

ANT COMMUNITY STRUCTURE: EFFECTS OF PREDATORY ANT LIONS¹

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Abstract. This study examined the responses of ground-foraging ants to larval ant lions (Neuroptera: Myrmeleontidae). In central Oklahoma, these sit-and-wait arthropod predators are restricted by abiotic factors to sheltered cliff bases. A high-density ant lion zone forms an effective “minefield” of predation for local ant assemblages. The density of ant-nest entrances and the number of pitfall-trap captures of ant foragers were significantly lower in the ant lion zone than in the adjacent forest or grassland. Differences in ant abundance could not be attributed to differences in thermal microhabitat within and outside the ant lion zone. Over a 24-h period, ants foraged continuously at tuna-fish baits placed on the forest floor, but never utilized baits placed within the ant lion zone. Field behavioral tests with individual ant foragers confirmed that the risk of predation from ant lions was high for common ant species in the assemblage. Among species, predation risk was negatively correlated with worker body mass.

Manipulative field experiments tested whether ants use biotic or abiotic cues to avoid ant lion aggregations. Ants foraged readily at baits on the forest floor and baits placed in the center of experimental sand patches, but they avoided baits placed in sand patches that contained ant lions. Ant foraging was also substantially lower in patches from which ant lions had been removed 3 h prior to the start of the experiment. Ant foraging was slightly reduced in patches with artificial ant lion pits that had never contained predators. These experiments suggest that ants use biotic cues associated with the presence or recent presence of predators. Previous studies have not implicated predation as an important factor structuring ant communities. This study suggests that predators can have important community-wide impacts on the distribution, abundance, and behavior of ground-foraging ants.

Key words: *abundance; ant; ant lion; behavior; community; distribution; foraging; predation; rarefaction.*

INTRODUCTION

There is considerable evidence that the presence of a predator can influence prey populations, even in the absence of direct predation (Sih 1987, Lima and Dill 1990). These indirect effects (*sensu* Miller and Kerfoot 1987) include induced shifts in the behavior (Neill 1990), morphology (Appleton and Palmer 1988), and life history (Washburn et al. 1988, Crowl and Covich 1990) of prey. Indirect effects may have important consequences for the population dynamics of predators and prey (Ives and Dobson 1987, Abrams 1990) and for the growth of competing prey populations (Kotler and Holt 1989, Osenberg et al. 1992). At the community level, indirect effects may be responsible for higher order interactions (Werner 1992), habitat associations (Jeffries and Lawton 1984), and regional differences in community structure (Schluter 1988).

Shifts in foraging behavior and habitat use by prey in the face of predation risk are especially well documented (Sih 1987, Neill 1990, Nonacs and Dill 1991). The particular foraging strategy employed depends on the perceived and actual risk of predation, the quality of the foraging reward, and the extent to which animals

can behaviorally control the risk of predation (Fraser and Huntingford 1986, Lima and Dill 1990). Unfortunately, the responses of prey to predators can be difficult to study in the field because predators are simultaneously reacting to movements of prey (Sih 1984). The clearest cases may be those in which the predator is limited in movement by abiotic factors or other mechanisms that are unrelated to predation (Connell 1975). In these cases, the response of the prey to the predator must be distinguished from the correlated response of the prey to abiotic factors.

In this study, I examine the distributional and behavioral responses of an assemblage of ground-foraging ants to high-density aggregations of predaceous ant lion larvae (Neuroptera: Myrmeleontidae). In central Oklahoma, these larvae are restricted by abiotic factors to the sheltered bases of cliff ledges (Gotelli 1993), where they effectively constitute a “minefield” of predators. I tested the null hypothesis that the spatial distribution of nest entrances, the short-term activity of foragers, and the long-term abundance of foragers were similar in the presence and absence of ant lion predators. I conducted a series of field experiments to quantify the risk of predation to foragers of different species and to reveal the biotic and abiotic cues potentially used by prey to avoid predators.

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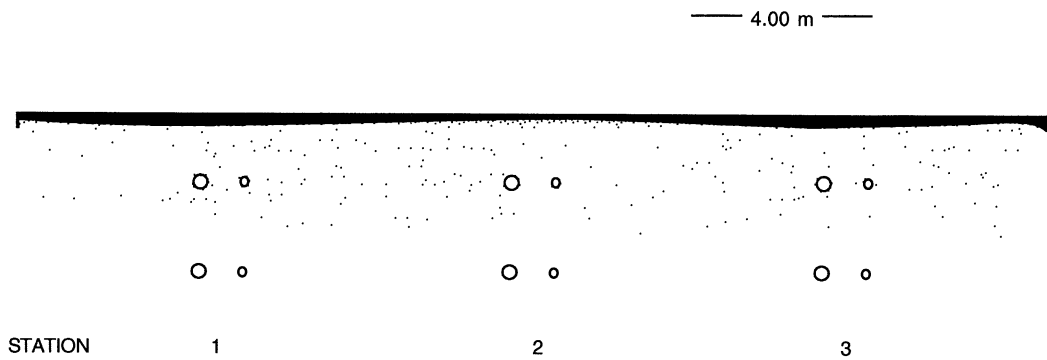


FIG. 1. Layout of pitfall traps. The black region represents the cliff ledge, and the shaded region represents the ant lion zone. At each cliff ledge, six stations were established, with large and small pitfall traps placed inside and outside the ant lion zone.

