



Response of pit-building antlions to repeated unsuccessful encounters with prey

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Pit-building antlion larvae are sit-and-wait predatory insects that construct conical pits, from which they ambush prey, in sandy soils. We examined the behavioural responses of antlions to the detection of various sized prey, which they were not allowed to capture. We found that antlions responded faster to smaller prey items, probably because larger prey may be considered a source of disturbance rather than a food source. Antlion response time to provided prey decreased after feeding and was negatively correlated with antlion body mass. Both of these results were indicative of a response to prey that depended on both internal and external factors. Pit dimensions increased with time at a constant rate among antlions in the unsuccessful prey capture or fed groups, but at a decelerating rate in the unfed control group. Contrary to our expectation, we could not detect differences in the rate of mass loss between antlions that were unfed and those experiencing unsuccessful prey captures. We also posited that antlions should exploit a specific prey type more efficiently as the number of encounters they had with it increased. However, there was no support for this prediction in our study. Exploring the responses of predators to prey in general, and in light of the conditions characterizing their natural habitat in particular, can improve our understanding of how predators adapt to cope with environmental variability.

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Animals are susceptible to cues and they rely on information when making decisions, such as where to forage and with whom to mate. Animals can forage more efficiently if, after the predator recognizes a foraging opportunity, it adjusts its behaviour accordingly to increase the probability of encountering more prey (Iwasa & Higashi 1981; Dall et al. 2005). Two main types of information are used while foraging: external information gathered from the environment (e.g. pheromones) and internal information (e.g. hunger level), both of which can markedly influence searching behaviour (Bell 1990; Ferran & Dixon 1993). Foraging predators commonly encounter prey items, and every such experience is of some informative value to the forager, which can learn how best to attack or handle the same prey item in future encounters. The effect of experience on foraging behaviour has been extensively studied in widely foraging animals (e.g. Stephens 2007). For instance, once a prey item is encountered, many animals switch from an extensive search mode (i.e. moving more directionally) to an area-restricted search (i.e. using more tortuous movement) to locate more prey nearby (e.g. Nakamuta 1985; Bell 1990). Other common responses

of widely foraging predators to prey encounter may be the formation of a search image or simply searching more slowly (e.g. Nams 1997).

Considerably fewer studies on information use by sit-and-wait predators exist (but see Riechert & Luczak 1982; Uetz 1992; Scharf & Ovadia 2006). This is probably because until recently the behaviour of sit-and-wait predators has been considered as stereotypic or automatic and they were simply not expected to show flexible behaviour (Krink & Vollrath 1997; Napolitano 1998). This perception is far from being true, since sit-and-wait predators show a variety of flexible behaviours, depending on information gathered from the environment. For example, Li & Lee (2004) and Loria et al. (2008) have shown that trap-building predators (i.e. web-building spiders and pit-building antlions) reduce their foraging activity in response to predation risk, as has been repeatedly demonstrated in widely foraging predators (Lima 1998). Prey encounter rate may be a reliable indicator to the predator of the prey abundance in a specific habitat, even when prey is detected but not consumed (Nakamuta 1985; Nakata 2007). Repeated encounters with the same prey type may also lead to decreased handling times or faster responses to that specific prey (e.g. Riechert & Luczak 1982; Morse 2000; Warburton & Thomson 2006). Changes in prey type may result in modifications of trap size or shape. For instance, when antlion larvae encounter large ants,

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they construct deeper pits than they do for smaller ants (Lomascolo & Farji-Brener 2001). Similarly, spiders fed with crickets built stiffer webs than those fed with flies (Tso et al. 2007).

We used pit-building antlion larvae as a model system to investigate several related aspects of the foraging behaviour of sit-and-wait predators. Antlion larvae are a good model system for studying foraging behaviour in sit-and-wait predators, because they are not yet in a reproductive stage, meaning that they focus most of their efforts on foraging. Furthermore, the foraging intensity and effort of trap-building predators can be easily evaluated by studying the construction and maintenance processes of their traps (Eltz 1997; Herberstein et al. 2000). We have already demonstrated that biotic (e.g. prey size; Scharf et al. 2009a) and abiotic (e.g. photoperiod; Scharf et al. 2008) factors affect the foraging decisions of antlion larvae, such as whether to construct a pit and how much to enlarge it. The goal of this research was to study how information on prey existence in the surrounding habitat affects antlion decision making and foraging behaviour. Specifically, we studied how an unsuccessful prey encounter affects antlion foraging decisions, such as pit enlargement and response times to provided prey.

