Journal of Insect Behavior, Vol. 16, No. 6, November 2003 (© 2003)

Microhabitat Selection by Antlion Larvae, Myrmeleon Crudelis: Effect of Soil Particle Size on Pit-Trap Design and Prey Capture

Alejandro G. Farji-Brener[1]

Accepted July 16, 2003; revised August 19, 2003

Selective pressure for choosing an adequate habitat should be strong in semisedentary animals because they have limited mobility once established. I examined microhabitat preferences and the adaptive value of these preferences in the antlion larva Myrmeloen crudelis, *a semisedentary insect that digs pit traps in soils to capture small arthropods. I tested the habitat preferences of* M. crudelis *between two soil types in a tropical dry forest of Costa Rica. Specifically, I compared the soil particle composition size within and outside antlion aggregations and manipulated the availability of fine- and coarse-grained soil to assess how differences in soil grain size affect the design and performance of larval traps. Adjacent to antlion pits the soil was composed of a greater proportion of fine-grained particles (<2 mm) than soil 1 m away from the pits. A set of experiments demonstrated that (1) in the presence of equal availability of fine- and coarse-grained soils, all larvae built their pits in fine-grained soil; (2) the larvae required less time to start and finish traps in fine-grained soil; (3) the larvae constructed larger and deeper pits in fine-grained soil; and (4) prey capture increased greatly in fine-grained traps compared with coarse-grained traps. Antlion larvae respond to variations in the proportion of fine particles in the soil, suggesting that antlion aggregations result from an active microhabitat selection. The preference for fine-grained soils is adaptive since pits constructed in such substrate are functional for longer periods and much more successful in trapping prey than pits in coarse-grained soil. Sit-and-wait predators that use sessile traps are spatially constrained to track prey abundance. Therefore, the ability to detect and select microhabitats with better*

---

[1] Lab. Ecotono, Depto. de Ecología, CRUB-UNC, Unidad Postal Universidad del Comahue, 8400, Bariloche, Argentina. e-mail: alefarji@crub.uncoma.edu.ar, alefarji@yahoo.com.

0892-7553/03/1100-0783/0 © 2003 Plenum Publishing Corporation

conditions that enhance capture success may be under strong selection for this type of organism.

KEY WORDS: antlion larvae; Costa Rica; habitat selection; pit design; prey capture; soil; tropical dry forest.

INTRODUCTION

Patchy environments offer a wide variety of habitats for animals to live in. Habitat selection occurs when an individual chooses an area from a set of sites that differ in characteristics that may affect its fitness (Rosenzweig, 1981). The evolutionary importance of habitat selection is based on the assumption that animals actively select habitats in which they show enhanced performance relative to habitats that were not selected. However, little evidence of habitat preference and its adaptive value is available (Martin, 1998).

Habitat selection has been studied primarily in mobile animals, especially birds (Cody, 1981; Danchin *et al.*, 1998; Martin, 1998; Rolstad *et al.*, 2000). However, many organisms are entirely or partially sessile, and local conditions entirely determine their growth, survivorship, and reproduction. Therefore, selective pressures for choosing an adequate habitat should be strong in organisms with limited mobility, making these animals ideal subjects for the study of habitat selection (Orians, 1991). In this study, I examined microhabitat preferences and the adaptive consequences associated with these preferences in antlion larvae, a semisedentary insect.

Antlion larvae (*Neuroptera: Myrmeleontidae*) are sit-and-wait predators that dig pits in loose soil to capture small arthropods that fall into these funnel-shaped traps. These larvae are commonly known as antlions because ants are the most common arthropod in their pit traps (Wilson, 1974). Antlion larvae primarily inhabit warm regions, and they are spatially restricted to open areas with loose soil substrata, which are sheltered from the rain (Wheeler, 1930).