MATERIALS AND METHODS

Study sites

Ant assemblages were examined at three sandstone cliff ledges in Caddo County, Oklahoma. These sites support dense aggregations of larval ant lions (*Myrmeleon immaculatus* and *M. crudelis*) in a well-defined zone 1–2 m wide at the base of each cliff. High soil surface temperatures and disturbance from rainfall restrict both predator species to this sheltered microhabitat (Gotelli 1993). Both ant lion species pass through three larval instars, and second and third instars are common through most of the year. The two species are not spatially segregated within the ant lion zone (Gotelli 1993). Although their morphology and feeding habits are similar, *M. immaculatus* is larger and less common than *M. crudelis* in Caddo County.

The background habitat beyond the cliff ledge differs among sites: open, disturbed prairie (Salyer East); narrow, partly shaded rock ledge (Salyer West) and mesic, forested canyon floor (Pugh Canyon). All sites have a southeast exposure and are separated from one another by 0.5–3 km. See Gotelli (1993) for full site descriptions and a map.

The mosaic of prairie and forest vegetation in these canyons supports over 30 species of ants (M. Albrecht, unpublished data). Numerically dominant species include *Monomorium minimum*, *Pheidole bicarinata*, *Pheidole dentata*, *Conomyrma flava*, *Crematogaster punctulata*, and *Solenopsis* spp. (primarily *Solenopsis molesta*).

Pitfall traps

Ant abundance and species richness were estimated from annual pitfall trap catches of individual ant foragers. At each site, a permanent array of six pitfall-trap stations was established parallel to the cliff ledge, at 6-m intervals. At each station, one large (50 mm diameter) and one small (32 mm diameter) polyvinyl chloride (PVC) sleeve (100 mm in length) were permanently buried and capped, within 0.75 m of one another. Large and

small traps were placed both within and 1 m beyond the ant lion zone (Fig. 1). The permanent PVC sleeve allowed traps to be inserted and removed with almost no disturbance to the surrounding substratum.

At each trapping date, I removed the caps and inserted a large (38 mm diameter) or small (25 mm diameter) glass jar, rimmed with foam insulation. Each jar was filled to a depth of 25 mm with ethylene glycol, a preservative and fixative, and the inner rim was coated with FLUON, a slippery industrial lubricant. Traps were run for 72 consecutive hours in July of each year from 1989 to 1993. Cores remained capped between trapping intervals. Ants were the most abundant arthropod in pitfall trap catches, and all individuals were counted and identified to species whenever possible. In July of 1992, the contents of two traps were lost to small mammals.

Measurement of soil surface temperatures

Because of obvious differences in canopy cover, the three sites varied in thermal exposure from the relatively warm and exposed prairie site (Salyer East) to the cooler, more mesic forest site (Pugh Canyon). But even within sites, certain stations were characteristically warm or cool. Thermal constraints may be an important limit to ant foraging and activity (Rogers 1974, Briese and Macauley 1980) and could account for variation in pitfall trap catches. To quantify microhabitat variation in thermal conditions, I measured soil surface temperature at each station at 0900, 1200, 1500 and 1800 with a Cole-Parmer Infrared Thermometer (model number 08407-10). I measured soil surface temperatures in July of 1992, concurrent with pitfall trapping. Because of time constraints, I could measure soil temperatures at only one site each day (Salyer East: 3 July 1992; Salyer West: 8 July 1992; Pugh Canyon: 6 July 1992). Peak air temperatures in the shade were similar on 3 July 1992 (28.5°C) and 6 July 1992 (28°), but were higher on 8 July 1992 (33.5°). At all sites, soil surface temperatures peaked at 1200. If the stations were ranked on the basis of total degree-hours, these

rankings would correspond with soil surface temperature at 1200, which was used as a simple thermal index to correlate with pitfall catches.

Statistical analysis of pitfall trap data

I analyzed species richness, total abundance, and abundance of the six most common species with a mixed-model repeated-measures analysis of variance. The within-subjects factor was years (1989–1993) and the between-subjects factors were sites (Salyer East, Salyer West, Pugh Canyon), microhabitats (predators present, predators absent), and trap sizes (small, large). Stations (1–6) were nested within sites. All factors in the model were random except microhabitats, which was fixed. Data were logarithmically transformed [$\ln(n + 1)$] before analysis to correct for non-normality. I deleted third-order and fourth-order interaction terms from the analyses, unless they were indicated by a significant lack-of-fit test. Tests were based on the 5 yr of July samples from 1989 to 1993. Similar patterns were found in 1994, and in a set of seasonal data from May, June, and July of 1989 (see Fig. 5 in Gotelli 1993).

