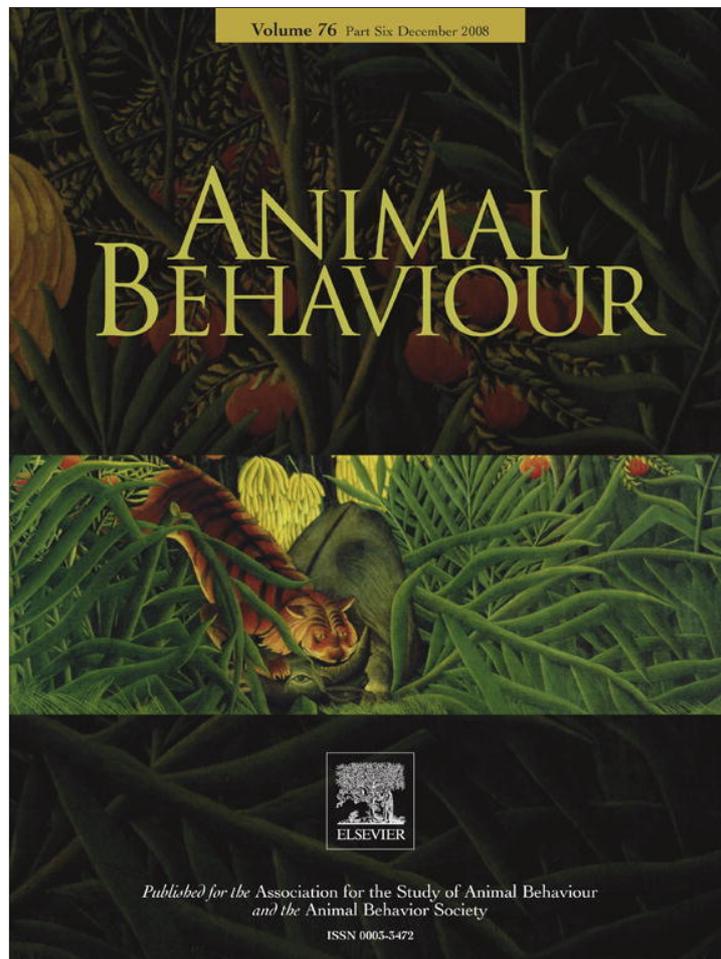


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Foraging behaviour and habitat selection in pit-building antlion larvae in constant light or dark conditions

INON SCHARF, AZIZ SUBACH & OFER OVADIA

Department of Life Sciences, Ben-Gurion University of the Negev

(Received 7 May 2008; initial acceptance 22 July 2008;
final acceptance 14 August 2008; published online 15 October 2008; MS. number: 08-00289R)

Pit-building antlion larvae are small sit-and-wait arthropod predators that dig conical pits in sandy soils. We investigated the effect of exposure to constant light versus constant dark conditions on antlion behaviour. Antlions tended to relocate less often, construct pits more frequently and construct larger pits in constant light. We interpret this as an indication of dichotomous behaviour under light versus dark conditions such that antlion larvae hunt during the day and modify their positions at night. Antlion larvae immediately responded to the complete switch in this illumination treatment and adapted their behaviour to fit the new conditions. Prey capture success did not differ between the constant light and constant dark conditions. When provided with a choice between light and dark conditions, the vast majority of larvae preferred the former. Those that preferred constant dark, however, were on average larger than those that preferred constant light. We thus suggest that since larger antlion larvae possess larger fat reserves, they can afford reductions in foraging activity (possibly to increase safety). An examination of the antlion trade-off between their preference for light and their preference for sand depth (which may affect their ability to evade predators) showed that their response to illumination was much more prominent, irrespective of the sand depth. Finally, combining light with other factors such as temperature and density may further elucidate microhabitat selection in pit-building antlion larvae.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.

Keywords: antlion larvae; habitat selection; movement; *Myrmeleon hyalinus*; Myrmeleontidae; photoperiod; sit-and-wait predator

The majority of animals are significantly influenced by photoperiod. It can directly affect the intensity and duration of crucial behavioural activities, such as foraging (e.g. De Block & Stoks 2003), reproduction and oviposition (e.g. Omkar & Pathak 2006; Homeny & Juliano 2007), and can also indirectly affect life history decisions, such as the induction of diapause in insects (Danilevskii 1965, page 40; Speight et al. 1999, page 30). For life history events, photoperiod is considered a more reliable predictive signal than other exogenous factors such as temperature (Bradshaw & Holzapfel 2007).

Photoperiod can affect behaviour through a number of mechanisms. An animal's innate capabilities dictate its preference to be active either during the day (diurnal) or

during the night (nocturnal; e.g. Tobler et al. 1998). Hence, animals can benefit by reducing activity when their predators are active (e.g. Lima 1998; Lang et al. 2006). For instance, nocturnal gerbils, *Gerbillus andersoni allenbyi*, reduce their activity on full-moon nights owing to their increased chances of being preyed upon by nocturnal predators, such as barn owls, *Tyto alba* (Kotler et al. 1984). On the other hand, since photoperiod can change the activity of potential prey, predators should adjust the timing of their foraging behaviours to match those of their prey more closely (e.g. Van Laerhoven et al. 2003; Sabato et al. 2006).