Antlions usually react to oncoming prey after sensing vibrations transmitted through the sand (Devetak 1998). Based on the prediction that animals will respond faster to prey as they encounter it more often (Riechert & Luczak 1982; Uetz 1992; Morse 2000), we tested whether the response times of antlions to the prey items provided decrease with training over time. Antlions may also respond faster to prey as they encounter it more often simply because they are kept in a more alert or vigilant state compared to a situation where they have no indication of the existence of prey in their immediate surroundings, often leading to a reduced metabolic rate to save energy. This behaviour is an example of the use of information related to prey existence in the environment. Learning by experience or the relationship between a predator's vigilant status and response times to prey have rarely been studied in trap-building predators (but see Jenkins 1994; Guillette et al. 2009). We also predicted that, after feeding, antlions would have longer response times to prey provided, similar to the effects of hunger and satiation on responses to prey in other taxa (e.g. Persons 1999). The effects of hunger level and prey size on response times to prey have rarely been studied in trap-building predators (but see Griffiths 1980). Next, we tested the effects of unsuccessful prey encounters on pit characteristics. We hypothesized that, similar to other arthropods, pit-building antlion larvae will invest more resources in foraging, in this case constructing larger pits than a control group, in response to unsuccessful prey encounters. This behavioural change should be based on the information of prey existence nearby. Such responses to unsuccessful prey encounters have rarely been studied in trap-building predators (but see Nakata 2007). Finally, we tested whether antlions that repeatedly failed to subdue and consume the prey would be more successful exploiting a prey item when finally allowed to consume it compared to a control group that had not been provided with prey throughout the experiment. We based this assumption on the more vigilant state expected among antlions that were repeatedly exposed to prey. We also tested whether these antlions experiencing unsuccessful prey encounters lost more mass than those in the control group, owing to their higher vigilant state which is likely to be sustained by higher metabolic rates.

METHODS

Study Species and Habitat of Origin

Myrmeleon hyalinus (Neuroptera: Myrmeleontidae) is the most abundant pit-building antlion in Israel. The larva attains a maximal

length of about 10 mm and a body mass of up to 0.06 g before pupating. Similar to other sit-and-wait predators, antlion larvae are generalist predators, and they feed on small arthropods (mainly ants) that fall into their pits. *Myrmeleon hyalinus* larvae develop through three instar stages (lasting about 1 year) and then enter pupation (lasting about 1 month), from which they emerge as short-lived, weak-flying adults (lasting about 1 week; Simon 1988). Capable of inhabiting different types of sandy soils, *M. hyalinus* larvae are found in high densities in shaded areas under trees, bushes and rocks. The *M. hyalinus* larvae for this research were collected under several tamarisk trees located in Nahal Secher (31° 06' N, 34° 49' E), a sandy area 15 km south of the city of Beer-Sheva, Israel. Nahal Secher is an extension of the sand belt of northern Sinai, and it receives around 150 mm of rainfall per year.

Experimental Procedure

We first tested for the effects of unsuccessful prey encounters on the response times of antlions to prey and on their body mass. These two response variables are expected to be correlated with metabolic rate. We collected 81 antlion larvae and brought them to the laboratory where they were fed with small flour beetle larvae (weighing about 1 mg), starved for 14 days, and weighed using an analytical scale (accuracy of 0.1 mg). They were then placed in round cups (diameter = 8.5 cm, sand depth = 6 cm) under identical day:night photoperiods (12:12 h) and divided into three treatment groups (each consisting of 27 individuals), characterized by similar initial body size distributions: (1) subjects unsuccessfully encountering a small prey item (mean \pm 1 SE = 4.8 ± 0.2 mg); (2) subjects unsuccessfully encountering a large prey item (26.5 ± 0.6 mg); (3) control group, with no prey encounter. In the first two treatments ('unsuccessful prey encounter' treatments), prey items (flour beetle larvae) were placed in the centres of the antlion pits. However, antlions were not allowed to consume the prey item, which we removed with forceps either 30 s after the prey item was put in the pit or immediately the antlions responded to the prey item, whichever occurred first. Based on previous experience, antlions usually either respond fast to prey (<20 s) or do not respond at all. Therefore, a cutoff point of 30 s for prey removal was reasonable. Antlions responded to the prey by moving, throwing sand particles in its direction and/or attempting to capture the prey with their mandibles. We documented the time it took for each antlion larva to show any of the behavioural responses described above. We repeated the procedure described above four times (on days 2, 5, 6 and 7 from the beginning of the experiment). At the end of this session (day 8), antlions were weighed and their growth rates were calculated to test whether loss of mass was consistent among treatments. Antlion larvae underwent two additional, successive unsuccessful prey encounter events (on days 12 and 13), after which they were fed with flour beetle larvae (day 14, mean weight of prey \pm 1 SD = 3.2 ± 0.9 mg, $N = 106$), which they were allowed to capture and consume. On day 15, antlions were weighed and the respective growth efficiency was calculated for each subject using the following formula: $(\text{Mass}_{\text{after}} - \text{Mass}_{\text{before}}) / \text{Mass}_{\text{beetle}}$.

