# COMPETITION AND COEXISTENCE OF LARVAL ANT LIONS

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*Abstract.* What factors permit the coexistence of competing species? In central Oklahoma, the predaceous ant lions *Myrmeleon crudelis* and *M. immaculatus* live in dense aggregations at the sheltered bases of cliff ledges. Three larval instars of each species act as predators and competitors of one another. In controlled field experiments, mortality of second and third instars increased with density, although intra- and interspecific effects were indistinguishable. The presence of third-instar larvae did not affect recruitment or survivorship of first-instar larvae. In all experiments, mortality was predictable on the basis of body mass and larval density, but not species identity. Increased food supply shortened development time and increased adult body mass but did not affect mortality. Larvae near the front of the ant lion aggregation grew faster due to greater food availability but suffered greater mortality in the pupal stage. Although food and space were limiting, neither species was excluded because (1) intra- and interspecific effects were similar; (2) third-instar larvae could not suppress the recruitment of first-instar larvae; and (3) recruitment was patchy in time and space. Oviposition behavior and interactions among adult ant lions may also contribute to larval coexistence.

*Key words: ant lion; cannibalism; coexistence; competition; food and space limitation; insect; intraguild predation; larvae; life history; predation; recruitment.*

## INTRODUCTION

The coexistence of species remains a central, unsolved problem in community ecology (Case and Diamond 1986, Gotelli and Graves 1996). If a pair of species consumes shared resources, why doesn't one member of the pair go extinct? Traditionally, there have been three kinds of answers. First, factors such as predation or disturbance may suppress densities to chronically low levels, so that shared resources never become limiting (Connell 1975, Sousa 1984). Second, coexistence on a local scale may be transitory, but regional coexistence may be maintained through immigration and patch dynamics (Hanski 1983, Wilson 1992). Third, competitors may partition available resources so that species coexist in a stable equilibrium, but at a lower abundance than they would in the absence of a competitor (MacArthur 1972, Tilman 1982).

Resource use and morphology of adult organisms have provided the traditional framework for studying resource partitioning (Wiens 1982). However, different size and age classes in a population may effectively function as different ''species'' in resource use (Wilson 1975, Polis 1984), particularly in animals with complex life histories (Wilbur 1988). Moreover, many species adopt different trophic roles depending on their stage or size (Werner and Gilliam 1984). Some species pairs may interact both as competitors and as predators of one another (Polis and McCormick 1987, Wissinger 1989, Moran 1995). This phenomenon of intraguild predation is widespread in nature (Polis et al. 1989)

and may enhance or destabilize the coexistence of competing species (Polis and Holt 1992).

In this paper, I describe the results of six manipulative field experiments and one laboratory experiment designed to test for the effects of intraguild predation on the coexistence of two species of larval ant lion (Neuroptera: Myrmeleontidae). My experiments manipulate food, spatial arrangement, and larval density, and assess their effects on different combinations of species and larval instars. The results provide insight into mechanisms that promote species coexistence.

## MATERIALS AND METHODS

### The study system

Ant lion larvae are ideal for studying species coexistence. Larvae are sit-and-wait predators that capture arthropod prey—including other ant lions—in sand pits (Plate 1) (Wheeler 1930, Topoff 1977). There are three larval instars. Larval development in the field takes 1–2 yr, so overlapping generations of larvae coexist. Larvae pupate in the soil, and adult ant lions emerge in the spring and summer. The adult ant lion is short lived; it ecloses, mates, and oviposits in the soil (Wheeler 1930).

