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The effect of sand depth, feeding regime, density, and body mass on the foraging behaviour of a pit-building antlion

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Abstract. 1. Pit-building antlions are small sit-and-wait arthropod predators, which dig conical pits in sandy soils. We studied how biotic (conspecific density and feeding regime) and abiotic (sand depth) factors affect pit diameter and depth, while taking into account the larval body mass.

2. Pit diameter increased with larval body mass at a decelerating rate. In addition, larger larvae tended to relocate less frequently than smaller ones.

3. Sand depth positively affected overall pit size, while increasing conspecific density had a weaker but negative effect on pit size.

4. Feeding the antlions resulted in an increase in pit diameter compared with an unfed control group. However, as prey size increased this positive effect diminished. This result suggests that the existence of prey provides information about the quality of the microhabitat, triggering pit extension. However, similarly to the reduction in the foraging effort of saturated predators, antlions provided with large prey invested only little effort in pit enlargement.

5. Antlions were previously shown to be sensitive to prey and conspecific vibrations in the sand. We thus expected the feeding regime of the neighbour to affect antlion behaviour – surrogate of discriminating between local and global shortage of prey. Nevertheless, antlions with fed neighbours (a local prey shortage) did not show different behaviour compared with a control group in which both antlions were unfed (a global prey shortage).

Key words. Body mass, foraging mode, Myrmeleontidae, sit-and-wait predators.

Introduction

Pit-building antlions can be classified as sit-and-wait predators, as they invest no energy or time in searching for prey, but need only a suitable place to construct a specific trap (Riechert, 1992). In active or mobile predators, foraging effort is usually reflected in the time and energy devoted for searching (O'Brien *et al.*, 1990), while in trap-building predators, foraging effort is reflected in the amount of energy invested in the process of trap construction and maintenance (Uetz, 1992; Eltz, 1997). Furthermore, the decision of sit-and-wait predators to relocate (i.e. to construct a new trap elsewhere) is analogous to the decision of an active predator to leave the current patch and search for a more profitable one (e.g. Harwood *et al.*, 2003; Miyashita, 2005). The decisions of how much effort should be invested in foraging or when it would be optimal to leave a patch have been extensively studied in active predators (e.g. Perry & Pianka, 1997). However, considerably fewer papers have treated traps of sit-and-wait predators in a similar manner and studied the effect of different biotic (e.g. prey abundance, prey size, prey type, and predator presence) and abiotic factors (e.g. microhabitat characteristics) on the effort invested in trap construction and maintenance (e.g. Lomascolo & Farji-Brener, 2001; Farji-Brener, 2003; Nakata, 2007). The present study focuses on testing the effect of larval body mass, conspecific density, feeding regime, and sand depth on pit characteristics.

Body mass can have dramatic influences on antlions' fitness, life history, and behaviour. For instance, larger antlion larvae can resist starvation better than smaller ones (Griffiths, 1991; Arnett & Gotelli, 2003). This same trend exists also in antlion

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adults (Scharf *et al.*, 2008a). Additionally, larger larvae can handle a wider spectrum of prey sizes, as their ability to handle the larger prey items does not reduce their ability to handle smaller ones (Heinrich & Heinrich, 1984; Scharf & Ovadia, 2006). Previous studies have illustrated that pit diameter and larval body mass are positively correlated (Youthed & Moran, 1969; Heinrich & Heinrich, 1984; Allen & Croft, 1985; Griffiths, 1986). In contrast to body mass, conspecific density often has a negative effect on the pit size of antlions (Youthed & Moran, 1969; Day & Zalucki, 2000; Devetak, 2000). This effect is usually explained by reduced space or interference competition (e.g. by sand throwing; Matsura & Takano, 1989).

Sand depth is an important characteristic of the habitat antlion larvae inhabit (Loria *et al.*, 2008). This is because the ability of the larvae to evade predators, which can hunt them mainly on or close to the sand surface, may be strongly constrained by sand depth (Loria *et al.*, 2008). Additionally, sand depth can strongly constrain pit depth to the extent that it will no longer be an effective trap for large arthropod prey. Sandy habitats largely vary in the degree of sand stabilization (Danin, 1978). Consequently, there is a large variance in sand depths which antlion larvae can experience.