Both food availability and habitat potentially restrict the spatial distribution of antlion populations. However, local distribution of antlion pits is not significantly correlated with prey availability (Gotelli, 1993; Crowley and Linton, 1999), and many ant species effectively avoid antlion aggregations (Gotelli, 1996, 1997). In contrast, several studies have shown that abiotic factors, such as soil moisture, litterfall abundance, temperature, rainfall, and soil compactness, may restrict the habitat available to antlions (McClure, 1976; Simberloff *et al.*, 1978; Boake *et al.*, 1984; Marsh, 1987; Lucas, 1989; Gotelli, 1993; Gatti and Farji-Brener, 2002). For example, Boake *et al.* (1984)

found that antlion larvae were absent from shaded patches of damp soil. Also, antlion larvae are spatially restricted to bare soil because leaf litter greatly reduces capture efficiency (Griffiths, 1980a). In central Oklahoma, antlions are restricted to the sheltered bases of cliff edges because outside of these zones the interaction between rainfall and temperature leads to the formation of a persistent soil crust, which larvae are unable to penetrate (Gotelli, 1993). A similar situation occurs in tropical dry forests of Costa Rica, where soil compactness limits pit abundance in ant-acacia clearings (Gatti and Farji-Brener, 2002).

Considering the hunting behavior of antlion larvae, microhabitat selection may be strongly influenced by soil characteristics (Gotelli, 1993). Thus, it is expected that selection of a suitable substrate for pit construction may initiate a dramatic cascade of consequences for antlion fitness. It is possible that soil characteristics affect construction and maintenance of pit traps, causing substantial differences in metabolic costs for antlion larvae (Griffiths, 1980a; Lucas, 1985). Furthermore, the physical properties of the substratum (i.e., soil grain size) are likely to affect pit morphology (Lucas, 1982), and thus prey capture (Lucas, 1982; Wilson, 1974; Griffiths, 1980a, 1986; Lomascolo and Farji-Brener, 2001), which in turn determines the duration of larval development and adult body size (Goteli, 1997). Despite these findings, microhabitat selection by antlions in relation to soil structure and its potential consequences on individual fitness have not been experimentally tested.

In tropical dry forest of Costa Rica, the most abundant antlion species, *Myrmeleon crudelis*, is restricted to bare soils along forest trails, at the bases of large trees, below cliff overhangs, and underneath logs (McClure, 1976). However, this species does not occupy its entire potential range within these zones. Although the larvae can move along the soil surface to build a new trap (Wilson, 1974; Heinrich and Heinrich, 1984; Crowley and Linton, 1999), dense aggregations of active traps are frequently found surrounded by trap barren areas apparently favorable for larval establishment.

In this study, I investigated the importance of soil structure (grain particle size) in determining the distribution of *Myrmeleon crudelis* at a local scale. Specifically, this study tests whether antlion larvae actively select microhabitats with fine-grained soils by (1) comparing the soil particle size where traps are constructed and adjacent areas without traps and (2) experimentally testing the existence of habitat selection and the adaptive value associated with these preferences. The availability of fine- and coarse-grained soils for antlion larvae was manipulated to assess the influence of soil types on different aspects of pit-building behavior and prey capture.

METHODS

Antlion Natural History

Adult antlions are nocturnal, short-lived, and feeble flyers. After mating, females lay many eggs in the soil (an average of 20 in captivity) from which larvae emerge. A newly eclosed larva digs a conical pit in dry, loose substrate protected from wind and rain. Some larvae later move on the soil surface, searching for a more suitable place to build a pit. To begin the construction of a pit, the larva moves backward, forming a circle on the soil surface. Then, digging deeper, it spirals toward the center, loosening soil particles, which are thrown out of the trap with a flicking motion of the head. Finally, the larva buries itself at the bottom of the pit; only its head and open jaws are visible. When an insect falls into the trap, the antlion attempts to grab it with its elongate, curved mandibles. If the attempt fails and the prey starts to scramble up the slope of the pit, the antlion tosses up soil particles by violently flipping its head, creating minilandslides that drag the prey back into its jaws. Captured prey are digested externally and consumed via the mandibles. When the prey's fluids are completely consumed, the larva throws the carcass out of the pit (Wilson, 1974). The duration of the larval stage is highly variable, requiring at least one to two summer seasons to mature (Gotelli, 1993). Antlion larvae are sessile predators but semisedentary animals (Heinrich and Heinrich, 1984), and larvae can move up to 2 m every 5–70 days along the soil surface to build a new pit (Wilson, 1974; Heinrich and Heinrich, 1984; Crowley and Linton, 1999).

Study Site and Methodology

This study was conducted at Palo Verde National Park, Guanacaste Province, Costa Rica (10°N, 85′W), which includes part of the southernmost Mesoamerican tropical dry forest. The region is highly seasonal, with annual rainfall averaging 1500 mm and a mean annual temperature of 27°C. *Myrmeloen crudelis* is the most common antlion larva in the area; it digs conspicuous conical pits in soils along forest trails, in forest clearings along streams, and near buildings (Wilson, 1974; McClure, 1976).

