

The interplay between foraging mode, habitat structure, and predator presence in antlions

Reut Loria · Inon Scharf · Aziz Subach · Ofer Ovadia

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Abstract Antlion larvae are sand-dwelling insect predators, which ambush small arthropod prey while buried in the sand. In some species, the larvae construct conical pits and are considered as sit-and-wait predators which seldom relocate while in other species, they ambush prey without a pit but change their ambush site much more frequently (i.e., sit-and-pursue predators). The ability of antlion larvae to evade some of their predators which hunt them on the sand surface is strongly constrained by the degree of sand stabilization or by sand depth. We studied the effect of predator presence, predator type (active predatory beetle vs. sit-and-pursue wolf spider), and sand depth (shallow vs. deep sand) on the behavioral response of the pit building *Myrmeleon hyalinus* larvae and the sit-and-pursue *Lopezus fedtschenkoi* larvae. Predator presence had a negative effect on both antlion species activity. The sit-and-wait *M. hyalinus* larvae showed reduced pit-building activity, whereas the sit-and-pursue *L. fedtschenkoi* larvae decreased relocation activity. The proportion of relocating *M. hyalinus* was negatively affected by sand depth, whereas *L. fedtschenkoi* was negatively affected also by the predator type. Specifically, the proportion of individual *L. fedtschenkoi* that relocated in deeper sand was lower when facing the active predator rather than the sit-and-pursue predator. The proportion of *M. hyalinus* which constructed pits decreased in the presence of a predator, but this pattern was stronger when exposed to the active predator. We suggest that these

differences between the two antlion species are strongly linked to their distinct foraging modes and to the foraging mode of their predators.

Keywords Myrmeleontidae · Foraging mode · Anti predator behavior · Sand depth · Model selection

Introduction

Predation often operates as a strong selection force shaping various traits of the prey, such as behavior (e.g., Lima 1998a), morphology (e.g., Relyea and Auld 2004), and life history (e.g., McPeck and Peckarsky 1998). In general, a potential prey should take at least some measures against predators (e.g., reducing activity) because the failure of avoiding predation has crucial consequences, even as a single event. Often, there is no clear behavioral response of the prey to predation risk, and one may interpret it as if the prey ignores the predator. Clearly, this is not the case because even when the marginal benefit of foraging is greater than the marginal cost, and there is no immediate change in the prey foraging behavior, the cost associated with predation risk is also taken into consideration (Brown 1988; Brown and Kotler 2004). The effects of predators on individual prey may also have important consequences for population and community dynamics (e.g., Wooster and Sih 1995; Agrawal 2001; Schmitz et al. 2004). These effects can be direct, i.e., where predators directly consume prey, or indirect, where the prey reduces its foraging and mating activity time, owing to the risk of predation (Abrams et al. 1996; Werner and Peacor 2003). Both effects are likely to result in a decrease in the per capita population growth rate of the prey (e.g., Stamp and Bowers 1991; Lima 1998b). Individual prey often decrease their activity time when

Reut Loria and Inon Scharf contributed equally to the paper.

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R. Loria · I. Scharf (✉) · A. Subach · O. Ovadia
Department of Life Sciences,
Ben-Gurion University of the Negev,
P.O. Box 653, Beer-Sheva 84105, Israel
e-mail: schari@bgu.ac.il

exposed to predation (e.g., Lima 1998a; Templeton and Shriener 2004); however, this behavioral response can be context dependent. For example, it has been suggested that predators differing in their foraging mode (active vs. sit-and-wait predators) should induce different behavioral prey responses (e.g., Lima 1998b; Sih et al. 1998; Schmitz and Suttle 2001). Indeed Schmitz and Suttle (2001) illustrated that grasshoppers switch their diet only when facing a sit-and-wait spider predator but not a more actively hunting spider. Other studies examining context-dependent prey responses distinguish between predator taxa (e.g., vertebrates vs. invertebrates), type of attack (e.g., aerial vs. aquatic), or habitat structure and complexity (e.g., existence of shelter; e.g., Wooster and Sih 1995; Krupa and Sih 1998; Templeton and Shriener 2004; Rodriguez-Prieto et al. 2006).

