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ANT LION ZONES: CAUSES OF HIGH-DENSITY PREDATOR AGGREGATIONS[1]

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Abstract. In this study, I describe the causes of persistent small-scale zonation in a terrestrial arthropod community. In central Oklahoma, two species of predaceous, pit-building ant lion larvae (*Myrmeleon immaculatus* and *M. crudelis*) coexist in a narrow, high-density (>50 animals/m^2) zone at the base of sandstone cliffs, where they are sheltered from rain and afternoon sun. Although larval movement is frequent and abundance within the zone varies seasonally, ant lions are rarely found >2 m from the cliff base.

I used field experiments and observations to test four hypotheses that could explain the maintenance of the ant lion zone: (1) zonation because of habitat availability; (2) zonation because of food availability; (3) zonation because of increased surface temperatures in exposed microhabitats; (4) zonation because of increased soil moisture and disturbance in exposed microhabitats.

Ant lions are probably not limited to the cliff base by the presence of rocks or vegetation, because there was no correlation between ant lion density and available habitat. The availability of prey also does not appear to limit ant lion distribution: ant abundance in pitfall traps was significantly higher outside the ant lion zone than within.

Outside the ant lion zone, soil surface temperatures reach lethal levels in the afternoon sun. However, third-instar larvae of *M. immaculatus* transplanted in dry, sifted soil suffered little mortality over a 4-d period. Larvae transplanted into exposed sites gained significantly more mass than larvae transplanted into the ant lion zone, probably because of differences in food availability.

Small-scale manipulations within the ant lion zone revealed that ant lion numbers decreased significantly over a 5-d period in response to both moisture (misting) and disturbance (pit-filling). In a recolonization experiment, the recovery time of patches exposed to a single "rainfall" treatment was extremely long: defaunated "rainfall" patches did not achieve the pit densities of defaunated control patches until after 84 d.

Rainfall limits ant lion distribution through an interaction with temperature. Transplant experiments on natural substrata revealed the nature of this interaction. Within the ant lion zone, the soil remains dry and ant lion larvae bury themselves more rapidly in the sun than in the shade. Outside the ant lion zone, rainfall leads to the formation of a persistent soil crust. Larvae are unable to penetrate this crust, and they succumb to high temperatures in the sun.

Because both species of ant lions are restricted to a narrow spatial zone, the probability of interspecific and intraspecific interactions (including competition, predation, and cannibalism) is increased. Such interactions may affect the density of both species within the ant lion zone. The abundances of *M. crudelis* and *M. immaculatus* were negatively correlated in quadrats from the center of the ant lion zone. Across the ant lion zone, the relative abundance of the two species also differed significantly, although the differences were not consistent among sites. Because of overriding abiotic constraints, neither species can achieve an ideal free distribution with respect to food resources.

High-density predator aggregations may also affect prey community structure. Arthropod abundance was low within the ant lion zone, perhaps because of direct predation by ant lions or predator avoidance behavior by prey. Although the ant lion zone is caused by the interaction of abiotic factors, high-density predator aggregations have important biotic consequences for the population dynamics of the predators and the spatial distribution of their prey.

Key words: abundance; distribution; disturbance; ideal free distribution; lethal temperatures; Myrmeleontidae; Neuroptera; prey abundance; rainfall; terrestrial; zonation.

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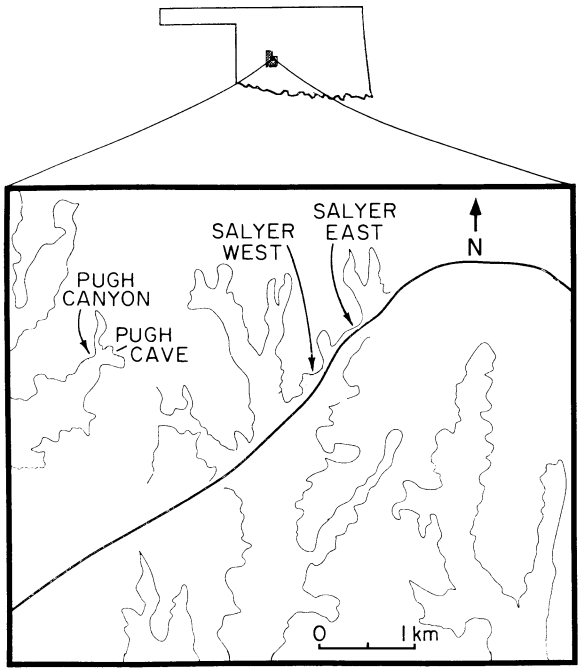

FIG. 1. Location of study sites in Caddo County, Oklahoma.

INTRODUCTION

The abundance of plants and animals varies systematically along spatial gradients (Whittaker 1967, Louda 1989). In many cases, populations are spatially restricted to discrete zones, which may be persistent features of the landscape (Paine and Levin 1981). Three classes of hypotheses may account for zonation: (1) physiological limitations imposed by spatial gradients in abiotic factors, such as temperature (Wethey 1983), salinity (Snow and Vince 1984), or desiccation stress (Stotz 1979); (2) species interactions, caused by spatial gradients in the presence of competitors (Grace 1987), predators (Paine 1974), or prey (Terborgh 1977); (3) recruitment limits, caused by spatial gradients in the dispersal of seeds (Rabinowitz 1978) or larvae (Grosberg 1982). The latter mechanism may be particularly important for plants and sessile invertebrates, which can disperse only during the recruitment phase of the life history.

Because biotic and abiotic factors covary along spatial gradients, an experimental approach is usually necessary to reveal the particular combination of factors at work. Experimental studies of zonation in marine intertidal communities have been especially successful (Paine 1977), probably because zonation in that habitat occurs on such a small spatial scale (<10 m). In contrast, most examples of terrestrial zonation occur on much larger spatial scales (>100 m). Although a few systems have been studied experimentally (Bartholomew 1970, Brown 1971, Louda 1982), the causes of zonation in many terrestrial communities are elusive (Whittaker 1967, Smith 1977, Terborgh 1977, Graves 1988).

In this study, I reveal the causes of small-scale zonation patterns in a terrestrial arthropod community. In central Oklahoma, larvae of two species of ant lion (Neuroptera: Myrmeleontidae) co-occur in a distinct zone at the base of sandstone cliffs. The pit-building and feeding behavior of ant lions has been well studied (Wheeler 1930, Topoff 1977, Lucas 1982), because these predatory larvae are long-lived, hardy, and amenable to experimental manipulation. These features also make ant lions ideal subjects for experimental field studies.