I conducted field measurements and a series of experiments to determine whether (1) soil particle size differs between microhabitats with and without antlion pits, (2) antlion larvae actively select fine-grained soil to construct their pits, (3) microhabitat selection (if it exists) affects the time invested in trap construction and trap design, and (4) changes in pit design (induced by the substrate in which the trap is built) affect capture success. These experiments were conducted during the dry seasons of 1995–1998.

To test for differences in soil particle size between substrate with and without antlion pits, I followed Gotelli's (1993) methodology. I collected three soil samples from nine randomly chosen areas occupied by antlion pits (hereafter referred to as antlion zones) and the same number of samples from areas 1 m away from pits. These control areas were apparently favorable for larval establishment. An antlion zone was defined as a portion of soil ($\approx 50 \times 50$ cm) with more than five pit traps. Each sample consisted of ≈ 100 g from the upper 5 cm of the soil. Soil samples were air-dried for 5 days and then subdivided by grain size using a series of sieves (<2, 2–6, and >6 mm). Sieved fractions were individually weighed, and the weight converted to percentages of the total sample. These percentages were arcsine transformed and analyzed with a two-way ANOVA, where soil grain size and location (occupied and unoccupied areas) were fixed factors. The interaction between factors tests for differences in the overall distribution of particle size inside and outside the antlion zone.

To assess experimentally the importance of microhabitat preference by antlion larvae between soils with different-sized grains, I collected soil samples around antlion zones. The soil samples were first separated with a series of screen sieves into two types: henceforth referred to as fine-grained (75% of soil particles <2 mm) and coarse-grained (50% of soil particles between 2 and 6 mm and 50% >6 mm). Then each of 70 individual containers (60×25 cm, 25 cm deep) were filled with fine-grained soil in one half and with coarse-grained soil in the other half in order to offer simultaneously equal availability of both soil types to larvae. The cardinal direction of soil types inside each container was randomly assigned. I collected 70 *Myrmeleon crudelis* larvae from different sites in the forest (second and third instars). Each larva was measured (body length) and carefully placed in the center of an individual container (time zero, T_0). In this experiment, larvae were maintained in enclosures that restricted their movement but were allowed to construct natural feeding pits in either soil type. For each larva, I measured the lapse of time from T_0 to the moment when the larvae started digging the trap (pit-building initiation time, T_i) and the time spent in constructing the pit (referred to as pit-building time, T_b). After 24 h, which is sufficient to dig a pit (McClure, 1976; Heinrich and Heinrich, 1984; Lomascolo and Farji-Brener, 2001; Gatti and Farji-Brener, 2002), I counted the number of pits dug in each soil type. For each trap I carefully measured the pit diameter and depth (in millimeters). The pit angle (angle of repose) was calculated from the diameter and vertical depth of the pit. I used a chi-square test to determine whether the construction of a pit was independent of the substrate grain size. If larvae do not select fined-grained soils where they dig their pits, a similar number of pits is expected in each soil type. Because all larvae preferred the half of the fine-grained soil of the container to construct their pits ($\chi^2 = 70$,

$P < 0.0001$), I collected 70 more larvae from the forest for the second experiment (second and third instars). In this experiment, each larva was measured (body length) and placed in an individual container (30 × 20 cm, 25 cm deep) filled with coarse-grained soil only. One day later, the number of pits built was counted. I used a chi-square test with Yates correction (Zar, 1999) to determine whether the pit construction was independent of the soil type. In this second experiment, I also measured T_i, T_b, and pit diameter, depth (mm), and angle.

To assess the effect of soil grain size on pit design, 50 larvae were randomly selected from the containers in which all the pits had been excavated in fine-grained soil and carefully transferring them to new individual containers filled with only coarse-grained soil. Another 50 larvae were randomly selected from the coarse-grained containers and carefully transplanted to new individual containers filled with only fine-grained soil. After 24 h, I measured T_i, T_b, and pit diameter, depth, and angle in all the pits built. In this crossover experimental design, each larva was considered as its own control (before and after the transfers). Thus, I used paired t-tests to detect changes in pit digging times (T_i and T_b), pit size, pit depth, and pit angle between pits built by each larvae in fine-grained and coarse-grained soil. Once this experiment was finished, I used the same containers (50 fine- and 50 coarse-grained, with active traps) to measure pit capture success. As the size of antlion larvae did not differ between soil treatments ($t = 0.5$, df $= 98$, $P > 0.45$), capture success was related to pit design rather than larval dimensions.