Several studies showed that sit-and-wait arthropod predators that were fed, reduced their trap size and trap maintenance compared with an unfed control group (antlions: Arnett & Gotelli, 2001; Lomascolo & Farji-Brener, 2001; spiders: Lubin & Henschel, 1996). However, opposite or different results were also obtained (antlions: Griffiths, 1986; Eltz, 1997; spiders: Segoli *et al.*, 2004). Heinrich and Heinrich (1984) reported a more sophisticated pattern in antlions: A short-term starvation brought about an increase in pit size compared with a control fed group, while larvae experiencing a long-term starvation showed decreased pits compared with the control group.

Sit-and-wait predators, such as spiders and antlions, often use the rate of prey arrivals to assess the profitability of their habitat, but it is sometimes almost impossible to evaluate the quality of the site. For example, a very variable environment, in which prey arrivals fluctuate temporally, is hard to follow (Griffiths, 1986; Nakata & Ushimaru, 1999). The response of sit-and-wait predators should therefore differ when the shortage in prey is temporal versus spatial. In other words, when located in a poor site, it should be beneficial to relocate, but if the shortage in prey arrivals is global (temporal shortage, such as a poor season) it should be better to reduce activity until conditions improve (Griffiths, 1986; Eltz, 1997; Scharf & Ovadia, 2006). Previous studies have shown that antlions and spiders respond differently to a gradual decrease in prey arrivals and an abrupt and complete stop of arrivals (Vollrath, 1985; Jenkins, 1994). The first scenario may indicate a global temporal shortage while the second may indicate a sudden deterioration of the trap location. Nevertheless, Griffiths (1986) and Caraco and Gillespie (1986) suggested that antlions cannot distinguish between local and general shortage of prey and therefore should only rarely relocate.

We report on a series of three behavioural experiments in the pit-building antlion, *Myrmeleon hyalinus* (Olivieri, 1811; Neuroptera: Myrmeleontidae), testing for the effect of its body mass, conspecific density, feeding regime, and sand depth on its pit characteristics and relocation rate. The first experiment examined the effect of the larva body mass, conspecific density, and sand depth on the pit diameter and depth. Previous studies usually used a fixed sand depth and modified only the sand particle size (e.g. Youthed & Moran, 1969; Farji-Brener, 2003; but see Loria *et al.*, 2008). The second experiment examined the change in pit diameter in response to varying prey body masses. The third experiment aimed at testing whether an antlion can distinguish between local and global prey shortage [as opposed to Griffiths' (1986) view].

In the following paragraph we provide detailed predictions for all experiments. First, we hypothesised that pit diameter should increase with larval body mass, but at a decelerating rate. The reason for this is that antlions probably reach some asymptotic mass and then wait for a proper timing for pupation. Therefore, at high masses antlions should not increase pit dimensions, as prey is needed only for maintenance and not for further growth. To test our hypothesis, we adopted the thorough statistical examination of model selection, which allows a comparison to be made among several competing models describing the relationship between pit diameter and body mass. Second, and based on previous studies, we expected that pit size should decrease with increasing conspecific density, owing to mutual interference. Third, we hypothesised that sand depth should increase overall pit size. Fourth, we predicted that as the size of the prey items provided increase, antlion larvae should neglect pit maintenance (and consequently pits should get smaller) compared with larvae which received no or small-sized prey. Finally, we predicted that feeding the antlion's neighbour would cause the unfed antlions to relocate more often. In other words, when neither antlion encounters prey, the shortage should be perceived as global, whereas when only the neighbour encounters prey, the shortage should be perceived as local and thus, encourage relocation. We based this prediction on the ability of antlions to sense vibrations of prey through the sand (Devetak *et al.*, 2007; Fertin & Casas, 2007) and to sense conspecific activity (Prado *et al.*, 1993).