In Caddo County, Oklahoma, *Myrmeleon crudelis* and *M. immaculatus* coexist at the sheltered bases of sandstone cliffs, where densities can exceed 100 larvae/m². Both species are restricted to this microhabitat by rainfall and high temperature in exposed areas (Gotelli 1993). Within the ant lion zone, there is no spatial segregation of the two species, although their numbers are negatively correlated in small-quadrat samples (Go-
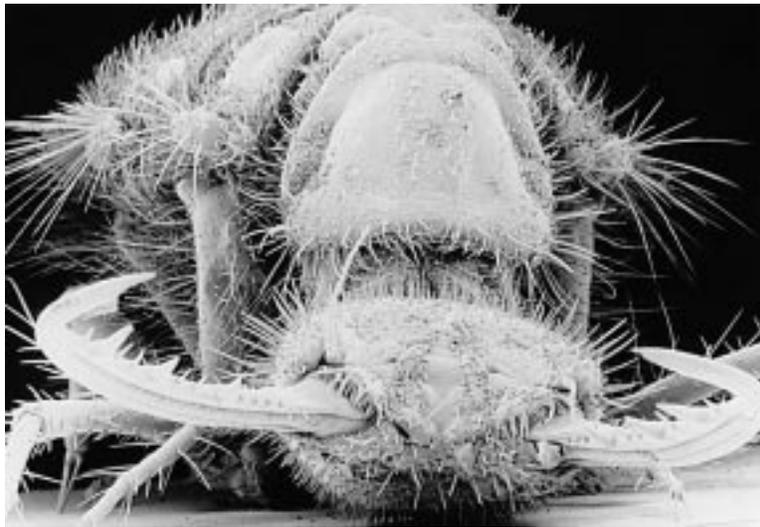
PLATE 1. Head and jaws of third-instar larva of *Myrmeleon immaculatus*. Photo courtesy of Dr. Kathleen Shields, USDA Forest Service.

telli 1993). Species coexist stably in this region, and I have collected both species at a number of cliff ledges in Caddo County (Salyer East, Salyer West, Pugh Canyon, North Canyon) for the past 7 yr.

Third-instar larvae of *M. immaculatus* are larger than those of *M. crudelis* (Lucas and Stange 1981), but there is considerable overlap of body size and feeding habits among all instars. Ants are the most common potential prey item in pitfall catches (Marsh 1987, Lucas 1989, Gotelli 1993, 1996), and the probability of capture is inversely related to ant body size (Gotelli 1996). However, field experiments reveal that ants can detect and effectively avoid high-density ant lion aggregations (Gotelli 1996).

Collectively, these observations suggest that both space and food may be limiting resources for ant lion larvae. Space is probably limiting because abiotic factors restrict both species to a specialized microhabitat. Food is probably limiting because the most common prey taxon is effective at avoiding ant lion aggregations. In the following sections, I describe field experiments that test for the effects of space and food limitation and reveal the mechanisms of species coexistence. Because of the potential for complex trophic interactions, different larval instars are treated as different "species" in intra- and interspecific competition experiments.

### Overview of the experiments

I conducted six field experiments and one laboratory experiment to test for the effects of competition among larvae for food or space (Table 1). In all experiments, larvae were maintained in enclosures that restricted their movement but allowed them to construct natural feeding pits and intercept ambient prey. The following section describes the methods and procedures that are common to all of the experiments. Then I provide details for each experimental manipulation.

### Field procedures

In Experiments 1–5, larvae were collected randomly from the field and returned to the laboratory for identification, weighing, and treatment assignment. Larvae were identified to species by the width : length ratio of the head capsule and by the pigmentation pattern on the head capsule. Both traits vary predictably between species (Lucas and Stange 1981). Larval stages were determined by head capsule width. Each larva was weighed to the nearest 0.1 mg in the laboratory and assigned randomly to one of the experimental treatments. One-way ANOVAs confirmed that there were no significant differences ($P > 0.30$) in initial body mass of individuals of the same stage and species that were assigned to different treatments. Within a replicate, each larva was uniquely marked with a tiny spot of colored enamel paint on the dorsal side of the abdomen. Larvae were held in plastic dishes (12 cm diameter, 2 cm depth) filled with 270 g of oven-dried sand collected from the ant lion zone. Larval densities in these experiments bracketed the range of densities typically encountered in the field (Gotelli 1993).

