



The involvement of sand disturbance, cannibalism and intra-guild predation in competitive interactions among pit-building antlion larvae

Erez D. Barkae*, Inon Scharf, Aziz Subach, Ofer Ovadia

Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel

ARTICLE INFO

Article history:

Received 14 January 2010

Received in revised form 17 March 2010

Accepted 21 May 2010

Keywords:

Competition experiment

Exploitation competition

Interference competition

Myrmeleontidae

Sit-and-wait predator

ABSTRACT

Competition in trap-building predators such as antlion larvae is a complex biotic interaction, potentially involving exploitation competition, sand throwing (i.e., interference competition), cannibalism and intra-guild predation. We investigated the short-term behavioral and developmental responses of the strict sit-and-wait antlion predator *Myrmeleon hyalinus* to sand disturbance (i.e., quantification of the impact of severe sand throwing), and to con- and hetero-specific competition by a larger sit-and-pursue antlion species *Lopezus fedtschenkoi*. We found that antlions subjected to sand disturbances reduced their pit construction activity and relocated less often. Furthermore, the reduction in pit construction activity was stronger among antlions subjected to disturbances prior to feeding. Almost no death occurred during the sand disturbance experiment, but as expected, disturbances caused reductions in the relative growth rates of antlions. This negative effect was stronger in the group exposed to sand disturbances prior to feeding. The presence of the sit-and-pursue competitor led to reductions both in pit construction and in relocation activities of *M. hyalinus*. Although the per-capita food supply was identical in both experiments, only 48% of *M. hyalinus* larvae survived the competition experiment, and this pattern was consistent between the con- and hetero-specific treatments. However, in the presence of hetero-specific competitors, the relative growth rate of surviving larvae was significantly lower than that measured in the presence of con-specific competitors. Our study demonstrates that investigating the different components of complex biotic interactions can markedly improve our understanding of how these different factors interact to influence the behavior and life history of organisms.

© 2010 Elsevier GmbH. All rights reserved.

1. Introduction

Competitors can interact indirectly via the depletion of shared limited resources (i.e., exploitation competition; Schoener, 1983), and simultaneously be engaged in direct negative interactions with each other, arising from territoriality, aggression, overgrowth, undercutting, allelopathy or even predation (i.e., interference competition; Schoener, 1983). One of the classical examples of such combined biotic interactions is intra-guild predation, i.e., the killing and eating of species that use similar resources and are thus potential competitors (Polis et al., 1989; Polis and Holt, 1992). An in-depth review by Polis et al. (1989) indicated that intra-guild predation is a common and often important interaction in a diverse array of communities including arachnids (Polis and McCormick, 1987), insect predators (Gotelli, 1997; Felix and Soares, 2004) and lizards (Adolph and Roughgarden, 1983). Intra-guild predation directly and indirectly influences the population size, stability and resilience of different species in the community, thus also hav-

ing important consequences on community structure and function (reviewed in Polis et al., 1989; Polis and Holt, 1992). This type of interaction intensifies as density increases, and is therefore often viewed as a mechanism for relaxing competition between potential competitors (Polis et al., 1989; Polis and Holt, 1992). Previous studies have illustrated that intra-guild predation is more likely to occur when the size differences between related species in the community are considerable, so that the smaller species or stage class falls within the normal prey size range of the larger species (Polis et al., 1989; Polis and Holt, 1992). This prediction also means that increased foraging activity will expose smaller individuals in particular to predation by larger con- or hetero-specific competitors (Polis et al., 1989). Indeed, small odonate larvae are consumed by larger con-specifics more often when they adopt an active rather than a sit-and-wait foraging mode (Johansson, 1993).

Ecologists have long recognized that investigating the different components of complex biotic interactions is crucial for the understanding of community dynamics (e.g., Polis and Holt, 1992; Schoener, 1993; Abrams et al., 1996; Schmitz et al., 2004). For example, Amarasekare (2002) developed an analytical model to investigate how exploitation and interference competition interact to influence community structure. According to this model, species

* Corresponding author. Tel.: +972 8 6461359; fax: +972 8 6472648.

E-mail address: barkae@bgu.ac.il (E.D. Barkae).

coexistence cannot occur under classical interference competition involving only costly interference mechanisms (e.g., territoriality, aggression, overgrowth, allelopathy), even if the species inferior at resource exploitation is superior at interference (Amarasekare, 2002). However, if the species involved in costly interference competition are also engaged in beneficial interference mechanisms (e.g., predation or parasitism), coexistence is possible via such a trade-off between exploitation and interference (Amarasekare, 2002).

Pit-building antlion larvae are an excellent model system for studying complex biotic interactions, since they often interact via exploitative competition (McClure, 1976; Simberloff et al., 1978; Matura and Takano, 1989; Griffiths, 1993), sand throwing (i.e., interference competition; Wilson, 1974; Linton et al., 1991), cannibalism (Griffiths, 1991, 1992) and intra-guild predation (Gotelli, 1997). Previous studies on antlions have illustrated that competition causes an increase in relocation rate (Griffiths, 1992; Day and Zalucki, 2000), decreases pit construction rate (McClure, 1976; Matura and Takano, 1989) and reduces pit size (Youthed and Moran, 1969; Griffiths, 1991; Day and Zalucki, 2000). Pits are extremely important for the effective capture of prey items (Mansell, 1988; Lucas, 1989; Griffiths, 1992; Devetak et al., 2005), and must conform to certain size (Wilson, 1974; Griffiths, 1980, 1986) and slope parameters to ensure efficient predation (Lucas, 1982). In addition to requiring increased metabolic expenditure (Lucas, 1985), relocation exposes the relocating larvae to a higher predation risk (Lucas, 1986; Matura and Takano, 1989; Hauber, 1999; Gatti and Farji-Brener, 2002). Obviously, the immediate result of both interference competition (in the form of sand throwing) and exploitation competition is the loss of foraging opportunities, which in turn can bring about increased metabolic expenditure and increased risk of cannibalism or intra-guild predation, especially among the relocating larvae.

