

# Spatiotemporal Variation in Antlion (Neuroptera: Myrmeleontidae) Density and Impacts on Ant (Hymenoptera: Formicidae) and Generalized Arthropod Foraging

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**ABSTRACT** Antlion larvae that construct conical pits to capture prey may strongly affect foraging of ants and other arthropods, yet are usually abundant only in sheltered microhabitats. Larval antlion (*Myrmeleon crudelis* Walker) densities increased in exposed areas in central Texas in late summer and early autumn of 1998, presumably because of extended dry conditions. I conducted a study to quantify larval antlion pit densities in sheltered and exposed areas over time, and to examine the effect of variation in pit density on the foraging activity of ants and other arthropods. Isolated rainfall events decreased pit densities in exposed areas, sometimes to zero, but pit densities returned to high levels as the soil dried out. Pitfall traps at sheltered sites caught significantly fewer ants and other arthropods inside antlion zones (i.e., areas of high antlion density) than in adjacent areas without antlions. At exposed sites, pitfall traps caught significantly fewer ants in antlion zones when pits were present (dry conditions) than when they were absent (wet conditions); there was no significant difference in foraging outside the antlion zones in wet compared with dry conditions. Significantly fewer ants were caught inside antlion zones at sheltered sites (that were permanent) compared with exposed sites (that were transient), although pit densities were similar at both types of sites. Attraction of ants to baits revealed similar patterns. Spatiotemporal variation in antlion pit densities and the associated predation risk to ants and other arthropods may result in behavioral modifications of foraging patterns, higher mortality rates, or both.

**KEY WORDS** antlion zone, Formicidae, *Myrmeleon crudelis*, Myrmeleontidae, predation risk

ANTS ARE IMPORTANT COMPONENTS of many terrestrial ecosystems. The Formicidae is both taxonomically diverse (an estimated 15,000 living species) and geographically widespread (present everywhere but the polar regions) (Bolton 1994). Accordingly, a great variety of life histories, morphologies, and foraging strategies exists. Despite the diversity that characterizes this subfamily, the single most important factor limiting many ant populations is thought to be intra- or interspecific competition with other ants. Indeed, many studies have conclusively demonstrated the importance of competition in structuring ant communities (Wilson 1971, Cole 1983, Fellers 1987, Ward 1987, Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990, Porter and Savignano 1990, Morrison 1996, Holway 1999).

Predators, pathogens, and parasites may also be capable of limiting ant populations under certain conditions (Hölldobler 1970, Edwards et al. 1974, Feener

1981, MacKay 1982, Waller and Moser 1990, Briano et al. 1995, Orr et al. 1995, Porter et al. 1995, Gotelli 1996, Morrison 1999), yet such organisms have not received as much attention as competitors. One reason may be that the effects of some members of the former group are more restricted in space or time. For example, antlions (Neuroptera: Myrmeleontidae) are ant predators that are common in many regions, although most pit-building species are found only in sheltered locations where dry, loose soil makes pit construction possible (Topoff 1977). Antlion pits may become very dense in such areas, and their presence may greatly reduce ant foraging activity (Gotelli 1993, 1996). These sheltered areas represent a very small proportion of the overall landscape, however.

During extended dry conditions, however, soil in exposed areas may become suitable for pit construction, and antlion larvae may become more abundant and widespread, resulting in an increased predation risk for foraging worker ants and other arthropods. Predation risk is known to be an important factor influencing foraging decisions in animals in general (Lima and Dill 1990; Sih 1992, 1994; Kats and Dill 1998; Lima 1998; Lima and Bednekoff 1999) and ants in

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particular (e.g., Nonacs 1990, Nonacs and Dill 1990). A greater predation risk associated with higher larval antlion densities may result in decreased foraging activity, greater mortality of foragers, or both.

In the summer of 1998, larval antlion densities in some areas of central Texas reached unusually high levels, and a study was initiated to elucidate their effects on ants and other arthropods. The following questions were addressed: 1) How did antlion pit densities in exposed areas vary over a period of 1 yr, and how did these densities compare with those in sheltered areas? 2) What environmental factor(s) was correlated with variation in antlion pit densities in exposed areas? 3) Did the presence of antlion pits affect the foraging of ants and other arthropods in the same way in sheltered and exposed areas?

### Materials and Methods

Antlion larvae (Neuroptera: Myrmeleontidae) are predators of small arthropods. The construction of funnel-shaped pits to capture prey occurs within the tribe Myrmeleontini (New 1986), and is characteristic of the genus *Myrmeleon* (Lucas and Stange 1981). The nocturnally active, winged adults oviposit in substrates composed of small, dry, loose particles; and developing larvae construct conical pits to capture prey. While antlion larvae feed on a diversity of arthropods, ants usually comprise the majority of the prey items (Topoff 1977).

