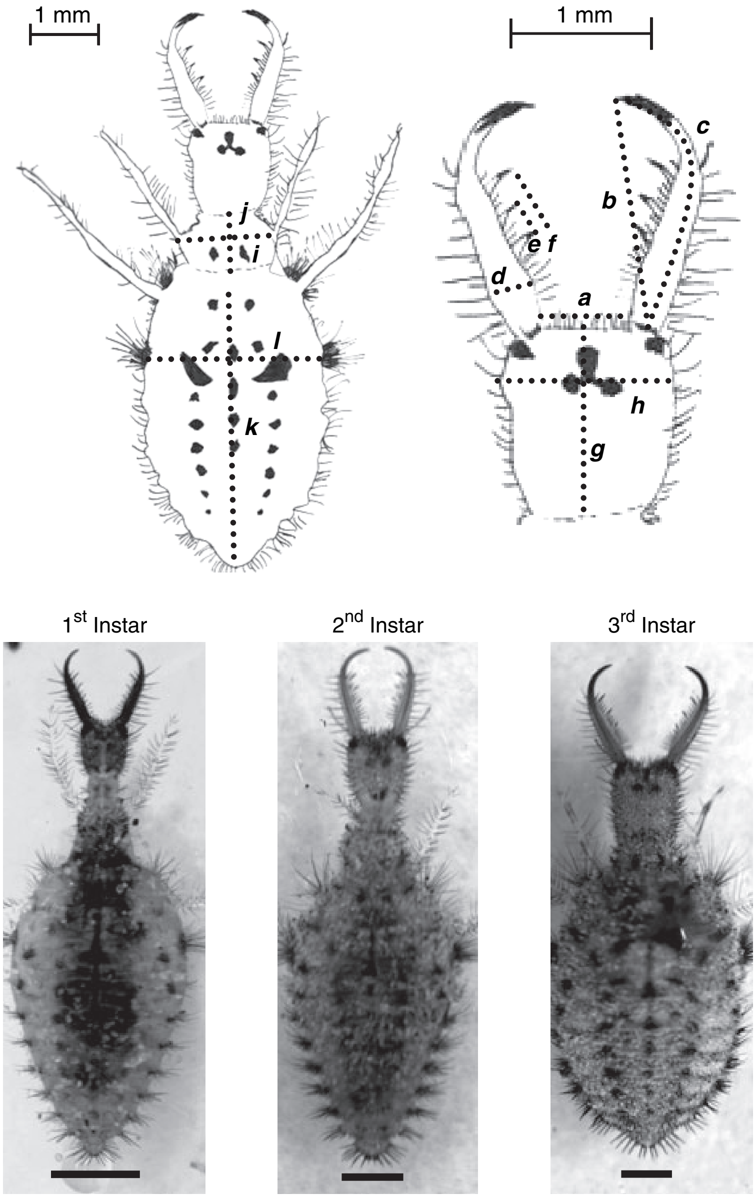

Fig. 2 (a) Drawing of a *Myrmeleon hyalinus* larva. The morphological measurements taken are marked with letters: distance between mandibles (*a*), mandible length (*b*), curved mandible length (*c*), mandible width (*d*), distance between mandible first and third tooth (*e*), distance between mandible second and third tooth (*f*), head length (HL) (*g*), head width (HW) (*h*), thorax width (*i*), thorax length (*j*), abdomen length (*k*) and abdomen width (AW) (*l*). (b) Photos of three *Myrmeleon hyalinus* instars. Instars were statistically distinctive mainly based on HW, HL and AW (see *Results*). During ontogeny, the head becomes relatively larger, the mandibles shorter and wider, and both head and mandibles increase in relative size with respect to the abdomen. Black lines represent 1mm length.

used the estimated growth rates (r) and a three-way ANOVA to study the possible differences among the five populations, between the two climate treatments, and among the three instars. Growth rates were log transformed prior to analysis to verify the assumption of normality. In addition, for those larvae that pupated, we tested for differences in the final body masses measured before pupation using a two-way ANOVA (population and climate treatment as factors).

Pupation and mortality rates

To evaluate the effect of population and climate treatment on pupation and mortality rates, we used the Cox proportional hazards regression model (Kleinbaum & Klein, 2005; p. 83), which is given by:

$$\mu(x;z) = \mu_0(x)\exp\left(\sum \beta_i z_i\right),$$

where $\mu(x, z)$ is either pupation or mortality rate. The baseline hazard function, $\mu_0(x)$, is a function of either time or body mass, i.e. we used both a model with x = time (representing pupation or mortality per unit time) and a model with x = body mass (representing size-specific rates, i.e. pupation or mortality per unit body mass). The effects of population and climate treatment are contained in z, which is a vector of covariates. Finally, the regression coefficients to be estimated, β_i, represent the independent effect of each covariate. In our model, we also included a possible population-by-climate treatment interaction term. These survival analyses were performed using S-PLUS 2000.