To test whether changes in pit design (induced by substrate characteristics) affect pit efficiency, I experimentally examined prey-capture success by placing ants in containers with different soil types and recording whether they escaped from the pit (see Heinrich and Heinrich, 1984). I used this technique instead of placing the ants with forceps directly into the pits (as in Wilson, 1974; Griffiths, 1980, 1986; Lomascolo and Farji-Brener, 2001), because it better reflects the natural history of prey capture (see Heinrich and Heindrich, 1984). Ants were used as prey in the feeding experiment since they are the major food source of antlions in nature (Griffiths, 1980a; Gotelli, 1993). I used *Pseudomyrmex spinicola* ants of similar size (ca. 6 mm long), an abundant ant species in the study area. Each individual ant was observed until it was captured by a larva or escaped from the pit. Capture success or failure was scored for the events when the ant fell into the pit, and only first encounters were used. Chi-square test with Yates correction was used to determine if capture success of a pit was independent of pit substrate. In each capture failure, I measured the time (in seconds) that the ant remained in the pit (T_e) as an indirect measure of trap efficiency. Then I compared T_e in pits dug in coarse- versus fine-grained soil using the nonparametric Mann–Whitney test. All experimental groups for a given experiment were observed simultaneously, so variations in temperature and other environmental variables should not influence the differences detected between groups.

RESULTS

In the field, soil in areas occupied by antlion larvae showed a greater proportion of fine-grained particles than the soil 1 m away. While the percentage of particles <2 mm was higher in soil inside antlion zones, outside antlion zones there was a higher percentage of particles >6 mm ($F_{2,48} = 15.1$, $P < 0.001$; Fig. 1). The association between fine-grained particles and pits could be simply a reflection of the fact that antlion pit construction alters soil particle size. Nonetheless, the preference for fine-grained soil to dig pits was experimentally confirmed. Given equal availability of soil types, all larvae ($n = 70$) selected fine-grained soil to dig their pits, strongly suggesting an active preference for this microhabitat. Moreover, soil trails revealed that several larvae (≈70%) explored the coarse-grained substrate, yet none made obvious attempts to dig a pit in it. In addition, whereas 100% of the antlions from the first experiment dug their pits in fine-grained soil, only 86% larvae from the containers filled only with coarse-grained soils dug their pits ($\chi^2 = 8.7$, df = 1, $P < 0.03$).

Both the time elapsed to the start of digging (T_i) and the construction time (T_b) differed between the two soil types. T_i and T_b were three and two times greater when the larva was in coarse-grained soil (paired *t*-tests, $t = 57.8$ and 35.2, df = 49, both *P*'s < 0.0001; Fig. 2). Pit design was also different for both soil types. An antlion larva digs larger and deeper pits in fine-grained soils (Table I).

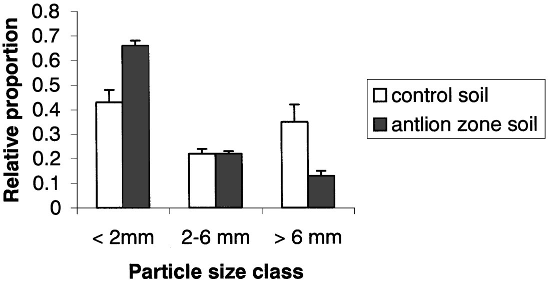

Fig. 1. Size of soil particles within and away from zones occupied by antlion larvae ($N = 9$ zones). Each bar represents the average (+SE) mass of nine soil samples.

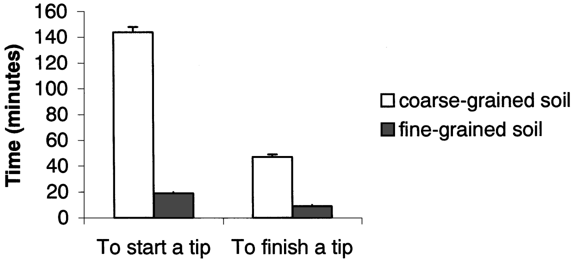

Fig. 2. Time required for an individual antlion larva to start digging a pit (T_i) and to finish a pit once started (T_b) in fine- and coarse-grained soils. Each bar represents the average (+SE) of 50 larvae (see text for further explanations).