Using only data from the large pitfall traps in July 1992, I compared trap catches in protected and exposed microhabitats, with soil surface temperature as a covariate. The simple patterns in the data did not justify a more complex analysis. I also compared species richness in exposed and protected microhabitats with rarefaction (Hurlbert 1971, Simberloff 1972). Rarefaction curves give the expected species number in a small random subsample of individuals from a collection. For each site and year, I pooled the data from the pitfall traps of the six exposed stations to estimate the full species-abundance distribution. I then rarefied this collection down to an equivalent number of individuals collected from the six stations within the ant lion zone. Confidence intervals about the expected species richness were calculated using the variance estimate in Heck et al. (1975). This test compares species richness in and out of the ant lion zone after adjusting for differences in abundance (James and Rathbun 1981).

Spatial pattern of nest entrances

During July of 1992, I mapped all nest entrances that could be found within and adjacent to the ant lion zone at each site along a 10–15 m transect parallel to each cliff ledge. Tuna-fish baits were used to lure ant foragers from nest entrances, which were then marked with flagging and located with a pair of x - y coordinates.

Risk of predation

For several ant species at the Pugh Canyon site, I estimated the probability of death by introducing foragers into the ant lion zone. Ten workers each of *Camponotus modoc* (major worker), *C. modoc* (minor worker), *Aphaenogaster texana carolinensis*, *Crematogaster laeviscula*, *Pheidole dentata* (minor worker), and *Monomorium minimum* were tested. Individual foragers were

collected with a suction aspirator from tuna-fish baits, and then dropped from a height of 5 cm over a haphazardly chosen location at the midpoint of the ant lion zone. I followed each individual until it was captured by an ant lion larva, escaped to the front of the ant lion zone, or successfully reached the cliff base at the back of the ant lion zone. The probability of death was defined as the proportion of those 10 workers that was successfully captured by ant lions. The probability of capture by an ant lion was measured for each prey species as (total number of ants captured per total number of ant lions encountered). An ant lion encounter was defined as an ant entering or partially entering an ant lion pit and eliciting a sand-throwing response from the predator. These experiments were conducted on several days in May and June of 1991. At that time in the year, the ant lion zone is dominated by second- and third-instar larvae of both *Myrmeleon crudelis* and *M. immaculatus*. The different instars and predator species encountered by ants were not distinguished in this experiment.

Between 3 and 10 workers each of *Camponotus modoc* (minor worker), *Aphaenogaster texana carolinensis*, *Crematogaster laeviscula*, *Pheidole dentata* (minor worker), and *Monomorium minimum* were desiccated to a constant mass to estimate individual body mass of each species. Body masses were then correlated with the probability of capture by ant lions.

Foraging behavior

To assess the foraging behavior of ants in the face of predation risk, I established bait stations in the presence and absence of ant lion predators. Each bait station consisted of 50 g of drained tuna fish (Bumblebee, oil-packed) placed on a 12.5 × 20 cm lined index card. Tuna fish represents a high-quality concentrated protein reward for ant foragers. In central Oklahoma, the ant species that forage at tuna-fish baits are the same ones that are found at insect carcasses and carrion in the field. Presence of species at tuna-fish baits is also correlated with pitfall-trap captures (M. Albrecht, unpublished data). Tuna-fish baits are usually colonized by ants within 2–10 min of placement.

On 25 June 1991, 20 bait stations were established at the Pugh Canyon site. At 6 m intervals, I placed one bait station in the center of the ant lion zone and a parallel station on the forest floor, 2 m beyond the edge of the ant lion zone. Bait stations were established at 0800 and censused hourly for 24 h. At each census, I recorded the species identity and abundance of ants at baits. For baits in the ant lion zone, I looked carefully for evidence of ongoing predation in nearby ant lion pits. Baits that were depleted by ant foraging were replenished during the experiment.

Foraging cue experiments

I constructed artificial ant lion patches on the forest floor in order to reveal the biotic and abiotic cues used by ants in avoiding predators. Each patch consisted of

25 kg of oven-dried sifted soil that was originally collected from the ant lion zone. The sand was arranged in a circular disk, 1 m in diameter and ≈ 3 cm deep. Into this patch, I introduced 30 second- and third-instar larvae of *M. crudelis* and *M. immaculatus*. This is comparable to predator densities in the ant lion zone. Eighty to 90% of these larvae established feeding pits in the sand patches.

At 1400, I placed tuna-fish bait on a 12.5×20 cm index card in the center of each artificial patch. Patches were established near a 1.2-km footpath through the forest at the Pugh Canyon site. All patches were in full shade and separated from one another by >10 m. Baits were monitored hourly from 1500 to 2000. I established two types of control patches and three treatments as follows:

Sand control. These patches received only a tuna-fish bait and no other manipulation.

Forest floor. Tuna-fish baits were established directly on the forest floor, without sand or ant lions present.