This study was conducted from 15 August 1998 to 30 August 1999 on the grounds of the University of Texas' Brackenridge Field Laboratory (BFL; Austin, TX). BFL contains numerous overhanging limestone cliffs and several abandoned structures (without floors) that create ideal antlion habitat, and antlion larvae were common in these areas for at least several years before the initiation of this project (unpublished data). Two major habitat types were defined for the purpose of this study: 1) "Sheltered" areas were regions immediately beneath abandoned structures that provided protection from rain and direct overhead sunlight (but not from running water during flooding, or sunlight at low angles). The soil was dry, fine, mostly free of vegetation, and represented ideal antlion habitat. 2) "Exposed" areas were defined as having no solid protection (i.e., rock, building materials) within a few meters above ground level, but most were beneath tree canopies of varying coverage, which allowed rain and some degree of direct, overhead sunlight to penetrate. Exposed areas also contained open patches of loose soil, primarily from disturbances (see *Discussion*). All antlion larvae examined from both sheltered and exposed sites were *Myrmeleon crudelis* Walker. At least 49 species of ants were present at BFL (Morrison 2002).

Three permanent strip transects were established in exposed areas of BFL on 15 August 1998 to document variation in pit density in exposed areas over time. Each transect was 8 m long and 0.5 m wide. Antlion pits were counted along each transect from 15 August 1998 to 30 August 1999. Counts were conducted several

days per week in the autumn of 1998, when pit densities were highest and most variable, and at least once every 2 wk thereafter. Transects were located along wildlife (primarily white-tail deer, *Odocoileus virginianus* [Boddaert]) trails, and the disturbance of the soil by passing animals prevented overgrowth of vegetation throughout the year.

Six permanent rectangular study plots were established on 8 August 1998 to compare pit densities in exposed and sheltered areas. Three plots were located in sheltered areas, under abandoned structures that had solid roofs and were open on one, two, or all sides. At these plots, antlion pits were abundant in the area protected from falling rain (i.e., immediately underneath the roof), but rare outside this area. Three plots were in exposed areas with mostly bare soil. The exposed plots consisted of a concentration of antlion pits surrounded by an area with few antlions.

At each plot, the area of dense antlion pits (i.e., the antlion zone) was circumscribed and measured. Antlion zones varied from 6.5 to 15.0 m<sup>2</sup>. A subplot of each antlion zone was delimited, and all pits in this subplot were counted and measured. Subplots were established in the central portion of the antlion zone, in a region representative of the overall plot. Subplots ranged from 3.2 to 4.3 m<sup>2</sup>. A wooden scaffold was placed over the plots to accurately measure pit diameters from directly above, without disturbing any of the pits. All antlion pits in the subplots at all six sites were measured at five intervals: August and December 1998; and March, June, and August 1999.

Pitfall trapping was conducted on 4 dates (8, 27, 31 August and 8 October 1998) at each of the 6 study plots. On each date, 10 traps were set out at each plot, 5 inside and 5 outside the antlion zone. Pitfall traps were plastic vials (3 cm diameter × 5.5 cm deep), and contained propylene glycol as a preservative. The 3-cm-diameter mouth of the pitfall traps approximated an average size antlion pit. The traps were placed out between 16:00 and 18:00 and were left out for 24 h.

Baits were set out on 9 and 28 August, 1 September, and 9 October 1998. Six baits were used at each of the six study plots, three inside and three outside the antlion zone. The baits were ≈3-g sections of Oscar Mayer hot dogs (pork and turkey), placed on 5 × 5-cm white plastic cards. Baits in direct sun were shaded. Baits were set out between 16:00 and 18:00. After 1 h, the number and species identities of all ants present on the cards were recorded.

Pitfall traps and baits were always located inside the subplots where pits were measured when placed inside the antlion zone, and away from any visible pits when placed outside the antlion zone. Those placed outside were never located >1 m away from the boundary of the antlion zone. Baiting trials were always conducted after pitfall traps had been collected, to prevent recruitment to baits biasing pitfall trap catches. More pitfall traps than baits were used because some pitfalls were disturbed by nocturnally active mammals. Pitfall traps that were disturbed were not included in the analyses. Baits, which were left out for only 1 h, were never disturbed.

During two of the sample periods (27–28 August and 31 August–1 September), the soil was dry, and many pits were present inside the exposed antlion zones. During the other two periods (8–9 August and 8–9 October), the soil in open areas was moist from recent rainfall, and no pits were visible inside the exposed sites when baits and pitfall traps were placed out. (Antlion larvae may have been present, but simply unable to construct pits in the moist soil.) Pit densities inside the sheltered sites were not obviously affected by these rainfall events. Thus, two time periods were sampled: with and without recent rainfall.

Specimens caught in pitfall traps were sorted to order except for Oligochaeta, Diplopoda, and Gastropoda, which were sorted to class. Collembolans were not counted, but recorded as present or absent. The Formicidae were further sorted to species, and all other taxa to morphospecies. Ants that recruited to baits were determined to species. Reference specimens of ants have been deposited at BFL.