Methods

Study species and habitat of origin

Myrmeleon hyalinus is the most abundant pit-building antlion in Israel. The larva maximal length is approximately 10 mm long (Simon, 1988), and it can attain a body mass of up to 0.06 g before pupating (personal observations). Similarly to other sit-and-wait predators, antlion larvae are generalist predators that capture small arthropods (mainly ants) falling into their pits (Simon, 1988). *Myrmeleon hyalinus* larvae develop through three instar stages (the larval phase may last up to 1 year; Scharf *et al.*, 2008b), enter pupation and then short-lived weak-flier adults emerge. The pupa stage duration lasts approximately a month and the adults live for about a week, under laboratory conditions (Scharf *et al.*, 2008a). The mass at eclosion is an important life-history trait, especially in adult insects (such as antlions), which do not feed frequently (McPeek & Peckarsky, 1998). Its effects on survival and rate of mass loss, and also its dependence on growth temperature were studied elsewhere (Scharf *et al.*, 2008a). Adults usually mate and oviposit between May and September (Simon, 1988). *Myrmeleon hyalinus* larvae are capable of inhabiting different types of soils (Simon, 1988). They are found in shaded areas under trees, bushes, and rocks, where they occur in high densities. These areas of high antlion densities were named *antlion zones* by Gotelli (1993), and are maintained by the larvae dependence on specific physical conditions, such as adequate soil, shelter from rain, and temperature. Previous research on *M. hylainus* concentrated on the behaviour and life history of different populations. Scharf *et al.* (2008b) showed that along the steep climatic gradient in Israel (from the Mediterranean climate in the north to the desert in the south) body size and the period spent as larvae decreased. Two additional behavioural experiments showed that *M. hylainus* actively select shaded microhabitats (Scharf *et al.*, 2008c) and decrease pit construction activity when exposed to predation risk (Loria *et al.*, 2008).

Previous studies on antlions have shown that populations of the same species may differ in their pit maintenance behaviour (Arnett & Gotelli, 2001). To minimise such genetic effects on pit construction and maintenance, we collected the larvae under several different tamarisk trees (to reduce relatedness) located at Nahal Secher (N31°06′, E34°49′), i.e. a single population. This sandy area, about 15 km south of the city of Beer-Sheva, Israel, is an extension of the sand belt of northern Sinai. Nahal Secher receives around 150 mm of rainfall per year, and can be divided into areas of shifting/mobile sand, semi-stabilized sand, and stabilized sand (Danin, 1978).

The sand used in all experiments was also brought from Nahal Secher (i.e. habitat of origin). We did not manipulate the grain size and only removed large particles (e.g. leaves and seeds). Sand composition was identical in all experiments and we only varied sand depth. In the first experiment, we used two different sand depths, shallow (2 cm) and deep (4 cm). In all other experiments a constant depth of 4 cm was used. Newly collected larvae were used in each of the three experiments.

First experiment: effect of density and sand depth on pit characteristics

We collected 70 antlion larvae in the field and brought them to the lab. For this experiment we chose only third instar larvae, in order to minimise the effect of body mass on pit size. Body mass of those larvae was 22 ± 0.74 mg (mean ± 1 S.E.; the smallest third instar larvae in *M. hyalinus* are about 7 mg; I. Scharf, pers. obs.). The larvae were fed with one flour beetle larva (of approximately 1 mg), starved for a week and were afterwards placed in aluminum trays (25 × 17 cm) at varying densities (one or four individuals per tray) and sand depths (2 or 4 cm). After 2 days of habituation, pit diameter and depth were measured using a digital caliper (accuracy of 0.1 mm). A previous study indicated that a 2-day period is sufficient for pit construction (Scharf *et al.*, 2008c). The above protocol was replicated three times, using the same individuals randomly assigned to treatments [$n = 138$ ($n_{t=1} = 58$, $n_{t=2} = 42$, $n_{t=3} = 38$), because not all individuals constructed a pit). We performed a Principal Component Analysis (PCA) on log-transformed pit diameter and pit depth, in order to reduce the number of dependent variables and because of the high correlation between pit diameter and depth (Manly, 2005, ch. 6). Data were analysed using a fully-factorial mixed ANCOVA model, with PC1 as the response variable. Density and sand depth were treated as fixed effects, replication number as a random effect, and body mass as a covariate. When testing for the effect of the treatment on the change in pit size, we had to use the mean sum of squares of the two-way interaction terms (sand depth or conspecific density × replication) and its degrees of freedom (rather than those of the error term) in the calculation of the F statistics and significance level. We also present the correlation between pit depth and diameter. All experiments were conducted in the laboratory with a constant temperature of approximately 25 °C.