In Experiments 1, 3, and 4, each dish was covered with 2 mm mesh netting to prevent the escape of larvae. However, the mesh did not prevent the escape of tiny first-instar larvae in Experiment 3. Large prey items may have been excluded by this mesh, although smaller prey did enter the dishes. In the recruitment experiment 5, the dishes were open so that females could oviposit in them. Dishes were randomly placed on the soil surface in the ant lion zone. Each dish was separated by 0.25 m from its nearest neighbor. During transport to and from the laboratory, larvae were segregated into

TABLE 1.  Summary of field and laboratory experiments.

| Experiment | Treatments | Duration (d) | Replication |
|---|---|---|---|
| 1. Effects of intraspecific competition on mortality of 2*Mc*. | 2*Mc* (1,2,4,8) | 47 | 20 |
| 2. Effects of intraspecific competition on mortality of fed 2*Mc* (laboratory). | 2*Mc* (1,2,4) | 25 | 24 |
| 3. Effects of intraspecific competition and presence of 3*Mi* on disappearance of 1*Mi*, 1*Mc*. | 1*Mi* (1,2,7)  1*Mc* (1,2,7)  3*Mi* (0,1) | 43 | 36 |
| 4. Effects of intra- and interspecific competition on mortality of 3*Mi* and 3*Mc*. | 3*Mi* (1), 3*Mi* (2), 3*Mi* (4)  3*Mc* (1), 3*Mc* (2), 3*Mc* (4)  3*Mc* (1) 3*Mi* (1), 3*Mc* (2) 3*Mi* (2) | 40 | 32 |
| 5. Effects of year, site, 3*Mi*, 3*Mc* and sham ant lion pits on recruitment of 1*Mi* and 1*Mc*. | Year (1992, 1993)  Site (SE, SW, PC, NC)  Treatment (3*Mi*, 3*Mc*, sham pit, control) | 100 d each year | 128 |
| 6. Effects of spatial position within the ant lion zone on growth and emergence of 3*Mc*. | Position (edge, center) | 80 | 37 |
| 7. Effects of food supplementation on growth, length of larval life, and adult emergence of 3*Mi*. | Diet (control, food supplement) | 46 | 40 |

*Notes:* Numerals and lowercase letters refer to instars and species. For example, 3*Mi* = third-instar *M. immaculatus*; 1*Mc* = first-instar *M. crudelis*. Numbers in parentheses refer to abundance levels in different treatments. Replication gives the total number of independent replicates in each experiment. Site abbreviations are SE = Salyer East, SW = Salyer West, PC = Pugh Canyon, and NC = North Canyon.

individual plastic containers to prevent them from eating one another. The fate of each larva (living, pupated, or dead) was scored at the end of the experiment. In the competition experiments with second- or third-instar larvae (Experiments 1, 2, and 4), dead larvae always showed wounds or punctures, indicating cannibalism or interspecific predation as the cause of death.

Experiments 6 and 7 also used similar methods. In these experiments, third-instar larvae were collected from the field, measured, and randomly assigned to treatments. Each larva was maintained individually in a plastic drinking cup filled with 500 g of sifted, oven-baked sand collected from the study site. Larvae constructed normal pits and fed actively in these containers. Each cup was buried in the ant lion zone with the lip of the cup flush with the adjacent sand surface. This configuration prevented the ant lion from escaping but allowed access to ambient prey resources and a natural background of thermal, photic, and moisture regimes. All larvae showed evidence of feeding during this experiment, and control larvae showed significant gains in mass in the absence of food supplements. Every 15 d, larvae were transported to the laboratory, weighed to the nearest 0.1 mg, and returned to the field within 48 h. Pupae were reared in the laboratory at room temperature (25°C) under a 12:12 L:D photoperiod and monitored daily until adult emergence. Adults in Experiment 6 were frozen upon emergence and then weighed to the nearest 0.1 mg. Adults in Experiment 7 were weighed immediately after emergence. Dead larvae in Experiments 6 and 7 did not show signs of predation or cannibalism.

### Statistical analyses

In the interest of brevity, I do not present ANOVA tables, although these are available from the author

upon request. Unless otherwise stated, interaction terms were nonsignificant ($P > 0.10$). I analyzed the data from Experiments 1–5 in two ways. First, I computed for each species the percentage mortality in a replicate as the response variable. Data were arcsine square-root transformed before analysis. These ANOVAs (or MANOVAs) tested for treatment effects, usually in a mixed-model ANOVA. Density levels were designated as random effects, because a number of possible density levels could have been used. However, results were qualitatively similar when density was treated as a fixed effect.