My field experiments and correlative data tested four hypotheses for the maintenance of ant lion zones: (1) zonation because of habitat availability; (2) zonation because of food availability; (3) zonation because of lethal surface temperatures in exposed microhabitats; (4) zonation because of increased soil moisture and disturbance in exposed microhabitats. These hypotheses are neither exhaustive nor mutally exclusive, but they do provide a framework for gathering correlative data and designing appropriate field experiments.

METHODS

Ant lion life history

Adult ant lions are feeble fliers, nocturnally active, and short lived (Wheeler 1930). Females lay eggs in the soil. Larval development is quite variable in length, but larvae probably require at least one to two summer seasons to mature. For example, *Myrmeleon crudelis* larvae maintained with ad libitum food in the laboratory (at 21°C) required 6 mo for development from first instar to adult (N. J. Gotelli, *unpublished data*). Wheeler (1930:109) noted that the larval life of ant lions is longer than that of most other insects because of an intermittent food supply (see also Griffiths 1991).

First-instar larvae recruit through midsummer, so that population abundance is greatest during the fall. Abundances decline through winter, and populations are sparsest in spring. However, qualitative censuses indicate that seasonal variation in larval abundance does not alter the zonation pattern. Third-instar larvae construct a sand-covered cocoon, from which adults (in a laboratory study) emerge in 4 wk (N. J. Gotelli, *unpublished data*).

In central Oklahoma, both *Myrmeleon crudelis* and *Myrmeleon immaculatus* co-occur in sheltered microhabitats. *M. immaculatus* is the larger of the two species, although there is considerable overlap in the body sizes of first- and second-instar larvae. The two species can be distinguished on the basis of pigmentation patterns on the ventral surface of the head (Lucas and Stange 1981). These patterns appear to be retained through all three larval instars.

Study sites

The study was conducted in Permian sandstone canyons of Caddo County, Oklahoma (Fig. 1). Canyon

floors are cooler and more mesic than surrounding uplands (Rice 1960), and many canyons support disjunct remnants of eastern deciduous forest vegetation (Little 1939). Three cliff bases that differ in background habitat were used. (1) Salyer East is a treeless hillside that is the most arid of the three sites. Dominant vegetation includes Johnson grass, weeping lovegrass, and witch grass. (2) Salyer West is a narrow cliff ledge partly shaded by an open canopy of sugar maple, soap berry, and redbud. (3) Pugh Canyon is a mesic canyon floor, shaded by a closed canopy of sugar maple, hackberry, and American elm. The site is the most mesic and shaded of the three. Because the sites encompass three rather distinct habitats, "site" was treated as a fixed factor in all analyses of variance.

Measurement of population density and habitat availability

I collected data on habitat structure and ant lion pit density during May 1990, when population sizes were near their seasonal minimum. I reasoned that habitat preferences will be most obvious when they are not complicated by habitat shifts that may occur at high densities. At each site, I censused 10 belt transects perpendicular to the cliff wall. Transects were 3 m in length and evenly spaced at 3-m intervals. This transect length provided roughly equal numbers of quadrats inside and outside the ant lion zone, although the width of the zone varied among sites. Along each transect, I measured ant lion pit abundance and available habitat in 12 contiguous square quadrats of 0.0625 m^2 (0.25 m per side). In each quadrat, I counted the number of pits whose centers fell within the quadrat boundaries. As in Boake et al. (1984), $\approx$70% of the pits were occupied by ant lions. A minimum of 0 and a maximum of 9 pits per quadrat were recorded. These numbers were converted to pit densities per square metre for analysis.

To measure habitat availability, I placed a clear plexiglass sheet, marked with 20 randomly placed points, over each quadrat (Greig-Smith 1983). The same array of 20 points was used to census all quadrats. I recorded the substrate type (soil, rock, or vegetation) beneath each point. Vegetation included living plants and accumulated leaf litter. Points over rock or vegetation were judged unsuitable for establishment of ant lion pits. These data were converted to a percent available habitat (= percent soil) for analysis. Available habitat in individual quadrats ranged from 0 to 100%.

I analyzed these data at large and small spatial scales. At the large scale, I averaged the abundance and habitat data across the 10 transects within a study site. Using these averages, I tested for a significant correlation (Pearson's r) between average density and average habitat availability across the ant lion zone. At the small spatial scale, I calculated the correlation coefficient between density and habitat availability within each transect. The histogram of 10 correlation coefficients from each study site reveals any tendency for an association between habitat availability and pit density.

To examine the distribution of both species across the width of the ant lion zone, I collected individual ant lions from the outer, middle, and inner edges of the ant lion zone at each site. In September 1990, I collected 10 ant lions from each zone by sampling individual pits at 3-m intervals. Individuals were sampled without regard to pit size or larval instar. For each site, I used a G test to reveal whether the relative abundances of the two species varied as a function of distance from the cliff wall. I also calculated the correlation coefficient between abundance of *M. immaculatus* and abundance of *M. crudelis* in the 12 control plots that were established in the center of the ant lion zone for the rainfall press experiment.

To test for habitat differences in soil particle size, I gathered three soil samples each from within and 1 m outside the ant lion zone at all study sites. With a hand trowel, I collected $\approx$150 g of the top 5 cm of soil. Sample locations were chosen randomly. Soil samples were air-dried for 5 d, then sorted in a screen sieve series (sieve opening sizes: 3.8, 1.0, 0.4, and 0.2 mm). Individual sieve fractions were weighed, and masses converted to percentages of the total sample. These percentages were analyzed with a MANOVA, which tests for differences in the overall distribution of particle sizes inside and outside the ant lion zone. Soil temperatures were measured with a k series thermocouple probe.

Prey availability

At each site, I established six permanent pitfall trap stations, at 6-m intervals. At each station, one large (50 mm diameter) and one small (32 mm diameter) polyvinyl chloride plastic (PVC) pipe sleeve (100 mm in length) were permanently buried and capped, within 0.75 m of one another. Large and small traps were situated within and 1 m beyond the ant lion zone. The permanent PVC sleeve allowed traps to be inserted and removed with virtually no disturbance to the surrounding substratum. In exposed microhabitats, trapping did not disturb the soil crust; in the ant lion zone, ant lions established pits directly next to the sleeve.