Finally, antlions from the two unsuccessful prey encounter treatments were presented with either small or large prey items and the effect of recent feeding on response time to prey was measured.

We next tested for the effect of an unsuccessful encounter with prey on pit diameter. We collected 92 additional antlion larvae and brought them to the laboratory where they were fed with small flour beetle larvae (weighing about 1 mg), starved for 14 days, and weighed using an analytical scale (accuracy of 0.1 mg). They were then placed in round cups (diameter = 8.5 cm, sand depth = 6 cm) under identical day:night photoperiods (12:12 h) and divided into

three treatment groups ($N = 31$, 31 and 30, respectively), characterized by similar initial body size distributions: (1) subjects unsuccessfully encountering a small prey item (mean \pm 1 SE = 2.8 ± 0.8 mg); (2) subjects encountering and consuming a small prey item (of a similar mass to group 1); (3) subjects unfed and undisturbed. We let the antlions construct pits a day after stocking, measured their pit diameter and then carried out the treatments, which were repeated on 2 successive days. Pit diameters were measured a day after each treatment.

Statistical Analyses

We used a repeated measures ANCOVA (Zar 1999) to test for the effects of prey size, time and initial antlion body mass on antlion response times to unsuccessful prey encounters. A repeated measures ANCOVA was also used to contrast the response times of antlions measured during the last unsuccessful prey encounter event with those observed after actual feeding took place. In both analyses, we included only antlions that responded to prey (i.e. responded within 30 s), while using body mass (covariate) and prey size (small versus large) as between-subjects factors and time (i.e. prey encounter events) as the within-subject factor. All possible interaction terms were included in these two analyses. ANCOVA was used to test for the effects of the unsuccessful prey encounter treatment, initial body mass (covariate) and their respective interaction term on the rate at which antlions lost mass during the experiment (the relative growth rate of antlions was negative because they were not fed). Finally, ANCOVA was also used to test for the effects of the unsuccessful prey encounter treatment, initial body mass (covariate) and their respective interaction term on antlion growth efficiency, measured after actual feeding took place.

Regarding the second experiment, a new variable, the proportion of change in pit diameter, was calculated, according to the following equation: $[(\text{Pit diameter}_{t+1} - \text{Pit diameter}_t) / \text{Pit diameter}_t]$. This variable was used instead of pit diameter to neutralize possible effects of initial differences between experimental groups, before we applied the different treatments. A repeated measures ANCOVA was used to explore the effects of treatment (unsuccessful prey encounter, prey encounter and consumption and control) and antlion body mass (covariate) as the between-subjects factors and time (prey encounter events) as the within-subject factor on the change in pit diameter. All interaction terms were included in this analysis. Response times and the changes in pit diameter were all log transformed because they were not normally distributed.

RESULTS

Response Times to Prey

Antlions usually responded to prey within the first 30 s (88.5% of all trials) and responded significantly faster to smaller than to larger prey items (Fig. 1a). Response times did not vary significantly among the four unsuccessful capture events (i.e. experience or time), nor as a function of antlion body mass. The three-way interaction term (prey encounter event*prey size*antlion body mass), and the two-way interaction terms (prey size*antlion body mass and prey size*prey encounter event) were not significant. See Table 1 for a statistical summary of the results. Analysis of the response times of antlions to unsuccessful capture before and after actual feeding resulted in a complex pattern. The three-way interaction term (before/after feeding*prey size*antlion body mass) was marginally significant. Specifically, prior to feeding, a small prey was attacked very fast, independent of the antlion body mass