In a complementary set of analyses, I treated larval fate (e.g., living, molted, pupated, dead) as the response variable in a nominal logistic regression. In these analyses, each larva served as a replicate, and the factors were treatment and initial body mass. These analyses violated the assumption of independence of larvae within a replicate, but they revealed the effects of body size on larval fate, which could not be accommodated in conventional ANOVAs. As will be shown, the effect of body size on larval fate was often more important than the effects of intra- or interspecific competition.

### Experiment 1. Intraspecific competition among second-instar M. crudelis

In this field experiment, I tested for intraspecific competition among second-instar larvae of *M. crudelis*. Larvae were collected from the field on 28 June 1992 and assigned randomly to one of four density treatments: one, two, four, or eight larvae per replicate, with five replicates per treatment. The surface area of each enclosure was ≈0.011 m², so larval density in this experiment varied from ≈90 to 720 animals/m². These densities bracketed the range of natural densities typ-

ically encountered for second-instar larvae. At the highest density of eight larvae per container, there was not enough space for all larvae to construct feeding pits. Treatments were established at Pugh Canyon on 30 June 1992, and the experiment was run until 16 August 1992. The fate of each larva (living, molted to third instar, or dead) was scored at the end of the experiment. Dead larvae always showed wounds or punctures, indicating cannibalism as the cause of death. Five out of the 75 larvae used were missing at the end of the experiment. I conservatively classified those individuals as ''living'' in the analyses, but results were qualitatively similar when missing larvae were deleted from the analyses.

I computed the percentage mortality in each replicate and analyzed the data as a one-way ANOVA using the four density treatments, and as a simple linear regression with $\log_{10}$(larval density) as the predictor variable. I also used the nominal regression model to assess the effects of treatment and initial body size on larval fate (dead, living, or molted to third instar) at the end of the experiment.

### Experiment 2. Intraspecific competition among fed second-instar M. crudelis

This experiment was similar to Experiment 1, except that it was conducted in the laboratory so that larvae could be fed. Larvae were collected from the field in Oklahoma on 28 March 1995 and mailed overnight to Burlington, Vermont. No mortality of larvae occurred during shipping. Larvae were not weighed initially in this experiment, but they were assigned randomly to one of three density treatments: one, two, or four larvae per replicate, with eight replicates per treatment. Larvae were held in 10 cm diameter plastic cups half filled with sand. The experiment was maintained in a Percival growth chamber at 26°C, 60% relative humidity, on a 12:12 L:D photoperiod. Daily, each ant lion larva with a pit was fed one *Tribolium confusum* larva. The fate of each ant lion larva (living, dead) was scored at the end of the experiment. No larvae were lost or missing, and all corpses showed evidence of cannibalism.

### Experiment 3. Effects of intraspecific competition and presence of third-instar M. crudelis on first instars of M. crudelis and M. immaculatus

This experiment tested the responses of first-instar larvae of each species to differences in first-instar density (one, two, or seven larvae) and to the presence or absence of a single third-instar larva of *M. crudelis*. Thus, the experiment addresses the ability of new first instars to persist in the presence of established third-instar larvae. First-instar larvae of both species were collected from the field on 30 August 1993 and assigned randomly to one of the six treatment combinations (three density levels × two third instar levels). For each species, there were three replicates of each of the six treatment combinations.

TABLE 2. Treatment combinations in a field experiment testing for intra- and interspecific competition among third-instar larvae (Experiment 4).

| Number of *M. immaculatus* larvae | Number of *M. crudelis* larvae | | | |
|---|---|---|---|---|
| | 0 | 1 | 2 | 4 |
| 0 | | a | b | c |
| 1 | d | g | | |
| 2 | e | | h | |
| 4 | f | | | |

*Note:* Letters indicate the eight treatment combinations that were established. Intraspecific comparisons were: a, b, c and d, e, f; interspecific comparisons were: e, g, b and f, h, c.

Larval density in this experiment varied from ≈90 to 630 animals/m², bracketing the range of densities typically encountered for recruiting first-instar larvae. In the presence of a third-instar *M. crudelis,* there was not enough room for all first-instar larvae to establish feeding pits in the highest density treatment of seven larvae/replicate. Treatments were established on 1 September 1993 and ran until 13 October 1993. The fate of each larva (living, molted to second instar, or missing) was scored at the end of the experiment. Dead larvae were not found in this experiment.