Treatment (1)—*Ant lion patches.* Foraging by ants in patches with ant lions was compared to foraging on sand control and forest floor patches. This experiment tested the effect of the presence of ant lion predators on foraging by ants. The experiment was carried out on 7 August 1991.

Treatment (2)—*Empty ant lion pits.* The ant lions in the previous experiment were removed from their pits 3 h prior to the start of the census. I carefully removed each individual ant lion with a plastic spoon. This experiment tested the effect of recent predator occupancy on foraging by ants. The experiment was carried out on 8 August 1991.

Treatment (3)—*Artificial ant lion pits.* A new array of patches was constructed on 23 August 1991. For the treatment patches, I used a plastic spoon to construct artificial ant lion pits. Ant lions were never introduced into these patches. This experiment tested the effect of ant lion trap structure on foraging by ants.

For each experiment, I established a treatment patch and the two controls in alternating order along the footpath. For each treatment and the two controls, there were five replicates, except for the ant lion and empty pit treatments, which had four replicates each. Weather conditions were comparable on all 3 d, and there were no differences in average ant abundance at the forest floor treatment on the 3 d ($F_{2,12} = 1.6$, $P = 0.24$).

The number of ants per bait of all species was compared with a repeated-measures ANOVA. The within-subjects factor was time and the between-subjects factor was treatment. I chose not to analyze the data for individual species because their appearance at baits was spatially patchy, and because there was turnover in species composition at baits. Patterns for total ant abundance were similar to patterns for individual species, but the number of replicates did not justify a MANOVA or other more complex statistical design. Repeated-measures ANOVAs and simple linear contrasts were used to compare particular subsets of treatments.

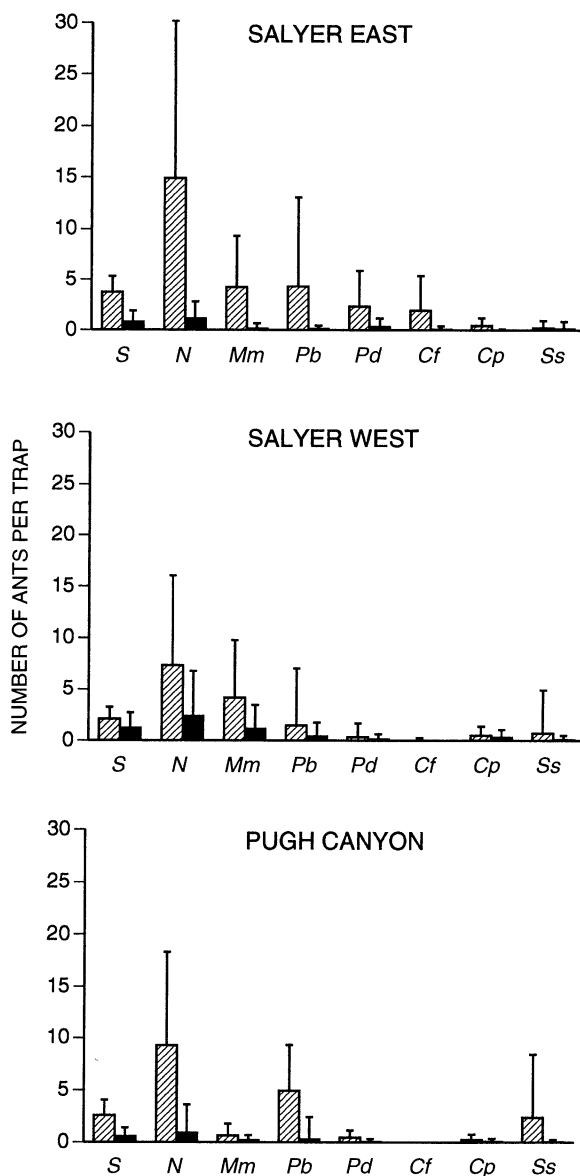


FIG. 2. Average abundance of ants collected annually in large pitfall traps at three sites (1989–1993). Hatched bars = ant lions absent. Solid bars = ant lions present. Vertical bars are 1 SD about the mean. *S* = species richness; *N* = total ant abundance; *Mm* = abundance of *Monomorium minimum*; *Pb* = abundance of *Pheidole bicarinata*; *Pd* = abundance of *Pheidole dentata*; *Cf* = abundance of *Conomyrma flava*; *Cp* = abundance of *Crematogaster punctulata*; *Ss* = abundance of *Solenopsis* spp. (mostly *Solenopsis molesta*).

RESULTS

Pitfall trap data

The analysis of pitfall traps revealed consistently fewer ants in the presence of ant lions (Fig. 2). Although the ANOVA revealed other sources of variation due to site, year, station, and trap size, the main result was that species richness, total abundance, and abundance of all the common species (except *Pheidole den-*

TABLE 1. Summary of analyses of variance for yearly pitfall trap catches (1989–1993). Each column represents a different response variable. S = total species number; N = total ant abundance. Other columns are for total abundance of particular species. Each row represents a different effect in the analysis of variance. Stations are nested within sites. Microhabitats are traps placed within and outside the ant lion zone (see Fig. 1). Degrees of freedom are indicated in parentheses. Significant effects are indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The linear contrast tests the hypothesis that pitfall catches were significantly different within and outside the ant lion zone.