These changes in pit design had severe consequences for capture success. While 44 of 50 ants were captured in pits dug in fine-grained soils, only 26 of 50 were captured in pits in coarse-grained soils ($\chi^2 = 13.8$, df $= 1$, $P < 0.001$; Fig. 3). Furthermore, ants that fell into pits dug in coarse-grained soil were retained in the pit for 12 ± 3 s before escaping, whereas the few ants that escaped from pits dug in fine-grained soil were retained in the pits for 29 ± 7 s before escaping (mean ± SE, $U = 132$, $n_1 = 24$, $n_2 = 6$, $P = 0.02$).

DISCUSSION

Habitat selection is a hierarchical process in which an organism makes a series of decisions about the use of different patches within its potential range (Orians and Wittenberger, 1991). On a scale of several meters, absence of litterfall, consistency of the soil, and protection from rain can spatially restrict antlion distribution to specific areas (McClure, 1976; Simberloff *et al.*, 1978; Gotelli, 1993; Gatti and Farji-Brener, 2002). This study confirms that

Table I. Mean (±SE) Diameter, Depth, and Pit Angle of the Pits of the Antlion Larva *Myrmeleon crudelis* in Fine- and Coarse-Grained Soils

	Soil type				
	Coarse-grained	Fine-grained	t^a	df	P
Diameter (mm)	26 ± 1	39 ± 3	7.9	49	<0.001
Depth (mm)	12 ± 1	18 ± 2	5.5	49	<0.001
Angle (deg)	40 ± 1	39 ± 1	0.7	49	0.54

[a] The t-values come from paired t-tests (see text for methodological details).

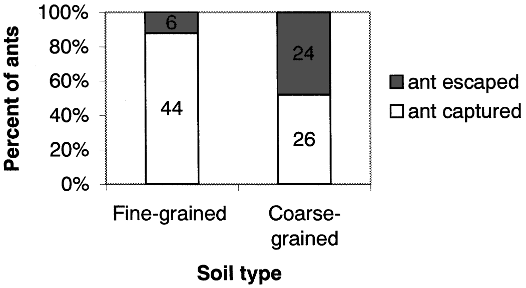

Fig. 3. Percentage of ants that escaped from or were captured in pits dug in fine- and coarse-grained soils. A total of 100 pits was used (50 in each kind of soil).

antlions also respond to smaller-scale variation in features of their potential environments (e.g., the proportion of fine particles in the soil), supporting the hypothesis that antlion larvae fine-tune their microhabitat selection in a hierarchical order (Lucas, 1989).

At the study area, the proportion of fine-grained particles in the soil was significantly greater within the antlion zones than outside them (Fig. 1). This result differs from that reported by Gotelli (1993), who found similar soil particle size within antlion zones and 1 m away from the area of the pits. However, Gotelli's (1993) study was conducted in a sandstone canyon, where soil within and outside antlion zones was mostly composed of particle sizes <2 mm in diameter. On the contrary, soils analyzed in my study was mainly composed of soil particles <2 mm in diameter in those areas occupied by antlion larvae, but this size class of particle dropped to 40% outside occupied areas (Fig. 1). The relative proportion of soil particle sizes probably is not a key factor determining microhabitat preferences in areas where soil is homogeneous and consists of mostly fine-grained particles, as in sandstone canyons (Gotelli, 1993). However, in dry tropical forests, soil is more heterogeneous and includes patches of larger particle size that enable microhabitat selection by antlions for soil with more fine-grained particles (see also Lucas, 1982).

One alternative hypothesis to explain the observed spatial aggregation of antlion larvae in patches of fine-grained soil is that such patchy distribution is a consequence of the behavior of adult female antlions. Adult neuropterans (lacewings) probably oviposit in opens areas (Wheeler, 1930; Lucas, 1989), but larvae are relatively mobile and often travel several meters to relocate their pit (Heinrich and Heinrich, 1984; Crowley and Linton, 1999). Therefore, female oviposition behavior may contribute to the initial spatial variation in pit density but not to the maintenance of the aggregated distribution of larvae (Gotelli, 1993).