In addition to its effects on foraging activity, photoperiod can play a dominant role in habitat selection by animals across taxa (e.g. Baker & Ball 1995; Belmain et al. 2000; Drolet et al. 2004). For example, an ophiuroid species has been shown to select microhabitats with reduced light and possible shelter (Drolet et al. 2004). It is probable that such

Correspondence: I. Scharf, Department of Life Sciences, Ben-Gurion University of the Negev, POB 653, Beer-Sheva 84105, Israel (email: schari@bgu.ac.il).

decisions are similarly related to improved foraging success or to the increased probability of escaping predators.

As noted above, photoperiod is an important trigger for many life history events, one of the most common examples being the onset of diapause in insects as daylength decreases (e.g. Speight et al. 1999, page 30; Bradshaw & Holzapfel 2007). In addition, many other aspects of life history are affected by photoperiod. For instance, final mass before metamorphosis is reduced and the duration of the larval period in insects is shortened in response to a decrease in daylength (e.g. De Block & Stoks 2003; Homeny & Juliano 2007; but see Gotthard 2004 for a more complex response when temperature is also involved).

The dependence of sit-and-wait predators, such as pit-building antlion larvae and web-building spiders, on their immediate surroundings for successful hunting means that exogenous factors largely dictate crucial behaviours, such as foraging and habitat selection (Herberstein & Fleisch 2003; Scharf & Ovadia 2006). For example, antlion larvae prefer to construct their pits in sand with small grains (Farji-Brener 2003; Devetak et al. 2005), in which pits can be larger and thus prey is caught more efficiently (Botz et al. 2003). Both ovipositing females and larvae can select their habitat (Farji-Brener 2003; Matsura et al. 2005). Habitat selection by the former, which is especially important in species that do not often relocate (Matsura et al. 2005), has rarely been investigated (Scharf & Ovadia 2006).

Some antlion species prefer shaded microhabitats to those exposed to direct sunlight when constructing their pits (Topoff 1977; Scharf et al. 2008); however, it is not clear whether this preference is based on thermoregulation (i.e. the sand heats up when exposed to the sun) or other unknown factors. Moreover, little is known about how the trade-offs between different microhabitat characteristics, such as shade and sand grain size, affect antlion larvae during habitat selection.

We used larvae of the pit-building antlion *Myrmeleon hyalinus* (Neuroptera: Myrmeleontidae) to study the effects of constant light versus constant dark conditions on foraging success and activity, as reflected in antlion larvae relocation events and the frequency of pit construction. We chose complete photoperiod manipulation to evaluate the full effect of light on antlion behaviour because any effects would probably be weaker with milder photoperiod manipulations. Furthermore, Youthed & Moran (1969a) have shown that antlions construct larger pits in summer than in winter, yet it is not clear whether this pattern resulted from differences in temperature or photoperiod between the two seasons. Our experimental design enabled us to disentangle the effect of light from that of temperature. Specifically, we predicted that constant light should result in larger pits and a lower pit relocation rate (i.e. light acts as a trigger for hunting). As for the ultimate reason, we suggest that the diurnal hunting behaviour of antlions may be related to when their prey are active, and may serve to improve the correlation between the antlion's and its prey's activity schedules. Antlion larvae have thermal responses similar to those of their prey (Marsh 1987), and it is plausible that the same is true when considering light (and not temperature).

In addition, we performed microhabitat selection experiments, which tested whether antlion larvae actively preferred constant light to constant dark conditions when both microhabitats were held at the same constant temperature. Another important characteristic of the habitat antlion larvae inhabit, sand depth (Loria et al. 2008), may strongly affect the ability of the larvae to evade predators, which can hunt them mainly on or close to the sand surface (Loria et al. 2008). A fully factorial experiment combining both illumination and sand depth treatments tested how the trade-offs between different microhabitat characteristics influenced microhabitat selection in *M. hyalinus* larvae. We predicted that antlion larvae would eventually be located in the constant light microhabitat, based on our prediction that exposure to light will reduce pit relocation (thus, under dark conditions they will relocate until they reach the illuminated area, and then will reduce movement and construct pits). Finally, we provided flour beetle larvae as prey items for antlions experiencing light and dark conditions. We predicted that capture success would be higher under light conditions, based on the assumption that pits will then be larger and more abundant.

METHODS

Study Site and Study Species

Populations of the same species may show different pit maintenance behaviours (Arnett & Gotelli 2001). To minimize such genetic effects on pit construction and maintenance, we collected *M. hyalinus* larvae under several different tamarisk trees (to reduce relatedness) located in Nahal Secher (31°06'N, 34°49'E), that is, from 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, semistabilized sand and stabilized sand. The sand used in all experiments was also brought from Nahal Secher, the habitat of origin. We did not manipulate sand grain size, but we did remove large particulate matter such as leaves and seeds. In all experiments sand composition was identical and the same antlions were used. To avoid data dependency, they were randomly assigned to treatments prior to each experiment.