At each trapping sequence, caps were removed and a large (38 mm diameter) or small (25 mm diameter) glass jar rimmed with foam insulation was inserted into the core. The insulation insured a tight seal between the edge of the jar and the PVC core. Each jar was filled to a depth of 25 mm with ethylene glycol, a preservative and fixative. The inner rim of each jar was coated with FLUON, a slippery industrial lubricant, to prevent prey from escaping (Marsh 1987). Traps were run for 3 d and two nights during dry weather in May, June, and July of 1989, and in July of 1990 and 1991. Only data from May of 1989 are presented here because results were similar at other times. Cores remained capped between trapping intervals.

Pitfall traps provide a reasonable estimate of prey availability, although capture rates by traps can be 95% higher than by ant lion larvae (Lucas 1989). In this study, number of ants per trap was taken as a simple index of relative prey availability. Not all ant species can be successfully attacked by ant lions, and ants are not the exclusive prey of ant lions. However, ants may be an important component of ant lion diet (Marsh 1987), and the pitfall catches of ants are representative of other arthropod prey taxa captured by ant lions. In central Oklahoma, such prey include small beetles, spiders, ticks, lepidopteran larvae, and other ant lion larvae.

Because small-scale variation within the ant lion zone was not of interest in this study, I ignored station number and analyzed the data as a three-way analysis of variance (microhabitat × site × trap size). Data were square-root transformed before analysis. As a second test of prey availability, I tallied the number of times ant abundance was greater for pitfall traps inside the ant lion zone than for corresponding traps outside the zone. Under the null hypothesis of no difference in prey ability, the ANOVA should reveal no significant effects of microhabitat, and the tallies of greatest prey abundance should not differ from a 50:50 distribution inside and outside of the ant lion zone.

Effects of moisture and disturbance: press experiment

Rainfall in exposed sites may limit ant lion distribution. This experiment was designed to measure changes in ant lion number in response to two components of rainfall: soil moisture and pit disturbance. The design is a "press" experiment (Bender et al. 1984) because treatments were maintained through time. At each site, 16 plots of 0.0625 m^2 were established in the center of the ant lion zone and flagged. Plots were randomly located, with the proviso that ant lion pits accounted for at least 66% of the plot area and that all plots were separated by at least 1 m. Plots at each site were assigned consecutively to one of four treatments:

1) Control (no moisture, no disturbance).

2) Misting (moisture, no disturbance). Each plot was gently misted with 1 L of water, applied over a 5-min period with an uncontaminated, pressurized insecticide mister. Existing ant lion pits were not eroded by this treatment.

3) Disturbance (no moisture, disturbance). Ant lion pits in each plot were gently filled in with dry sand. I was careful to avoid displacing animals with this treatment.

4) Rainfall (moisture, disturbance). Each plot was watered from a 1-L canteen held 1 m above the soil surface. This treatment mimicked the effects of a violent rainstorm by saturating and displacing soil. However, the effects of the treatment were modest compared to disturbances from natural storms.

Pretreatment pit numbers were counted in all plots. Plots were established on 20 May 1990. On the following 5 d, I counted active pits in all plots and then applied treatments. Treatments were reapplied daily because the misting and rainfall plots began drying out after 24 h. After 5 d, I collected the top 10 cm of soil in each plot, returned the samples to the laboratory, and counted number of living and dead ant lion larvae of each species.

If ant lions burrow deeply in response to moisture, this sampling technique may be biased against the moisture and rainfall treatments. To counter this potential bias, I waited 5 d and collected all additional ant lions (eight *M. immaculatus* and seven *M. crudelis*) from new pits in the moisture and rainfall treatments. Addition of these animals to the original counts did not qualitatively affect the results of the press experiment, so they are not reported here.

The design is a three-way multiple analysis of variance (moisture × disturbance × site). Response variables are the number of *M. crudelis* and *M. immaculatus* in each plot. Pretreatment pit numbers were used as an additive covariate. I also analyzed the data for each species separately with a three-way univariate analysis of variance. All data were square-root transformed before analysis.

Effects of rainfall: pulse experiment

The press experiment revealed effects of sustained moisture and disturbance on ant lion numbers. I also conducted a "pulse" experiment (Bender et al. 1984) to determine recovery time of plots disturbed by a single rainfall event.

For this manipulation, I used the control and disturbance quadrats from the press experiment. Forty-eight hours after the press experiment ended, I again defaunated the control and disturbance plots and replaced the soil with 1000 g of sifted, oven-dried soil (particle diameter < 0.4 mm) from the study site. Because both control and disturbance plots were recolonized within 24 h, I do not believe there were any carryover effects from the press experiment to the pulse experiment. The disturbance plots received a single rainfall treatment as described in the press experiment.

All plots were then censused nondestructively by counting number of ant lion pits approximately twice weekly through the summer of 1990. Although the design followed repeated-measures analysis of variance, there were too many time periods sampled to carry out this analysis. Instead, I used a two-way analysis of variance at each time period (site × treatment) to determine when there were no longer any significant differences between treatments in the number of ant lion pits.

Effects of temperature

To measure the effects of high temperatures on mortality and growth of ant lion larvae, I transplanted animals into different microhabitats inside and outside

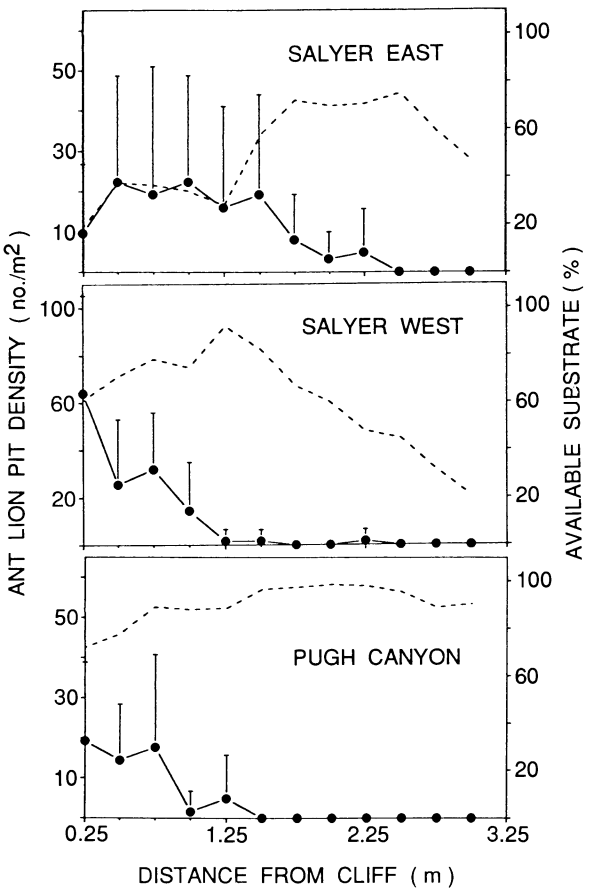

FIG. 2. Average habitat availability and average ant lion abundance across the ant lion zone. Each point connected by the solid line is the average density of ant lion pits based on 10 belt transects at each of three study sites (left ordinate). The vertical lines are ±1 SD. The dashed line is the average percentage of available habitat at each location (right ordinate). Salyer East, $r = -0.58$, $P < .05$; Salyer West, $r = 0.21$, $P > .20$; Pugh Canyon, $r = -0.77$, $P < .01$.