The association between soil grain heterogeneity and the presence of antlion aggregations in the field likely results from larval preferences: in the presence of equal availability of fine and coarse soils, all the sampled antlions actively selected fine-grained soil to dig their pits. Moreover, the soil tracks in the experimental containers revealed that most of the larvae selected fine-grained soil *after* having explored coarse-grained soil. This confirms a key assumption of habitat selection: animals actively explore, search, and discriminate among habitats before choosing a particular place for establishment (Rosenzweig, 1991). Habitat selection may also occur in response to certain habitat characteristics that are strongly associated with habitat quality. For example, if food availability or predation risk varies with abundance of plants in an area, different levels of plant density provides cues that facilitate habitat selection (Rolstad *et al.*, 2000). At the antlions temporal and spatial scale, the distribution of soil particle size is a consistent microhabitat characteristic that can predict habitat quality, and thus, the larvae are able to employ it to detect and choose among patches.

Although antlions can dig pits in coarse-grained soil, larvae always select fine-grained soil patches if they have a choice. What is the adaptive value of this preference? The behavior of habitat selection in antlions can also be analyzed as a simple cost–benefit relationship where the costs are those associated with pit construction and benefits result in prey capture (Griffiths, 1986). This study shows that excavating a pit in fine-grained soil results in higher benefits and lower costs for a larva than digging a pit in coarse-grained soil. The time elapsed to start digging a pit was greater in coarse-grained than in fine-grained soil (Fig. 2), probably because the larvae were searching for better patches to dig their pits. Larvae in containers with only coarse-grained soils showed two short-term behaviors: they buried themselves without digging pits or digging the pit required twice the investment in time than in fine-grained soil (Fig. 2). Larger soil particles are probably more difficult to handle for larvae (Lucas, 1982), and thus they require more time to dig functional pits. Regardless of the cause of this behavior, spending more time both to initiate and to dig the pit is costly for a larva. Nonfunctional pits decrease the total foraging time and increase the total energy expended in construction (Griffiths, 1980a; Crowley and Linton, 1999). Metabolic expenditures during pit construction are about an order of magnitude higher than metabolic rates at rest (Lucas, 1985). Longer times for pit construction thus require the use of more energy from reserves, with detrimental consequences to antlion growth (Griffiths, 1985). For example, the growth rate and mean weight of the antlions whose pits have been disturbed are almost 50% lower compared to those of undisturbed larvae of similar body size (Griffiths, 1980a).

Larvae that dig pits in fine-grained soil also accrue benefits other than having functional pits for longer periods. It has been shown that several features of pit design, such as depth, diameter, and pit angle, influence efficiency in prey capture (Wilson, 1974; Griffiths, 1980a, 1986; Lucas, 1982). This study demonstrates that the proportion of fine-grained particles in the soil affects dimensions of pit diameter and depth, features that directly affect trap capture success. Pits dug in fine-grained soil were 50% bigger, 50% deeper, and 100% more efficient in capturing prey than pits dug in coarse-grained soil (Table 1, Fig. 3). Pit diameter and depth are features of the trap that influence capture success by affecting the probability of prey encounter and prey retention, respectively (Griffiths, 1986; Lomascolo and Farji-Brener, 2001). For example, a 2-mm increase in diameter results in a 10% increase in capture success, regardless of the prey species (Griffiths, 1980a, 1986). Larger pits also capture a wider variety of prey types and sizes and decrease the time between captures compared with smaller traps (Griffiths, 1986; Crowley and Linton, 1999). Additionally, larger-diameter pits produce a more favorable thermal environment for larvae than smaller traps, extending larvae activity without exceeding the upper critical body temperature (Marsh, 1987). On the other hand, deeper pits reduce prey escape probability (Griffiths, 1980a, 1986; Lomascolo and Farji-Brener, 2001; see also Fig. 3), because capture success increases dramatically when ants cannot place their legs outside the pit (Griffiths, 1980a). Accordingly, ants escaped three times faster from pits dug in coarse-grained soil than from the pits dug in fine-grained soil (Fig. 2).

The low capture success of pits in coarse-grained soil has other indirect costs for antlions. Food-limited larvae build and repair their pits more frequently than well-fed larvae (Arnett and Gotelli, 2001), and they are more likely to abandon their pits (Griffiths, 1980a). Both activities, maintenance and relocation of pits, require a high amount of energy (Griffiths, 1980a, b, 1986; Lucas, 1985; Crowley and Linton, 1999) and may increase mortality risk (Simberloff *et al.*, 1978; Lucas, 1989).