We used the pit-building antlion *Myrmeleon hyalinus* (Neuroptera: Myrmeleontidae) as a model system to test the short-term responses (i.e., behavior and growth rate) of a strict sit-and-wait predator to con- and hetero-specific competition, potentially involving sand throwing, cannibalism and intra-guild predation. Since it was impossible to control for sand throwing in the competition experiment (without interfering with the spatial distribution of antlion larvae), we also examined the direct effect of sand disturbance, before or after feeding, on the behavior and growth rate of *M. hyalinus* larvae. Destroying antlion pits before or after feeding enabled us to evaluate the effect of severe sand throwing on antlion behavior and growth rate, and to separate the metabolic costs associated with pit reconstruction (i.e., pit destruction after feeding) from those caused by the loss of feeding opportunities (i.e., pit destruction before feeding) when foraging without a pit. It is well known that the hunting success of pit-building antlions foraging without a pit is substantially reduced (Griffiths, 1992). By holding the per-capita food supply constant in the sand disturbance and competition experiments, we could minimize the differences in exploitation competition between and within the two experiments (see Section 2.2).

We had two major working hypotheses. The first is related to the effect of sand disturbance on antlion behavior and growth rate while the other relates to the effect of competition on the same factors. First, we hypothesized that sand disturbance should elicit the behavioral responses of increased relocation and decreased pit construction rates. Since the antlion pit is extremely important for the effective capture of prey items (Mansell, 1988; Lucas, 1989; Griffiths, 1992; Devetak et al., 2005), we predicted that the negative effect of pit destruction prior to feeding on the larvae growth rate should be stronger than that of pit destruction after feeding. Second, cannibalism and intra-guild predation in antlion larvae are well documented (Griffiths, 1991, 1992; Scharf and Ovadia, 2006).

We thus posited that the presence of either con- or hetero-specific competitors would prominently affect antlion growth rate and behavior. Specifically, based on the large size differences between *M. hyalinus* and the hetero-specific competitor used in the current setting, *Lopezus fedtschenkoi* (Neuroptera: Myrmeleontidae), we predicted that the reduction in growth rates would be stronger in the hetero- than in the con-specific treatment. The expected behavioral response to either the cannibalism or the predation threat is a reduction in pit construction and relocation activities, as reflected in the foraging behavior of this trap-building species. Indeed, *M. hyalinus* was previously shown to reduce pit construction activity in response to the predation threat of a predatory ground beetle (Loria et al., 2008).

2. Methods

2.1. Study species

In early fall 2008 we collected 118 *M. hyalinus* larvae from Nahal Secher (31°06'N, 34°49'E), a sandy habitat area in the northern Negev desert about 15 km south of the city of Beer-Sheva, Israel, and brought them to the laboratory. *M. hyalinus* larvae are sit-and-wait predators constructing pits in shaded microhabitats under trees and bushes (Simon, 1988). The larva develops through three instar stages and undergoes complete metamorphosis. We also collected 30 *L. fedtschenkoi* individuals from the same region. *L. fedtschenkoi* is a nocturnal sit-and-pursue predator, which is active mainly on open dune slopes while changing its ambush position several times during the night but does not construct a pit (Simon, 1988; Loria et al., 2008). These two antlion species co-occur over a wide range of sandy habitats in Israel. In addition to the species' different foraging modes, they also substantially differ in body size. Specifically, *L. fedtschenkoi* is typically more than double the size of *M. hyalinus*, when considering the final mass prior to pupation. For instance, the body masses of third instar *M. hyalinus* and *L. fedtschenkoi* larvae are 0.026 ± 0.002 g and 0.058 ± 0.016 g (mean \pm 1 SD), respectively (Ovadia, unpublished data).

2.2. Experimental design

2.2.1. Sand disturbance experiment

We placed each of the 28 second instar *M. hyalinus* larvae into a separate 25 cm \times 17 cm aluminum tray, filled with 3 cm of sand. Trays were kept in an environmental chamber, which was set to mean September day/night temperatures (36.4°C/23.7°C) and relative humidity levels (19%/54%) characteristic of the southern hyper-arid region of Israel (i.e., Eilat) and an identical night/day photoperiod (12:12 h). Antlions were fed once a week with one flour beetle larva (mean beetle larva mass \sim 1 mg), introduced at a random position in the tray. Trays were randomly assigned to one of the following three treatments: (i) pit destruction 1 min prior to feeding ($n = 10$); (ii) pit destruction 24 h after feeding ($n = 10$); and (iii) a control treatment with no sand disturbance ($n = 8$). Sand disturbance in the first two treatments was performed once a week, by shaking the trays until the existing pits were fully covered with sand, forcing the antlions in the first treatment to forage without a pit. We ran the experiment for nine weeks. During this period, we recorded behavioral activity (i.e., relocation and pit construction) twice a week and weighed the antlions once a week using an analytical scale (CP224S; Sartorius AG, Goettingen, Germany; accuracy of 0.1 mg), which caused an additional pit destruction in all treatments. Behavioral observations took place before pit destruction and prior to weighing the antlions. The entire experimental protocol including exact chronological information on all experimental events is presented in Fig. 1A.

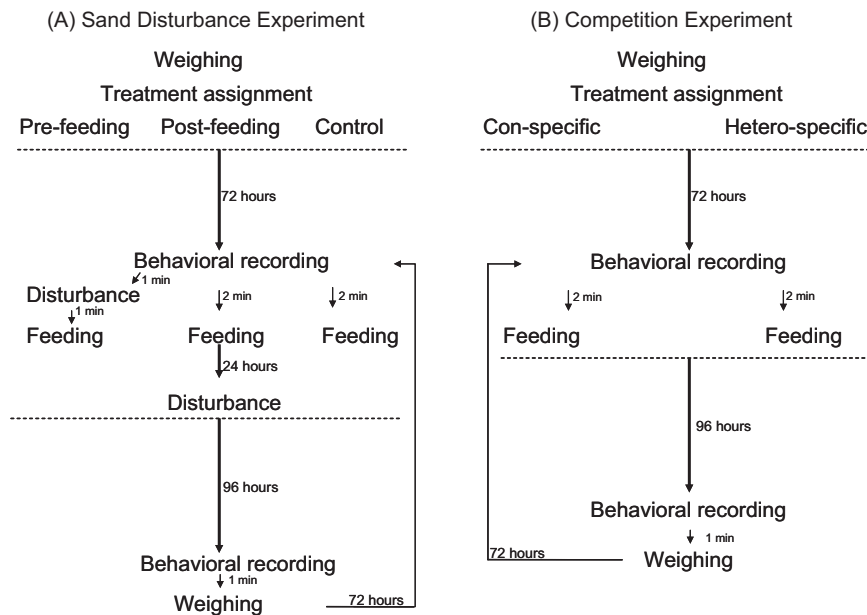


Fig. 1. A diagram presenting the experimental protocol of the (A) sand disturbance and (B) competition experiments, including the exact chronological information of all experimental events. Behavioral recording stands for recording pit construction and pit relocation.