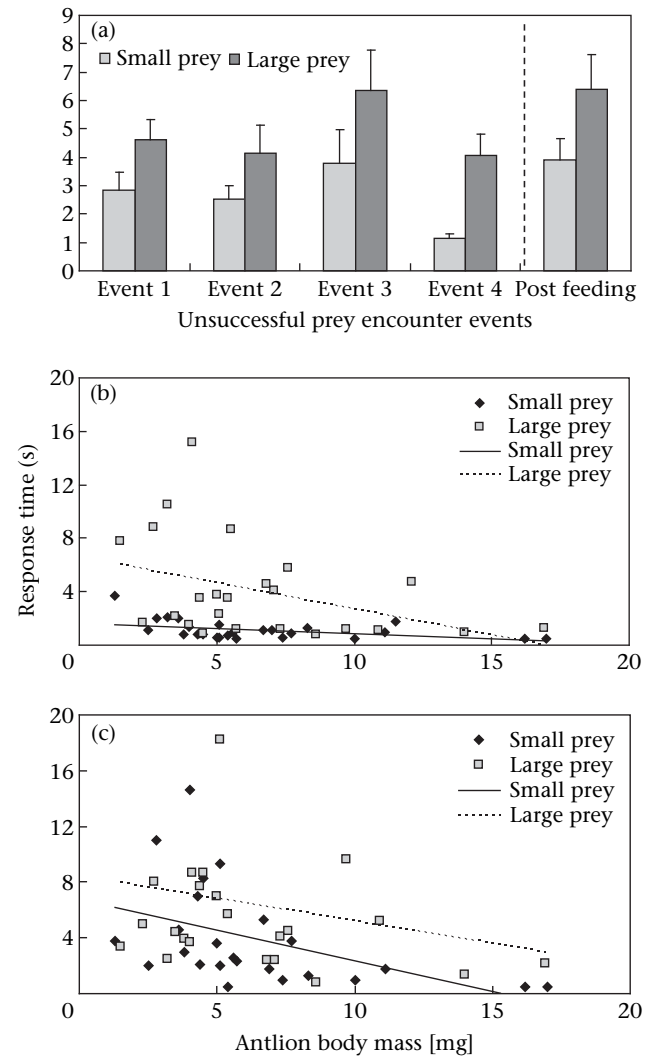


Figure 1. (a) Response times of antlion larvae to a provided prey item. 'Event 1–Event 4' stand for the four unsuccessful prey encounter events prior to actual feeding. 'Post feeding' stands for the unsuccessful prey encounter event after actual feeding. Error bars represent 1 SE. The dashed line represents the separation before and after the actual feeding event. (b) The response time to prey prior to actual feeding. (c) The response time to prey after actual feeding.

(Fig. 1b). In contrast, after feeding, the response time to small prey was dependent on the antlion body mass (Fig. 1c). Antlion response times to prey decreased with antlion body mass, and were faster when a smaller prey was provided. Finally, the response to prey after actual feeding took place was slower than that observed prior to actual feeding (Table 1).

Growth Rate and Growth Efficiency

Because antlions were not fed throughout the experiment, they lost body mass. The rate of mass loss (the relative growth rate) during the first experiment (i.e. 8 days with four unsuccessful prey encounter events) did not differ significantly between treatments (Table 1). Also, there was neither a significant initial body mass effect nor a prey size/control*antlion mass effect. Growth efficiency, that is, the efficiency of prey mass conversion into antlion body mass, neither varied significantly among treatments nor varied as a function of antlion body mass prior to feeding. Again, the