Results

Multivariate ontogenetic allometry

Antlion progression from one instar stage to the next is marked by a size increase in all traits (Fig. 2b; as the loadings of all traits on the first PC were all positive and significantly different from zero; see also Table S2 in the supplementary material). Using the ontogenetic variation of HW as a reference, most other traits grow with negative allometry relative to HW, and as such, their loadings are significantly less than 1. HL, however, grows isometrically with HW, and its loading is not significantly different from 1. The overall size and shape of the head, therefore, remains similar across larval stages. Only ML grows with positive allometry relative to HW (its loading is significantly larger than 1). Consequently, overall ontogenetic morphological change as an individual progresses through the larval stages can be summarized as follows: (i) all traits increase in their absolute size; (ii) the head becomes relatively larger; (iii) the mandibles become relatively shorter and wider (relative to head size) and relatively closer together on the head; (iv) using the abdomen as a reference, both head and mandibles increase their relative size during ontogeny, i.e. they grow with positive allometry (Fig. 2b).

Finally, canonical discriminant function analysis on morphology provided an expression for the maximal separation of instars (Fig. 3). Based on this expression, the trait best suited to discriminating between the larval stages is HW, and the second most indicative trait is HL. Other useful distinguishing traits include AW and all the mandible measures (excluding CML, which probably has a relatively large measurement error). Simon (1988) has

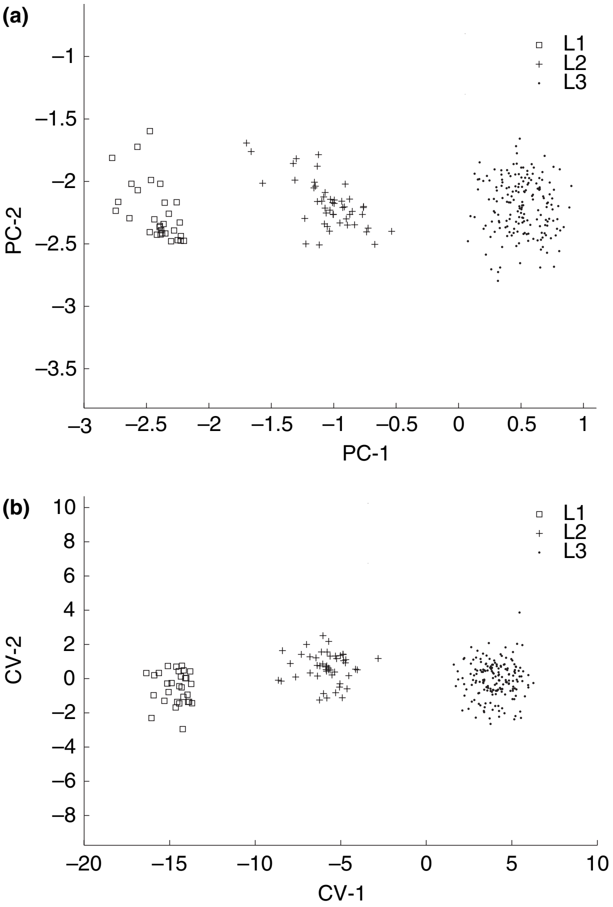

Fig. 3 (a) PCA of log-transformed morphological traits. Note how the three instars are separated along the first principal axis (accounting for 88.63% of the total morphological variation; Bootstrap 95% CI 86.16–90.55%), but not along any other principal component. PC1 describes the average ontogenetic allometry of all individuals from all populations (the relative growth of traits during the three larval stages). (b) Results of canonical discriminant function analysis of the morphological data set, using instar stage as a grouping variable. The first canonical variate, which provides the maximal separation among instars, is given by: CV-1 = 2.75DBM + 2.84ML + 2.55MW + 3.56HL + 6.65HW − 0.671T13 + 0.84T23 − 0.465TL − 1.5TW + 0.0196AL + 2.27AW + 1.24CML (Wilk's λ = 0.023; $P < 0.0001$; d.f. = 12, 239).

also used HW as the preferred trait for separating among the larval stages.