2.2.2. Con- and hetero-specific competition experiment

To disentangle the effects of density and competition, we used a substitutional experimental design. Specifically, we placed either four *M. hyalinus* larvae (con-specific treatment; two 1st instar and two 2nd instar) or two *M. hyalinus* larvae (one 1st instar and one 2nd instar) plus two 3rd instar *L. fedtschenkoi* larvae (hetero-specific treatment) into 25 cm × 17 cm aluminum trays, each filled with 3 cm of sand. Each of these two treatments was replicated 15 times. The large differences in body mass between the two antlion species in the hetero-specific treatment and between the instars in the con-specific treatment aimed at intensifying the risk of predation by con- or hetero-specific competitors (i.e., cannibalism and intra-guild predation, respectively). Note that a three- to fourfold-size difference may also exist among *M. hyalinus* larvae of the same developmental stage.

To facilitate individual identification, larvae of the same developmental stage, placed into a single tray, were selected so that their size differences were evident throughout the entire experiment. Doing so enabled us to document the specific changes in mass and growth rate of each *M. hyalinus* larva. Trays were kept in an environmental chamber set to the same conditions as described for the sand disturbance experiment. For the entire nine weeks of the experiment, the antlions were fed once a week with flour beetle larvae (mean larval mass ~1 mg). Specifically, we held the per-capita food supply constant at one prey item per individual by introducing four flour beetle larvae into each tray at random positions. By avoiding to feed the antlions directly in their pits, we ensured that the probability of prey approaching an antlion was equal for all individuals, and not biased towards antlions having pits. Moreover, *L. fedtschenkoi* does not construct a pit, and we were unable to locate its exact position and to feed it directly. Clearly, this feeding procedure also allows for one or a few larvae to catch more than one prey item while others may not capture prey at all, thus increasing the variance in growth rates among individuals within and among treatments. During the experiment, we recorded behavioral activity (i.e., relocation and pit construction) twice a week: before weighing the antlions and prior to feeding. Trays were sieved once a week in order to weigh the live antlions and to record the number of dead individuals.

All antlion larvae that participated in this experiment were accounted for (i.e., no individuals were missing). Larvae were weighed using the same analytical scale as described in the sand disturbance experiment. The entire experimental protocol including the exact chronological information of all experimental events is presented in Fig. 1B.

2.3. Statistical analysis

2.3.1. Analysis of behavioral data

Two complementary approaches were used to analyze the behavioral data. One focused on the overall cumulative effect experimental treatments had on pit construction and relocation activities, while the second dealt with the rate at which these behavioral events occurred.

The first approach was simply based on calculating the proportion of antlions that were involved in these behavioral activities. Specifically, because repeated observations on the same tray are not independent of each other, we calculated the proportion of pit construction or relocation events that occurred in each tray during the entire experimental period as the ratio between the observed cumulative and the maximum possible number of such events. For example, if trays were censused 18 times during the entire experimental period, and the number of antlion larvae in each tray was 4, the maximum possible number of pit construction events should be $18 \times 4 = 72$. For example, let us assume that during each census only two pits were recorded, meaning that the cumulative number of pit construction events was $2 \times 18 = 36$; thus, the proportion of pit construction events would be $36/72 = 0.5$. When death occurred in a particular tray, we recalculated the maximum possible number of pit construction events, and calculated the proportion of pit construction events accordingly. We tested whether the above calculated proportions of pit construction or relocation events were affected by sand disturbance or competition using one-way ANOVAs. In keeping with accepted practice for proportions (Sokal and Rohlf, 1995, p. 419), data were arcsine square root transformed prior to the analysis. Recall that we had a priori expectations that sand disturbance should result in increased relocation and decreased pit construction activities, and that these behavioral responses should be stronger in the group subjected to

sand disturbance prior to feeding compared to that subjected to sand disturbance after feeding. We thus specified a set of two linear orthogonal contrasts. The first contrast tested for differences between the sand disturbance treatments in the aggregate and the control group. The second contrast tested for differences between the group subjected to sand disturbance prior to feeding and that subjected to sand disturbance after feeding. There was no need to specify such orthogonal contrasts when analyzing the competition experiment which included only two experimental groups (i.e., con- and hetero-specific treatment). All the above statistical analyses as well as those of relative growth rates described below were performed using STATISTICA v6.0 (StatSoft, Ltd., Tulsa, OK, USA).

The second approach tested for the effects of sand disturbance or competition on the rate at which antlion larvae relocated or reconstructed pits using a Cox proportional hazards model (Hosmer and Lemeshow, 1999), with either the sand disturbance (control=0, post-feeding sand disturbance=1, and prior-to-feeding sand disturbance=2) or competition (con-specific=0 and hetero-specific=1) treatment, initial body mass and the respective interaction terms as covariates. Time-to-event data are commonly analyzed using this method, which enables one to evaluate the effects of different predictors (i.e., covariates) on the rate at which the event in focus (in our case, relocation or pit reconstruction) occurs independent of some time-varying background rate (Hosmer and Lemeshow, 1999). To control for repeated measurements on a subject – which, in our case, were trays that were repeatedly censused throughout the experiment – we used a robust jackknife variance estimator grouped by observations per tray (Lin and Wei, 1989). These statistical analyses as well as those described in the next section were performed using S-PLUS 2000 (MathSoft, Inc., Cambridge, MA, USA).

2.3.2. Analyzing mortality rates

We used a Cox proportional hazards model (described above) to test for the effect of potential cannibalism or intra-guild predation on the rate at which mortality events took place, with competition treatment (con-specific=0 and hetero-specific=1), initial body mass, and the respective interaction terms as covariates. Note that during the sand disturbance experiment all individuals except for two survived the experiment, thus precluding the need for such a survival analysis.

2.3.3. Calculating and analyzing relative growth rates

We calculated the instantaneous rate of change in antlion larvae body mass (i.e., relative growth rate) as the log ratio of two successive body mass measurements ($\ln[\text{mass}(t+\tau)/\text{mass}(t)]$) divided by the number of days that elapsed between the two measurements (τ , which in our case was 7 days). During each experiment, antlion larvae were weighed 10 times, meaning that we could calculate nine successive relative growth rate values per individual. Because successive measurements on the same individual are not independent of each other, we used repeated measures ANOVAs (von Ende, 2001) to test for the effect of sand disturbance or con- and hetero-specific treatments (i.e., between-subject factors), time (i.e., within-subject factor), and the respective interaction terms on the relative growth rate of antlions.