Factor	S	N	<i>Mono-</i> <i>morium</i> <i>minimum</i>	<i>Pheidole</i> <i>bicarinata</i>	<i>Pheidole</i> <i>dentata</i>	<i>Cono-</i> <i>myrma</i> <i>flava</i>	<i>Cremato-</i> <i>gaster</i> <i>punctulata</i>	<i>Solenopsis</i> spp.
Site (2)								
Year (4)								
Trap size (1)					*			
Microhabitat (1)	*		*					
Site × year (8)						***		***
Site × trap size (2)						***		
Site × microhabitat (2)		**		***		***		**
Year × trap size (4)					*	*		
Trap size × microhabitat (1)							*	
Year × microhabitat (4)			*	*	**			***
Station [site] (3)					*	***		*
Year × station [site] (4)						***		
Trap size × station [site] (3)						***		
Microhabitat × station [site] (3)	*	**		***		***	*	***
Linear contrast: predators absent vs. present	***	***	***	***		***	***	***

tata) were lower in the presence of ant lions (Table 1). The difference in abundance of ants within and outside the ant lion zone could not be attributed to differences in the thermal properties of the two microhabitats (Fig. 3).

Rarefaction comparisons of expected species richness within and outside the ant lion zone revealed few significant deviations (Table 2). In other words, ant species richness within and outside the ant lion zone was approximately comparable after adjusting for differences in total abundance (Fig. 4).

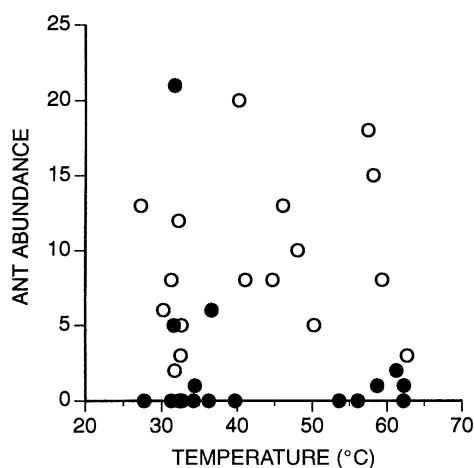


FIG. 3. Ant abundance in pitfall traps (July 1992) as a function of soil surface temperatures measured at noon. ○, ant lions absent; ●, ant lions present. Soil surface temperature was a nonsignificant covariate ($P > 0.05$) and did not account for the difference in pitfall catches in the presence and absence of ant lion predators.

Density of nest entrances

At Salyer West and Pugh Canyon, no ant nest entrances were found within the ant lion zone. At Salyer East, only a single nest entrance of *Monomorium minimum* was discovered within the ant lion zone, in a vertical crack of the rock wall. Outside the ant lion zone, nest entrance density ranged from 0.10 (Salyer West) to 0.20 (Pugh Canyon) to 0.58 (Salyer East) nest entrances/m².

Risk of predation

For several ant species at Pugh Canyon, the probability of capture during a single encounter with an ant lion was substantial. The overall risk of predation was high, and for most species, none of the 10 workers introduced into the ant lion zone escaped (Table 3). The probability of capture was negatively correlated with worker body mass (log-log transformed data, $r = -0.91$, $P = 0.03$).

Foraging behavior

Tuna-fish baits placed in exposed microhabitats were rapidly colonized by ant foragers, and baits were continuously occupied for 24 h. Average ant abundance peaked at dusk and near midnight, and reached a minimum near noon and dawn. In contrast, none of the baits within the ant lion zone was ever colonized over the 24-h period (Fig. 5). I also found no evidence of ongoing predation by ant lions on ants during the course of this experiment.

One potential problem with this experiment is that the two treatments may not have been independent because of their spatial proximity. In other words, ants

TABLE 2. Comparison of observed and expected ant species number from pitfall traps in the presence or absence of ant lion predators. The observed number of ant species in the presence of ant lions is shown, with the expected number in the absence of predators generated from rarefaction. Asterisks indicate species richness values that are >1.96 standard deviations from the expectation.