of the ant lion zone. On 15 June 1990, I collected ≈60 third-instar larvae of *M. immaculatus* at Pugh Cave, a cliff ledge that was not used in any of the field experiments (Fig. 1). Larvae were brought to the laboratory and individually weighed to the nearest 0.1 mg. Forty-eight hours later, I transplanted these animals into one of three microhabitats at Pugh Canyon and Salyer East: control (within the ant lion zone), bare zone (just beyond the ant lion zone, usually characterized by no vegetation) or exposed (1 m beyond the edge of the ant lion zone). These three zones represent a gradient of increased exposure to high daytime temperatures.

I placed each animal in a marked, 470 mL (16 oz.) plastic drinking cup with 750 g of sifted, oven-dried soil (<0.4 mm particle diameter) from the site. The outer rim of each cup was coated with STICKY-TRAP to prevent prey from entering. Each cup was buried with a 2-cm lip projecting above the soil surface. Eight to ten cups were placed in each of the three microhabitats in the two sites, spaced at 1-m intervals.

My plan was to end the experiment after 20 d of dry weather and measure survivorship and mass loss of exposed and protected animals that were starved. Two unexpected factors disrupted this design. First, blowing sands quickly coated the sticky trap in all three microhabitats so that prey were not excluded. Second, a violent weather front passed over the study site 3 d after the experiment was set up, forcing me to terminate it prematurely. Nevertheless, daytime air temperatures exceeded 33°C during this time period. In laboratory experiments, ant lion larvae may succumb to high temperatures within 5 h (Lucas 1989), so the field experiment should have been long enough to reveal any major effects of high temperature on mortality. Survivorship was evaluated with a G test, and body mass was analyzed with an analysis of covariance using initial body mass as the covariate.

Behavioral observations

The transplant experiment revealed the importance of temperature to survivorship and growth of animals

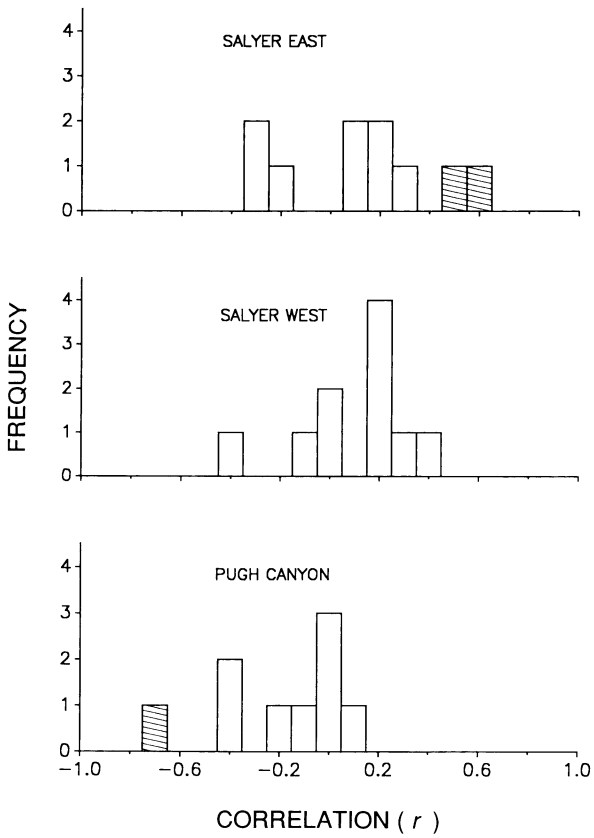

FIG. 3. Correlation coefficients (Pearson's r) for the relationship between ant lion density and available habitat. Each sample is based on 12 contiguous, 0.0625-m² quadrats censused in a transect across the ant lion zone. Hatched bars indicate significant correlations ($P < .05$).

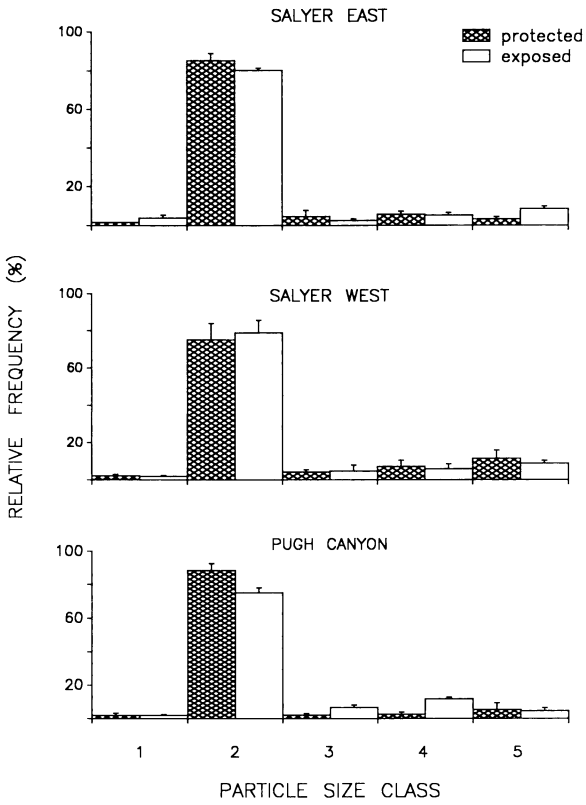

FIG. 4. Soil particle size within (= protected) and outside (= exposed) the ant lion zone. Each histogram bar represents the average percentage by mass of three soil samples. The vertical lines are 1 SD. Particle size classes are: (1) <0.2 mm diameter; (2) 0.2–<0.4 mm; (3) 0.4–<1.0 mm; (4) 1.0–<3.8 mm; (5) ≥3.8 mm.

in artificial (dried, sifted) substrata. I also wished to determine the behavioral responses of larvae on natural substrata to temperature. A canopy shades the Pugh Canyon site in the morning hours, creating shaded and sunlit microhabitats within and outside the ant lion zone. I transplanted three third-instar larvae of *M. immaculatus* into each of these four microhabitats. For each larva, I recorded movement and the time in seconds until the animal reburied itself. A different larva was used in each trial. The experiment was conducted at 1100 on the morning of 25 June 1990 under a clear sky (air temperature 29°C).