3. Results

3.1. Sand disturbance experiment

As expected, the proportion of *M. hyalinus* individuals that constructed pits was relatively high and it significantly differed among treatments (one-way ANOVA; $F_{2,25} = 8.42$; $P = 0.0016$; Fig. 2A). In agreement with our predictions, sand disturbance

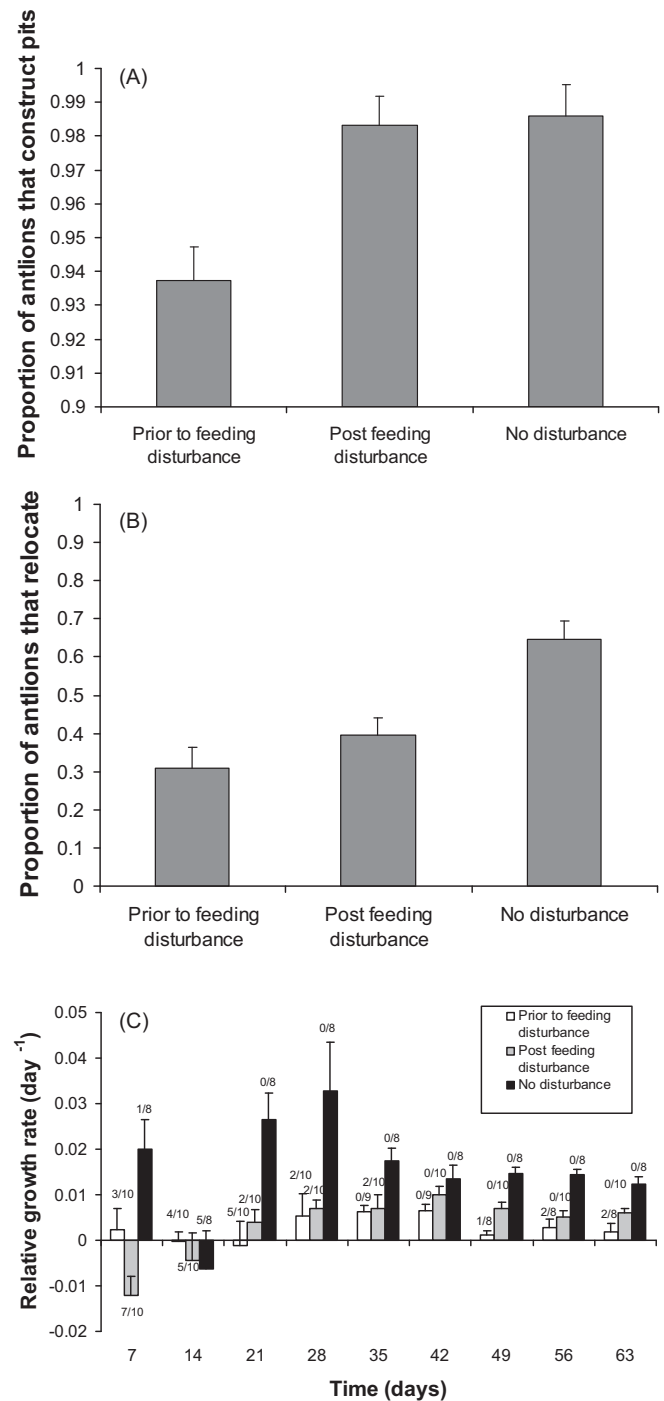


Fig. 2. Effect of sand disturbance on *M. hyalinus* behavior and growth rate. (A and B) Sand disturbance prior to feeding reduces both the proportion of pits constructed (A) and the proportion of relocating individuals (B). (C) Pre-feeding sand disturbance (white) was also associated with the strongest reduction in the relative growth rate. Error bars stand for 1 SE. Numbers above bars represent the proportion of *M. hyalinus* larvae having negative growth rates out of those antlions which survived up to this stage of the experiment. The initial number of larvae in each of the sand disturbance groups was 10 and that of the control group was 8.

caused a reduction in the proportion of individuals that constructed pits (0.9603 ± 0.0082 , mean ± 1 SE) relative to that observed in the undisturbed control group (0.9861 ± 0.0091 ; first orthogonal contrast, $t = 2.1395$; $P = 0.0424$; Fig. 2A). Furthermore, this reduction in pit construction activity was stronger in the group subjected to sand disturbance prior to feeding (0.9373 ± 0.0100)

Table 1

The results of a Cox proportional hazards model examining the effects of initial body mass (measured in mg), sand disturbance (control = 0, post-feeding = 1, and prior to feeding = 2) or competition (con-specific = 0 and hetero-specific = 1) on pit reconstruction and relocation rates, and on the survival of *M. hyalinus* larvae. Since there was almost no mortality during the sand disturbance experiment, the survival analysis was applicable only in the competition experiment.^a

Experiment	Event in focus	Covariate	e^{β}	z	P	Model statistics
Sand disturbance	Pit construction	Treatment	0.926	-3.25	$P = 0.001$	LRT = 2.14, d.f. = 2, N.S.
		Initial body mass	0.977	-1.47	N.S.	
		Interaction			N.S.	
	Relocation	Treatment	0.657	-3.233	$P = 0.001$	LRT = 20.6, d.f. = 2, $P < 0.0001$
		Initial body mass	0.979	-0.328	N.S.	
		Interaction			N.S.	
Competition	Pit construction	Treatment	0.625	-5.97	$P < 0.0001$	LRT = 22.9, d.f. = 2, $P < 0.0001$
		Initial body mass	1.079	1.44	$P < 0.0001$	
		Interaction			N.S.	
	Relocation	Treatment	0.309	-3.798	$P = 0.0001$	LRT = 35.6, d.f. = 2, $P < 0.0001$
		Initial body mass	1.039	0.533	N.S.	
		Interaction			N.S.	
	Mortality	Treatment	0.499	-1.14	N.S.	LRT = 33.2, d.f. = 3, $P < 0.0001$
		Initial body mass	0.396	-2.89	$P = 0.003$	
		Interaction	1.586	1.3	N.S.	