Digging a pit in coarse-grained soil decreases, directly or indirectly, the probability of prey captures. However, I did not correlate capture success with larval fitness because I did not measure larval survival, larval growth rate, or number of offspring per adult. However, other studies have demonstrated that food is one of the most important limiting resources for antlion larvae (Griffiths, 1980b, 1986, 1991; Lucas, 1985; Gotelli, 1993; Crowley and Linton, 1999). For example, antlions fed with three additional ants per week shorten the duration of larval life by 40%, gained significantly more mass, had decreased mortality rates, developed into larger pupae, and emerged with a significantly greater mass as adults compared with controls (Griffith, 1980b; 1985; Gotelli, 1997). Therefore, the reduction of capture success in coarse-grained soil that I found in this study probably affects larval fitness directly.

Although abiotic factors appear to determine the spatial patchiness of antlions' distribution (Lucas, 1982; Boake *et al.*, 1984; Gotelli, 1993; Gatti and Farji-Brener, 2002), there are several biotic consequences of this spatial aggregation. First, as they are restricted to specific microhabitats, the distribution of larvae may not be associated with their resources (e.g., ant nests) on a microscale. Similar constraints have been described for antlions in sandstone canyons (Gotelli, 1993) and in a tropical dry forest in Costa Rica (Gatti and Farji-Brener, 2002), showing how abiotic constraints may produce deviations from an ideal free distribution (see Fretwell and Lucas, 1970). Second, as antlions are spatially restricted to discrete sites where prey abundance may be low and unpredictable (Lucas, 1985; Griffiths, 1986; Gotelli, 1993), the probability of competition and cannibalism may increase (Lucas, 1989; Gotelli, 1997). These intraspecific interactions likely affect the dynamics of antlion populations (Gotelli, 1993). Third, since ants—the most common food resource for antlions—avoid foraging within antlion zones (Gotelli, 1996), pit-trap aggregations may affect prey abundance and distribution, which in turn may influence capture success.

The theory of habitat selection is based largely on studies of mobile animals (Rosenzweig, 1981). Regardless of their general immobility, sedentary organisms (including plants) can cope with much of the small-scale variability in their habitat by shortterm, reversible adjustments to environmental changes. For example, plants can exploit favorable or avoid unfavorable patches via the selective placement of roots and ramets (Evans and Cain, 1995; Gersani *et al.*, 1998, 2001). Sedentary ant nests, by adjusting their foraging trail ends, can discriminate and selectively reach patches with a greater abundance of resources (Lopez *et al.*, 1993). However, sessile predators such as antlions are unable to track prey abundance because abiotic factors often restrict the location of their traps (Gotelli, 1993; Crowley and Linton, 1999; Gatti and Farji-Brener, 2002). Therefore, behavioral adjustments that maximize capture success given the constraints imposed by abiotic environmental conditions should be under strong selective pressure in this group of animals. The antlions' ability to detect and select microhabitats where they can modify their pit design to improve its capture efficiency is probably one of these behavioral adjustments selected.

ACKNOWLEDGMENTS

I appreciate the helpful comments of M. "Larva" Tadey, G. Barrantes, B. Wcislo, Frank Joyce, C. Peñaloza, N. Gotelli, and two anonymous reviewers. I also thank the Organization for Tropical Studies (OTS) for facilitating this work at the Palo Verde Biological Station and 1995–1998 OTS Spanish courses for their help in the field.

REFERENCES

Arnett, A., and Gotelli, N. (2001). Pit-building decisions of larval ant lions: Effects of larval age, temperature, food and population source. *J. Insect Behav.* **14:** 89–97.

Boake, C., Andow, D., and Visscher, K. (1984). Spacing of ant-lions and their pits. *Am. Midl. Nat.* **111:** 192–194.

Cody, M. (1981). Habitat selection in birds: The roles of vegetation structure, competitors, and productivity. *BioScience* **31:** 107–113.

Crowley, P., and Linton, M. (1999). Antlion foraging tracking prey across space and time. *Ecology* **80:** 2271–2282.

Danchin, E., Boulinier, T., and Massot, M. (1998). Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* **79:** 2415–2428.

Evans, J., and Cain, M. (1995). A spatially explicit test of foraging behavior in a clonal plant. *Ecology* **76:** 1147–1155.

Fretwell, S. D., and Lucas, H., L. Jr. (1970). On territorial behavior and other factors influencing habitat distribution in birds. Theoretical development. *Acta Biotheor.* **19:** 16–36.