Morphological variation among populations

Univariate analysis was used to test for the effect of population on each of the 12 morphometric measures (see Table S3 in the supplementary material). To avoid confounding effects due to differences in the initial stage distribution among populations, we analysed the traits of second and third instar individuals separately. First instar individuals did not provide an adequate sample size. Figure 4 (and Table S3) presents the results of such univariate tests and trends of variation across populations respectively. Some traits showed clear trends of variation across populations that were also consistent between instars. Mandible length (ML and TML) and thorax width (TRW) decreased from north to south, and HW was larger in the Mediterranean populations (Rishon-LeZion and Caesarea). Additionally, DBM and TRL decreased from north to south only for the third instars. Finally, the Nahal Secher population was deviant in several traits (e.g. HL and MW).

Using multivariate analysis on log-transformed trait values, we found that the morphology of antlion larvae differed significantly among instars, and among populations (Table S3). Compared with the very sharp separation into larval stages (Fig. 3), the separation among populations is less clear (Wilk's λ for separation among populations: 0.558 and 0.7 for second and third instars respectively; Wilk's λ for separation among instars: 0.023).

Larval body mass and growth trajectory

We tested for the effect of instar, population, climate treatment and all possible interaction terms on the relative growth rate (log transformed). The only significant effects were those of instar ($F_{2,240} = 5.02$, $P = 0.0073$) and the instar-by-climate treatment interaction term ($F_{2,240} = 3.85$, $P = 0.0227$). Relative growth rate increased with instar, and it was higher in the desert