^a The expected change in the rate at which antlions reconstructed their pits, relocated, or died as a function of one unit change in each of the above-mentioned covariates can be estimated using the exponent coefficient (e^{β}). For example, the shift from con- to hetero-specific competition should decrease pit reconstruction rate by a factor of 0.625 (i.e., a reduction of 37.5% in pit reconstruction rate). The significance level of each of the estimated coefficients was computed using a z-test often referred to as Wald's test. LRT is a likelihood ratio test done by contrasting the solution obtained after fitting the model with a null model that includes the initial value of the coefficients.

compared to that subjected to sand disturbance 24 h after feeding (0.9833 ± 0.0085 ; second orthogonal contrast, $t = -3.5018$; $P = 0.0018$; Fig. 2A). We found significant differences in the proportion of relocating antlions among treatments ($F_{2,25} = 11.0929$; $P = 0.0003$; Fig. 2B). However, in contrast to our expectations, sand disturbance also led to a significant reduction in the proportion of relocating antlions relative to that of the control group (sand disturbance: 0.3519 ± 0.0357 ; control: 0.9833 ± 0.0085 , first orthogonal contrast, $t = 4.5133$; $P = 0.0001$; Fig. 2B). There were no significant differences in the proportion of relocating individuals between antlions experiencing sand disturbance prior to and after feeding (pre-feeding: 0.3095 ± 0.0533 ; after feeding: 0.3944 ± 0.0464 ; second orthogonal contrast, $t = -1.3476$; $P = 0.1899$; Fig. 2B). As predicted, the relative growth rate of *M. hyalinus* larvae experiencing sand disturbance was significantly lower than that observed in the control group (repeated measures ANOVA: $F_{2,23} = 28.798$; $P < 0.0001$; Fig. 2C). There were significant time ($F_{8,184} = 5.857$; $P < 0.0001$) and time \times sand disturbance effects ($F_{16,184} = 2.765$; $P = 0.0005$; Fig. 2C), indicating that changes in growth rates over time were not consistent across treatments. Indeed, the average growth rate of antlions subjected to pre-feeding sand disturbances did not deviate significantly from zero (i.e., no change in body mass) during the entire experimental period except for the fifth and sixth weeks when growth rates were positive. In contrast, in the group that experienced sand disturbance 24 h after feeding, average growth rates were negative during the first week, did not vary significantly from zero during the second and third weeks, and were positive from the fourth week onward (Fig. 2C). The control group showed on average positive growth rates throughout the entire experimental period except during the second week, and overall, there was an increase in growth rate until the fourth week, but then it decreased to a lower positive level that remained constant until the end of the experiment (Fig. 2C).

Using a Cox proportional hazards model, we found that sand disturbance caused a significant reduction in the rate at which *M. hyalinus* larvae reconstructed their pits or relocated ($P < 0.0001$; Table 1). Initial body mass did not have any observable effect on either rate and there was no significant sand disturbance \times initial body mass interaction (Table 1), indicating that pit reconstruction and relocation rates were not affected by the initial body masses of the antlions and that this pattern was consistent among treatments.

With the exception of two larvae from the group subjected to sand disturbance prior to feeding, all antlion larvae survived until the end of the experiment.

3.2. Competition experiment

As predicted, the presence of *L. fedtschenkoi* caused a significant reduction in the proportion of *M. hyalinus* larvae that constructed pits (0.8042 ± 0.0162 and 0.7089 ± 0.0345 for the con- and hetero-specific treatments, respectively; $F_{1,28} = 6.7733$, $P = 0.0146$; Fig. 3A) or that relocated (0.6074 ± 0.0289 and 0.1644 ± 0.0424 for the con- and hetero-specific treatments, respectively; $F_{1,28} = 73.149$, $P < 0.0001$; Fig. 3B). *M. hyalinus* larvae in the con-specific treatment exhibited positive growth rates, which were significantly higher than those of the hetero-specific group throughout the entire experimental period (repeated measures ANOVA $F_{1,26} = 14.783$, $P = 0.0007$; Fig. 3C). There were significant time effects ($F_{8,208} = 2.53$, $P = 0.012$) and marginally significant time \times treatment effects ($F_{8,208} = 1.951$, $P = 0.054$), suggesting that the change in growth rate over time was not consistent between the two treatments. Indeed, in the presence of *L. fedtschenkoi*, the average growth rates of *M. hyalinus* larvae did not vary significantly from zero during the first three weeks of the experiment, but from the fourth week onward positive growth rates were measured (Fig. 3C). In contrast, antlions in the con-specific group showed on average positive growth rates throughout the entire experimental period, which were higher in the first four weeks of the experiment and later decreased to a lower positive level that remained constant until the end of the experiment (Fig. 3C).

Using a Cox proportional hazards model, we found that the presence of *L. fedtschenkoi* led to a significant reduction in the rate at which *M. hyalinus* larvae reconstructed their pits or relocated ($P < 0.0001$ in both cases; Table 1). We found that the mean initial body mass of antlion larvae was positively related to the rate at which they reconstructed their pits ($P < 0.0001$; Table 1), but no such effect on relocation rate could be detected (Table 1). In contrast to the almost 100% survival rate of *M. hyalinus* during the sand disturbance experiment, only 48% of *M. hyalinus* larvae survived the competition experiment, with most of the mortality (>85%) occurring during the first four weeks of the experiment. Using a Cox proportional hazards model, we found that the initial body masses