Date	Salyer East		Salyer West		Pugh Canyon	
	Predators absent	Predators present	Predators absent	Predators present	Predators absent	Predators present
Large pits:						
May 1989	6.67	8	4.06	5	2.24	3
June 1989	4.43	4	8.82	10*	2.34	2
July 1989	3.33	3	5.94	6	2.87	4
July 1990	3.92	4	3.38	5	1.61	1
July 1991	4.27	3	1.00	1	0.00	0
July 1992	3.29	3	2.60	3	4.71	4
July 1993	5.95	6	4.45	6	1.47	1
Small pits:						
May 1989	2.87	4	5.60	5	2.52	3
June 1989	3.15	4	4.22	6*	1.86	3
July 1989	2.46	2	3.94	3	2.68	3
July 1990	3.70	3	4.15	5	3.06	5*
July 1991	1.00	1	0.00	0	1.00	1
July 1992	2.47	2	2.44	3	1.00	1
July 1993	6.00	5	1.70	3*	0.00	0

may have been absent from the ant lion zone *because* they were feeding at baits on the adjacent forest floor. To test this hypothesis, I repeated the experiment on 28 June 1991 with a different spatial array of replicates. Five bait stations were placed within the predator aggregation spaced along the first 30 m of the ant lion zone, and five bait stations were placed on the adjacent forest floor along the next 30 m of the ant lion zone.

This spatial arrangement ensured that foraging responses in the ant lion zone were independent of foraging responses on the forest floor. I censused these baits for 6 h and obtained identical results to those of the full 24-h census. In other words, ants avoided foraging at baits within the ant lion zone even when no other baits were offered in the immediate area.

Foraging cue experiments

Effects of ant lion predators.—Ant foraging differed significantly among the forest floor, sand control, and ant lion treatments ($F_{2,11} = 8.56, P = 0.005$). In five out of the six censuses, ants never foraged at baits in ant lion patches, whereas ants readily foraged at the forest floor and at sand controls ($F_{1,8} = 0.49, P = 0.50$; Fig. 6a).

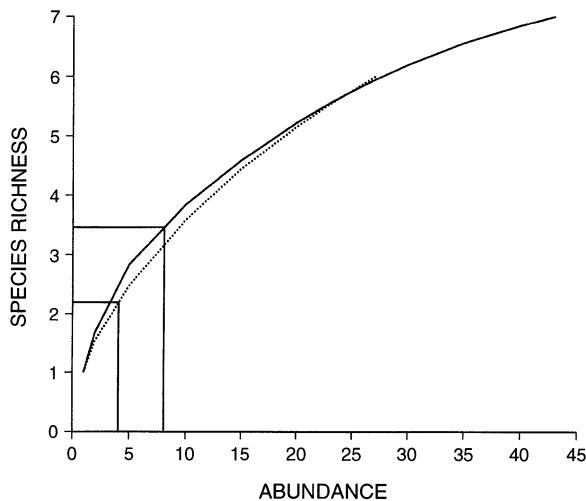


FIG. 4. Rarefaction curve of expected ant species richness in the absence (solid curve) and presence (dotted curve) of ant lion predators. Data from pooled large trap pitfall catches at Salyer West, July 1989 collection. The x axis is the abundance in the collection, and the y axis is the expected species richness, based on a random subsample of the assemblage. The vertical lines indicate the average abundance of pitfall traps in presence and absence of predators, and the horizontal lines indicate the corresponding expected species richness. From Gotelli and Graves (1996).

TABLE 3. The probability of death (PD) for ants entering the ant lion aggregation, and the probability of successful capture (PC) for individual ant lion-ant encounters. Ten workers of each of the common prey species were aspirated from tuna-fish baits and introduced individually into the center of the ant lion zone (though not directly into a predator's pit). The probability of death (PD) was defined as the proportion of those ten workers that was successfully captured by ant lions. The probability of capture (PC) was measured for each species as (total number of ants captured per total number of pits encountered). An encounter was defined as an ant entering or partially entering an ant lion pit and eliciting a sand-throwing response from the predator.

Ant species	PD	PC
<i>Camponotus modoc</i> (major worker)	0.60	0.26
<i>Camponotus modoc</i> (minor worker)	0.90	0.60
<i>Aphaenogaster texana carolinensis</i>	1.00	0.83
<i>Crematogaster laeviscula</i>	1.00	1.00
<i>Pheidole dentata</i> (minor worker)	1.00	0.91
<i>Monomorium minimum</i>	1.00	1.00

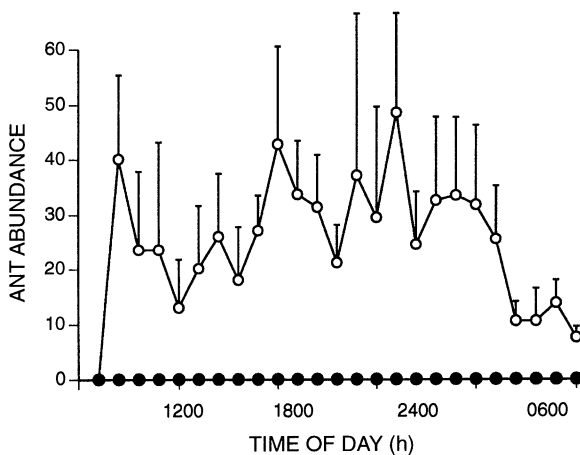


FIG. 5. Average number of ants per bait at tuna-fish bait stations placed within natural predator aggregations (●) and on the adjacent forest floor (○) during a 24-h census. Both treatments were established at 0800 and censused hourly. Vertical lines are 1 SD. $n = 10$ in each treatment.