Second experiment: change in pit diameter in response to different prey body masses and the effect of antlion body mass on the diameter of the pit constructed

We collected 85 antlion larvae in the field and brought them to the lab. In this experiment, we aimed to investigate the effect of antlion body mass on the diameter of the pit constructed also. Therefore, we collected antlions of different instars and masses (first, second, and third instars were approximately 33%, 40% and 27%, respectively, of the larvae collected. Body mass was 5.4 ± 0.64 mg; mean ± 1 S.E.). The larvae were fed with one flour beetle (of about 1 mg), starved for a week and afterwards were placed in pairs in aluminum trays (25 × 17 cm) with a partition in the tray centre. We documented the pit diameter a day after the experiment began. Antlions were then divided into four groups, based on the size of the flour beetle larvae given (a. no prey; b. small prey, mean of 0.85 mg; c. medium prey, mean of 1.98 mg; d. large prey, mean of 3.79 mg). We measured pit diameter once more, a day after the prey was given. We calculated the proportion of change before and after feeding $\left(\frac{Pit_{after} - Pit_{before}}{Pit_{before}}\right)$ and compared the different groups using a one-way ANCOVA.

We used the arcsine transformation, common when analysing proportions (Sokal & Rohlf, 1995, pp. 419–421). We also presented the relationship between antlion body mass and pit diameter. We tested whether linear regression, order two polynomial regression or a hyperbolic saturation equation best fit this relationship. For this purpose, we used a procedure of model selection called *second-order Akaike information criterion* (hereafter AICc) usually used for a relatively small sample size (number of parameters divided by the sample size is less than 40; Burnham & Anderson, 2002).

Third experiment: testing antlion response to local shortage of prey

We collected 95 antlions of various masses and instars (Body mass was 3.9 ± 0.42 mg (mean ± 1 SE); first, second, and third instars were approximately 48%, 34%, and 18%, respectively, of the larvae collected) in the field and brought them to the lab. Antlions were fed with one flour beetle (of approximately 1 mg), starved for a week and were then placed in aluminum trays (25 × 17 cm), separated by a piece of cardboard, in pairs of similar body mass [the mean distance ($\pm$1 SE) between antlions in each pair was 7.28 ($\pm$0.27) cm]. In the treatment group, only one antlion out of each pair was fed (one flour beetle larva every 2 days) while the other did not receive prey. In the control group, neither antlion was fed. We documented pit diameter and relocation events 1, 5, and 7 days after the experiment began. A second replication of this experiment was performed using 82 additional larvae, which were raised in the laboratory about 2 months prior to the experiment. We calculated the proportion of change in the pit diameter and compared the unfed antlions in the treatment with the unfed antlions in the control group (to study whether antlions distinguish between local and global shortage), as well as the fed antlions to the unfed antlions in the whole experiment (to study whether fed antlions move less frequently) using a two-way mixed ANCOVA model with replication as a random variable. When testing for the effect of the treatment on the change in pit diameter, we had to use the mean sum of squares of the interaction term (treatment replication) and its degrees of freedom (rather than those of the error term) in the calculation of the F statistics and significance level. We tested for the factors affecting the rate of relocation events (i.e., antlion body mass, replication number, the antlion was fed/unfed, the neighbour was fed/unfed) using survival analysis (Cox regression model; Kleinbaum & Klein, 2005, p. 83).

Results

First experiment: effect of body mass, density, and sand depth on pit characteristics

There was a positive correlation between pit depth and pit diameter (Fig. 1A; $r = 0.779$, $P < 0.001$, $n = 138$). Coefficients were estimated using type-two regression [slope equals to 0.425 with CI of (0.368, 0.484) and constant equals to –0.065 with CI of (–0.335, 0.193)]. To reduce the number of dependent variables and due to the high correlation between pit diameter and depth, we performed a PCA. The first PC explained 89.5% of the variance. PC1 loadings were both positive ($\mathrm{PC1} = 0.2626 \times \text{pit diameter} + 0.3735 \times \text{pit depth}$) and can therefore be considered as a surrogate for pit size.

Sand depth induced an increase in pit size (i.e. in PC1) ($F_{1,2} = 126.81$, $P = 0.0078$; Fig. 1b). Doubling sand depth increased pit diameter and depth from 4.16 ($\pm$0.14) to 5.17 ($\pm$0.14) and 1.58 ($\pm$0.07) to 2.20 ($\pm$0.07) respectively (mean $\pm$ 1 SE). Pit dimensions increased from the first to the second replication, but decreased in the third replication ($F_{2,125} = 6.77$, $P = 0.0016$). The effect of density on PC1 was insignificant, ($F_{1,2} = 2.93$, $P = 0.229$; Fig. 1b). Increasing density caused a decrease in the mean pit diameter and depth from 4.97 ($\pm$0.16) to 4.36 ($\pm$0.11) and 1.93 ($\pm$0.10) to 1.84 ($\pm$0.06) (mean $\pm$ 1 SE). When examining each replication separately, the effect of density on pit size was significant only in the first replication ($F_{1,53} = 8.60$, $P = 0.0049$). In this experiment, body mass had no effect on either pit diameter or depth, probably because all antlions were relatively large (>10 mg) and all were third instar larvae.