Myrmeleon hyalinus is the most abundant pit-building antlion in Israel. The larva attains a maximal length of about 10 mm (Simon 1988). Similar to other sit-and-wait predators, antlion larvae are generalist predators that capture small arthropods that fall into their pits (Simon 1988). The larvae develop through three instar stages (the larval phase may last up to a year; Scharf et al., in press), enter pupation, and then short-lived, weak-flying adults emerge. Under laboratory conditions the pupal stage lasts about a month, after which the adults that emerge live about a week (Scharf et al., in press). Adults usually mate and oviposit between May and September (Simon 1988). The larvae are capable of inhabiting different types of soils (Simon 1988). They are found in shaded

experiment. A single antlion was placed in the middle of each tray. Larvae and pit positions were recorded 1 and 5 days after stocking. To formulate the relationship between the antlion's preferred location and its body mass while avoiding pseudoreplication, we separately analysed data from the first and fifth days using logistic regression.

Next, we examined the responses of 112 antlion larvae to the combined effect of both illumination and sand depth treatments. Using a partial horizontal partition buried in the sand, we created two equal-sized microhabitats: shallow sand (1 cm) and deep sand (3 cm). A single antlion larva was placed in the centre of each tray and randomly assigned to one of the following four treatments: (1) the entire tray exposed to constant light; (2) the entire tray exposed to constant dark; (3) constant light over shallow sand/constant dark over deep sand; (4) constant light over deep sand/constant dark over shallow sand (Fig. 1b, c). We recorded the antlion's position (shallow or deep sand) and the proportion of antlions constructing pits 1 and 5 days after stocking. Data analysis began with chi-square tests to determine whether frequencies of microhabitat choice, within each treatment and during each of the two repeated measurements, differed significantly from the null expectation of equal frequencies. Next, we used log-linear models to test for differences between the first and second treatments where the entire tray was exposed to either constant light or constant dark. In this case, significant results should indicate differences in the preference for shallow or deep sand, which were also affected by light, while nonsignificant results should show that the effect of sand depth was consistent between the two illumination treatments. Similarly, we used log-linear models to compare the responses of the antlion larvae to the combined effect of illumination and sand depth between the third and fourth treatments, where selection for both microhabitat characteristics was allowed. In this case, significant results should indicate that light had a stronger effect than sand depth while nonsignificant results should demonstrate the opposite. The proportion of antlions constructing pits was analysed similarly.

RESULTS

When comparing the behaviour of antlion larvae exposed to constant light with those under constant dark conditions, we found three trends: light decreased the tendency of the larvae to relocate, but it also increased their tendency to construct pits, which were larger than those constructed under constant dark conditions. A logistic regression indicated that there was also a strong significant increase, consistent over time, in their tendency to relocate in the constant dark treatment (day 1: $P = 0.001$, odds ratio = 0.001; day 5: $P < 0.0001$, odds ratio = 0.080; Fig. 2a). Similarly, the proportion of pits constructed was higher among larvae exposed to constant light conditions (day 1: $P = 0.0001$, odds ratio = 5.903; day 5: $P < 0.0001$, odds ratio = 14.040; Fig. 2a). On day 1, the tendency of the larvae to relocate was negatively correlated with body size ($P = 0.047$, odds ratio = 0.967). Additionally, the interaction term, illumination treatment*body mass,

was significant ($P = 0.022$, odds ratio = 1.043), indicating that the decreased relocation tendency observed among larger larvae was stronger under constant dark conditions. Neither trend was significant on day 5 (mass: $P = 0.479$; interaction term: $P = 0.260$).

On both days, we could not detect a significant effect of body mass on the tendency to construct pits nor was there a significant illumination treatment*body mass interaction (day 1: body mass: $P = 0.191$; interaction term: $P = 0.333$; day 5: body mass: $P = 0.134$; interaction term: $P = 0.594$). Pit diameter was positively correlated with larval body mass ($r = 0.544$, $\chi^2_1 = 55.15$, $P < 0.001$). To control for this effect, we performed a repeated measures ANCOVA with body mass as a covariate. Our analysis indicated that pits constructed under constant light were larger than those constructed under constant dark conditions, but this pattern diminished over time (a significant time*treatment interaction term: $F_{1,61} = 7.707$, $P = 0.007$; Fig. 2b).

The same behavioural response was also evident after switching the illumination treatment between the two experimental groups. Relocation was more frequent under constant dark conditions (day 1: $P = 0.003$, odds ratio = 0.0005; day 5: $P < 0.0001$, odds ratio = 0.024; Fig. 3a), and it was consistent over time. The frequency of pit construction was lower among antlion larvae under constant dark conditions (day 1: $P = 0.004$, odds ratio = 1.030; day 5: $P < 0.0001$, odds ratio = 7.701; Fig. 3a), and it was qualitatively consistent over time. On day 1, relocation was