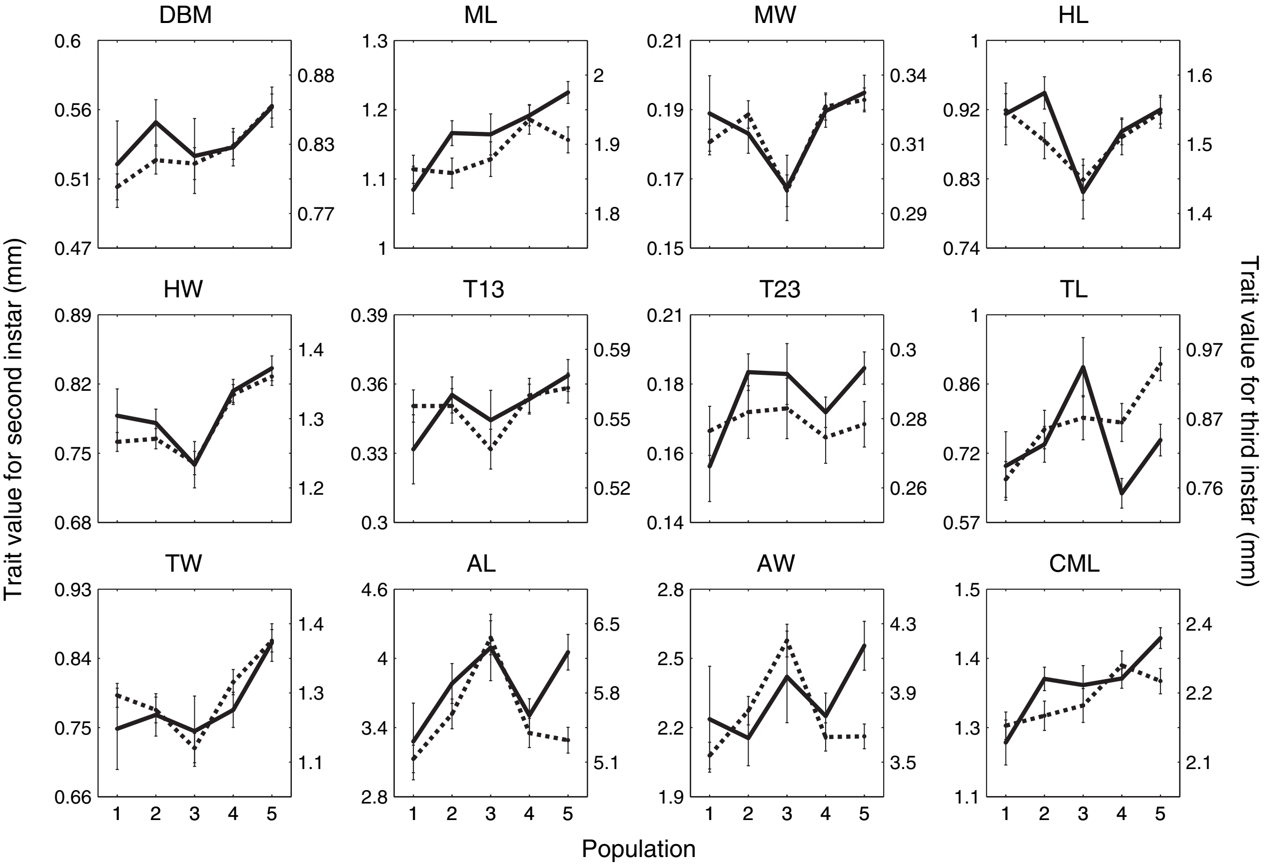

Fig. 4 Univariate analyses of each morphological trait for the second (dashed lines) and third (black lines) instar stages (see also Table S3 in the supplementary material). Populations are arranged from south to north: Hatzeva (1), Holot Agur (2), Nahal Secher (3), Rishon-LeZion (4) and Caesarea (5). The *X*-axis represents populations (from south to north) and the *Y*-axis represents the mean trait value ± SE. Generally speaking, most traits increase along the south–north gradient and are usually similar between second and third instars.

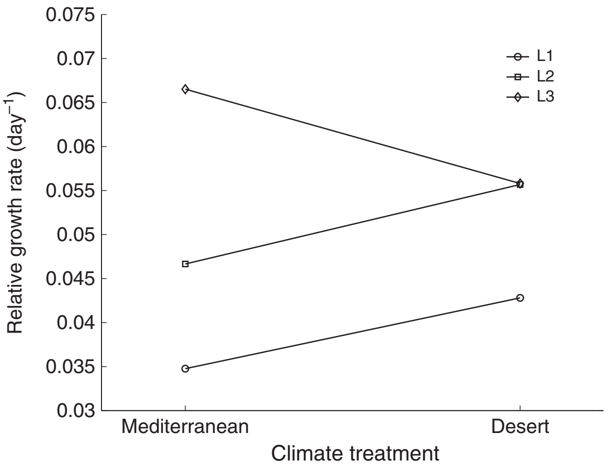

Fig. 5 Reaction norm of growth rates for different instar stages in the two climate treatments. The first and second instars grow faster in the desert climate treatment; the third instar grows faster in the Mediterranean climate treatment.

climate treatment for the first and second instar but lower for the third instar (Fig. 5).

We tested for differences in final larval body mass before pupation (log transformed) among populations and climate treatments. Larvae differed across populations and climate treatments ($F_{4,320} = 9.74$, $P < 0.0001$ and $F_{1,320} = 8.96$, $P = 0.003$ respectively). Mediterranean populations pupated at larger body masses than desert populations, and a clear gradient in body masses was observed (Fig. 6). Additionally, pupation in the desert climate treatment occurred at smaller body masses compared with the Mediterranean climate treatment (Fig. 6). The climate treatment-by-population interaction term was nonsignificant. However, a power analysis showed that the probability of committing a type 2 error is large (> 0.8), indicating that an interaction may nevertheless exist.

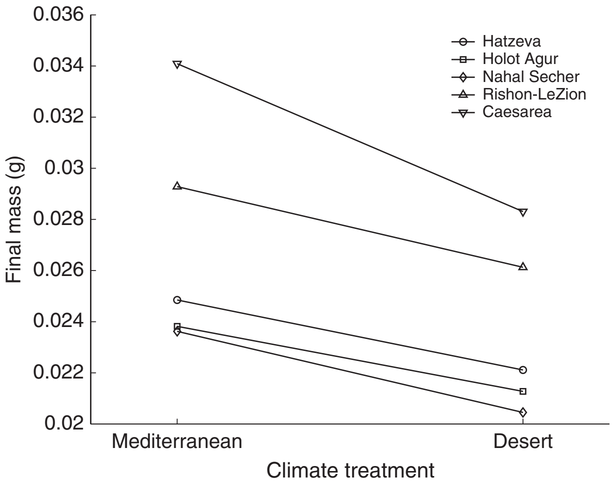

Fig. 6 Reaction norm of final body mass before pupation for different populations in the two climate treatments. Mediterranean populations (Caesarea and Rishon-LeZion) are larger than desert populations (Nahal Secher, Holot Agur and Hatzeva) and show less variation in final body mass between the two climate treatments.

Pupation and mortality rates

We tested for differences in pupation rate as a function of time and body mass across populations and climate treatments. Pupation rate as a function of time differed across populations ($z = -3.652$, $P = 0.0003$, $e^{\beta} = 0.634$), and it showed the same trend as a function of body mass ($z = -3.04$, $P = 0.0023$, $e^{\beta} = 0.679$). In general, southern desert populations pupated faster (and at smaller body masses) than northern Mediterranean populations, and larvae in the desert climate treatment pupated faster (and at smaller body masses) than larvae in the Mediterranean climate treatment (Fig. 7). Although the population-by-climate treatment interaction term was nonsignificant ($P = 0.11$ and 0.15 for time and body mass respectively), Fig. 7 suggests that the rearing environment (i.e. the climate treatment) exerts a differential effect on pupation rates (in the case of Fig. 7, pupation rate per body mass). In other words, the Hatzeva population showed no difference in the pupation rate between climate treatments (i.e. fixed response), and the Caesarea population showed the largest difference in pupation rate between the climate treatments (i.e. flexible response).