Table 1
Summary of statistical analyses

	df	F	P
Effect of unsuccessful prey capture on response times of antlions to prey*†			
Antlion body mass (ABM)	1, 36	2.468	0.125
Prey size (PS)	1, 36	10.75	0.002
Prey encounter events (PEE)	3, 108	0.007	0.999
PS*ABM	1, 35	1.322	0.258
PEE*ABM	3, 108	0.999	0.396
PEE*PS	3, 108	1.383	0.252
PEE*PS*ABM	3, 105	1.112	0.348
Comparison of response times of antlions to prey before and after actual feeding*			
Antlion body mass (ABM)	1, 41	27.58	<0.0001
Prey size (PS)	1, 41	5.588	0.023
Before/after feeding (BAF)	1, 41	13.04	0.0008
PS*ABM	1, 41	0.153	0.698
BAF*ABM	1, 41	0.446	0.508
BAF*PS	1, 41	0.153	0.698
BAF*PS*ABM	1, 41	3.686	0.062
Effect of unsuccessful prey capture on the growth rate of antlions†			
Prey size/control (PS)	2, 66	1.911	0.156
Antlion initial body mass (ABM)	1, 66	0.215	0.645
PS*ABM	2, 64	0.089	0.915
Effect of unsuccessful prey capture on antlions' growth efficiency†			
Prey size/control (PS)	2, 64	1.301	0.279
Antlion initial body mass (ABM)	1, 64	0.075	0.785
PS*ABM	2, 62	0.289	0.750
Effect of unsuccessful prey capture on the change in pit diameter of antlions*†			
Feeding treatment (FT)‡	2, 72	1.045	0.357
Antlion body mass (ABM)	1, 72	3.695	0.059
Time/feeding events (T)	1, 72	1.927	0.169
FT*ABM	2, 70	1.398	0.254
T*FT	1, 72	5.242	0.008
T*ABM	1, 72	0.408	0.525
T*FT*ABM	2, 70	0.135	0.874

Significant or marginally significant results are marked in bold.

* Repeated measures ANCOVA.

† Significance levels after excluding nonsignificant higher order interaction terms from the analysis.

‡ The feeding treatment included three groups: a group encountering and consuming the prey, a group encountering but not consuming the prey and an unfed, undisturbed group.

interaction term prey size/control*antlion body mass was not significant (Table 1).

Change in Pit Diameter

There was a significant prey encounter event*treatment interaction. Specifically, pit diameter increased with time at a constant rate in the unsuccessful prey encounter and encounter and consumption groups, but at a decelerating rate in the unfed control group (Fig. 2). All other factors were not significant, except for body mass which was marginally significant (Table 1).

DISCUSSION

We were able to show in this study that antlions responded to unsuccessful prey encounters by increasing investment in foraging. The response times of antlions to prey prior to actual feeding or to smaller prey were shorter than those observed after actual feeding took place or among those provided with larger prey. Yet, we could not detect any change in the response times of antlions to prey as a function of repeated encounters with the same prey type, nor was there a difference in the rate of mass loss between antlions repeatedly experiencing unsuccessful encounters with prey and those left undisturbed.

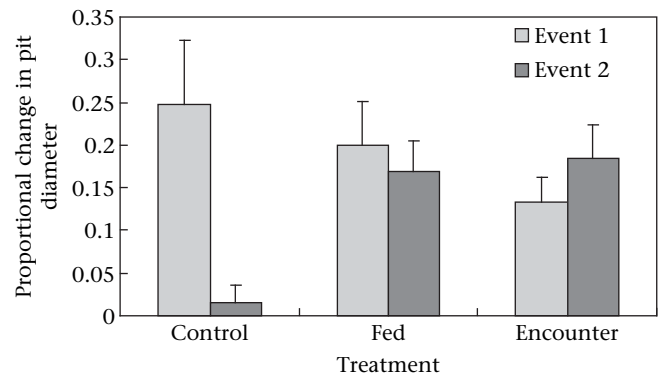


Figure 2. The proportion of change in pit diameters over time in the three treatments: control group, fed group and the group experiencing unsuccessful encounters with prey after the first and second feeding/unsuccessful encounter events. Error bars represent 1 SE.

Antlions responded to unsuccessful prey encounters by increasing pit diameter, in a similar way to the increase observed among those that were allowed to subdue and consume the prey. This response was consistent over time in these two treatment groups but weakened with time in the unfed control group (Fig. 2, Table 1). We can thus determine that an unsuccessful prey encounter is enough to trigger further investment of antlions in foraging, reflected by trap enlargement, as was also shown in spiders (Nakata 2007). Detection of prey without capture is sufficient to trigger a change in the search pattern of widely foraging predators as well (e.g. Nakamuta 1985). The trap is constructed and then slightly increased on the following day (this procedure may represent a stepwise pit construction, as also reported by Heinrich & Heinrich 1984). At this stage, the antlion waits for cues pointing to the existence of prey nearby. If such cues are available (e.g. a prey item is captured or even unsuccessfully attacked) further investment in the trap can be seen. Otherwise, the antlion maintains only the initial increase in pit size and waits for some time for prey to arrive. Finally, it may decide to relocate (Jenkins 1994; Scharf & Ovidia 2006). We interpret the response of antlions to unsuccessful encounters as a measure of evaluating their immediate habitat: pits are enlarged faster and more intensively when there is some indication of the existence of prey nearby. In other words, antlions invest more in habitats where the expected benefit of prey arrivals is higher.