Variation in the distribution of pit sizes was analyzed by  $\chi^2$  tests of homogeneity (Daniel 1990). All pits in the three plots for each type of site (sheltered or exposed) were combined. Comparisons of pit size distributions were made between the sheltered and exposed sites in August 1998, and among the five different sampling dates for the sheltered sites. Average pit size was also evaluated in the same comparisons, by a two-tailed *t*-test and a one-way analysis of variance (ANOVA), respectively. Data were log transformed to normalize the distributions. Because antlion larvae of the same size constructed relatively larger pits in the sheltered areas (unpublished data), comparisons of pit size and distribution were made to elucidate the relative predation risk to potential prey, rather than to indicate differences in larval antlion size or age.

Three-way ANOVAs were used to analyze the pitfall trap data. The three factor levels were site (sheltered vs exposed), location (inside vs outside the antlion zone), and moisture (wet vs dry; i.e., with vs without recent rainfall). All factors in the model were fixed. Four separate analyses were conducted for: 1) total number of ant species, 2) total number of ant individuals, 3) total number of nonant morphospecies, and 4) total number of nonant individuals. Log transformations ( $\ln[n + 1]$ ) were performed to normalize the data before analyses. After the ANOVAs, four contrasts of treatment means were evaluated by the Bonferroni method of multiple comparisons (Neter et al. 1985).

Ant recruitment to baits was measured as the number of individual workers on the bait cards summed over all species after 1 h. Ant recruitment was compared for the six treatments (outside sheltered sites, dry; outside sheltered sites, wet; outside exposed sites, dry; outside exposed sites, wet; inside exposed sites, dry; inside exposed sites, wet; in which wet and dry refer to the soil) by a one-way ANOVA. Because no ants were found inside the sheltered sites in wet or dry conditions, these two treatments were not included. A one-way ANOVA was used in this analysis because interest was on whether recruitment varied among the

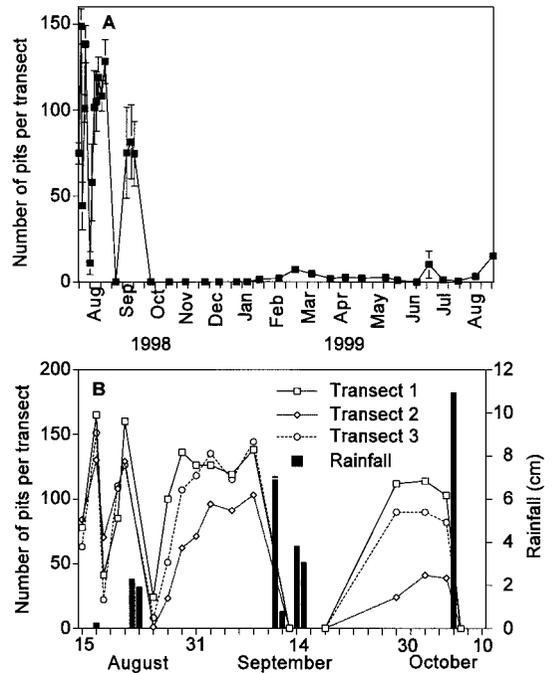


Fig. 1. (A) Abundance of antlion pits over 1 yr along the strip transects. Points represent averages of the three transects; error bars indicate 1 SE. (B) Abundance of antlion pits along each of the three strip transects and rainfall events in the late summer and early fall of 1998.

six treatments that had foraging ants. StatView 5.0.1 (SAS Institute, Cary, NC) was used for all statistical analyses.

Results

Antlion pit densities varied greatly over time in exposed areas. Along the three strip transects, pit densities were highest from August to early October 1998 (Fig. 1A). In mid-October 1998, pit densities declined to zero; pits were present at very low densities in the spring and summer of 1999. Pits were not censused before 15 August 1998, but, qualitatively, it was observed that in the preceding 3 yr, in exposed areas, pit densities did not reach the levels observed in the summer of 1998 (unpublished data).

The relatively high pit densities recorded in August–October 1998 followed a period of low rainfall that allowed soil in exposed areas to become dry enough for pit construction. The 30-yr average rainfall in Austin, Texas, for the 4-mo period April–July is 32.7 cm (National Climatic Data Center, Asheville, NC). Actual rainfall for April–July 1998 was only 10.1 cm (31% of 30-yr average). Conversely, the relatively low pit densities observed in the summer of 1999 followed a relatively wet April–July, in which rainfall was 39.8 cm (122% of 30-yr average).

Although densities of antlion pits along the three strip transects reached high levels during August–October 1998, pit numbers varied greatly during this

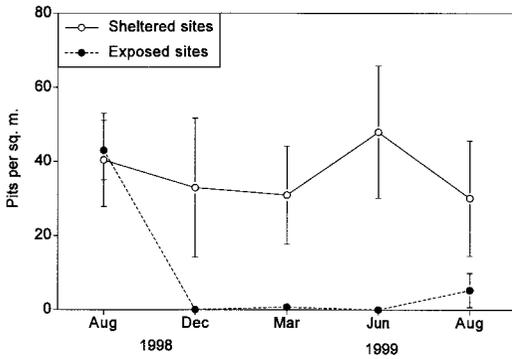


Fig. 2. Mean density of antlion pits at the sheltered and exposed sites over 1 yr. Error bars represent 1 SE.

time period. Pit densities always decreased after measurable precipitation, and increased back toward their original levels as the soil dried out again (Fig. 1B). There was a strong negative correlation between pit density (averaged over the three transects) and rainfall (cumulated over the previous 3 d) ( $r = -0.80$ ;  $F = 28.29$ ;  $df = 1, 16$ ;  $P = 0.0001$ ). After heavy rains in the month of October 1998 (31.47 cm, 360% of normal), no pits were found again until January 1999 (Fig. 1A). The absence of pits in the late autumn and early winter may have been because of numerous factors, including increased rainfall, lower temperatures, and accumulation of leaf litter.