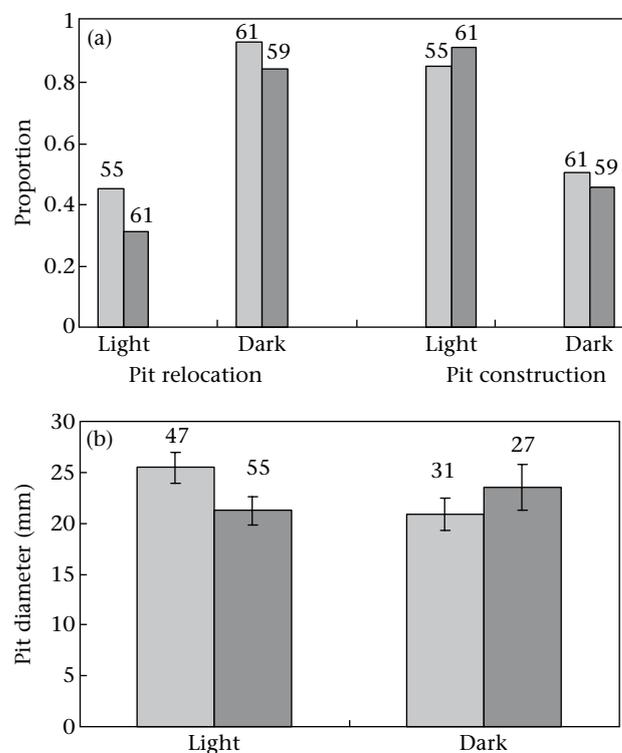


Figure 2. (a) The proportion of antlion larvae relocating and constructing pits and (b) pit diameter under constant light and dark conditions 1 day (lighter columns) and 5 days (darker columns) after stocking. Error bars and numbers above columns represent 1 SE and sample size, respectively.

negatively correlated with larval body mass, and there was an almost significant illumination treatment*body mass interaction ($P = 0.080$, odds ratio = 0.967 and $P = 0.054$, odds ratio = 1.049 for body mass and the interaction term, respectively), indicating that the decreased relocation tendency observed among larger antlion larvae was stronger under constant dark conditions. Neither trend was significant on day 5 (mass: $P = 0.213$; interaction term: $P = 0.798$).

On day 1, larval body mass was positively correlated with the tendency to construct pits, and there was a significant illumination treatment*body mass interaction (mass: $P = 0.004$, odds ratio = 1.030; interaction term: $P = 0.053$, odds ratio = 0.974), implying that the increased tendency to construct pits observed among larger larvae was stronger under constant dark conditions. However, neither of these two trends was significant on day 5 (mass: $P = 0.487$; interaction term: $P = 0.382$).

Pit diameter was positively correlated with larval body mass ($r = 0.602$, $\chi^2_1 = 64.64$, $P < 0.001$). Using a repeated measures ANCOVA with body mass as a covariate, we found that pit diameter was significantly smaller among antlion larvae under constant dark than those exposed to constant light conditions ($F_{1,52} = 6.371$, $P = 0.015$; Fig. 3b). This pattern did not change significantly over time (nonsignificant time*treatment interaction: $F_{1,52} = 0.084$, $P = 0.772$).

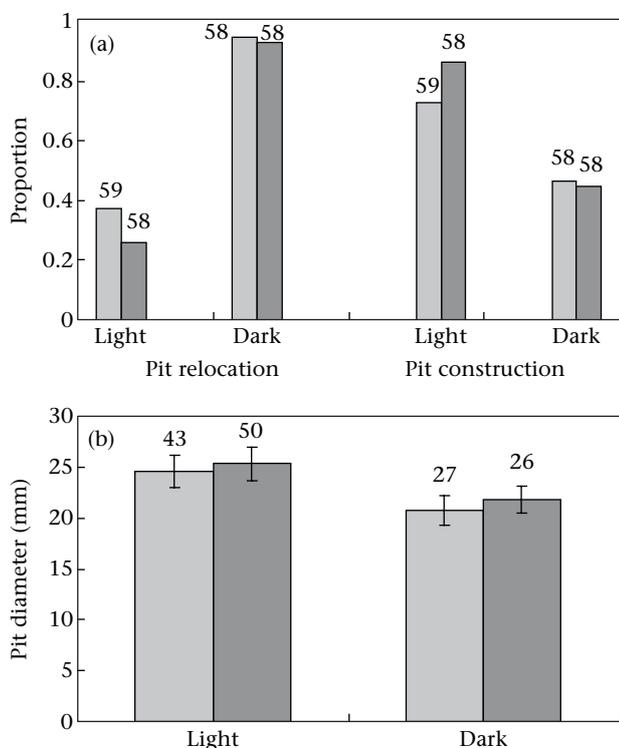


Figure 3. (a) The proportion of antlion larvae relocating and constructing pits and (b) pit diameter under constant light and dark conditions 1 day (lighter columns) and 5 days (darker columns) after stocking trays with the larvae and after changing illumination treatments (see Methods; first experiment). Error bars and numbers above columns represent 1 SE and sample size, respectively.

The success of the antlions in capturing prey did not differ between the constant light and constant dark treatments ($\chi^2_1 = 0.30$, $P = 0.86$). However, capture success was positively correlated with the body mass of the larvae (see below). When antlions were placed in pairs and fed with two prey items, the probability of both prey items being consumed was negatively correlated with the body mass of the smaller antlion larva within each pair (logistic regression: $P = 0.014$ for the mass and $P = 0.002$ for the constant). The odds ratio was 1.029, meaning that an increase of 0.1 mg in the body mass of the smaller antlion larva within each pair increased the probability that both prey items will be consumed by 2.85%.