For a similar analysis performed on mortality rates, the five populations were combined into three groups (Mediterranean, arid and hyper-arid regions) to compensate for the low number of mortality events. The effects of region and region-by-climate treatment interaction on mortality rate as a function of time were marginally significant (region: $z = -1.80$, $P = 0.072$, $e^{\beta} = 0.438$; interaction: $z = 1.66$, $P = 0.097$, $e^{\beta} = 1.635$). The same trend was observed when substituting body mass for time, but in this case both effects were significant (region: $z = -1.95$, $P = 0.05$, $e^{\beta} = 0.406$; interaction: $z = 2.12$, $P = 0.034$, $e^{\beta} = 1.879$). The climate treatment affected mortality only through the interaction term, such that the difference in mortality rate between the two climate treatments is more pronounced in populations of the Mediterranean region than in populations from the arid or hyper-arid regions. In other words, desert populations tended to have similar mortality rate in both climate treatments, whereas Mediterranean populations experienced higher mortality under desert conditions.

Discussion

Investigating trait variation across geographical and ecological gradients is an integral part of the study of evolution and adaptation. In this study, we investigated

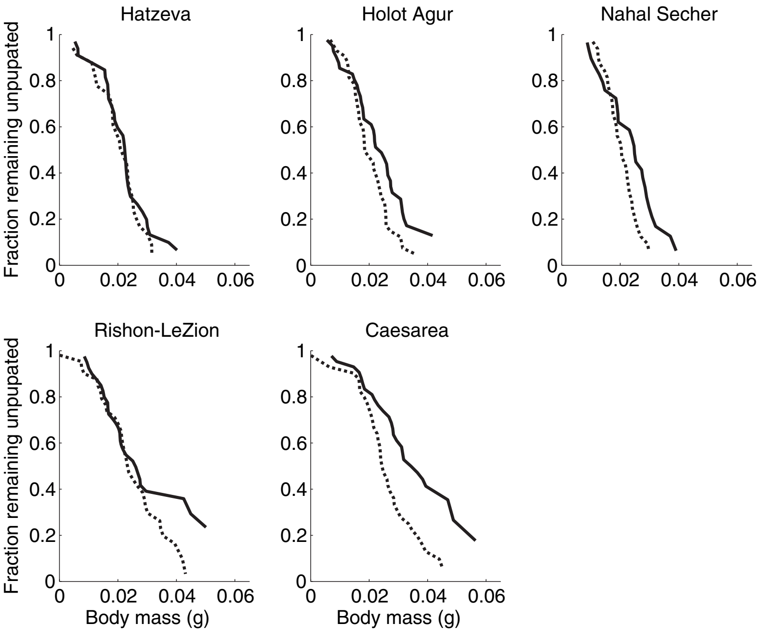

Fig. 7 Pupation rate for the five populations in the Mediterranean (black lines) and desert (dashed lines) climate treatments. Pupation was usually faster in the desert climate treatment and faster for desert populations. Mediterranean populations showed larger differences in pupation rates between the two climate treatments than did desert populations.

M. hyalinus populations across a steep climatic gradient (i.e. from a Mediterranean climate in Israel's north to a desert climate in the south) via a transplant experiment that used environmental chambers to distinguish between the fixed and plastic responses of the antlion to climate. In addition, we studied the ontogenetic growth of antlion larvae, providing a quantitative way to differentiate between instar stages. To the best of our knowledge, this is one of the first studies contrasting morphology and life history of the same species in both desert and nondesert environments. Our experiment was controlled for temperature and humidity, which are among the most important factors differentiating between the Mediterranean and desert region. Clearly, some additional differences may exist between these two climatic regions. For example, sand particles along the Mediterranean cost are coarser than those in the desert and the perennial plant cover is denser. Further research should examine to what extent such additional factors can explain the variability in morphology or life history which we could not account for in our study.