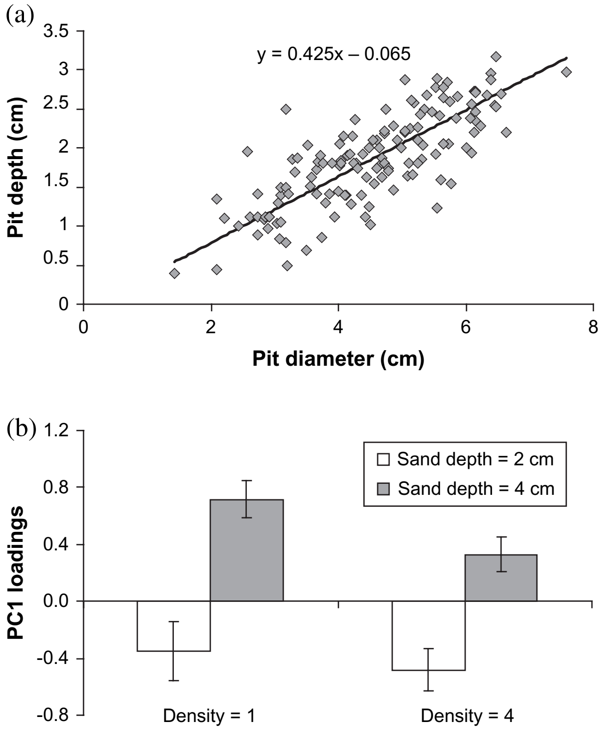

Fig. 1. (a) The relationship between pit diameter and pit depth of antlion larvae (original data, prior to the log transformation used in the statistical analysis), based on results obtained in the first experiment (see Results). The correlation is significant ($r = 0.779$, $P < 0.001$, $n = 138$). The coefficients were estimated using type-two regression [slope (with CI) = 0.425 (0.368, 0.484), constant (with CI) = –0.065 (–0.335, 0.193)]. (b) The effect of sand depth and conspecific density on pit size (PC1 loadings). Pit size is positively correlated with sand depth and negatively correlated with conspecific density.

Second experiment: change in pit diameter in response to different prey body masses and the effect of antlion body mass on the diameter of the pit constructed

The proportion of change in pit diameter after providing prey, differed significantly among the four groups of prey size ($F_{3,77} = 4.072$, $P = 0.0097$), while the effect of body mass was not significant ($F_{1,77} = 0.786$, $P = 0.38$). The most prominent increase in pit diameter was evident in the group which received the smallest prey size. However, the increase in pit diameter gradually diminished as prey size increased. In the control group which received no prey, there was only a marginal increase in pit diameter (i.e. a humped shape pattern; Fig. 2a). In this experiment, pit diameter increased significantly as a function of the larval body size, at a decelerating rate (Fig. 2b). To find which function best fits this relationship, we compared three models: linear regression, order two polynomial regression, and a nonlinear regression of hyperbolic saturation equation. The AICc