The average density of antlion pits in the sheltered plots remained relatively high throughout the year, ranging from 30 to 50 pits per  $m^2$  (Fig. 2). The average density of antlion pits in the exposed sites was similar to that for the sheltered sites in August 1998, but declined to zero by the December census and remained near zero until the following August census, when  $\approx 5$  pits per  $m^2$  were recorded. This is the same general pattern as found in the strip transects (compare with Fig. 1A).

In August 1998, an average of 40.4 pits/ $m^2$  was recorded from the three sheltered sites, whereas an average of 43.0 pits/ $m^2$  was found in the three exposed sites. The overall distributions of pit sizes were different for the exposed and sheltered sites ( $\chi^2 = 56.2$ ,  $df = 24$ ,  $P = 0.0002$ ,  $\chi^2$  test of homogeneity). The average pit diameter was not significantly different, however ( $27.0 \pm 13.5$  vs  $26.7 \pm 10.2$  mm [mean  $\pm$  SD], sheltered vs exposed, respectively;  $P = 0.26$ , two-tailed  $t$ -test).

Over the year, the distribution of pit sizes in all three sheltered sites considered together varied significantly ( $\chi^2 = 479.8$ ,  $df = 116$ ,  $P < 0.0001$ ,  $\chi^2$  test of homogeneity). Average pit diameter also varied significantly ( $F = 65.2$ ;  $df = 4, 2190$ ;  $P < 0.0001$ ; one-way ANOVA), ranging from a low of  $16.2 \pm 8.3$  mm in December 1998 to a high of  $26.9 \pm 13.5$  mm in August 1998.

A total of 2,283 specimens was recorded from pitfall traps (not including Collembolans). Overall, ants accounted for 68% of the individual specimens. The

ANOVAs revealed no three-way interactions for any analysis. For both ant species and ant individuals, the interaction between site and location was highly significant. For both nonant morphospecies and nonant individuals, the interaction between location and moisture was highly significant. The importance of the interaction between site and moisture varied among the dependent variables (Table 1).

Four contrasts of interest revealed the following patterns (Table 2; Fig. 3): 1) At sheltered sites, traps caught less where antlion pits were present (inside, wet and dry conditions) than where they were absent (outside, wet and dry conditions). This was true for ant species and individuals as well as nonant morphospecies and individuals. 2) Inside antlion zones at exposed sites, more ant species and individuals were caught during moist conditions when antlion pits were absent, than during dry conditions when they were present. This contrast revealed no significant differences for nonants. 3) Outside antlion zones at exposed sites, there were no significant differences between wet and dry conditions for ant species, ant individuals, or nonant morphospecies. More nonant individuals were caught during dry than wet conditions. 4) Traps caught less inside sheltered sites where antlion pits were present (wet and dry conditions) than inside exposed sites where antlion pits were present (dry conditions only). This was true for ant species and individuals, and nonant individuals, but not nonant morphospecies.

In other words, at sheltered sites there were lower catches of all potential antlion prey, on the basis of both species richness and numerical abundance, where antlion pits were present than where they were absent. In comparisons of exposed sites, more ants were caught inside the antlion zone during moist conditions, when pits were absent, than during dry conditions, when pits were abundant. No significant difference was found for ants between wet and dry conditions outside the antlion zones. There were no significant differences for any of the comparisons of nonants at the exposed sites except that more nonant individuals were caught outside the antlion zone when it was dry. Finally, more ants and nonants (on an abundance basis only) were caught inside the exposed sites when pits were present than inside the sheltered sites (which always contained pits).

Fifteen ant species were captured in pitfall traps over the course of this study (Table 3). At sheltered sites, *Solenopsis invicta* Buren was the most common ant species, being very abundant outside, but rare inside, the antlion zones (20.36 vs 0.13 individuals/trap, respectively). At the exposed sites, 3 *Pheidole* species, *P. floridana* Emery, *P. bicarinata* Mayr, and *P. dentata* Mayr, were more common than other species, both inside and outside the antlion zones. The sheltered sites tended to be surrounded by open, sunny areas that represented favorable habitat for *S. invicta*, while the exposed areas were more shaded. Overall, similar numbers of species were caught outside the sheltered areas compared with inside and outside the exposed areas (12, 10, and 11 species, respectively). In

**Table 1. Summary of three-way ANOVA results for the pitfall trap data; four different dependent variables were evaluated**