Myrmeleon hyalinus populations differed in their rates of pupation, mortality and relative growth and also in their final body masses before pupation. Pupation rates and final body masses also varied between the climate treatments. In general, desert populations (i.e. Nahal Secher, Holot Agur and Hatzeva) pupated faster and at smaller body masses in comparison with Mediterranean populations (i.e. Caesarea and Rishon-LeZion) (Figs 6 and 7). Two complementary explanations are offered for this pattern. First, the shorter duration of peak prey abundance in the desert, compared with the Mediterranean region, may select for faster development, even at the cost of small body mass at pupation, as predicted by life-history models and demonstrated empirically (e.g. Kozlowski & Wiegert, 1986; De Block & Stoks, 2004). Second, mean summer temperature in the desert region is significantly higher than that in the Mediterranean region, and the lower humidity characterizing desert region sharpens this difference. Based on the temperature–size rule (Sibly & Atkinson, 1994), antlions from colder environments are larger and develop more slowly. The second explanation is supported by the evidence, which showed that antlions grown in the Mediterranean climate treatment reached higher body masses before pupation, demonstrating at least some level of plasticity.

The largest and smallest differences between the climate treatments in pupation rates and final body masses were exhibited by the most northern and the most southern populations, Caesarea and Hatzeva respectively (Figs 6 and 7). Although the interaction term (population-by-climate treatment) was nonsignificant, Fig. 7 suggests that the Hatzeva population showed the lowest plasticity, whereas the Caesarea population the highest. This pattern is consistent with previous studies, showing that populations accustomed to stressful conditions show little change in life-history traits even when exposed to better conditions (Ward & Slotow, 1992; Niewiarowski & Roosenburg, 1993; but see Arendt & Wilson, 1997). However, relative to the Mediterranean regions, desert regions show higher variation in both the seasonal and annual precipitation, and they are also characterized by steeper temperature differences between summer and winter and day and night. Therefore, we expected that the level of plasticity would be higher in the desert regions owing to the seasonal fluctuations and high stochasticity, but this was not the case. This prediction may be somewhat simplistic. Indeed, Iwasa

(1991) claims that a poor environment, even with some variability, and an occasional supply of nutrients, would select for a fixed response. Generally speaking, it is possible that as environmental stochasticity increases, phenotypic plasticity initially increases. When the environment becomes too difficult to predict and follow, however, phenotypic plasticity decreases. In the case of increased environmental stochasticity, a uniform solution may be selected (i.e. canalization).

Mortality rates differed across regions (Mediterranean, arid and hyper-arid), but the interaction term, region-by-climate treatment, is the more revealing factor. The population of the hyper-arid region showed the smallest difference in morality rates between the climate treatments, whereas the Mediterranean region populations showed the largest differences between regional mortality rates and coped with the desert climate treatment less successfully. Gotthard *et al.* (1994) exposed a similar pattern in a butterfly species, where a population originating in a less stressful environment had lower survival rates under poor conditions than a population experiencing poor conditions in its natural habitat. This may be a good example of the trade-off between growth rate and mortality risk, which is expressed mainly under the more inferior conditions. Further research should investigate mortality levels in the field, which may differ from those observed under laboratory conditions.

Growth rate positively correlated with instar, providing evidence for exponential growth up to a certain limit – larval body mass before pupation. A simple explanation may be the broader range of prey sizes larger antlions can handle compared with smaller ones, which can only handle small prey items (e.g. Heinrich & Heinrich, 1984). The ability of the third instar to handle larger prey items may be explained by the increases in size, head-to-body ratio and mandible 'robustness' (they become wider and relatively shorter), relative to those characters in the first and second instar stages (Fig. 2b). Compared with the Mediterranean climate treatment, growth rates were larger for the first and second instars but smaller for the third instar in the desert climate treatment. Although not immediately evident, one possible explanation for this pattern is that larger larvae suffer from high temperatures and low humidity to a greater extent than do the smaller ones, but this suggestion is open to discussion. It is also possible that the feeding levels were relatively high for the smaller larvae and the earlier instars but were less satisfactory for the larger larvae, as all larvae were fed the same amounts of food. Such a feeding policy may have caused a food shortage for the larger larvae, and therefore, the third instars were the most strongly affected group. It is also possible that slow third instar growth results from a costly, faster growth in the earlier first and second instar stages.

Arnett & Gotelli (1999b) compared the life-history traits of northern (Connecticut and Rhode Island) and southern (Georgia and South Carolina) USA antlion populations. Their experiment is similar in many respects to ours, and a comparison between the results may provide interesting insights. In both experiments, the northern populations achieved larger body masses before pupation, despite the shorter times to pupation in the northern populations in their experiment. This difference results in higher growth rates in the northern than in the southern populations in their experiment, but no difference was revealed between populations in our experiment. Arnett and Gotelli suggested that the shorter times to pupation in northern populations is a result of the shorter season in the northern USA. We suggest the same, but for the desert (i.e. the southern) populations, where spring is shorter and summer is harsh. Moreover, in contrast to the northern USA, the Mediterranean climate lacks frosts. In both cases, lower temperatures in the north form a probable explanation for differences in body mass in accordance with the temperature–size rule, although Arnett and Gotelli suggested food availability as the major factor affecting differences in body mass. When antlion growth in the environmental chambers is examined, our southern populations showed lower plasticity levels (in final body masses) than did the northern populations (Figs 6 and 7). Arnett & Gotelli (1999b) transplanted a northern population (Connecticut) in a southern site (Oklahoma) and vice versa. Their results are similar: southern populations showed less difference between the two sites than northern populations (see Fig. 5 in their paper). However, another experiment with additional temperature and feeding regime treatments showed more complex trends (see Fig. 3 in their paper).