In the microhabitat selection experiment, when we allowed the antlion larvae to select between either constant light or constant dark conditions, the majority chose the former (chi-square test for equal probabilities: $\chi^2_1 = 59.71$, $P < 0.0001$; Fig. 4a), and this preference did not change over time ($\chi^2_1 = 0.49$, $P = 0.48$). However, there was a negative correlation between the body mass of the larvae and their preference for constant light conditions, which slightly increased over time (day 1: mass: $P = 0.089$; constant: $P = 0.001$, day 5: mass: $P = 0.003$; constant: $P = 0.0005$). The odds ratio (for day 5) was 0.965, meaning that an increase of 0.1 mg in antlion body mass reduced the preference for the constant light microhabitat by 3.51%. The probability that a pit would be constructed was consistent between treatments and did not vary significantly over time or body masses (day 1: location: $P = 0.87$; mass: $P = 0.36$; constant: $P = 0.53$; day 5: location: $P = 0.98$; mass: $P = 0.13$; constant: $P = 0.98$).

The second and more complex microhabitat selection experiment (Fig. 1) revealed slightly more complicated results (Fig. 4b). As a first step, we tested whether antlion larvae were equally distributed between the shallow and deep sand microhabitats in each of the four illumination treatments. In all treatments except the second (constant dark over both shallow and deep sand) there was an unequal distribution of larvae between shallow and deep sand, which was consistent over time (Table 1). When allowed to select between the constant light and constant dark conditions, antlion larvae preferred the former irrespective of sand depth. When both the shallow and deep sand microhabitats were under constant dark conditions, antlion larvae showed no preference for either shallow or deep sand. However, when both were exposed to constant light conditions, they preferred the shallow to the deep sand microhabitat (Fig. 4b, Table 1).

A between-treatment-pair comparison of pit positions showed that pit positions were significantly different between the first (constant light over both shallow and deep sand) and second (constant dark over both shallow and deep) treatments (a significant treatment*position interaction term; Table 1). This pattern was consistent over time (neither interaction term, time*treatment*position and time*position, was significant; $\Delta G_1 = 0.10$, $P = 0.75$ and $\Delta G_1 = 0.07$, $P = 0.79$, respectively). Specifically, antlions exposed to constant dark conditions had no clear preference for either the shallow or the deep sand microhabitat, but when exposed to constant light

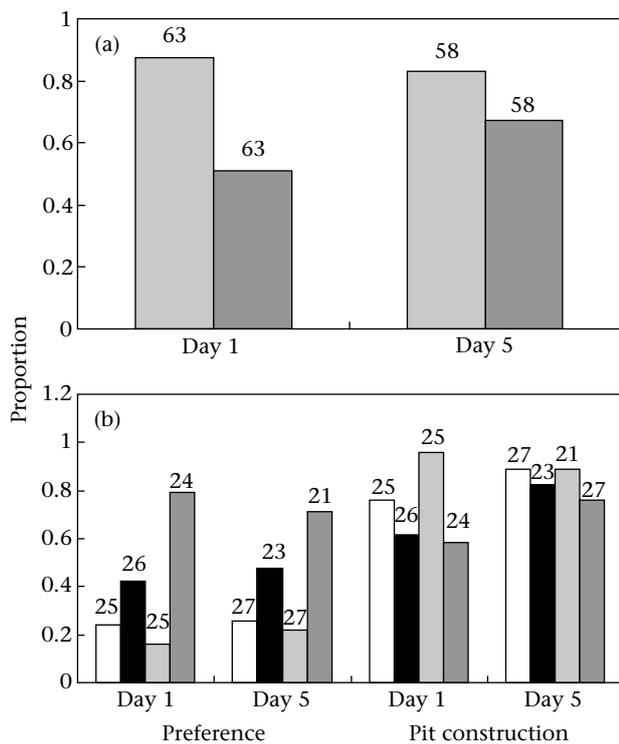


Figure 4. (a) Proportion of antlion larvae preferring constant light (lighter columns) and constructing pits (darker columns) 1 and 5 days after stocking in the simple microhabitat selection experiment. (b) Proportion of antlion larvae preferring deep sand and proportion constructing pits 1 and 5 days after stocking in the complex microhabitat selection experiment. Treatments include (bars from left to right): (1) the entire tray exposed to constant light (white columns); (2) the entire tray exposed to constant dark (black columns); (3) constant light over shallow sand/constant dark over deep sand (lighter columns); (4) constant light over deep sand/constant dark over shallow sand (darker columns). Numbers above columns represent sample size.

conditions, larvae showed a clear preference for the shallow sand. Similarly, pit positions were significantly different between the third (constant light over shallow sand) and fourth (constant light over deep sand) treatments (the interaction term illumination treatment*position was significant; Table 1), while there was no detectable effect of time (neither interaction term, time*treatment*position and time*position, was significant; $\Delta G_1 = 0.64$, $P = 0.42$ and $\Delta G_1 = 0.11$, $P = 0.74$, respectively). These results indicate that light is indeed the dominant factor influencing microhabitat selection in *M. hyalinus* larvae.