Source	df.	MS	F	P
Ant species				
Site	1	11.034	97.40	<0.0001
Location	1	10.814	95.46	<0.0001
Moisture	1	0.236	2.08	0.1521
Site × location	1	2.827	24.95	<0.0001
Site × moisture	1	0.502	4.43	0.0375
Location × moisture	1	0.029	0.25	0.6160
Site × location × moisture	1	0.087	0.77	0.3821
Error	110	12.461		
Ant individuals				
Site	1	20.195	43.58	<0.0001
Location	1	63.183	136.36	<0.0001
Moisture	1	0.461	1.00	0.3208
Site × location	1	23.256	50.19	<0.0001
Site × moisture	1	11.228	24.23	<0.0001
Location × moisture	1	1.055	2.28	0.1342
Site × location × moisture	1	0.021	0.05	0.8327
Error	110	0.463		
Nonant morphospecies				
Site	1	1.850	10.23	0.0018
Location	1	5.735	31.71	<0.0001
Moisture	1	1.184	6.55	0.0118
Site × location	1	0.143	0.79	0.3750
Site × moisture	1	0.774	4.28	0.0409
Location × moisture	1	1.582	8.75	0.0038
Site × location × moisture	1	0.172	0.95	0.3316
Error	110	0.181		
Nonant individuals				
Site	1	3.33	8.22	0.0050
Location	1	22.61	55.77	<0.0001
Moisture	1	11.73	28.93	<0.0001
Site × location	1	0.580	1.43	0.2343
Site × moisture	1	0.156	0.38	0.5365
Location × moisture	1	7.627	18.81	<0.0001
Site × location × moisture	1	0.047	0.12	0.7342
Error	110	0.405		

contrast, pitfalls inside the sheltered areas captured only 4 ant species (Table 3).

Twenty-one invertebrate groups (primarily orders; see *Materials and Methods*) were caught in pitfall traps over the course of the study (Table 4). As observed with ants, a similar taxonomic richness was captured outside the sheltered areas and inside and outside the exposed areas, whereas ≈30% fewer groups were captured inside the sheltered areas.

The baits confirmed the same general patterns as the pitfall traps. The total number of baits that were

discovered by ants and to which recruitment occurred was similar for all treatments except inside the sheltered antlion zones, where no ants were found (Fig. 4a). Although pitfall trapping revealed the species richness of ants to be similar at the sheltered and exposed sites, the number of ant species recruiting to baits was higher at the exposed sites (Fig. 4b). Eight species of ants were attracted to baits at the exposed sites: *Crematogaster laeviuscula* Mayr, *Monomorium minimum* (Buckley), *P. bicarinata*, *P. floridana*, *Pheidole dentata*, *Pachycondyla harpax* (F.), *S. invicta*, and

**Table 2. Contrasts of treatment means evaluated by the Bonferroni method of multiple comparisons (Neter et al. 1985)**

Contrast	Ant species	Ant individuals	Nonant morphospecies	Nonant individuals
1) Antlion pits present vs absent at sheltered sites	**	**	**	**
2) Antlion pits present (dry) vs absent (wet) inside exposed sites	*	**	NS	NS
3) Antlion pits absent outside exposed sites: wet vs dry	NS	NS	NS	**
4) Antlion pits present at sheltered sites vs present at exposed sites	**	**	NS	*

For each significant contrast, pitfall trap catches of the respective groups were less for the first combination of factor level means specified in the contrast.

\*, Significant at family confidence coefficient of 0.90. \*\*, Significant at family confidence coefficient of 0.99. NS, not significant.

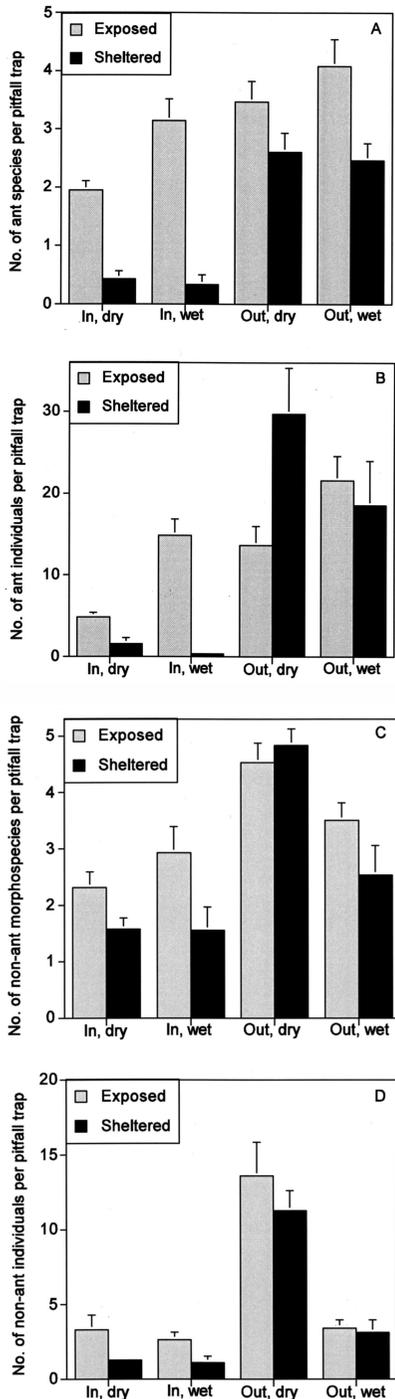


Fig. 3. Summary of pitfall trap captures by site, location, and moisture for (A) ant species, (B) ant individuals, (C) nonant morphospecies, and (D) nonant individuals. In = inside the antlion zone. Out = outside the antlion zone. Dry = dry soil. Wet = moist soil from recent rain. Error bars represent 1 SE.