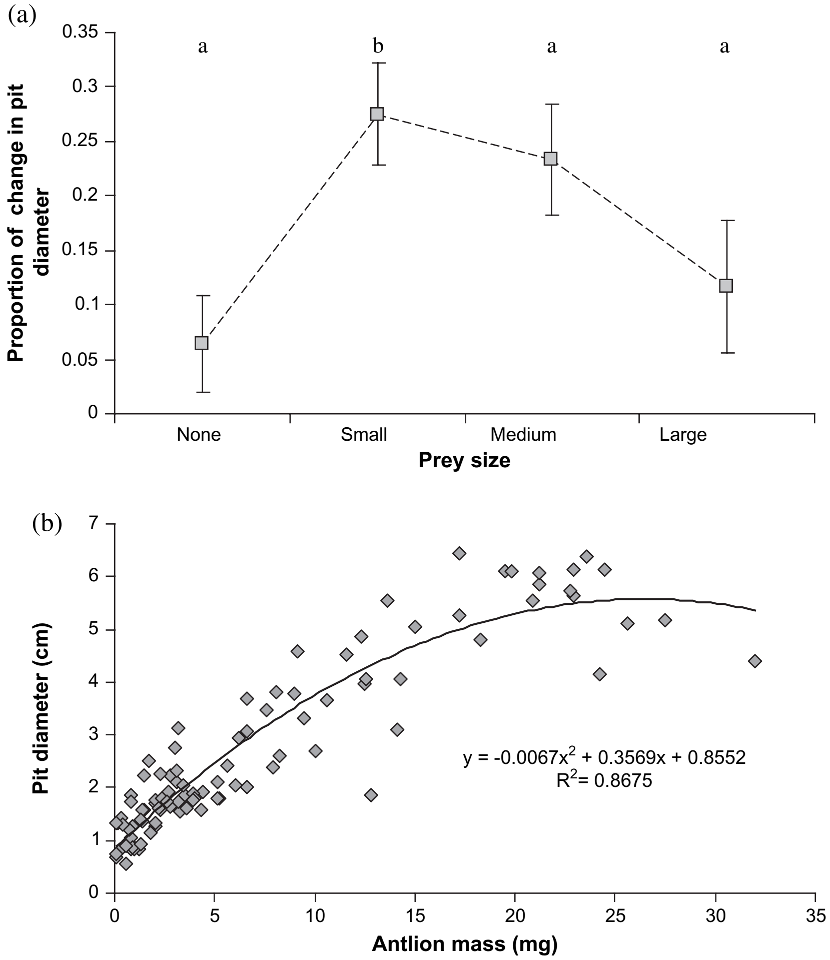

Fig. 2. (a) Proportion of change (original data, prior to the arcsine transformation used in the statistical analysis) in pit diameter as a function of the prey size provided. Prey was classified as 'small' (mean of 0.85 mg), 'medium' (mean of 1.98 mg), and 'large' (mean of 3.79 mg). A control group received no prey. The most prominent increase in pit diameter was evident in the group receiving the small prey, followed by the group receiving medium and large prey. The group receiving no prey showed only a slight increase in pit diameter. (b) Pit diameter as a function of antlion body mass. Using a second-order Akaike information criterion (AICc), we show that a polynomial regression or a hyperbolic saturation equation fits this relationship better than a simple linear regression. The equation of a second-order polynomial regression is shown, based on the second experiment (see Results).

scores of both the polynomial regression and the non-linear regression were substantially lower than that of the linear regression and therefore, both can be considered (Table 1; note that the difference between these two functions is very low: 0.51).

Third experiment: testing antlion response to local shortage of prey

Using Cox's regression, we found that the feeding regime of neither the focal antlion nor its neighbour (i.e. fed or unfed neighbor) had a significant effect on the relocation rate. The tendency of antlions to relocate the pit was negatively correlated with their body mass. Additionally, we found that in the second replicate, where the experimental population was raised for a longer period under laboratory conditions, the tendency to relocate was higher than that of the one kept in the laboratory only for a week (Table 2; Fig. 3). A similar trend was evident for pit diameter. There was no effect of feeding regime of either the focal or the neighbour antlion on the proportion of change in pit diameter, and there was also no effect of body mass or the number of replications (feeding regime of the neighbour: $F_{1,1} = 0.07$, $P = 0.831$; body mass: $F_{1,1} = 0.72$, $P = 0.552$; replication: $F_{1,1} = 0.97$, $P = 0.505$; feeding regime of the focal antlion: $F_{1,1} = 0.36$, $P = 0.552$).

Discussion

Trap characteristics of trap building predators vary as a function of different constraints imposed by the habitat they occupy and can also be modified by the predator, whose aim is to maximise the chances of catching prey (Lomascolo & Farji-Brener, 2001; Nakata, 2007). Trap size and other traits can therefore be viewed as the foraging or searching effort invested by more active predators. We showed here that antlion larvae modify their pit diameter (and sometimes depth) as a response to sand depth, conspecific density, and feeding regime (but not as a response to the feeding regime of the nearest neighbour). Some of these changes in the pit characteristics should be considered as a constraint (e.g. the decrease in pit depth when sand is shallow), while others should be viewed as adaptations to cope with the variability in prey abundance (e.g. the increase in pit diameter after capturing a prey item).