A between-treatment-pairs analysis of the proportion of pits constructed showed no detectable difference between the first (constant light over both shallow and deep sand) and second (constant dark over both shallow and deep) treatments (Table 1), meaning that the preference for deep or shallow sand was not affected by the illumination treatment. The only significant pattern was the positive effect of time (a significant time*pit interaction term: $\Delta G_1 = 4.43$, $P = 0.035$). In contrast, there was a significant difference between the third (constant light over shallow sand) and fourth (constant light over deep sand) treatments. In other words, constant light over shallow sand caused more antlions to construct pits than constant light over deep sand. This may indicate that antlions prefer building pits in shallow sand (a significant illumination treatment*pit interaction term; Table 1). There was no time effect (neither interaction term, time*treatment*pit and time*pit was significant; $\Delta G_1 = 0.69$, $P = 0.41$ and $\Delta G_1 = 0.35$, $P = 0.55$, respectively).

DISCUSSION

Light is an important exogenous factor that can strongly affect behaviour and life history (e.g. Danilevskii 1965; Tobler et al. 1998; Herberstein & Fleisch 2003; Bradshaw & Holzapfel 2007). In this study, we have shown that antlion larvae responded strongly to changes in light conditions, such that when exposed to constant light, their

Table 1. Results of the complex microhabitat selection experiment

	Treatment	Day	Test	P	Remarks
Distribution of larvae between shallow and deep sand*	1	1	6.76	0.009	Preference for shallow sand
	1	5	6.26	0.012	
	2	1	0.62	0.43	No preference
	2	5	0.04	0.83	
	3	1	11.56	0.001	Preference for light & shallow sand
	3	5	8.33	0.004	
	4	1	8.17	0.004	Preference for light & deep sand
4	5	3.86	0.05		
Difference in distribution between pairs of treatments†	1 & 2	1, 5	4.45	0.035	Light affects preferred position and sand depth
	3 & 4	1, 5	32.77	<0.0001	
Differences in proportion of pits constructed between pairs of treatments†	1 & 2	1, 5	1.72	0.190	No differences in proportion of pit construction
	3 & 4	1, 5	10.47	0.001	

The treatments were as follows: (1) the entire tray exposed to constant light; (2) the entire tray exposed to constant dark; (3) constant light over shallow sand/constant dark over deep sand; (4) constant light over deep sand/constant dark over shallow sand. Positions and pits were recorded after 1 and 5 days.

*Analysed with chi-square tests for equal probabilities.

†Analysed with log-linear models (ΔG_1).

tendency to relocate was lower, and they constructed pits, which were also larger than those constructed under constant dark conditions, at a higher rate. Furthermore, when offered a choice between constant light and constant dark conditions, the larvae almost always preferred the former, even when an additional factor was involved (i.e. sand depth in our experiment). As far as we know, this is the first study showing behavioural responses to light in pit-building antlion larvae (for the effect of light on life history, see Furunishi & Masaki 1983). Youthed & Moran (1969a) showed that pits constructed in summer are larger than those constructed in winter, but this effect cannot be related only to photoperiod or light, since temperature is also known to affect pit diameter and antlion activity (Youthed & Moran 1969b; Arnett & Gotelli 2001).

Our results suggest that antlion larvae prefer to hunt during the day and to relocate and improve their positions at night. However, the factors behind these behavioural differences are not known. It is possible that antlion larvae adjust the timing of their hunting activity to that of their prey, a common behavioural trait of numerous other predators (e.g. Sabato et al. 2006). A previous study supports such possible adaptation, since antlion larvae are known to adjust their thermal activity range to that of their potential prey (Marsh 1987). An alternative explanation may be related to antlion predators rather than to their potential prey. When relocating, antlion larvae are probably more vulnerable to predation (Gatti & Farji-Brener 2002; Scharf & Ovadia 2006), so they should avoid moving during the day when their potential predators (such as birds) are active. Other potential prey species behave similarly (e.g. Kotler et al. 1984; Lang et al. 2006). A previous study showed that antlion larvae are sensitive to the presence and activity of potential predators, and when exposed to predators they reduce relocation and pit construction activities (Loria et al. 2008). Therefore, it is also possible that since light is correlated with the presence of potential predators, antlion larvae avoid relocation when exposed to light. When the constant light treatment was replaced with constant dark conditions, antlion larvae responded immediately (as described above), and showed no traces of their behavioural responses to the former treatment, showing that the antlion's behavioural response to light is both flexible and easily induced. Such an experimental design (i.e. switching between treatments) may elucidate the issues of how much time animals need to adjust their behaviour to new surroundings, and of how memory and experience affect that behaviour.

Since antlion larvae showed distinctive behaviours under the two illumination treatments and since hunting success is positively correlated with pit size (Griffiths 1980; Scharf & Ovadia 2006), we expected that prey capture success would be higher under constant light conditions. Previous studies also indicated a positive correlation between activity in preferred light conditions and capture success (e.g. Van Laerhoven et al. 2003; Omark & Pathak 2006). However, we did not detect such a trend, finding rather that the capture success was similar across treatments. This surprising result suggests that antlion larvae without pits or with small pits could compete

equally well with those possessing large, fully constructed pits. Nevertheless, this statement should be treated with caution, since the prey we used is not the natural prey of antlions nor is it adapted to move efficiently on sand. Moreover, it is also possible that the flour beetle larvae travelled around the entire surface of the small tray, thus making it unnaturally easy for the antlion larvae to catch them.

We also found a correlation between antlion mass and the ability to catch prey, such that smaller larvae caught significantly fewer prey. It is likely that pit size affected capture success after all (based on the positive correlation between antlion mass and pit diameter), as was also reported in previous studies showing that larger antlion larvae can cope with a larger spectrum of prey sizes than smaller antlions (e.g. Youthed & Moran 1969a).