Gatti, G., and Farji -Brener, A. G. (2002). Low density of antlion larvae (*Myrmeleon crudelis*) in ant-acacia clearings: High predation risk or inadequate substrate? *Biotropica* **34**(3): 358–362.

Gersani, M., Abramsky, Z., and Falik, O. (1998). Density–dependent habitat selection in plants. *Evol. Ecol.* **12:** 223–234.

Gersani, M., Brown, J., O, Brien, E., Maina, G., and Abramsky, Z. (2001). Tragedy of the commons as a result of root competition. *J. Ecol.* **89:** 660–669.

Gotelli, N. (1993). Ant lion zones: Causes of high-density predator aggregations. *Ecology* **74:** 226–237

Gotelli, N. (1996). Ant community structure: Effects of predatory ant lions. *Ecology* **77:** 630–638.

Gotelli, N. (1997). Competition and coexistence of larval ant lions. *Ecology* **78:** 1761–1773.

Griffiths, D. (1980a). The feeding biology of antlion larvae. Prey capture, handling and utilization. *J. Anim. Ecol.* **49:** 99–125.

Griffiths, D. (1980b). The feeding behavior of ant-lion larvae: Growth and survival in Morter obscurus. *Oikos* **34:** 364–370.

Griffiths, D. (1985). Phenology and laval-adult size relations in the antlion Macroleon quinquemaculatus. *J. Animal Ecol.* **54:** 573–581.

Griffiths, D. (1986). Pit construction by antlion larvae: a cost-benefit analysis. *J. Anim. Ecol.* **55:** 39–57.

Griffiths, D. (1991). Food availability and the use of storage of flat by antlion larvae. *Oikos* **60:** 162–172.

Heinrich, B., and Heinrich, M. (1982). The pit-foraging strategy of the ant lion, *Myrmeleon immaculatus* de Geer (Neuroptera: Myrmeleontidae). *Behav. Ecol. Sociobiol.* **14:** 151–160.

Jaenike, J., and Holt, R. (1991). Genetic variation for habitat preference: Evidence and explanations. *Am. Nat.* **137** (Suppl.): S67–S115.

Lomascolo, S., and Farji-Brener, A. G. (2001). Adaptive short-term changes in pit design by antlion larvae (Myrmeleon sp.) in response to different prey conditions. *Ethol. Ecol. Evol.* **13:** 395–399.

López, F., Acosta, F., and Serrano, J. M. (1993). Responses of trunk routes of a harvester ant to plant density. *Oecologia* **93:** 109–113.

Lucas, J. (1982). The biophysics of pit construction by antlion larvae (Myrmeleon, Neuroptera). *Anim. Behav.* **30:** 651–664.

Lucas, J. (1985). Melabolic rates and pit construction costs of two antlion species. *J. Anim. Ecol.* **54:** 295–309.

Lucas, J. (1989). Differences in habitat use between two pit-building antlion species: Causes and consequences. *Am. Midl. Nat.* **121:** 84–98.

Lucas, J., and Brockmann, H. (1981). Predatory interactions between ants and antlions. *J. Kans. Entomo. Soc.* **54:** 228–232.

Marsh, A. (1987). Thermal responses and temperature tolerance of a desert ant-lion larva. *J. Therm. Biol.* **12:** 295–300.

Martin, T. (1998). Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79:** 656–670.

McClure, M. (1976). Spatial distribution of pit making antlion larvae (Neuroptera: Myrmeleontidae): Density effects. *Biotropica* **8:** 179–183.

Orians, G. (1991). Habitat selection: Preface. *Am. Nat* **137** (Suppl.): S1–S4.

Rolstad J., Loken, B., and Rolstad, E. (2000). Habitat selection as a hierarchical process: The green woodpecker at the northern edge of its distribution range. *Oecologia* **124:** 116–129.

Rosenzweig, M. (1981). A theory of habitat selection. *Ecology* **62:** 327–335.

Rosenzweig, M. L. (1991). Habitat selection and population interactions: The search for mechanism. *Am. Nat.* **137:** S5–S28.

Simberloff, D., King, L., Dillon, P., Lowrie, S., Lorence, D., and Schilling, E. (1978). Holes in the doughnut theory: the dispersion of antlions. *Brenesia* **14:** 13–46.

Wheeler, W. (1930). *Demons of the Dust*, Norton, New York.

Wilson, D. S. (1974). Prey capture and competition in the antlion. *Biotropica* **3:** 187–193.