RESULTS

Habitat availability

The ant lion zone did not coincide with the availability of substrate for pit construction. At Salyer East and Pugh Canyon, habitat availability actually increased away from the cliff ledge, resulting in a negative correlation between average pit density and habitat availability (Fig. 2). At a smaller spatial scale, there was also no consistent relationship between density and habitat availability within a transect. Although a few transects at each site yielded significantly positive or negative associations, most correlations between density and habitat availability within individual transects were nonsignificant (Fig. 3). Finally, soil particle size did not differ consistently between microhabitats (Wilks' $\lambda = 1.44$, $P = .31$ [SAS 1988]). Both within and outside the ant lion zone at all three sites, the soil was well sorted, consisting mostly of fine-grained particles (Fig. 4).

Prey availability

At all sites, ant abundance in pitfall traps was significantly greater outside the ant lion zone than within (Fig. 5). In 30 of 36 paired comparisons of pitfall traps, abundance of ants (and most other arthropod taxa) was greater outside the zone than within ($P < .0001$; binomial test). Differences among sites and trap sizes were not statistically significant (Table 1).

Effects of rainfall: press experiment

Both moisture and disturbance reduced the ant-lion abundance over a 5-d period. Moisture, disturbance, and initial pit density had simple additive effects on ant lion numbers; there were no differences among sites in the final number of ant lions and no significant in-

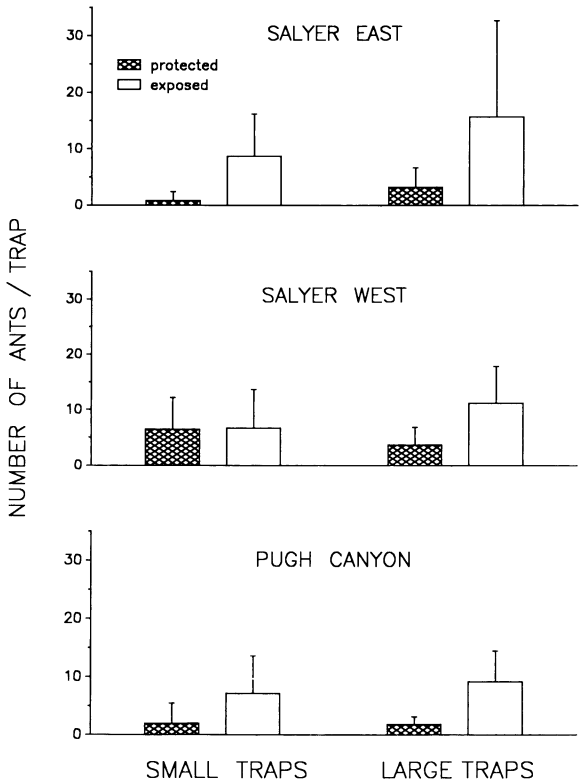

FIG. 5. Ant abundance within (protected) and outside (exposed) the ant lion zone. Each histogram bar is the average of six pitfall traps over a 3-d period (29–31 May 1989). Vertical bars are 1 SD. For details of trap size and placement, see *Methods: Prey availability.*

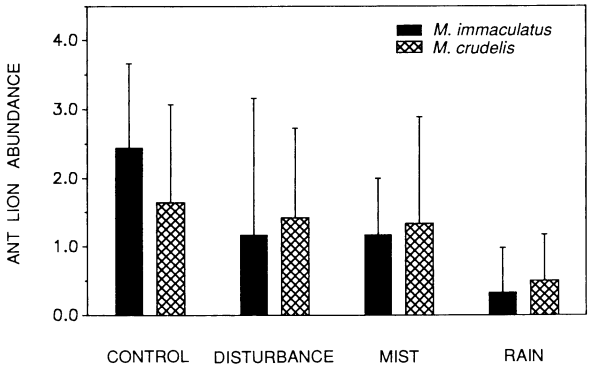

FIG. 6. Abundances of *Myrmeleon crudelis* and *M. immaculatus* after four consecutive days of exposure to moisture and disturbance. Each histogram bar shows the average abundance in 12 plots (4 each at three sites). The vertical lines are 1 SD. Treatments are control: no manipulation; misting: daily gentle misting of each 0.0625-m^2 plot with 1 L of water; disturbance: daily hand-filling of all ant lion pits in each plot; rainfall: daily violent watering of each plot with 1 L of water.

teraction terms in the multiple analysis of variance (Table 2). Both species showed similar reductions in number owing to moisture and disturbance (Fig. 6), but the effects were weak and nonsignificant for *M. crudelis,* strong and significant for *M. immaculatus* (Table 3). All animals collected at the end of the experiment were alive, with the exception of two individuals of *M. crudelis* from the rainfall treatment.

At two sites, effects of daily disturbance were also evident in changes in pit number through time (Fig. 7). Disturbance did not appear to affect pit number at the Salyer East site, although variances were large, and a site effect was not detected in the repeated-measures analysis of variance (Table 4).

Effects of rainfall: pulse experiment

The single rainfall treatment had both short-term and long-term effects on the recolonization of defaunated quadrats. In the short run, the number of ant lion pits in control plots returned to approximate pretreatment levels within 2 wk, whereas treatment plots showed little colonization by this time (Fig. 8). At 25 d posttreatment, there was a significant correlation between pit number and initial pit number for control plots ($r^2 = 0.58$, $P < .01$), but no correlation for treatment plots ($r^2 = 0.00$, $P > .50$).

After 25 d, both control and treatment curves began to rise as new first-instar larvae recruited into the population (Fig. 8). At each sampling date, I compared pit numbers with a two-way analysis of variance (site ×

TABLE 1. ANOVA for effects of pitfall trap size, microhabitat (inside and outside the ant lion zone), and site on ant abundance over a 3-d trapping period.