The microhabitat selection experiment shows once more that antlion larvae positions are not solely determined by the ovipositing female; rather, the larvae actively select preferred microhabitats, which in our case was the one exposed to constant light conditions. In previous studies of microhabitat selection, antlion larvae showed a preference for a specific sand particle size (Farji-Brener 2003; Devetak et al. 2005). Ovipositing females of *M. bore* show a similar preference (Matsura et al. 2005). However, this finding regarding adult behaviour is more relevant in species, such as *M. bore*, that rarely relocate. This is clearly not the case in our study species, *M. hyalinus* (e.g. Scharf et al. 2008; this study). Furthermore, our results indicate that larval body mass affected the choice between the two light treatment microhabitats (those choosing the constant dark side were larger). We suggest that such constant dark conditions may provide some shelter from diurnal predators (and it may explain the higher activity levels under dark conditions). However, it may also involve the usual trade-off between foraging and safety, in the form of a reduced chance to capture prey (Lima 1998). Larger antlion larvae may occupy the safer microhabitat while smaller ones must forage either because of smaller fat reserves or simply because they have to grow. A further study of the interplay between antlion size, its physical state and microhabitat preference may contribute to the understanding of state-dependent decisions in antlion larvae.

Based on the combined experiment examining light and sand depth preferences, we suggest that the larval preference for constant light conditions may be stronger than those involving sand type or depth. A preference for the shallow sand was expressed only when the whole experimental unit was exposed to constant light. Moreover, similar to a previous experiment (Loria et al. 2008), antlion larvae constructed pits in shallow sand more often than in deep sand. It is difficult to explain this counterintuitive preference for building pits in the shallow sand, because deeper sand enables the antlions to construct larger pits which in turn enable them to capture larger prey items. Again, it is possible that thermoregulation considerations are involved (i.e. faster warming after sunrise). Another possible explanation, which remains to be tested, is that the pit structure is more stable and is better supported by a hard surface beneath the sand. Therefore, a prey

falling into the pit constructed in shallow sand would cause less damage to the pit structure.

Previous studies that did not control for temperature showed that antlion larvae in general, and this species in particular, prefer shaded microhabitats to those exposed to direct sunlight (Topoff 1977; Scharf et al. 2008). However, we have shown that when temperature is being controlled, this preference is reversed, which may indicate that temperature is a stronger force than light in dictating pit location. Investigating the exact importance of each of these two exogenous factors for microhabitat selection requires manipulating both light and temperature independently of each other.

In summary, antlion larvae showed distinct behaviours under constant light and constant dark conditions. They moved more under constant dark but constructed more pits under constant light conditions. When given a choice, they preferred constant light conditions, although we could not show that there are differences in hunting success between the constant light and dark conditions. Future studies should investigate the connection between the preference for light and that for other suitable habitat characteristics, such as temperature and sand types, and expand the focus to examine the relationship between the preference for light and biotic factors, such as prey abundance and conspecific density.

Acknowledgments

The research was supported by Israel Science Foundation Grants 1084/05 and 1399/05 (to O.O.).