Antlion larvae are sand-dwelling insect predators, which ambush small insect prey while buried in the sand. In some species, the larvae construct conical pits and are considered as strict sit-and-wait predators which seldom relocate while in other species, they ambush prey without a pit but change their ambush site much more frequently, possibly to compensate for their smaller attack radius (Cain 1987; Scharf and Ovadia 2006). Here, we classify the foraging mode of this latter group as ‘sit-and-pursue’ (similar to Schmitz and Suttle 2001). Antlion larvae are also exposed to predation pressure by other sand dwelling predators at higher trophic levels such as spiders and predatory beetles. The ability of antlion larvae to evade such predators, which can hunt them mainly on or close to the sand surface, may be strongly constrained by the degree of sand stabilization or by sand depth. We studied the effect of predator presence, predator type (active predatory beetle vs. sit-and-pursue wolf spider), and sand depth (shallow vs. deep sand) on the behavioral response of pit-building and sit-and-pursue antlion larvae. We hypothesized that in the presence of a predator, both species will reduce activity (i.e., as measured in this experiment: proportion of relocating individuals, movement distance, and pit construction). This activity reduction should be greater when exposed to the active predatory beetle, which covers a greater area, resulting in a higher probability to encounter antlion prey. In addition, we anticipated that this pattern will be stronger in the more active antlion species (the sit-and-pursue one) because its movement can result in higher probability of being encountered by the predator but will weaken when antlions are not offered possible shelter from the predator (i.e., shallow sand), and there is no advantage for reducing activity.

Studies investigating the interplay between the foraging modes of the prey and the predator suggest that sit-and-wait predators mainly catch active or moving prey and that active predators usually search for sedentary prey (e.g., Huey and Pianka 1981; Greef and Whiting 2000). In

addition, theoretical studies suggest that when the active predator moves fast relative to the prey, there is only a little difference between the encounter rates of the active predator with either moving or sedentary prey (e.g., Werner and Anholt 1993; Scharf et al. 2006). As a result, a sit-and-wait predator may pose a particular threat to the moving prey while the active predator poses a threat to both types of prey. We, therefore, hypothesized that the pit-building antlion larvae would respond strongly to the active predatory beetle, while the response of the sit-and-pursue antlion would be consistent between the two predator types.

Methods

Study species and habitat of origin

Myrmeleon hyalinus and *Lopezus fedtschenkoi* (Neuroptera: Myrmeleontidae) co-occur over a wide range of sandy areas in Israel (Ovadia O., unpublished data). Both species ambush small insect prey, but they differ in their foraging mode and microhabitat preference. The pit-building antlion *M. hyalinus* is a classical sit-and-wait predator, which prefers shaded microhabitats under trees or bushes, and it rarely relocates after constructing a pit (Simon 1988). In contrast, *L. fedtschenkoi* is a sit-and-pursue predator, which is mainly active on open dune slopes, changing its ambush site several times during the night without constructing a pit (Simon 1988). We collected about 50 *M. hyalinus* and 40 *L. fedtschenkoi* individuals from Nahal Secher, (31°06' N, 34°49' E), a sandy area in the Northern Negev desert, about 15 km south of the city of Beer-Sheva, Israel. This region is an extension of the sand belt of Northern Sinai and is usually divided into areas of shifting or mobile sand, semi-stabilized sand, and stabilized sand. We also collected two abundant sand dwelling predators of antlions (12 of each) from the same area: a carabid beetle, *Anthia sexmaculata* (Coleoptera: Harpalidae), which actively searches for prey, and a sit-and-pursue wolf spider (Araneae: Lycosidae).

Experimental system and study design

We constructed 40 small enclosures, 1.5×1 m each, made of 20 cm plastic sheets attached to wooden planks, and filled with 10 cm sand (deep sand) brought from the habitat of origin. To manipulate sand depth we randomly placed pieces of plywood (1.5×1 m each) in half of the enclosures and covered them with 0.5 cm (shallow) sand. Antlions were fed with flour beetle larvae ad libitum and then starved for a week before starting the experiment. Predators were provided with flour beetle larvae on a daily basis, because they might not survive a long starvation period. The experiment consisted of eight main treatments (two