In accordance with most of the previous studies, we have shown that pit size decreases with density (Youthed & Moran, 1969;

Table 1. Three models describing the relationship between antlion body mass and pit diameter (sample size = 97). The model which fitted best was selected using a second-order Akaike information criterion (AICc). The best model was scored as zero and the rest are scaled in ascending manner (ΔAICc). Likelihood values (L) and Akaike weights (w) are also presented. RSS and # Par. stand for residual sum of squares and number of parameters in the model.

Regression	Equation	RSS	# Par	AICc	ΔAICc	L	w
Linear	$y=a+bx$	51.77	2	–22.45	13.32	0.0013	0.001
Polynomial	$y=a+bx+cx^2$	36.42	3	–35.26	0.51	0.7749	0.436
Hyperbolic saturation	$y=a\left(\frac{(x-c)}{b+(x-c)}\right)$	35.99	3	–35.77	0	1	0.563

Table 2. The effect of the replication (1 = first and 2 = second), body mass (mg), feeding of the focal antlion (0 = unfed, 1 = fed) and feeding of its neighbour (0 = unfed, 1 = fed) on relocation events. The coefficient (ß) for each factor was estimated using a Cox proportional hazard model and tested for its significance. The expected change in the time to relocation per one unit change in each of these covariates was predicted using the exponent coefficient ($e^{ß}$). For example, an increase of 1 mg in body mass decreases the antlion's probability of relocation by a factor of 0.82.

Replication		Body mass		Antlion is fed		Neighbour is fed		
$e^{ß}$	Stat.	$e^{ß}$	Stat.	$e^{ß}$	Stat.	$e^{ß}$	Stat.	Model statistics
5.86	$z = 8.44$ $P < 0.001$	0.82	$z = -5.69$ $P < 0.001$	–	NS	–	NS	LRT = 94, d.f. = 4, $P < 0.001$

Day & Zalucki, 2000; Devetak, 2000; but see Matsura & Takano, 1989), but this pattern was only evident during the first replication of the experiment. We suggest that the effect of density declined with time in our experiment, as the proportion of antlions constructing pits in the second and third replications was smaller than that of the first replication (100%, 75%, and 74% of the antlions constructed pits in the first, second, and third replications of this experiment, respectively). As fewer antlions constructed pits, the effect of mutual disturbance in the high-density treatment was not as prominent as in the first replication. Although these modifications of the traps are probably a constraint (i.e. pit depth in shallow sand is obviously restricted), they are highly relevant to antlions in their natural habitat, where they occur at varying densities and sandy soils of different types and depths. As pit diameter and depth are correlated with the success of prey capture (Heinrich & Heinrich, 1984; Scharf & Ovadia, 2006), these factors should also be correlated with growth rate and other life history traits.

Pit diameter increases with antlion body mass at a decelerating rate (Fig. 2b). This trend was also reported for other pit-building antlion species (e.g. Heinrich &Heinrich, 1984; Griffiths, 1986) and web-building spiders (e.g. Miyashita, 2005), even though a linear relationship is sometimes reported between body length and trap size (assuming that body mass is similar to length^3, the same trend is still valid). It is probable that at extremely large masses, antlions show smaller pits than expected (i.e. the curve tends to bend down) due to pit neglect. The reason for this is that antlions no longer need prey and just wait for the appropriate time for pupation. In the first experiment, such a pattern (i.e. a positive correlation) was not evident probably because most antlions were third instar larvae (i.e. the asymptote or the maximal pit diameter had already been achieved).

The effect of the size of prey captured by the antlion larvae on the proportion of change in the pit diameter had a complex trend, contrary to our prediction. As prey size increases, antlions initially increase their pits, but later on, when prey is relatively large, the increase in pit diameter diminishes. This result agrees only partially with previous studies, which found a decrease in trap size with the amount or frequency of prey given to a trap-building predator (Lubin & Henschel, 1996; Lomascolo & Farji-Brener, 2001), and does not agree with other studies which found no change in trap size as a function of feeding regime or prey size (e.g. Eltz, 1997). However, we suggest that the trend we report here is more realistic. Antlions receiving no prey have no information to count on and therefore, should not invest additional effort in their traps. On the contrary, receiving a large quantity of prey satiates the antlion to such an extent that it no longer needs to invest in capturing prey, for at least a short time