Our study makes the important contribution of showing that response times to prey are context dependent. Specifically, we have shown that smaller prey were attacked faster than larger prey, hungrier antlions attacked prey faster than satiated ones, and larger antlions attacked prey faster than smaller ones (Fig. 1). Prior to actual feeding, antlions responded very fast to small prey, irrespective of their size (Fig. 1b); however, the response to small prey after feeding was dependent on antlion body mass. This suggests that the prey antlions consumed during feeding was not enough to satiate the larger antlions, but was sufficient for the smaller ones. The reduction in response times to potential prey when predators are hungrier and the shorter response times to larger prey are consistent with the measured response times of another species of pit-building antlion (Griffiths 1980) and of several species of web-building spiders (Riechert & Luczak 1982; Persons 1999). One possible reason for the slower response times to larger prey is that, because of its large size, the prey was incorrectly perceived as a source of disturbance instead of as a potential meal. Although many trap-building and sit-and-wait predators can handle prey items much larger than their own body

sizes, overly large prey can harm the trap and/or the trap-building predator itself, and should thus be attacked with some caution (Diaz-Fleischer 2005).

We also predicted that antlions would respond faster to potential prey after several unsuccessful prey capture attempts, which may indicate the existence of more prey in their immediate surroundings. Moreover, as predators become more familiar with a specific type of prey, the probability of the predator attacking increases and the time needed to initiate an attack decreases (Riechert & Luczak 1982; Morse 2000). Similarly, widely foraging predators engage more easily in an area-restricted search and hesitate less before attacking prey when familiar prey is encountered (Ferran & Dixon 1993; Punzo 2000, page 164). This was not the case, however, in either Griffiths' (1980) study, or in our experiment: despite the foraging experience antlions accrued during the experiments, there was no significant reduction in their response times to prey. Olive (1982) also failed to show a modified behavioural response in a web-building spider.

As already described, response times of antlions to prey varied with their hunger level and body mass as well as with prey size, but were independent of foraging experience. It is plausible that familiarity with a specific prey type is not required for an initiation of an attack in these opportunistic sit-and-wait predators, which are restricted mostly by prey size and less by its type (Simon 1988; Napolitano 1998). Moreover, even when the total time devoted to attack and consumption decreases with experience, not all stages can become more efficient. In a parasitic wasp, for example, paralyzing prey becomes faster with experience, but the burial of prey and oviposition do not (Punzo 2000, page 164). Alternatively, it is also possible that response times, when referring to prey type, are canalized to achieve some optimum or average capture success in different situations (Olive 1982).

Finally, we expected antlions that were unsuccessful at capturing prey to lose more mass during the experiment because of their increased metabolic rates compared to the control group. Starved predators often react by reducing their metabolic rate, minimizing the negative effects a long starvation period may have on their body mass and survival (Wang et al. 2006). However, as antlions were receiving cues that prey were available nearby, the reduction in metabolic rate might interfere later on with their ability to capture oncoming prey. Additionally, antlions that were intensively fed lost weight more rapidly than antlions that were not fed prior to a period of starvation (Scharf et al. 2009b). This suggests that when antlions encounter prey, they are probably in a more physiologically active mode that enables them to attack and exploit prey more efficiently. Although such a preattack physiological state should incur some energetic costs, this was not the case with the antlions in our experiment: they did not lose mass when they encountered prey but were not allowed to consume it. Our only explanation is that the metabolic rates of antlions are generally low and the experiment was too short to observe such a response (Lucas 1985). We also could not find any effect of experience on the conversion efficiency of prey mass into predator body mass, although such differences were evident in Scharf et al. (2009b) who examined the effects of starvation on conversion efficiency in this same antlion species.

In conclusion, we have shown that the antlion's tendency to attack prey depends on a combination of several factors. We have also shown that pit enlargement depends on some cue of prey existence, even without a successful prey capture. Together with other recent studies on antlion behavioural flexibility (Guillette et al. 2009; Scharf et al. 2009a), we provide here strong evidence for the existence of complex context-dependent behaviour in antlions, to a much larger extent than has been previously expected.

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