Source of variation	df	MS	*F*
Trap size	1	2.118	1.50
Site	2	2.057	1.46
Microhabitat	1	43.282	30.71***
T × S	2	1.081	0.77
T × M	1	1.545	1.10
S × M	2	4.186	2.97(*)
T × S × M	2	0.273	0.19
Error	60	1.409	

*** $P < .001$, (*) $.05 < P < .10$.

TABLE 2. MANOVA for the effects of initial pit density, moisture, and disturbance on the numbers of *M. immaculatus* and *M. crudelis* in manipulated plots. Initial density is treated as an additive covariate. The *F* ratio is Wilks' lambda (SAS 1988).

Source of variation	df	*F*
Initial density	2,33	4.29*
Disturbance	2,33	16.07***
Moisture	2,33	10.49***
Site	4,66	0.45
D × M	2,33	0.28
D × S	4,66	0.17
M × S	4,66	1.37
D × M × S	4,66	0.56

* $P < .05$, *** $P < .001$.

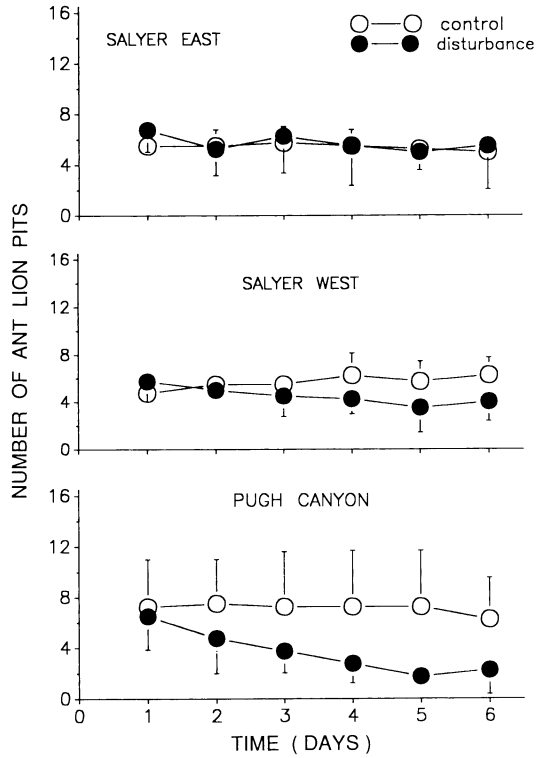

FIG. 7. Pit abundances in control and disturbance plots. Each point is the average of four plots. Vertical bars are 1 SD. Control plots were unmanipulated. Ant lion pits in disturbance plots were filled in after each daily census. Pretreatment values are shown on day 1.

TABLE 3. Univariate ANOVAs for effects of initial pit density, moisture, and disturbance on the numbers of *Myrmeleon immaculatus* and *M. crudelis*.

Source of variation	df	*F* (*M. crudelis*)	*F* (*M. immaculatus*)
Initial density	1	0.24	4.78*
Disturbance	1	1.17	17.14**
Moisture	1	2.71	7.50**
Site	2	0.07	0.68
D × M	1	0.57	0.10
D × S	2	0.29	0.01
M × S	2	0.30	2.02
D × M × S	2	0.45	0.46

* $P < .05$, ** $P < .01$.

treatment, with pretreatment pit number as an additive covariate). These analyses (results not presented here) revealed a significant treatment effect ($P < .05$), but no site or interaction effects, at every sampling date until 13 August 1990. For several time periods beyond this, control averages still exceeded treatment averages, and the probability value was suspiciously small ($.05 < P < .10$). Thus, a minimum of 84 d was required for recovery of plots that received a single rainfall treatment.

Effects of temperature

The cliff ledges provide shade from the afternoon sun, creating a dramatic spatial gradient of increasing soil surface temperature: average soil surface temperature at 1400 on a cloudless day (2 July 1990) was 51°C in the sun and 32°C in the shade. Microhabitat conditions in the transplant cups were comparable, although the oven-dried, sifted soil reached a higher surface temperature (in excess of 60°C) than did the natural substratum. In the exposed (full sunlight) treatment, however, soil temperature at a depth of 8 cm was only 35°C, comparable with surface temperature in the ant lion zone treatment (36°C). Perhaps as a consequence of this thermal refuge, there was essentially no mortality of third-instar *M. immaculatus* in any of the three treatments over the 4-d period. Of the 58 transplanted animals, only one larva in the "bare zone" treatment at Pugh Canyon died. No animals were missing at the end of the experiment. However, there were significant effects of microhabitat on mass gain: larvae in the exposed microhabitats gained more body mass than larvae in the bare zone or ant lion zone (Fig. 9). Slopes of the curves differed among treatments because small larvae in the exposed treatment gained more body mass than did large larvae (Table 5).

Behavioral observations

Within the ant lion zone, burial times for third-instar *M. immaculatus* were significantly longer under shade than under sun. Outside the ant lion zone, larvae under shade appeared to be unable to bury themselves; they sat motionless for over 15 min, although they occasionally probed the soil crust with the tip of the abdomen. In contrast, larvae under sun moved rapidly in an irregular half circle until they encountered a patch of shade and immediately stopped moving. Animals that remained under full sun outside of the ant lion zone became torpid after 2 min and died after 3 min (Table 6).

DISCUSSION

The ant lion zone appears to result from an interaction between rainfall and temperature. Neither factor acting alone would be likely to limit larval distribution. Not only could third-instar larvae of *M. immaculatus* survive high soil surface temperatures, they actually gained more mass outside the ant lion zone (Fig. 9), probably because of greater food availability (Fig. 5). Similarly, although rainfall and disturbance reduced ant lion numbers, these factors were not an important source of mortality, and never led to the complete elimination of ant lions from a patch (Fig. 6). However, larvae cannot dig in rain-soaked soil, and they succumb to high temperatures in the sun (Table 6).

Soil surface temperatures on natural substrata and in the transplant experiment exceeded lethal limits (46°C for first-instar larvae) determined in laboratory studies of temperature tolerance (Lucas 1989). *M. immaculatus* probably survived in these transplants because of a thermal refuge in deeper soil. Larval movement (Topoff 1977), pit location (Klein 1982), and orientation within a pit (Green 1955) are all affected by high surface temperatures. If the soil is loose and friable (as in the transplant experiment), high surface temperatures may not act as a lethal limit to distribution. However, a single rainshower makes the crust impenetrable, so that temperature becomes a limiting factor. As a consequence, the "recovery time" of patches hit by rain is extremely long, even though the soil surface is dry within 10 days.