The morphological differences among populations were not always consistent across the traits measured or among the instars. We suggest three main generalizations for our data (Fig. 4): first, similar trends were exhibited across most traits for second and third instars. Second, for at least one instar group, most traits increased in size from the desert to the Mediterranean populations. This trend was more apparent in traits related to the mandibles and thorax. This study showed that Mediterranean populations achieved higher body masses before pupation, and it is possible that larger mandibles enable them to grow more. The head is also wider in Mediterranean populations, possibly to support larger mandibles. Third, the Nahal Secher population was atypical in many traits (e.g. HW, HL and MW).

In this study, we have shown that antlion populations differ in life-history traits and morphology between desert and Mediterranean regions. However, not all these differences are fixed; rather, some of them are sensitive to the environment. As our artificial experimental environment representing desert and Mediterranean climates varied in both temperature and humidity, we cannot isolate each factor's contribution with respect to the trait plasticity we observed. Testing reaction norms across different humidity levels was significantly less popular in previous studies than testing them across different temperatures (but see Ward & Slotow, 1992). Antlions' water needs are satisfied exclusively by their prey. Therefore, we suggest that investigating the effect of humidity on antlion life history may provide intriguing results, especially when combined with different feeding regimes. It is possible that large amounts of food may compensate for other stressful conditions, such as high temperature or low humidity, especially in the Mediterranean populations, which showed more flexible responses. Additionally, testing the effects of growing densities, interference and/or depletion on life history may also be productive: increased competition under stressful conditions will probably have a much greater effect on growth rate and mortality. In summary, we suggest that antlions are a good animal model for life-history studies in particular, because of their restriction to a specific area (the 'antlion zone') all their lives as larvae. The antlion's limited ability to change its habitat has probably selected for significant plasticity and variation in various life-history traits, as we have shown in this paper.

Acknowledgments

The research was supported by Israel Science Foundation Grant 1084/05 (to O.O.). We would like to thank Yoav Bartan, Hagai Guterman, Ron Rotkopf and Gal Yaacobi for their help in maintaining the antlions.

References

Angilletta, M.J. & Dunham, A.E. 2003. The temperature–size rule in ectotherms: simple evolutionary explanations may not be general. *Am. Nat.* **162**: 332–342.

Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quart. Rev. Biol.* **72**: 149–177.

Arendt, J.D. & Wilson, D.S. 1997. Optimistic growth: competition and ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution* **51**: 1946–1954.

Arnett, A.E. & Gotelli, N.J. 1999a. Bergmann's rule in the ant lion *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae): geographic variation in body size and heterozygosity. *J. Biogeogr.* **26**: 275–283.

Arnett, A.E. & Gotelli, N.J. 1999b. Geographic variation in life-history traits of the ant lion *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. *Evolution* **53**: 1180–1188.

Arnett, A.E. & Gotelli, N.J. 2003. Bergmann's rule in larval ant lions: testing the starvation resistance hypothesis. *Ecol. Entomol.* **28**: 645–650.

Ashton, K.G. 2004. Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. *Integr. Comp. Biol.* **44**: 403–412.

Augert, D. & Joly, P. 1993. Plasticity of age at maturity between two neighbouring populations of the common frog (*Rana temporaria* L.). *Can. J. Zool.* **71**: 26–33.

Blanckenhorn, W.U. & Demont, M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integr. Comp. Biol.* **44**: 413–424.

Bonte, D., Bossuyt, B. & Lens, L. 2007. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. *Behav. Ecol.* **18**: 438–443.

Case, T.J. 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus*. *Ecology* **57**: 313–323.

David, J.R., Gibert, P. & Moreteau, B. 2004. Evolution of reaction norms. In: *Phenotypic Plasticity* (T. J. DeWitt & S. M. Scheiner, eds), pp. 50–63. Oxford University Press, Oxford.

De Block, M. & Stoks, R. 2004. Life-history variation in relation to time constraints in a damselfly. *Oecologia* **140**: 68–75.