Effects of empty ant lion pits.—Ant foraging differed significantly among the forest floor, sand control, and ant lion removal treatments ($F_{2,11} = 5.17$, $P = 0.02$). Ant abundance was lowest for patches from which ant lions had been removed, whereas differences between forest floor and sand control treatments were not significant ($F_{1,8} = 1.89$, $P = 0.20$; Fig. 6b). At each census, a few foragers of different species were found in the treatment with empty ant lion pits. This is in contrast to the experiment with live ant lions, in which foragers almost never occurred (Fig. 6a).

Effects of artificial ant lion pits.—Ant foraging did not differ significantly among the forest floor, sand control, and artificial pit treatments ($F_{2,12} = 1.22$, $P = 0.33$). However, the interaction of time and treatment was significant ($F_{10,60} = 8.67$, $P < 0.001$), as was the linear contrast of empty pits vs. forest floor and sand controls ($F_{12,60} = 8.67$, $P < 0.001$). Although ants readily entered artificial ant lion pits, their movement seemed to be impeded, so that total numbers of foragers were reduced somewhat in this treatment (Fig. 6c).

DISCUSSION

A variety of circumstantial evidence suggests that dense aggregations of ant lion predators affect the distribution and abundance of ants: forager abundance in pitfall traps was consistently lower in the presence of ant lions (Figs. 2 and 4), and the rarefaction analysis suggested that the difference represented a random sample of individuals from the assemblage (Fig. 4). Ant nest entrances were seldom located within the ant lion zone, and ants never foraged at high-quality tuna-fish baits in the presence of ant lions (Fig. 5). The risk of death by predation was substantial for most ant species (Table 3), and was negatively correlated with worker body mass (see also Griffiths 1982, 1986). The

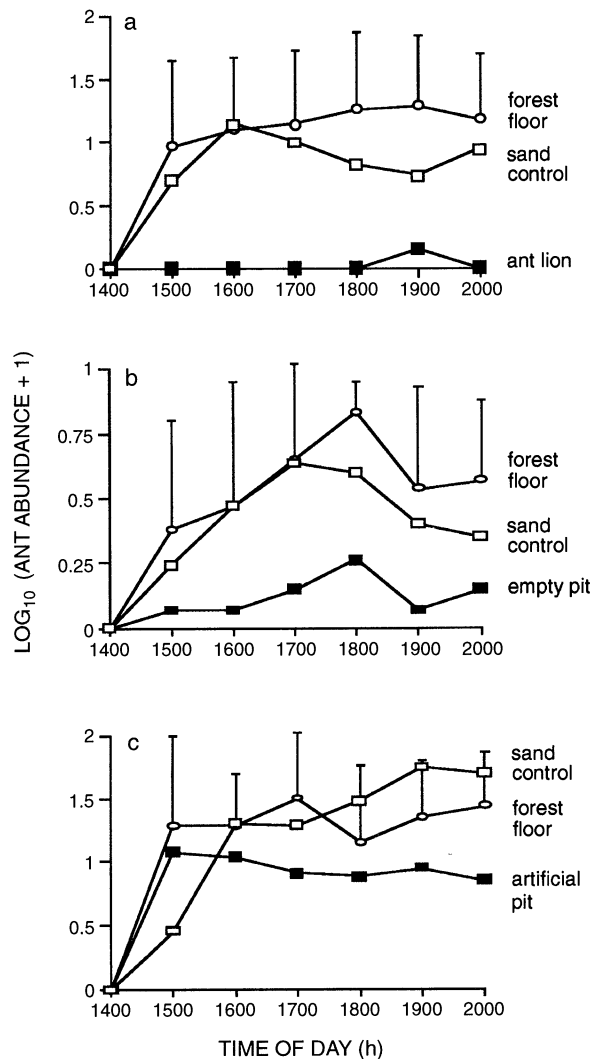


FIG. 6. Experimental manipulation of predation risk for ant foraging. Each graph gives the average number of ants per treatment over a 6-h census interval. In all graphs, the open circles are averages for baits placed directly on the forest floor. The vertical line is 1 SE. The open squares are averages for baits placed in a 1 m diameter circle of sand. Closed squares indicate the treatment group in each experiment. (a) Ant lion present. Sand patches contained 30 second- and third-instar larvae of *Myrmeleon crudelis* and *M. immaculatus*. (b) Empty ant lion pits. Animals from the experiment in (a) were removed from the sand patches 3-h prior to the start of the experiment. Ant lion pits were left intact in this treatment. (c) Artificial pits. Sand patches never had ant lions introduced, but artificial ant lion pits were constructed by spooning out soil to create pits. In all the experiments, there were significant differences among the treatments ($P < 0.05$), although means did not differ among the forest floor control groups ($P > 0.10$).

estimates of predation risk may be inflated because ants became agitated when handled. On the other hand, ants also became agitated after encountering ant lions, so the behavioral responses after an initial encounter with a predator were probably accurate.