antlion species \times two main predator treatments \times two levels of sand depth), in a randomized block design. These treatment combinations were replicated 35 times each. The predator treatment was basically divided into two categories (predator present and predator absent). The predator present treatment was divided into two additional sub-treatments, related to the predator type: active predator beetle and sit-and-pursue wolf spider. These sub-treatments were replicated 16–19 times each (total of 35). Immediately after sunset, predators were placed in the enclosures (zero or one individual per enclosure) and an hour later, antlion larvae were added (one individual per enclosure). We calculated the proportion of antlions that relocated, their relocation distance measured along their relocation path, and whether a pit was constructed (for *M. hyalinus* only) 4–5 h after they were stocked. To avoid interrupting the animals, relocation distances were taken using a measuring tape only after the experiment ended. Finally, antlions and predators were collected and brought back to the lab. This protocol was replicated seven times with an interval of 1–2 days between replications. Individual antlion were used more than once (three to four times) during the experiment, while the same predators were used each night. To avoid dependence of the data, both antlions and predators were randomly assigned to the different enclosures and experimental treatments.

Data analysis

Our dataset included binary response variables (the antlion relocated or did not relocate and constructed a pit or did not construct a pit). Thus, we had to adopt a statistical method that allowed analyzing contingency tables or frequencies of occurrence. Specifically, we used loglinear models (Sokal and Rohlf 1995, p 743) to test for differences in the effects of predator presence, predator type, and sand depth on the proportion of relocating antlion larvae between the two antlion species. This same approach was used to analyze the proportion of *M. hyalinus* that constructed a pit. Only biologically meaningful interaction terms (i.e., interaction terms which include the response variable – relocation or pit construction events) were considered in the models. Relocation distance is a continuous response variable and we, thus, used a fully factorial analysis of variance (ANOVA) (Sokal and Rohlf 1995, p 369) to test for the effect of predator presence and sand depth on relocation distance between the two antlion species. Predator type was not included in this analysis because in some treatments, antlion larvae did not relocate at all, and consequently, there was not enough power to test for such an effect. Relocation distances were log-transformed because they were not normally distributed. We used a model selection procedure (AIC) to choose the model that best explains our data, both

for the loglinear tests and ANOVA (Caswell 2001, p 332; Johnson and Omland 2004). All statistical procedures were executed using SYSTAT v 11 (SYSTAT Software Inc. San Jose, CA, USA).

Results

The sit-and-wait *M. hyalinus* responded mainly to the habitat structure by reducing its activity in deep sand. The sit-and-pursue *L. fedtschenkoi*, on the contrary, showed a more complex response and was affected by predator presence, predator type, and habitat structure. Both antlion species decreased their activity when exposed to predators. The proportion of individual *L. fedtschenkoi* that relocated was smaller, and their relocation distances were reduced, while a smaller proportion of *M. hyalinus* constructed pits.

The proportion of relocating antlions

The two antlion species responded differently to both sand and predator treatments, as reflected in the proportion of relocating antlions (Fig. 1; the four-way interaction term, antlion species \times sand depth \times predator type \times relocation

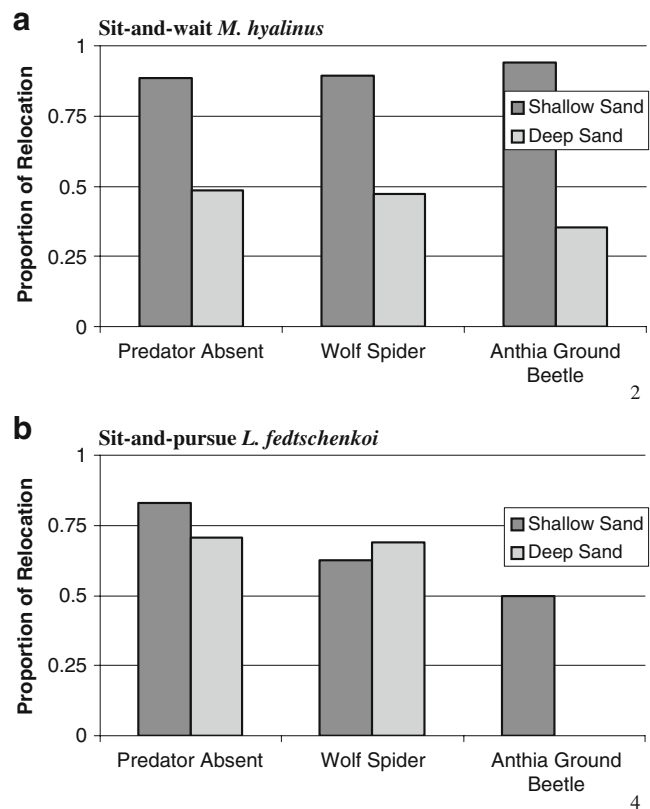


Fig. 1 The proportion of relocating *M. hyalinus* (a) and *L. fedtschenkoi* (b) in response to the sand depth (deep and shallow sand) and the predator treatment (predator absent, active predatory beetle or sit-and-pursue wolf spider present)