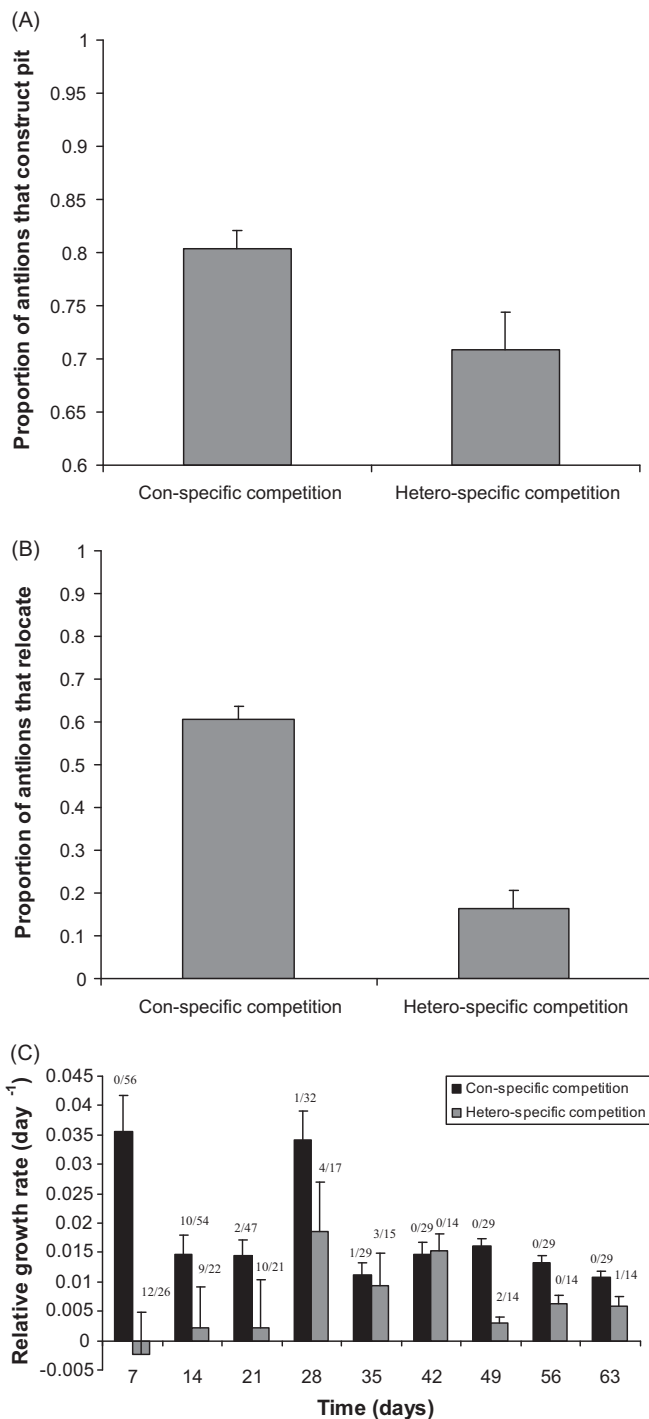


Fig. 3. Effect of competition on *M. hyalinus* behavior and growth rate. The proportion of pits constructed (A), the proportion of relocating individuals (B), and the relative growth rate (C) were lower in the hetero- than in the con-specific treatment. Error bars stand for 1 SE. Numbers above bars represent the proportion of *M. hyalinus* larvae having negative growth rates out of those antlions which survived up to this stage of the experiment. Since we used a substitutional experimental design, the initial number of *M. hyalinus* larvae in the con-specific group was 60 and that of the hetero-specific group was 30.

of *M. hyalinus* larvae significantly affected their survival rates. However, we did not detect any difference in survival rates between the two competition treatments, and there was no significant treatment \times initial body mass interaction (Table 1). It is important to note that there was no significant difference in the initial body size distribution of *M. hyalinus* larvae between the two competition treatments (two-sample Kolmogorov–Smirnov test, $P = 0.9762$).

4. Discussion

We report here on the short-term behavioral and developmental responses of the pit-building antlion *M. hyalinus* to sand disturbance (i.e., quantification of the impact of severe sand throwing) and to the presence of con- and hetero-specific larvae, two treatment strategies that simulate the combined effects of intra-specific competition and cannibalism and the effect of intra-guild predation, respectively. We showed that antlion larvae subjected to sand disturbance reduced their pit construction activity and relocated less often. Moreover, the reduction in pit construction activity was stronger among antlions subjected to disturbances prior to feeding. Although almost no death events were recorded during the sand disturbance experiment, as expected, it led to a reduction in the relative growth rates of antlions, and this negative effect was strongest in the group exposed to pre-feeding sand disturbances. The presence of the larger sit-and-pursue *L. fedtschenkoi* larvae caused the *M. hyalinus* larvae to reduce their pit construction and relocation activities more than the presence of con-specific competitors. Cannibalism and intra-guild predation are well documented in antlions (Griffiths, 1991, 1992; Gotelli, 1997; Scharf and Ovadia, 2006). Indeed, although the per-capita food supply in the competition experiment was identical to that in the sand disturbance experiment, only 48% of the *M. hyalinus* larvae survived the competition experiment; a pattern that was consistent in both the con- and hetero-specific treatments. Also, the relative growth rate of surviving *M. hyalinus* larvae was significantly lower in the presence of hetero-specific competitors than in the presence of con-specific competitors.

Antlions experience sand disturbances throughout their larval stage. Pit destruction, possibly the most common type of disturbance to befall antlions, may result from wind-blown sand movement, sand throwing by con-specifics or the activities of various animals on the sand dune surface. As described for other sit-and-wait predators such as the caddisfly (Beveridge and Lancaster, 2007), we report that the occurrence of disturbances was associated with a decreased individual growth rate, which was mainly caused by the high cost of repetitive pit construction (Lucas, 1985), but also by the loss of foraging opportunities when foraging without a pit (Mansell, 1988; Lucas, 1989; Griffiths, 1992; Devetak, 2005). In other words, there was a small but significant additive effect for the loss of feeding opportunities in addition to the cost of repetitive pit construction (i.e., the growth rate of individuals being disturbed before feeding was lower than that of those disturbed after feeding). Consequently, to offset the high cost of repeated pit construction, pits with smaller diameter may have evolved. Such a strategy, however, may lead to a subsequently lower prey encounter rate, thus reducing prey capture success (Griffiths, 1980, 1986; Heinrich and Heinrich, 1984). In the absence of competitors, antlions prefer to reconstruct their pits, regardless of the high metabolic cost, because a well-constructed pit can substantially increase their hunting success (e.g., Griffiths, 1992).

Contrasting the two experiments shows that the presence of hetero-specific competitors has the strongest negative effect on both pit construction and relocation activities of *M. hyalinus*. As we predicted, the lowest relocation rates were observed among *M. hyalinus* larvae in the hetero-specific treatment, but it also seems that this type of activity was lower among larvae experiencing a severe sand disturbance than among those in the con-specific competition experiment. The rate at which *M. hyalinus* larvae reconstructed their pits was relatively high irrespective of the timing of sand disturbances (i.e., prior to or after feeding, ~94% and ~98%, respectively). However, when exposed to competition, the tendency to construct a pit was substantially lower in both con- and hetero-specific treatments (~80% and ~70%, respectively).