These "natural experiments" are problematic to interpret, however, and do not necessarily implicate the importance of predators. For example, ants may avoid the ant lion zone because of abiotic factors such as soil texture or surface temperature. The analysis of thermal microhabitats (Fig. 3) does not support this interpretation, although these data must be interpreted cautiously because they do not reveal the critical temperature ranges experienced by ants in each microhabitat. Alternatively, the lack of foragers in the ant lion zone could be attributed entirely to the spatial arrangement of ant nest entrances, and energy constraints on colony foraging (Holder Bailey and Polis 1987). The data also do not indicate whether the influence of predators is primarily through direct or indirect effects.

Fortunately, the results of the manipulative field experiments allow us to distinguish among some of these alternatives. Abiotic limitations seem unlikely because ants readily foraged on sand patches that mimicked the substrate of the ant lion zone (Fig. 6a). The absence of ant foragers in the ant lion zone was similar to the virtual absence of foragers in small sand patches that contained ant lions. However, these sand patches were located randomly with respect to ant nest entrances, so the results cannot be attributed to the unique spatial arrangement of colonies. As in the natural experiment, predation of ants by ant lions was not observed during this experiment, suggesting that avoidance behavior is the primary determinant of reduced ant numbers within the ant lion zone.

The experiments also provide insight into the particular cues used by ants to avoid ant lions. Avoidance does not seem to be based on the physical structure of the ant lion trap because ants established foraging trails and recruited, though at reduced numbers, across a patch of artificial ant lion pits (Fig. 6c). Instead, foraging activity was suppressed only in the presence of living ant lions (Fig. 6a), or empty pits from which ant lions had recently been removed (Fig. 6b). These results suggest the possibility of a labile chemical cue associated with ant lions that is detected by ant foragers. If the cue were entirely visual or auditory, forager abundance should have returned to control levels when ant lions were removed. The presence of a few foragers at the removal treatment (Fig. 6b) suggests that these workers had located the food resource but did not recruit additional foragers. Further field and laboratory experiments are necessary to elucidate the precise nature of the cue, but it is clear that ants can effectively detect ant lion predators using cues that are directly associated with predators, and not simply their microhabitat.

Ant chemical communication is well documented (Hölldobler and Wilson 1990), and ants use short-lived alarm pheromones in response to nest disturbance or immediate threats to the colony (Hölldobler 1978). However, workers may respond to more distant threats that do not immediately endanger the colony. Foraging

activity is influenced by mortality risk, and the removal of aboveground workers often reduces colony activity levels (Gentry 1974, Munger 1984, Gordon 1986). Recent laboratory experiments have documented that ant foragers can communicate the risk of predation to nest-mates (Nonacs 1990), and that foraging responses represent a balance between patch rewards and foraging risks (Nonacs and Dill 1990, 1991, Nonacs 1991). The results of the current study suggest that these behaviors are generally important in nature, and that effective predator avoidance can affect distribution and abundance of ants at the community level.

Consequences of indirect effects

What are the consequences of ant avoidance behavior to both prey and predator populations? For ant populations, the effect is probably minimal. The ant lion zone is localized and limited in spatial extent. Moreover, ant lion feeding and pit-building activity reduce the amount of prey, carrion, seeds, and vegetation that could be used by ants (N. J. Gotelli, *personal observation*). Consequently, these are probably not areas of high-quality foraging to begin with, and hence their avoidance by ants probably entails a minimal energy cost.

However, the consequences of avoidance behavior are probably not trivial for the predators. Ants are the most common arthropod in pitfall trap catches, and represent a potentially important food source for ant lions. The avoidance behavior by common ant species may substantially reduce food resources for ant lions. Ongoing field experiments (N. J. Gotelli, *unpublished data*) indicate that ant lion life histories are phenotypically plastic, and that the length of the larval life can be greatly reduced by food supplementation. Moreover, food availability and length of the larval life may affect predatory and competitive interactions that control the coexistence of both ant lion species.

Organization of ant community structure

Ant communities are thought to be organized by competitive interactions (Fellers 1987, Porter and Savignano 1990), and, to a lesser extent, parasitism (Feener 1981). Until now, predation has not been considered an important biotic factor at the community level. Studies of predation have focused on specialist predators, such as horned lizards, and their effects on particular ant species (Munger 1984). The current study suggests that generalist ant predators, such as ant lions, can have community-wide impacts on distribution, abundance, and behavior of ground-foraging ants.

In summary, ecologists and naturalists have long emphasized the unique adaptations of ant lions for capturing prey. These include morphological specialization (Wheeler 1930), the unique geometry of the ant lion pit (Lucas 1982), and behavioral strategies for subduing large or risky prey (Eisner et al. 1993). This study shows that avoidance behaviors by ants may effectively

counter these adaptations and perhaps indicate rough parity in the "evolutionary arms race" between predator and prey.

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