At least 7 wk must pass before abundances fully recover (Fig. 8). On shorter time scales, ant lions move

TABLE 4. Repeated-measures ANOVA of ant lion pit number in disturbed and control microhabitats.

Source of variation	df	MS	*F*
Between-subjects effects			
Disturbance	1	4.304	4.15(*)
Site	2	0.246	0.24
D × S	2	1.98	1.91
Error	18	1.037	
Within-subjects effects			
Time	5	0.385	4.78**
T × D	5	0.437	5.43**
T × S	10	0.123	1.53
T × D × S	10	0.060	0.74
Error (Time)	90	0.081	

(*) $.05 < P < .10$, * $P < .05$, ** $P < .01$.

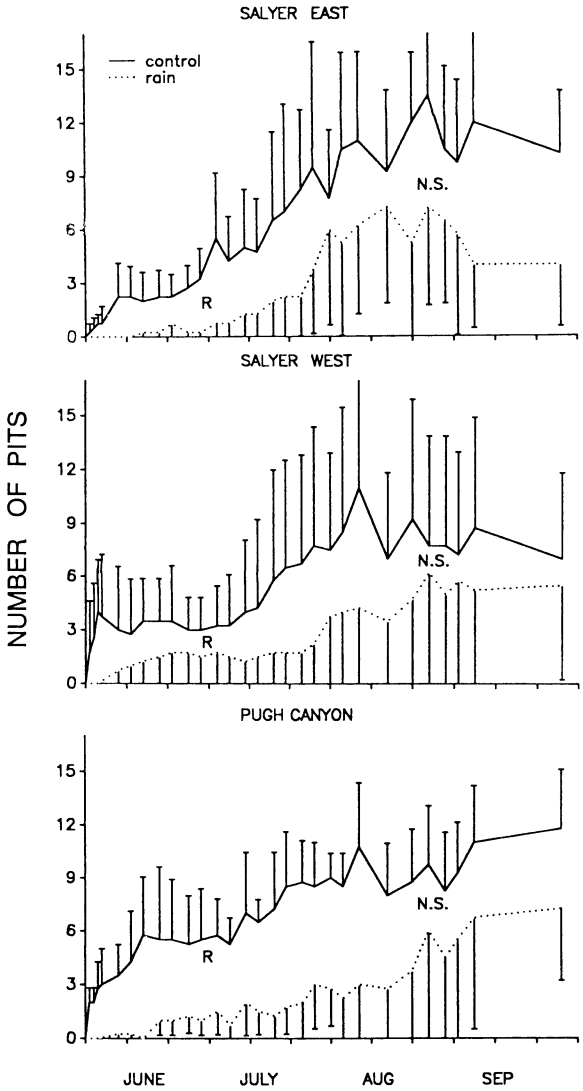

FIG. 8. Long-term recolonization of control and rainfall plots. Symbols as in Fig. 7. "R" is the time at which the pits of new first-instar larvae began appearing at all sites. "N.S." is the time at which the pit abundances in control and treatment plots no longer differed significantly ($P > .05$; two-way ANOVA).

TABLE 5. ANCOVA for final body mass of third-instar *M. immaculatus* transplanted into different microhabitats.

Source of variation	df	MS	F
Initial body mass	1	0.491	128.30***
Microhabitat	2	0.014	3.63*
Site	1	0.004	1.10
I × M	2	0.017	4.43*
I × S	1	0.004	1.07
M × S	2	0.001	0.47
I × M × S	2	0.002	0.50
Error	45	0.004	

* $P < .05$; *** $P < .001$.

TABLE 6. Average burial times and fates of third-instar *Myrmeleon immaculatus* transplanted into shaded and sun-lit microhabitats inside and outside the ant lion zone (means ± 1 SD). $N = 3$ for each group.

Microhabitat	Burial time (s)
Shaded, within zone	65 ± 22.9
Sun-lit, within zone	9.7 ± 9.1
Shaded, outside zone	··· [no burial]
Sun-lit, outside zone	··· [death]

in response to daily disturbances (Fig. 7). Pit construction is an important metabolic cost for ant lion larvae (Lucas 1985), and larvae apparently "fine-tune" their microhabitat choices within the ant lion zone (Lucas 1989). Simberloff et al. (1978) suggested that small-scale variation in moisture and microhabitat probably influenced pit placement, and Boake et al. (1984) found that *M. crudelis* was missing from shaded patches of damp, compacted soil. This study confirms experimentally that ant lions are responsive to small-scale spatial variation in both moisture and disturbance. Larvae also move in response to food deprivation, although only after several weeks of starvation (Heinrich and Heinrich 1984).

Although *M. immaculatus* and *M. crudelis* commonly occur in shaded microhabitats, larvae of other ant lion species occur in more exposed microhabitats. Even for these species, rainfall may have important consequences for distribution and abundance. For example, abundance of *Morter obscurus* in an exposed site in South Africa declined sharply following a heavy rainfall (Griffiths 1980). In South Florida, densities of *M. crudelis* in shaded microhabitats were ≈10 times

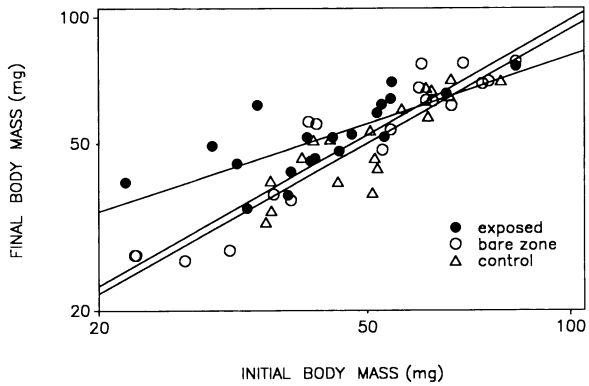

FIG. 9. Gains in body mass of third-instar *Myrmeleon immaculatus* transplanted into three microhabitats. Each point represents the initial and final mass of an individual larva. Final mass was measured after a 4-d transplant experiment. See text (*Methods: Effects of temperature*) for microhabitat descriptions. Regression lines were fit with a log-log transformation. For control larvae, $y = 0.171 + 0.900x$ ($r^2 = 0.734$; $P = .0001$); for bare zone larvae, $y = 0.183 + 0.905x$ ($r^2 = 0.889$; $P = .0001$); for exposed larvae, $y = 0.845 + 0.531x$ ($r^2 = 0.564$; $P = .0001$).