Pit construction activity was negatively affected by, in descending order of magnitude, hetero-specific competition, con-specific competition and sand disturbance. Indeed, previous studies have shown that competition intensity was negatively correlated with pit construction rates (McClure, 1976; Matsuura and Takano, 1989; Griffiths, 1991; Devetak, 2000). We interpreted the observed reduction in pit construction activity to mean that as the density of con- or hetero-specific competitors increased, some *M. hyalinus* larvae may have changed their foraging strategy from a sit-and-wait to a sit-and-pursue foraging mode, thus relying less on their pits as their preferred foraging tool. This hypothesis of a shift in foraging strategy was also supported by the fact that, from the fourth week onward, almost all *M. hyalinus* larvae in the competition experiment (>94%) as well as those subjected to disturbance prior to feeding (>89%) had positive growth rates, indicating that they can successfully capture prey even without a pit. *L. fedtschenkoi* is more than double the size of *M. hyalinus*. It is thus logical that a reduction in pit construction activity and/or a shift in foraging mode can substantially reduce the chances that *L. fedtschenkoi* larvae will locate and feed on *M. hyalinus* larvae, i.e., decrease the risk of intra-guild predation. Additionally, the sit-and-pursue foraging mode employed by *L. fedtschenkoi* may also result in pit destruction, as its movement over the sand surface can destroy pits constructed by *M. hyalinus*.

Pit construction activity is energetically costly (Lucas, 1985), and the lower prevalence of this type of activity among *M. hyalinus* larvae exposed to the risk of either cannibalism or intra-guild predation, compared to those experiencing sand disturbance, may also explain why the relative growth rates of the former were higher. Clearly, part of these differences in growth rates (especially those observed during the first four weeks of the experiment when most mortality occurred; see below) might also be attributed to cannibalism, which may provide an additional source of food. Our survival analysis indicated that an increase of one milligram in the initial body mass of *M. hyalinus* larvae exposed to the danger of either cannibalism or intra-guild predation decreased their mortality rate by ~60% (Table 1). Indeed, mortality occurred during the first four weeks of the experiment (>85%) and the victims were mainly first instar *M. hyalinus* larvae (13 out of 16 [81%], and 23 out of 31 [74%] cases in the con- and hetero-specific treatments, respectively). Previous research on *M. hyalinus* larvae has indicated that they can easily survive a starvation period of up to six weeks (Scharf et al., 2009). We thus suggest that most mortality events observed in our experiment were the result of intra-guild predation and cannibalism. Previous studies have shown that the victims of cannibalism are usually individuals in early developmental stages (Polis, 1981; Polis et al., 1989) and that survival rates are influenced by the within-population size structure (i.e., frequency dependence; Ovadia et al., 2007). Griffiths (1991, 1992) observed density-dependent cannibalism in antlions, especially when there were large size differences between conspecifics.

Evidently, growth rates are highly dependent on the size of the larvae. Since most mortality victims were first instar larvae, there was also a substantial reduction in the variances of the growth rates of surviving *M. hyalinus* larvae with time, and this pattern was consistent between the con- and hetero-specific treatments. The presence of the larger sit-and-pursue *L. fedtschenkoi* larvae led to a reduction in the growth rates of *M. hyalinus* larvae. Moreover, this pattern was more pronounced during the first four weeks of the experiment. We thus suggest that the reduction in growth rates observed during the first month should be attributed to the decreased incidence of cannibalism at the expense of increased intra-guild predation. The fact that during this period, growth rates of *M. hyalinus* larvae in the con-specific treatment were even higher than those of *M. hyalinus* larvae in the undisturbed control group

supports this assertion. However, from the fifth week onward, there was little or no mortality and almost all *M. hyalinus* larvae (>94%) had positive growth rates. This means that, in accord with our prediction, cannibalism and intra-guild predation acted as a mechanism for relaxing both interference (i.e., sand throwing) and exploitation competition.

Eltz (1997) illustrated that pit destruction of the antlion species *M. mobilis* had no significant effect on the pit relocation rate, but here we show that sand disturbance decreased the relocation rate. Note that rather than increasing the disturbance rate, as was done by Eltz (1997), we only changed disturbance timing. Moreover, Eltz destroyed the pits by filling them with sand, whereas in our study the entire tray was shaken. The divergent outcomes of these two methods of mimicking sand disturbances in nature may be differently perceived by the antlion: when the whole tray was shaken, relocation to different areas of the tray would probably not improve foraging success, but in the event of a more localized disturbance, a logical antlion strategy would be to relocate far from the source of the disturbance. This behavior is in accordance with observations made by Chmiel et al. (2000), who observed daily movements of the sit-and-wait spider *Argiope keyserlingi* in response to web damage. They reported that movement was in the direction away from the source of damage.

To conclude, we propose that the two antlion species interact at three different levels: (1) sand disturbance: the movement of *L. fedtschenkoi* individuals over the sand surface can destroy *M. hyalinus* pits; (2) exploitation competition: sharing and depleting the same limited potential prey; and (3) intra-guild predation by *L. fedtschenkoi*. Ultimately, the interactions between the two species lead to changes, such as in the foraging behavior of *M. hyalinus*. Furthermore, as was previously suggested by Amarasekare (2002), when the species that are involved in costly interference competition (e.g., sand throwing) are also engaged in beneficial interference mechanisms (e.g., predation), coexistence is possible via a trade-off between exploitation and interference. We thus suggest that this interplay between intra-guild predation (i.e., beneficial interference mechanism), sand throwing (costly interference mechanism) and exploitation competition plays an important role in promoting the coexistence of the various antlion species (~20 species, Simon, 1988) in the sandy areas of Israel.

Acknowledgments

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

References

- Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D.A., Yodanis, P., 1996. The role of indirect effects in food webs. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York, pp. 371–395.
- Adolph, S.C., Roughgarden, J., 1983. Foraging by passerine birds and *Anolis* lizards on St. Eustatius (Neth. Antilles): implications for interclass competition, and predation. *Oecologia* 56, 313–317.
- Amarasekare, P., 2002. Interference competition and species coexistence. *Proc. R. Soc. B: Biol. Sci.* 269, 2541–2550.
- Beveridge, O.S., Lancaster, J., 2007. Sub-lethal effects of disturbance on a predatory net-spinning caddisfly. *Freshw. Biol.* 52, 491–499.
- Chmiel, K., Herberstein, M.E., Elgar, M.A., 2000. Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. *Anim. Behav.* 60, 821–826.
- Day, M.D., Zalucki, M.P., 2000. Effect of density on spatial distribution, pit formation and pit diameter of *Myrmeleon acer* Walker (Neuroptera: Myrmeleontidae): patterns and processes. *Austral Ecol.* 25, 58–64.
- Devetak, D., 2000. Competition in larvae of two European ant-lion species (Neuroptera: Myrmeleontidae). *J. Neuropterol.* 3, 51–60.
- Devetak, D., 2005. Effects of larval antlions *Euroleon nostras* (Neuroptera: Myrmeleontidae) and their pits on the escape time of ants. *Physiol. Entomol.* 30, 82–86.