Gilchrist, G.W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* **146**: 252–270.

Goldreich, Y. 2003. *The Climate of Israel: Observation, Research and Application*. Kluwer Academic/Plenum Publishers, New York.

Gotelli, N.J. 1993. Ant lion zones: causes of high-density predator aggregations. *Ecology* **74**: 226–237.

Gotthard, K., Nylin, S. & Wiklund, C. 1994. Adaptive variation in growth-rate – life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* **99**: 281–289.

Heinrich, B. & Heinrich, M.J.E. 1984. The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae). *Behav. Ecol. Sociobiol.* **14**: 151–160.

Iwasa, Y. 1991. Pessimistic plant: optimal growth schedule in stochastic environments. *Theor. Pop. Biol.* **40**: 246–268.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigsten, P.J. 2001. Life history traits of brown trout vary with the size of small streams. *Funct. Ecol.* **15**: 310–317.

Karkach, A.S. 2006. Trajectories and models of individual growth. *Demogr. Res.* **15**: 347–400.

Keeley, E.R., Parkinson, E.A. & Taylor, E.B. 2007. The origins of ecotypic variation of rainbow trout: a test of environmental vs. genetically based differences in morphology. *J. Evol. Biol.* **20**: 725–738.

Kleinbaum, D.G. & Klein, M. 2005. *Survival Analysis: A Self-learning Text*, 2nd edn. Springer, New York.

Kozlowski, J. & Wiegert, R.G. 1986. Optimal allocation of energy to growth and reproduction. *Theor. Pop. Biol.* **29**: 16–37.

Langerhans, R.B., Layman, C.A., Langerhans, A.K. & DeWitt, T.J. 2003. Habitat-associated morphological divergence in two Neotropical fish species. *Biol. J. Linn. Soc.* **80**: 689–698.

McLaughlin, R.L. & Grant, J.W.A. 1994. Morphological and behavioral differences among recently emerged brook charr, *Salvelinus fontinalis*, foraging in slow running vs. fast running water. *Environ. Biol. Fish* **39**: 289–300.

McPeek, M.A. & Peckarsky, B.L. 1998. Life histories and the strengths of species interactions: combining morality, growth, and fecundity effects. *Ecology* **79**: 867–879.

Miaud, C., Guyétant, R. & Elmberg, J. 1999. Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): a literature review and new data from the French alps. *J. Zool. Lond.* **249**: 61–73.

Niewiarowski, P.H. & Roosenburg, W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* **74**: 1992–2002.

Nylin, S. & Gotthard, K. 1998. Plasticity in life-history traits. *Annu. Rev. Entomol.* **43**: 63–83.

Ray, C. 1960. The application of Bergmann's and Allen's rule to the poikilotherms. *J. Morphol.* **106**: 85–108.

Roderick, G.K. 1996. Insect populations: gene flow, phylogeography, and their uses. *Annu. Rev. Entomol.* **41**: 325–352.

Roff, D.A. 2002. *Life History Evolution*. Sinauer, Sunderland, MA.

Rowe, L. & Ludwig, D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**: 413–427.

Schlichting, C.D. & Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer, Sunderland, MA.

Sibly, R.M. & Atkinson, D. 1994. How rearing temperature affects optimal adult size in ectotherms. *Funct. Ecol.* **8**: 486–493.

Simon, D. 1988. *Ant-lions (Neuroptera: Myrmeleontidae) of the coastal plain: systematical, ecological, and zoogeographical aspects with emphasize on the coexistence of a species guild of the unstable dunes*, PhD thesis, Tel Aviv University, Israel.

Tracy, C.R. 1990. Differences in body size among chuckwalla (*Sauromalus obesus*) populations. *Ecology* **80**: 259–271.

Trussell, G.C. 2000. Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail. *Evolution* **54**: 151–166.

Van Buskirk, J. 2002. A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. *Am. Nat.* **160**: 87–102.

Walters, R.J. & Hassall, M. 2006. The temperature–size rule in ectotherms: may a general explanation exist after all? *Am. Nat.* **167**: 510–523.

Ward, D. & Slotow, R. 1992. The effects of water availability on the life history of the desert snail, *Trochoidea seetzeni*. *Oecologia* **90**: 572–580.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press, New York.

Supplementary material

The following supplementary material is available for this article:

Table S1 Climate data of the sites where antlion were collected.

Table S2 Results of principal component analysis on log-transformed morphometric traits.

Table S3 Results of univariate and multivariate analyses of intra-population variation in morphological traits.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1420-9101.2007.01453.x

Received 15 July 2007; revised 21 September 2007; accepted 26 September 2007