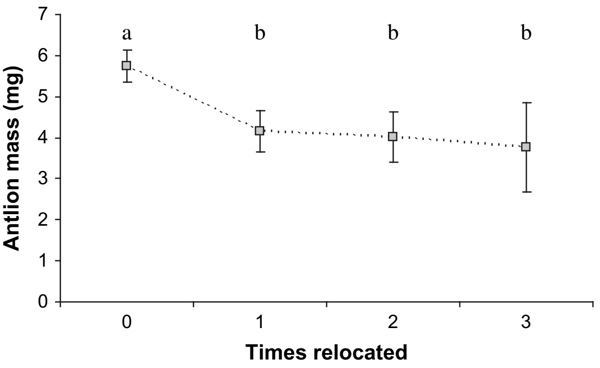

Fig. 3. The relationship between the number of times antlions relocated (1, 2 or 3) and their body mass (based on the third experiment; see Results). Larger larvae had lower probability of relocating. However, there were no significant differences in the body masses of antlions which relocated once, twice or three times.

period. This explanation may fit what has been reported before. However, when receiving only a small prey, the antlion may identify its location as profitable and may decide to invest more in capturing. Consequently, the size of the pit increases. The pattern we describe is analogous to the switch in foraging mode, from the active to the sit-and-wait mode, exhibited by some species of geckos, spiders and damselflies (e.g. Hirvonen, 1999). Hirvonen (1999) claims that at high prey densities, it is beneficial to reduce searching effort, because a high encounter rate is already achieved without spending much on searching. As prey abundance declines, it is first advantageous to adopt a more active foraging mode, but at low prey abundance, below a certain threshold, it is no longer worthwhile searching, as the cost associated with searching is too high relative to the expected foraging gain.

Previous studies showed that starved antlions sometimes do not construct larger pits; rather they increase the rate of pit relocation (Matsura & Murao, 1994; Eltz, 1997). These different responses may reflect distinct adaptations to deal with the shortage of prey. Specifically, the decision to relocate is negatively correlated with the ability of antlions, in the population under investigation, to cope with long periods of starvation by reducing their respiration rate (Matsura & Murao, 1994). Accordingly, a theoretical analysis suggested that the decision of whether to use a sit-and-wait tactic or a more flexible or active strategy is related to the food required for reproduction and the chance for reproductive failure (Caraco & Gillespie, 1986). As the expected number of prey captures exceeds the amount required, and as the chance for failure decreases, the strict sit-and-wait foraging mode becomes less advantageous.

Scharf and Ovadia (2006) suggested that antlions may be able to distinguish between global and local shortage of prey, owing to their ability to sense vibrations through the sand. Moreover, several studies suggested that at high densities antlions tend to relocate their pits more frequently, as a result of sand tossing by their neighbours (Matsura & Takano, 1989; Griffiths, 1993). As prey handling increases sand tossing, we predicted that feeding the neighbours should result in increased relocation rates of the focal individuals. Additionally, Prado *et al.* (1993) showed that antlions with small-sized neighbours relocated less often than those with larger neighbours. It thus suggests that antlions can sense the presence of different types of conspecific neighbours and respond by relocating. On the other hand, Griffiths (1986) suggested that antlion larvae have no such ability, and used this argument to explain why relocation events are rare. We could not support this prediction, related to the antlion's ability to distinguish between local and global shortage of prey. Nevertheless, it is still not an indication that antlions cannot follow spatial variation in their proximate habitat. One possible explanation is that the distances between the two antlions in each pair were too large for them to sense activity in the neighbour's pit. Although relocations in general were frequent, it is also possible that if the experiment had lasted for a longer period of time, more significant results would have been obtained. An additional pattern emerging from the analysis is the negative effect body mass has on the relocation events. Larger antlions have more fat reserves, are less sensitive to short-term fluctuations in prey arrivals, and can resist starvation for a longer period. This result is consistent with previous studies showing a similar pattern (Griffiths, 1993; Prado *et al.*, 1993).

In summary, although we could not detect an effect of the feeding regime of the antlion's neighbour on relocation rate or pit size, we showed here that antlion larvae change their foraging effort by modifications in the pit size as a result of biotic and abiotic factors: antlion feeding regime, prey size, antlion density, and sand depth. By comparing the modifications in pit size to flexibility in the foraging mode adopted by searching animals, we support the concept that the trap can be considered as a measure of the foraging effort invested by sit-and-wait predators.

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