- Devetak, D., Spornjak, A., Janzekovic, F., 2005. Substrate particle size affects pit building decision and pit size in the antlion larvae *Euroleon nostras* (Neuroptera: Myrmeleontidae). *Physiol. Entomol.* 30, 158–163.
- Eltz, T., 1997. Foraging in the ant-lion *Myrmeleon mobilis* Hagen 1888 (Neuroptera: Myrmeleontidae): behavioral flexibility of a sit-and-wait predator. *J. Insect Behav.* 10, 1–11.
- Felix, S., Soares, A.O., 2004. Intra guild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. *Eur. J. Entomol.* 101, 237–242.
- Gatti, M.G., Farji-Brener, A.G., 2002. Low density of ant lion larvae (*Myrmeleon crudelis*) in ant-acacia clearings: high predation risk or inadequate substrate? *Biotropica* 34, 458–462.
- Gotelli, N.J., 1997. Competition and coexistence of larval ant lions. *Ecology* 78, 1761–1773.
- Griffiths, D., 1980. Feeding biology of ant-lion larvae—prey capture, handling and utilization. *J. Anim. Ecol.* 49, 99–125.
- Griffiths, D., 1986. Pit construction by ant-lion larvae—a cost-benefit-analysis. *J. Anim. Ecol.* 55, 39–57.
- Griffiths, D., 1991. Intra-specific competition in larvae of the ant-lion *Morter* sp. and inter-specific interactions with *Macroleon quinquemaculatus*. *Ecol. Entomol.* 16, 193–202.
- Griffiths, D., 1992. Interference competition in ant-lion (*Macroleon quinquemaculatus*) larvae. *Ecol. Entomol.* 17, 219–226.
- Griffiths, D., 1993. Intra-specific competition in ant-lion (*Macroleon quinquemaculatus*) larvae in the field. *Oecologia* 93, 531–537.
- Hauber, M.E., 1999. Variation in pit size of antlion (*Myrmeleon carolinus*) larvae: the importance of pit construction. *Physiol. Entomol.* 24, 37–40.
- Heinrich, B., Heinrich, M.J.E., 1984. The pit-trapping foraging strategy of the antlion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae). *Behav. Ecol. Sociobiol.* 14, 151–160.
- Hosmer, D.W., Lemeshow, S., 1999. *Applied Survival Analysis: Regression Modeling of Time to Event Data*. Wiley, New York.
- Johansson, F., 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behavior and zooplankton availability. *Oikos* 66, 80–87.
- Lin, D.Y., Wei, L.J., 1989. The robust inference for the Cox proportional hazards model. *J. Am. Stat. Assoc.* 84, 1074–1079.
- Linton, M.C., Crowley, P.H., Williams, J.T., Dillon, P.M., Aral, H., Strohmeier, K.L., Wood, C., 1991. Pit relocation by antlion larvae—a simple-model and laboratory test. *Evol. Ecol.* 5, 93–104.
- Loria, R., Scharf, I., Subach, A., Ovadia, O., 2008. The interplay between foraging mode, habitat structure, and predator presence in antlions. *Behav. Ecol. Sociobiol.* 62, 1185–1192.
- Lucas, J.R., 1982. The biophysics of pit construction by antlion larvae (*Myrmeleon*, Neuroptera). *Anim. Behav.* 30, 651–664.
- Lucas, J.R., 1985. Partial consumption by antlion larvae. *Anim. Behav.* 33, 945–958.
- Lucas, J.R., 1986. Antlion pit construction and kleptoparasitic prey. *Fla. Entomol.* 69, 702–710.
- Lucas, J.R., 1989. The structure and function of antlion pits—slope asymmetry and predator–prey interactions. *Anim. Behav.* 38, 318–330.
- Mansell, M.W., 1988. The pitfall trap of the Australian ant-lion *Callistoleon illustris* (Gerstaecker) (Neuroptera, Myrmeleontidae)—an evolutionary advance. *Aust. J. Zool.* 36, 351–356.
- Matsura, T., Takano, H., 1989. Pit-relocation of antlion larvae in relation to their density. *Res. Popul. Ecol.* 31, 225–234.
- McClure, M.S., 1976. Spatial distribution of pit-making antlion larvae (Neuroptera: Myrmeleontidae): density effects. *Biotropica* 8, 913–922.
- Ovadia, O., Dohna, H.Z., Booth, G., Schmitz, O.J., 2007. Consequences of body size variation among herbivores on the strength of plant–herbivore interactions in seasonal environment. *Ecol. Model.* 206, 119–130.
- Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Evol. Ecol. Syst.* 12, 225–251.
- Polis, G.A., Holt, R.D., 1992. Intra-guild predation—the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7, 151–154.
- Polis, G.A., McCormick, S.J., 1987. Intra-guild predation and competition among desert scorpions. *Ecology* 68, 332–343.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intra guild predation—potential competitors that eat each other. *Annu. Rev. Ecol. Evol. Syst.* 20, 297–330.
- 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. *J. Insect Behav.* 19, 197–218.
- Scharf, I., Filin, I., Ovadia, O., 2009. A trade-off between growth and starvation endurance in a pit-building antlion. *Oecologia* 160, 453–460.
- Schmitz, O.J., Vlastimil, K., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7, 153–163.
- Schoener, T.W., 1983. Field experiments on inter-specific competition. *Am. Nat.* 122, 240–285.
- Schoener, T.W., 1993. On the relative importance of direct versus indirect effects in ecological communities. In: Kawanabe, H., Cohen, J.E., Iwasaki, K. (Eds.), *Mutualism and Community Organization: Behavioral Theoretical and Food-Web Approaches*. Oxford University Press, Oxford, pp. 365–411.
- Simberloff, D., Dilon, P., King, L., Lorence, D., Lowrie, S., Schilling, E., 1978. Holes in the doughnut theory: the dispersion of antlions. *Brenesia* 14, 13–46.
- Simon, D., 1988. Ant-lions (Neuroptera: Myrmeleontidae) of the costal 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, Israel.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, 3rd ed. Freeman, New York.
- von Ende, C.N., 2001. Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*, 2nd ed. Oxford University Press, New York, pp. 134–157.
- Wilson, D.S., 1974. Prey capture and competition in the antlion. *Biotropica* 6, 187–193.
- Youthed, G.J., Moran, V.C., 1969. Pit construction by myrmeleontid larvae. *J. Insect Physiol.* 15, 867–875.