*Solenopsis texana* Emery. Only three species of ants were attracted to baits at the sheltered sites: *M. minimum*, *P. floridana*, and *S. invicta*. There was no dif-

ference in recruitment to baits at any of the six treatments with ants ( $F = 1.47$ ,  $df = 107$ ,  $P = 0.21$ , one-way ANOVA).

### Discussion

The larvae of most antlion species usually construct pits in sheltered areas that are protected from direct sun, rain, wind, and disturbances from large animals (Haub 1942, Topoff 1977). The importance of shading from the sun, which results in lowered soil temperatures, has been emphasized as a primary mechanism for the observed distributions (Haub 1942, Klein 1982, Lucas 1989). In the only field manipulation of the factors underlying antlion zones, Gotelli (1993) concluded that an interaction of temperature and rainfall produced the observed distributions of *M. immaculatus* DeGeer and *M. crudelis* in central Oklahoma, and that neither factor acting alone would be likely to limit larval distribution.

Some species of antlion larvae do construct pits in areas with high soil temperatures (Marsh 1987, Lucas 1989). The temperature at the base of an antlion pit, however, is often much lower than the surface soil temperature (Green 1955, Gotelli 1993). Moreover, antlion larvae are able to regulate their thermal exposure by changing position in the pit, and, at extremely high temperatures, may enter a state of torpor (Green 1955). Additionally, antlion larvae are more likely to construct pits during cooler times of the day (Youthed and Moran 1969, Klein 1982). Thus, although high temperatures affect larval antlion activity, high temperatures per se may not be the most important factor limiting larval antlion distribution in many situations. In fact, Gotelli (1993) found no effect of temperature on mortality; moreover, larvae transplanted to exposed, higher temperature areas gained more biomass than those in shaded areas, presumably because of greater food availability.

Rainfall is an obvious variable limiting antlion distribution, as larvae can only construct pits in dry substrate. In fact, the phenology of some antlion species appears to be an adaptation to regular dry and rainy seasons (Griffiths 1985). Gotelli (1993) found significant effects of moisture on antlion abundance, and hypothesized that rainfall events prevent pit construction, after which larvae perish from high temperatures on the soil surface. This scenario may very well characterize some antlion zones, depending upon soil composition and sun exposure. The patterns of antlion abundance in the exposed areas documented in this work, however, can be entirely attributed to rainfall events without any interactions with high temperatures. Antlion pit abundances decreased dramatically after rainfall events and increased to previous levels as the soil dried out (Fig. 2). Moreover, all exposed areas were mostly shaded, and antlions were abundant in the exposed areas in the late summer and early autumn, when soil temperatures would have been highest.

Although a strong negative correlation between recent rainfall and antlion pit density was found for

**Table 3. Ant species caught in pitfall traps inside and outside the antlion zones at sheltered and exposed sites**

Species	Sheltered		Exposed	
	Inside	Outside	Inside	Outside
<i>Aphaenogaster texana</i> Wheeler		0.12 ± 0.55		
<i>Brachymyrmex depilis</i> Emery		0.06 ± 0.35	0.30 ± 0.77	1.34 ± 4.78
<i>Cyphomyrmex rimosus</i> (Spinola)	0.04 ± 0.21			
<i>Dorymyrmex flavus</i> McCook			0.12 ± 0.55	0.07 ± 0.32
<i>Forelius mccooki</i> (McCook)			0.03 ± 0.17	0.62 ± 1.12
<i>Monomorium minimum</i> (Buckley)		0.88 ± 1.45	0.88 ± 1.88	0.90 ± 1.21
<i>Pachycondyla harpax</i> (F.)		0.06 ± 0.24	0.03 ± 0.17	0.21 ± 0.37
<i>Paratrechina terricola</i> (Buckley)		1.03 ± 2.26		0.07 ± 0.23
<i>Pheidole floridana</i> Emery	0.04 ± 0.21	1.06 ± 2.25	2.42 ± 4.71	5.00 ± 4.88
<i>Pheidole bicarinata</i> Mayr		0.06 ± 0.24	1.55 ± 4.05	2.21 ± 3.46
<i>Pheidole dentata</i> Mayr		0.64 ± 0.81	2.15 ± 2.80	4.28 ± 4.02
<i>Solenopsis invicta</i> Buren	0.13 ± 0.34	20.36 ± 24.99	0.30 ± 1.05	1.14 ± 1.42
<i>Solenopsis texana</i> Emery	0.43 ± 1.67	0.52 ± 0.68	1.09 ± 2.14	1.21 ± 1.54
<i>Strumigenys louisianae</i> Roger		0.03 ± 0.17		
<i>Trachymyrmex turrifex</i> (Wheeler)		0.03 ± 0.17		
Number of individuals/trap	0.65 ± 1.70	24.85 ± 22.82	8.88 ± 7.32	17.03 ± 10.04
Total number of ant species/site	4	12	10	11