Table 1 A loglinear model testing for the effects of antlion species, sand depth, predator presence, and predator type on the proportion of antlions that relocated

Model number	Model components	LR χ^2	df	P-Value	AIC	ΔAIC
1	Anl \times Snd \times Prd, Anl \times Prd, Anl \times Snd, Snd \times Prd, Anl, Snd, Prd	4.072	7	0.7714	-9.928	2.575
2	Anl \times Snd \times Prd, Anl \times Prd, Anl \times Snd, Anl, Snd, Prd	5.497	9	0.7890	-12.503	0
3	Anl \times Snd \times Prd, Anl \times Prd, Anl \times Snd, Snd, Prd	8.187	10	0.6106	-11.813	0.690
4	Anl \times Snd \times Prd, Anl \times Snd, Snd, Prd	12.236	12	0.4269	-11.764	0.739
5	Anl \times Snd \times Prd, Snd, Prd	21.566	13	0.0625	-4.435	8.068
6	Anl \times Prd, Anl \times Snd, Snd \times Prd, Anl, Snd, Prd	11.804	9	0.2246	-6.196	6.306
7	Anl \times Prd, Anl \times Snd, Anl, Snd, Prd	16.071	11	0.1385	-5.929	6.574

The best fitted model was selected using the AIC. The best model was scored as 0 and the rest are scaled in ascending manner. Model #2 fits the data best, but models #3 and #4 should also be considered. Non-biologically meaningful interaction terms (i.e., those not involving the proportion of relocating antlions) were omitted from all the models. Note that main effects are included in all seven models and all model components presented in the table are associated with the response variable—relocation. For instance, Anl \times Prd is actually Anl \times Prd \times Relocation
Anl Antlion species, *Snd* sand depth, *Prd* predator presence and predator type

was included in the best model; Table 1). Because the two species differed in their response to the experimental manipulations, we next had to examine the response of each species separately (Table 2). In sit-and-wait *M. hyalinus*, the single important factor was sand depth: *M. hyalinus* relocated less in deep sand. In sit-and-pursue *L. fedtschenkoi*, the picture was more complicated. The response of the antlions to the predator was influenced by both sand depth and predator type (the triplet interaction term sand depth \times predator type \times relocation was included in the best model; Table 2). Specifically, the proportion of relocating individual *L. fedtschenkoi* in shallow sand was consistent between the two predator types; however, in deeper sand, when a refuge existed, more than 70% of the antlions facing the sit-and-pursue wolf spider relocated compared with none exposed to the active predatory beetle (Fig. 1).

Relocation distance

Sand depth had a negative effect on relocation distance, which was consistent between the two antlion species

(Fig. 2; the interaction terms involving antlion species were not included in the best model; Table 3). However, this response (i.e., an increase in sand depth associated with a decrease in movement distances) was stronger in the presence of a predator (a significant sand depth \times predator type interaction term; see also Fig. 2). A closer look in Fig. 2 and the second best model (Table 3; third row) suggest that some differences, nevertheless, exist between the two antlion species and that the two antlion species should be analyzed separately. In both species, there was a negative effect of sand depth on relocation distance (*M. hyalinus* $F_{1,92}=30.315$, $P<0.001$; *L. fedtschenkoi* $F_{1,79}=18.347$, $P<0.001$). Regarding the effect of predator presence, in *L. fedtschenkoi*, we could not detect a significant effect on relocation distance ($F=0.7$, $P_{1,79}=0.15$). In contrast, the presence of the predator caused a decrease in the relocation distance of *M. hyalinus* mainly in deep sand (a significant predator presence \times sand depth interaction term, $F_{1,92}=7.714$, $P=0.007$). We interpret this to mean that the two antlion species indeed responded differently to distinct combinations of sand depth and predator presence (as can be seen in Fig. 2; compare the difference in