References

- Arnett, A. E. & Gotelli, N. J. 2001. Pit-building decisions of larval antlions: effects of larval age, temperature, food, and population source. *Journal of Insect Behavior*, **14**, 89–97.
- Baker, R. L. & Ball, S. L. 1995. Microhabitat selection by larval *Chironomus tentans* (Diptera: Chironomidae): effects of predators, food, cover and light. *Freshwater Biology*, **34**, 101–106.
- Belmain, S. R., Simmonds, M. S. J. & Blaney, W. M. 2000. Behavioral response of adult deathwatch beetles, *Xestobium rufovillosum* de Geer (Coleoptera: Anobiidae), to light and dark. *Journal of Insect Behavior*, **13**, 15–26.
- Botz, J. T., Loudon, C., Barger, J. B., Olafsen, J. S. & Steeples, D. W. 2003. Effects of slope and particle size on ant locomotion: implications for choice of substrate by antlions. *Journal of the Kansas Entomological Society*, **76**, 426–435.
- Bradshaw, W. E. & Holzapfel, C. M. 2007. Evolution of animal photoperiodism. *Annual Review of Ecology, Evolution & Systematics*, **38**, 1–25.
- Danilevskii, A. S. 1965. *Photoperiodism and Seasonal Development of Insects*. Edinburgh: Oliver & Boyd.
- De Block, M. & Stoks, R. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology*, **16**, 986–995.
- Devetak, D., Spornjak, A. & Janzekovic, F. 2005. Substrate particle size affects pit building decision and pit size in the antlion larvae *Euroleon nostra* (Neuroptera: Myrmeleontidae). *Physiological Entomology*, **30**, 158–163.
- Drolet, D., Himmelman, J. H. & Rochette, R. 2004. Effect of light and substratum complexity on microhabitat selection and activity of the ophiuroid *Ophiopholis aculeate*. *Journal of Experimental Marine Biology and Ecology*, **313**, 139–154.
- Farji-Brener, A. G. 2003. Microhabitat selection by antlion larvae, *Myrmeleon crudelis*: effect of soil particle size on pit-trap design and prey capture. *Journal of Insect Behavior*, **16**, 783–796.
- Furunishi, S. & Masaki, S. 1983. Photoperiodic control of development in the antlion *Hagenomyia micans* (Neuroptera: Myrmeleontidae). *Entomologia Generalis*, **9**, 51–62.
- Gatti, M. G. & Farji-Brener, A. G. 2002. Low density of ant lion larva (*Myrmeleon crudelis*) in ant-Acacia clearings: high predation risk or inadequate substrate? *Biotropica*, **34**, 458–462.
- Gotelli, N. J. 1993. Ant lion zones: causes of high-density predator aggregations. *Ecology*, **74**, 226–237.
- Gotthard, K. 2004. Growth strategies and optimal body size in temperate Pararginiid butterflies. *Integrative and Comparative Biology*, **44**, 471–479.
- Griffiths, D. 1980. The feeding biology of ant-lion larvae: prey capture, handling and utilization. *Journal of Animal Ecology*, **49**, 99–125.
- Herberstein, M. E. & Fleisch, A. F. 2003. Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). *Austral Ecology*, **28**, 622–628.
- Homeny, R. H. & Juliano, S. A. 2007. Developmental response to a seasonal time constraint: the effects of photoperiod on reproduction in the grasshopper *Romalea microptera*. *Ecological Entomology*, **32**, 559–566.
- Kotler, B. P., Ayal, Y. & Subach, A. 1984. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. *Oecologia*, **100**, 391–396.
- Lang, A. B., Kalko, E. K. V., Roemer, H., Blockholdt, C. & Dechmann, D. K. N. 2006. Activity levels of bats and katydid in relation to the lunar cycle. *Oecologia*, **146**, 659–666.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent development from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **77**, 215–290.
- Loria, R., Scharf, I., Subach, A. & Ovadia, O. 2008. The interplay between foraging mode, habitat structure and predator presence in antlions. *Behavioral Ecology and Sociobiology*, **62**, 1185–1192.
- Marsh, A. C. 1987. Thermal responses and temperature tolerance of a desert ant-lion larva. *Journal of Thermal Biology*, **12**, 295–300.
- Matsura, T., Yamaga, Y. & Itoh, M. 2005. Substrate selection for pit making and oviposition in an antlion, *Myrmeleon bore* Tjeder, in terms of sand particle size. *Entomological Science*, **8**, 347–353.
- Omkar & Pathak, S. 2006. Effects of different photoperiods and wavelengths of light on the life-history traits of an aphidophagous ladybird, *Coelophora saucia* (Mulsant). *Journal of Applied Entomology*, **130**, 45–50.
- Sabato, M. A. L., de Melo, L. F. B., Vaz Magni, E. M., Young, R. J. & Coelho, C. M. 2006. A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. *Behavioural Processes*, **73**, 228–230.
- Scharf, I. & Ovadia, O. 2006. Factors influencing site abandonment and site selection in a sit-and-wait predator: a review of pit-building antlion larvae. *Journal of Insect Behavior*, **19**, 197–218.
- Scharf, I., Hollender, Y., Subach, A. & Ovadia, O. 2008. Effect of spatial pattern and microhabitat on pit construction and relocation in *Myrmeleon hyalinus* (Neuroptera: Myrmeleontidae) larvae. *Ecological Entomology*, **33**, 337–345.
- Scharf, I., Filin, I., Ben-Yehoshua, D. & Ovadia, O. In press. Phenotypic plasticity and variation in morphological and life-history traits of antlion adults across a climatic gradient. *Zoology*.
- Simon, D. 1988. Ant-lions (Neuroptera: Myrmeleontidae) of the coastal plain: systematical, ecological, and zoogeographical aspects with emphasis on the coexistence of a species guild of the unstable dunes. Ph.D. thesis, Tel-Aviv University.

- Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. 3rd edn. New York: W. H. Freeman.
- Speight, M. R., Hunter, M. D. & Watt, A. D. 1999. *Ecology of Insects: Concepts and Applications*. Oxford: Oxford University Press.
- Tobler, I., Herrmann, M., Cooper, H. M., Negroni, J., Nevo, E. & Achermann, P. 1998. Rest-activity rhythm of the blind mole rat *Spalax ehrenbergi* under different lighting conditions. *Behavioural Brain Research*, **96**, 173–183.
- Topoff, H. 1977. The pit and the antlion. *Natural History*, **86**, 65–71.
- Van Laerhoven, S. L., Gillespie, D. R. & Roitberg, B. D. 2003. Diel activity pattern and predation rate of the generalist predator *Dicyphus hesperus*. *Entomologia Experimentalis et Applicata*, **107**, 149–154.
- Von Ende, C. N. 2001. Repeated-measures analysis. In: *Design and Analysis of Ecological Experiments*. 2nd edn (Ed. by S. M. Scheiner & J. Gurevitch), pp. 134–157. Oxford: Oxford University Press.
- Youthed, G. J. & Moran, V. C. 1969a. The lunar-day activity rhythm of Myrmeleontid larvae. *Journal of Insect Physiology*, **15**, 1259–1271.
- Youthed, G. J. & Moran, V. C. 1969b. Pit construction by Myrmeleontid larvae. *Journal of Insect Physiology*, **15**, 867–875.