Numbers are mean ± 1 SD, pooled over wet and dry conditions.

autumn of 1998, this study was conducted over a single year, and annual patterns of pit density may vary, particularly in wetter years (i.e., 1999). Soil moisture was not quantified during this study, although this variable may be a good predictor of overall antlion pit density (i.e., in the transect censuses). Soil moisture was not measured during the pitfall trapping because interest was not on the degree of moisture, but simply whether the soil was too wet for pit construction. Manipulation of soil moisture was not done, but represents a way of isolating this effect from variables related to rainfall events (e.g., temperature, cloud cover).

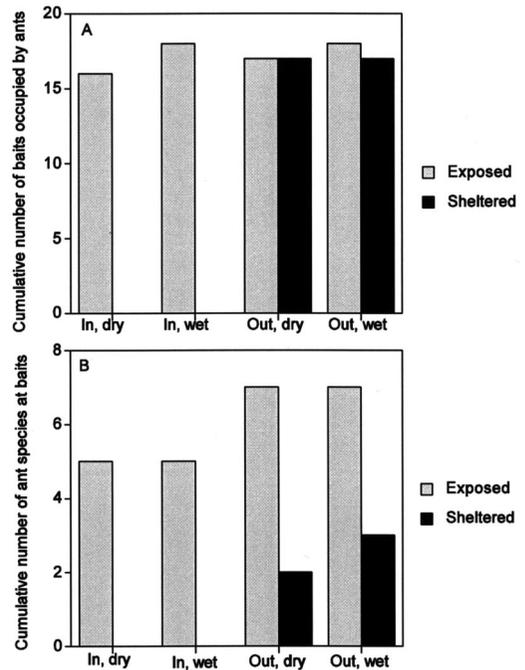
Disturbances that damage or destroy antlion pits (or kill antlions) are another obvious limiting factor. All

the exposed areas of this study (the three strip transects as well as the three study plots) were located in areas that received relatively frequent disturbance from large animals. The bare areas of loose soil inhabited by the antlions were apparently maintained by frequent disturbances from large animals, as areas adjacent to the animal trails were vegetated and contained little suitable habitat for antlion pits. Observations of the strip transects after deer were seen on the trail revealed that many pits were disturbed, but

**Table 4. Invertebrate groups caught in pitfall traps inside and outside the antlion zones at sheltered and exposed sites**

Taxa	Sheltered		Exposed	
	Inside	Outside	Inside	Outside
Acari	X	X	X	X
Araneida	X	X	X	X
Coleoptera	X	X	X	X
Collembola	X	X	X	X
Dermaptera		X	X	X
Diptera	X	X	X	X
Hemiptera			X	X
Homoptera		X		X
Hymenoptera (non-Formicidae)	X	X	X	X
Isopoda		X	X	X
Isoptera	X	X		
Lepidoptera		X	X	
Diplopoda			X	X
Neuroptera	X			
Oligochaeta				X
Orthoptera		X	X	X
Pseudoscorpionida			X	
Psocoptera		X		X
Gastropoda	X	X	X	X
Thysanoptera	X		X	X
Trichoptera		X		X
Total number of groups	10	15	15	17

An X represents the presence of the indicated taxa.



**Fig. 4.** Summary of baiting trials by site, location, and moisture for (A) number of baits occupied and (B) number of ant species at baits. Categories are the same as in Fig. 3. Error bars represent 1 SE.

within several hours were reconstructed (unpublished data). Thus, while such disturbances result in pit destruction and probably some mortality, such frequent disturbances appear necessary to maintain the appropriate microhabitat for antlion pit construction, at least in some exposed areas.

At the sheltered sites, pit densities remained relatively high throughout the year, although significant differences in the distribution of pit sizes and average pit size were documented. These differences may be attributable to the phenology of *M. crudelis*, as larger instars are relatively more abundant at certain times of the year (Lucas 1989). Another possibility is that although the sheltered sites were protected from falling rain, several heavy rainfall events occurred, resulting in runoff that flooded parts of the sheltered sites. This may have resulted in mortality of some larvae or a change in soil moisture that affected pit construction.

Relatively lower catches of ants and other arthropods in pitfall traps inside concentrations of antlion pits could result from either a decrease in foraging activity in these areas, an increase in mortality if ants or arthropods are preyed upon by antlions, or both. Fewer foraging ants at baits could be similarly interpreted. Examination of the ground surface around pits in both exposed and sheltered areas resulted in the discovery of few exoskeletons. It is likely that a behavioral impact on foraging is the primary mechanism at work, although this could not be determined with certainty. Thus, throughout the discussion, I will use the term "successful foraging" in interpreting pitfall catches, to indicate that ants or other arthropods were present in an area, apparently engaged in foraging, and that they had not fallen prey to antlions.