Table 2 A loglinear model testing for the effect of sand depth, predator presence, and predator type on the proportion of individual *M. hyalinus* and *L. fedtschenkoi* that relocated

	Model number	Model components	LR χ^2	df	P-Value	AIC	ΔAIC
<i>M. hyalinus</i>	1	Snd \times Prd, Snd, Prd	0.1649	2	0.9209	-3.8351	6.8317
	2	Snd \times Prd, Snd	0.2136	4	0.9947	-7.7864	2.8804
	3	Snd	1.3332	6	0.9698	-10.667	0
<i>L. fedtschenkoi</i>	1	Snd \times Prd, Snd, Prd	0.1861	2	0.9111	-3.8139	0.0752
	2	Snd \times Prd, Prd	2.1109	3	0.5497	-3.8891	0
	3	Prd	17.1493	5	0.00423	7.1493	11.038

The best fitted model was selected using the AIC. Factors are indexed as in Table 1: Sand depth (*Snd*), predator presence and predator type (*Prd*), and the proportion of antlions that relocated. In *M. hyalinus*, model #3 fits the data best; in *L. fedtschenkoi*, model #2. Non-biologically meaningful interaction terms (i.e., those not involving the proportion of relocating antlions) were omitted from all the models. Note that main effects are included in all models and all model components presented in the table are associated with the response variable—relocation. For instance, Snd \times Prd is actually Snd \times Prd \times Relocation

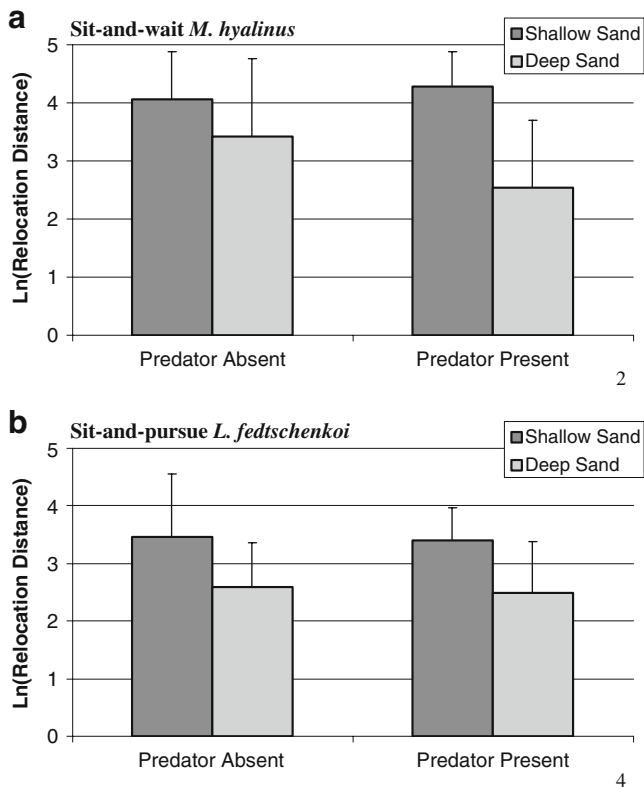


Fig. 2 The natural logarithm of the relocation distances of *M. hyalinus* (a) and *L. fedtschenkoi* (b) in response to the sand depth and predator presence (mean \pm 1 SD)

relocation distance over deep sand in the presence and absence of predator between the two antlion species).

The proportion of pit construction

Predator presence had a negative effect on the proportion of individual *M. hyalinus* that constructed pits (Fig. 3; the interaction term predator type \times pit construction was included in the best model; Table 4), but this decrease was sharper when the larvae were exposed to the active predatory beetle (Fig. 3). Antlions built slightly less pits in

deep sand compared to shallow sand across predator treatments (Fig. 3). However, this effect of sand depth should be considered with caution, because the rank of the second best model, which did not point on a sand depth effect, was close to the best model (Table 4).