The response variable was the percentage (arcsine square-root transformed) of larvae in a replicate that were missing at the end of the experiment. This measure includes both larval mortality and larval emigration out of the enclosures, which could not be distinguished. Treating each replicate as a single observation, I used a two-way mixed-model ANOVA to test for effects of density (one, two, or seven first-instar larvae) and third-instar *M. crudelis* (present or absent) on the percentage of larvae missing. Density was treated as a random factor and presence of a third instar was treated as a fixed factor. I also used a nominal logistic regression to test for effects of initial larval body mass on fate (living, molted to second instar, or missing) of larvae at the end of the experiment. Analyses were run separately for each species.

### Experiment 4. Effects of inter- and intraspecific competition on third-instar M. crudelis and M. immaculatus

In this experiment, I examined inter- and intraspecific competition between third-instar larvae of *M. crudelis* and *M. immaculatus*. Each treatment combination included one, two, or four larvae of one or both species. Forty larvae of each species were assigned to one of eight treatment combinations (Table 2), with four replicates per treatment. There were six single-species treatments with three density levels (one, two, or four larvae) for each species. There were two mixed-species treatments with two or four larvae total. This design allowed me to partition both intraspecific and interspecific density effects (Goldberg and Scheiner 1993).

Larvae were collected from the field on 30 June 1993. Larval density in this experiment varied from ≈90 to 360 animals/m². At the highest density of four larvae per container, there was not enough space for all larvae to construct feeding pits. Treatments were established on 2 July 1993, and the experiment was run until 11 August 1993. The fate of each larva (living, pupated, or dead) was scored at the end of the experiment. No larvae were missing at the end of this experiment.

To measure the effects of intraspecific density, I used a one-way ANOVA, comparing average mortality of treatments with one, two, and four larvae per replicate. To measure the effects of interspecific density, I used a two-way ANOVA, comparing average mortality in the treatments with two or four larvae. The two factors were mixture (single species, two species) and density (two larvae, four larvae). I also analyzed larval fate (living, pupated, or dead) as the response variable in a nominal logistic regression. In these analyses, each individual larva is a replicate, and the factors are treatment and initial body mass.

### Experiment 5. Effects of year, site, third-instar larvae, and sham ant lion pits on recruitment of first-instar *M. crudelis and M. immaculatus*

In the previous experiments, I experimentally manipulated ant lion density. In this recruitment experiment, density was the response variable, and the microhabitat was experimentally manipulated. ''Recruitment'' was defined as the appearance of tiny pits built by first-instar larvae in a replicate dish. Thus, recruitment may reflect female oviposition preferences, as well as early mortality or migration of first-instar larvae before pit construction (see Keough and Downes 1982).

Four treatments were established: (1) Control. Control dishes received oven-dried sand, but no other manipulation. (2) Third-instar *M. crudelis.* A single third instar larva of *M. crudelis* was placed in a replicate and allowed to construct a normal feeding pit. (3) Third-instar *M. immaculatus.* This treatment was identical to Treatment 2, except for the identity of the third-instar larva. (4) Empty pit. In this treatment, a sham ant lion pit 3 cm in diameter was constructed in each replicate.

This experiment was conducted during the recruitment season of 1992 and 1993 at four canyon sites: Pugh Canyon, Salyer East, Salyer West, and North Canyon (see Fig. 1 of Gotelli 1993 for a map). At each site, four replicates of each treatment were established in the ant lion zone in an alternating spatial arrangement, separated from one another by 0.2 m. There was a total of 128 replicates (four sites × four treatments × two years × four replicates) in the experiment.

Treatments were established early in June of each year, several weeks before the start of the recruitment season. The experiments were run until the middle of September, which is the end of the recruitment season.

I censused the treatments 3–5 times/wk during this period. Whenever first-instar pits were detected, the sand from that replicate was immediately replaced with fresh medium. The old sand was returned to the laboratory and sifted, and first-instar larvae were identified to species and counted. For Treatments 2 and 3, third-instar larvae that escaped, pupated, or died were immediately replaced.