Both the pitfall and bait data indicate that very little successful foraging by ants occurred within the antlion zones at the sheltered sites. Only 31% (4 of 13) of the ant species and 59% (10 of 17) of the total invertebrate groups recorded from the sheltered sites were found inside the antlion zones. In contrast, 91% (10 of 11) of the ant species and 79% (15 of 19) of the total invertebrate groups known from the exposed sites were found inside the antlion zones (Tables 3 and 4). The antlion zone is a permanent feature of the sheltered sites, and densities of antlion pits were observed to exhibit relatively little seasonal variation.

The cumulative numbers of both ant species and other taxonomic groups captured outside the sheltered antlion zones were similar to those captured outside the exposed antlion zones (Tables 3 and 4). Thus, the lower number of ant species and other invertebrates caught inside the sheltered antlion zones is not because of a lower species richness in the vicinity of the sheltered sites.

The pitfall data indicate that significantly more successful foraging by ants occurred within the antlion zones of the exposed sites than within those of the sheltered sites, even though antlion pit densities were slightly higher at the exposed sites. Successful foraging by ants was significantly greater within the antlion zones of the exposed sites when antlion pits were absent because the soil was too moist for pit construc-

tion, than when pits were present. The finding of no significant difference in successful ant foraging outside the antlion zone in wet vs dry conditions demonstrates that the differences documented inside the zone were not simply because of a variation in abiotic factors (i.e., relative humidity or soil moisture).

Ants and other groups of arthropods successfully foraged less in, or simply avoided traveling across, permanent antlion zones. Foraging in the transient antlion zones at the exposed sites in dry conditions was greater than that in the antlion zones at the sheltered sites, however, even though pit densities were similar. This suggests that, over the time scale considered, ants do not respond completely to temporal changes in predation risk in transient antlion zones.

Other factors in addition to predation risk may affect the activity of ant foragers in nature. For example, most permanent antlion zones are located in dry, loose soil with little or no vegetation present. This type of microhabitat probably represents a very poor food source for ants (or other arthropods) and, thus, is not an attractive foraging area. This may be especially true for antlion zones at the base of cliffs or other objects that may represent a terminal habitat edge for ant foragers (Gotelli 1993). An advantage of studying antlion zones under structures open on the sides is that areas adjacent to the antlion zone are accessible through the zone. Even if there is little food within the zone, ants may be expected to travel through the zone to forage on the other side.

It is possible that the observed variation in foraging activity between sheltered and exposed sites was affected to some degree by differences in the ant species diversity at the 2 types of sites, if some species reacted differently than others to this type of predation risk. Nine of the 15 ant species trapped in pitfalls were present at both types of sites, however, and the 6 species that were present at only 1 type of site were relatively rare ( $\leq 0.12$  individuals per trap for all but *Forelius mccooki* [McCook], which reached an abundance of 0.62 individuals per trap outside exposed sites). Yet some species (e.g., *S. invicta*, *P. bicarinata*) were more abundant at 1 type of site than another. Although elucidation of such variation was beyond the scope of this study, a species-by-species comparison of ant foraging behavior in a common habitat containing high densities of antlion pits would be an interesting future study.

Based on a study of antlions inhabiting cliff bases, Gotelli (1996) suggested that generalist ant predators such as antlions may have community-wide impacts on the distribution, abundance, and behavior of ants. This conclusion was supported by a finding of strong effects on ant foraging behavior, although the distribution of antlions was so spatially restricted (Gotelli 1993) that the magnitude of the overall effects at the community level must have been very small. However, if antlions (or other predators) are able to increase their distribution or abundance at certain times, as shown in this study, the overall degree of predation pressure on the community of ants and other arthropods may be much greater.

A large literature suggests that animals possess the ability to assess the relative risk from predators and alter their behavior accordingly (Lima and Dill 1990, Kats and Dill 1998, Lima 1998). Until recently, however, the effects of temporal variation in risk on prey behavior have been largely ignored. Yet, such temporal variation may be a fundamental driving force behind much of the antipredator behavior observed in nature (Lima and Bednekoff 1999, Sih et al. 2000). If periods characterized by a high risk of predation are relatively brief and infrequent, as in the exposed antlion areas of this study, theory predicts that the majority of feeding by prey animals should be allocated to low-risk situations (Lima and Bednekoff 1999). In the context of this study, relatively more foraging would be expected to occur at the transient antlion zones during wet conditions, when predation risk would be lower. Foraging of ants did appear to be less during periods of higher predation risk at the exposed sites, although foraging still occurred.

Few experiments have addressed temporal variation in predation risk, and more data are needed to fully understand the effects on prey behavior (Sih et al. 2000). This antlion/prey arthropod community represents an ideal system to test these ideas at the behavioral level.

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