Discussion

An individual prey usually reduces activity in response to the presence of predators, thus, balancing the benefits of foraging against costs, including the risk of predation (Brown 1988; Lima 1998a; Brown and Kotler 2004). We showed here that this response is context dependent, and we suggest that it changes as a function of the relationship between the predator and prey foraging modes and habitat structure, which constrains the ability of the prey to evade predators (shallow sand in this case). Clearly, in addition to their distinct foraging mode, our studied species differ in many other organismal traits. Therefore, the observed differences between the two antlion species might have been related to some additional differences which we abstracted. However, based on our understanding of the system, the foraging mode is an important behavioral difference between the two studied antlion species and is usually correlated with many additional traits (Huey and Pianka 1981). Furthermore, most of the results were consistent with our predictions and with the life history of the two antlion species.

The response to microhabitat structure, predator presence, and predator type was not consistent between the two antlion species. We suggest that these differences originate from the dissimilarity in the antlion foraging modes. The proportion of the sit-and-wait *M. hyalinus* larvae that relocated was affected exclusively by sand depth (they tended to relocate more in shallow sand), while the larvae of the sit-and-pursue *L. fedtschenkoi* were influenced by sand depth, predator presence, and the interaction between

Table 3 ANOVA testing for the effect of antlion species, sand depth, and predator presence on the distances moved while relocating

Model number	Model component	Number (N)	Parameters	RSS	AIC	ΔAIC
1	Main effects and all interactions	179	8	139.68	-3.284	4.180
2	Main effects; <i>Anl</i> \times <i>Snd</i> \times <i>Prd</i> , <i>Anl</i> \times <i>Snd</i> and <i>Snd</i> \times <i>Prd</i> interactions	179	7	140.32	-4.926	2.538
3	Main effects; <i>Anl</i> \times <i>Snd</i> \times <i>Prd</i> and <i>Snd</i> \times <i>Prd</i> interactions	179	6	141.09	-6.501	0.963
4	Main effects; <i>Snd</i> \times <i>Prd</i> interaction	179	5	142.98	-7.464	0
5	Main effects; <i>Anl</i> \times <i>Snd</i> and <i>Snd</i> \times <i>Prd</i> interactions	179	5	142.566	-5.692	1.772

The best fitted model was selected using the AIC. The best model was scored as zero and the rest are scaled in ascending manner. Model #4 fits the data best. Model #3 should also be considered

Anl Antlion species, *Snd* sand depth, *Prd* predator presence



Fig. 3 The proportion of *M. hyalinus* that constructed a pit in relation to sand depth and predator treatment (predator absent, active predatory beetle or sit-and-pursue wolf spider present)

these factors, thus demonstrating a more sophisticated behavior (Fig. 1; Table 2). Specifically, predator presence, and mainly the active predatory beetle, had a negative effect on the proportion of relocating *L. fedtschenkoi* larvae. Sand depth only slightly affected the proportion of relocating individual *L. fedtschenkoi* when the predator was absent or when the sit-and-pursue spider predator was present but when combining the active predator with deep sand, there were no relocation events at all. We suggest that *L. fedtschenkoi* is exposed to predation to a larger extent as a consequence of its more active foraging mode. In other words, because it covers a larger area, it has a higher chance of encountering a predator. Therefore, it should be more sensitive to predator activity and may also be more successful in quantifying the risk imposed by each type of potential predator. Furthermore, when *L. fedtschenkoi* larvae are exposed to an active predator, which covers a large area, and when a potential refuge (i.e., deep sand) exists, the best response would be to change their behavior and use this refuge; otherwise, if a refuge does not exist, there should be little or no change in activity. This pattern

(i.e., decrease in activity only when a refuge exists) was also reported in other taxa (e.g., Sih and Kats 1991; Lima 1998a). *M. hyalinus* generally relocated less and its predator avoidance behavior was solely related to the habitat structure. Previous studies suggest that pit-building antlions strongly depend on physical and microclimatological factors when choosing the preferred microhabitat (see Scharf and Ovadia 2006 for a review), and this study reinforces that conclusion from an additional aspect (i.e., the response to predation threat). It would be interesting in future research to design an experimental system which enables changes in the vertical locations of larvae in the sand to be followed to better demonstrate its possible usage as a shelter.