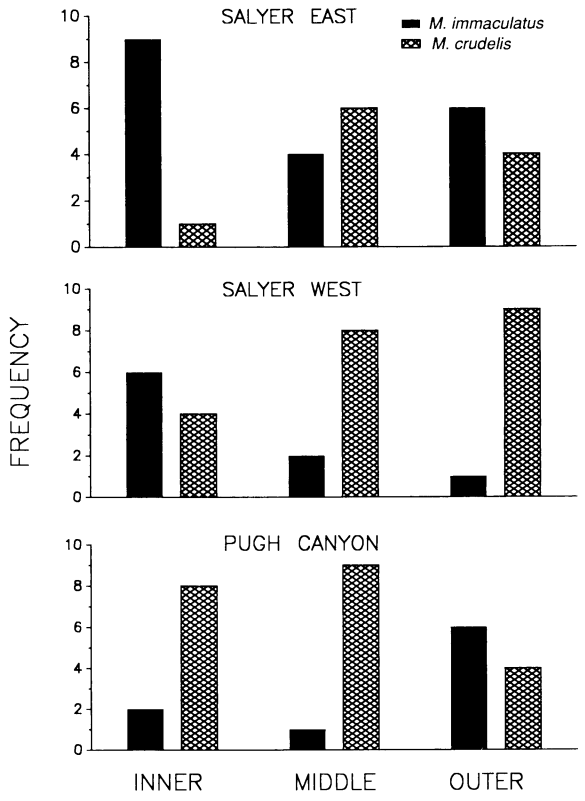

FIG. 10. Relative abundance of *Myrmeleon immaculatus* and *M. crudelis* at different locations within the ant lion zone. The inner samples were taken closest to the cliff wall, middle samples at the approximate midpoint of the ant lion zone, and outer samples at the distal edge. Salyer East ($G_2 = 6.01$, $P = .050$); Salyer West ($G_2 = 6.68$, $P = .035$); Pugh Canyon ($G_2 = 6.68$, $P = .035$).

higher than densities of *M. carolinus* in exposed microhabitats, which were characterized by high temperatures and frequent disturbance by rain (Lucas 1989).

As in Lucas' study, soil particle size was quite similar in shaded vs. exposed microhabitats. However, the soil in South Florida was mostly well-drained sand, so the effects of rainfall were less important than in central Oklahoma, where the soil probably has a higher clay content. Moreover, Lucas (1989) detected no spatial differences in prey availability, whereas, in this study, prey were consistently more abundant in exposed microhabitats.

Alternative hypotheses

Although the field experiments and observations point to the importance of abiotic factors in maintaining ant lion zones, it is important to consider mechanisms that were *not* tested in this study. Competition and predation are two such mechanisms that often lead to zonation. Ant lions could compete indirectly with plants for space, but the habitat surveys revealed an abundance of available habitat outside of the ant lion zone (Fig. 2). Similarly, competition for food is unlikely to limit distribution because food abundance is probably greater outside the ant lion zone (Figs. 5 and 9).

Although ant lions have been recorded in the stomach contents of lizards (Pianka 1975, Best and Gennaro 1985), there is little evidence of predation or parasitism on ant lions by other taxa (Lucas 1985). In this study, there were no missing animals or evidence of predation in the transplant experiment, suggesting that predation does not limit ant lion distributions.

Behavior of adult ant lions may also contribute to spatial pattern in the larval population. Lacewings probably oviposit in sheltered microhabitats (Lucas 1989; N. J. Gotelli, *personal observations*), but larvae are very mobile and often travel distances greater than the width of the ant-lion zone. Consequently, female oviposition behavior may contribute to the origin of the ant lion zone, but not to its maintenance.

Consequences of ant lion zones

Although the interaction of abiotic factors causes the ant lion zone, there are several biotic consequences of this restricted spatial distribution. First, ant lions are consistently denied access to exposed areas where food is more abundant. Similar foraging constraints have been described for desert spiders, which can spend little time in the most productive habitats because of thermal limits (Riechert and Tracy 1975). Intertidal gastropods are also denied access to patches of high prey abundance because heavy wave action restricts predators to crevices (Menge 1978).

Second, because both ant lion species are restricted to a spatially limited habitat, the probability of inter- and intraspecific encounters, including predation and cannibalism (Lucas 1989, Matsura and Takano 1989), is increased. These interactions may affect population dynamics and the probability of species coexistence (Polis et al. 1989). Species interactions are suggested by the negative covariation in abundances for the control plots ($r = -0.64$, $P = .03$; $n = 12$). These samples were taken from plots of homogeneous habitat in the center of the ant lion zone, so the pattern probably does not reflect subtle covariation with underlying habitat structure.

There is currently much interest in habitat selection and population interactions (Rosenzweig 1991), but ant lions in this system will never achieve an ideal free distribution (Fretwell and Lucas 1970) with respect to food supply because of overriding abiotic constraints. The geometry of the ant lion aggregation also establishes the potential for shadow competition (Wilson 1974, Linton et al. 1991) between animals in the front and back of the zone.

Interactions between the two species of ant lion may be mediated by the physical environment. Fig. 10 shows that the relative abundance of both species changed as a function of distance from the cliff wall. These patterns were not consistent from site to site, perhaps because of differences in local habitat or age structure of the

populations. A detailed analysis of inter- and intraspecific interactions is beyond the scope of this study. However, it is clear that the abiotic restriction of both species to a narrow, high-density zone greatly increases the chances for encounters between individuals.

Finally, physical constraints on predator distribution may have important consequences for prey community structure (Connell 1975). There may be a cause-and-effect relationship between high ant lion abundance and low prey abundance at cliff bases (Sih 1984). At least three hypotheses may account for reduced prey abundance: (1) direct predation by ant lions; (2) predator avoidance by prey; (3) prey responses to microhabitat gradients. Additional field experiments, including predator removals and microhabitat manipulations, are necessary to distinguish among these hypotheses. Preliminary results (N. J. Gotelli, *unpublished data*) suggest that ant lion predator aggregations are an important biotic constraint on foraging activity and nest placement of ants.

In summary, the zonation of plant and animal populations is a challenging ecological problem because abiotic and biotic factors covary along spatial gradients. In this study, habitat and food availability, temperature, moisture, and disturbance increase away from the cliff base. Although correlative data negated certain hypotheses, manipulative field experiments were necessary to reveal the interaction between temperature and rainfall that restricts ant lion distributions and causes high-density predator aggregations.

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