In the presence of predators, there was a significant decrease in the relocation distances of larvae of both antlion species (Fig. 2). Both antlion species decreased relocation distances in deep sand (suggesting again that deep sand provides some kind of a refuge), but predator presence had an effect only on *M. hyalinus* (Fig. 2). Because only relocating individuals were taken into consideration in this analysis, we suggest that *M. hyalinus* responded to the predator presence and type by changing relocation distances (i.e., moved shorter distances), whereas *L. fedtschenkoi* used a more extreme behavior: it either relocated or not, without changing its relocation distances.

A comparison of the pit construction behavior of *M. hyalinus* under different conditions showed that predator presence, predator type, and sand depth affected the proportion of pit construction (Fig. 3, Table 4). The effect of the predator was most prominent when comparing the active predator with the two other alternatives (predator absent and sit-and-pursue predator). When exposed to the active predator, *M. hyalinus* larvae constructed fewer pits. This observation is in accord with our prediction, and it is possible that an active predator, which covers a large area, interferes with the process of pit construction. It is also

Table 4 A loglinear model testing for the effect of sand depth, predator presence, and predator type on the proportion of antlions that constructed a pit

Model number	Model components	LR χ^2	df	P value	AIC	ΔAIC
1	Snd \times Prd, Snd	24.5468	4	<0.0001	16.547	20.802
2	Snd \times Prd, Prd	4.6226	3	0.2016	-1.377	2.878
3	Snd, Prd	3.7449	4	0.4416	-4.255	0
4	Prd	6.6661	5	0.2467	-3.334	0.921
5	Snd	40.2699	6	<0.0001	28.270	32.525

The best fitted model was selected using the AIC. The best model was scored as zero and the rest are scaled in ascending manner. Model #3 fits the data best, but model #4 should also be considered. Non-biologically meaningful interaction terms (i.e., those not involving the proportion of antlions that constructed a pit) were omitted from all the models. Note that main effects are included in all five models and all model components presented in the table are associated with the response variable—Pit construction. For instance, Snd \times Prd is actually Snd \times Prd \times Pit construction. Snd Sand depth, Prd predator presence and predator type

possible that the process of pit construction exposes the larvae to active predators, which visually detect their prey or can cover a larger area when searching for prey, in contrast to more sedentary predators with a smaller detection range owing to their limited searching area (Huey and Pianka 1981). There was also a difference in the frequency of pit construction as a function of sand depth: in deep sand, *M. hyalinus* larvae constructed fewer pits. This trend is counterintuitive, and we can only suggest an explanation. The shallow sand is perceived by *M. hyalinus* larvae as a dangerous habitat. It is possible that pit construction is used in this case to reduce the risk (pulling out an antlion from the sand is harder when a pit exists). This suggestion remains to be tested.

This study exemplifies how two similar antlion species, differing mainly in their foraging mode, respond differently to predators with distinct foraging modes and to microhabitat structure. It also shows that the interaction between microhabitat structure and predation risk is not trivial and differs between the two species (e.g., when exposed to sit-and-pursue predator, *L. fedtschenkoi* relocates more in deep sand than in shallow sand but the opposite pattern occurs when the predator is absent). Both antlion species are shown to reduce activity in the presence of predators. This activity reduction is prominent in the proportion of *L. fedtschenkoi* that relocated (Fig. 1) and in the proportion of pit construction of *M. hyalinus* (Fig. 3). This reduction in activity surely results in fewer captures of prey. Pit-building antlions that do not construct pits catch significantly fewer prey items (Griffiths 1992; Scharf and Ovadia 2006) and sit-and-pursue predators that remain inactive surely reduce their encounter rate with prey. We expected that the sit-and-pursue predator would pose a greater threat to *L. fedtschenkoi* than *M. hyalinus*. A support for this prediction is prominent in the relocation proportion of each species as a function of predator type in shallow sand (Fig. 1). *M. hyalinus* responded only to sand depth but *L. fedtschenkoi* showed a reduction in activity when a sit-and-pursue predator was present compared to the no predator treatment. In conclusion, predators have significant nonlethal effects on prey, in addition to numerical responses (almost no antlions were caught by the predators in our experiment). A next logical step should be combining the two predators in one enclosure and measuring the antlion response; it is possible that antlions would respond differently to this combination than to each predator separately (Sih et al. 1998). Furthermore, it would be also enriching to test whether long-term exposure to predation risk affects life history traits of these two antlion species and whether some compensation for reduced hunting success exists (e.g., better exploitation of each prey item caught).

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