Because recruitment was low (or zero) for most replicates, I summed the recruitment for each replicate across the entire season. The response variable was the number of first-instar larvae of *M. crudelis* and *M. immaculatus.* The design was a three-factor mixed-model MANOVA. The factors were site (four levels), treatment (four levels), and year (two levels). Site and year were random factors, and treatment was a fixed factor. The data were square-root-transformed before analysis.

In addition to the overall MANOVA, I tested two a priori contrasts. The first was the contrast of Treatment 1 to the average of Treatments 2, 3, and 4. This contrast tests whether recruitment was lower in the presence or the absence of an ant lion pit. The second contrast was between the average of Treatments 1 and 4 and the average of Treatments 2 and 3. This contrast tests whether recruitment was lower in the presence or the absence of living ant lions.

### Experiment 6. Effects of spatial position within the ant lion zone on growth and emergence of third-instar *M. crudelis*

Thirty-seven third-instar larvae of *M. crudelis* were collected in May 1992, sorted according to size and mass, and assigned randomly to one of two treatments, center or edge. Center animals ($n = 18$) were raised in the center of the ant lion zone. Edge animals ($n = 19$) were raised in the proximal region of the ant lion zone, farthest from the cliff wall where larval density was lowest (Fig. 1). These two microhabitats were separated by <1 m. No further manipulations were performed, and larvae were exposed to ambient food levels and abiotic factors in the two microhabitats. The experiment lasted for 80 d, until the last individual had pupated or died. In this analysis, the response variables were larval growth during the first 2 wk, larval duration, pupal duration, and adult body size. Each larva was treated as an independent replicate in an ANCOVA, using $\log_{10}$(initial body mass) as the covariate. Eleven larvae escaped during the course of the experiment and were not included in the analysis.

### Experiment 7. Effects of food supplementation on growth, pupation, and adult body size of third-instar *M. immaculatus*

Forty third-instar larvae of *M. immaculatus* were collected in May 1991, sorted according to size and mass, and assigned randomly to one of two treatments, control or food supplement. Control animals were allowed access to ambient food levels. Food supplement ani-
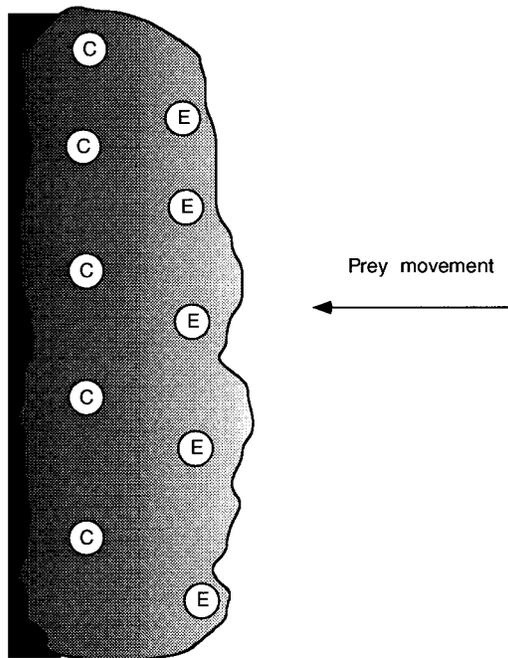
FIG. 1. Layout of field experiments to test for shadow competition (Experiment 6) and food supplementation (Experiment 7). The irregular polygon represents the ant lion zone, and the shading is proportional to natural ant lion density. The black bar represents the cliff ledge, and the arrow indicates the principal direction of prey entry. Each circle represents a plastic cup, buried flush with the soil surface and containing a single ant lion larva. In Experiment 6, half the larvae were transplanted to the edge of the ant lion zone (E) and half were transplanted to the center (C). In Experiment 7, all larvae were transplanted to the center of the ant lion zone, but half were given an additional food supplement of three ants per week.

mals were hand-fed an additional three minor workers of *Camponotus modoc* per week. All larvae were reared in individual cups embedded in the center of the ant lion zone (Fig. 1). Treatments were established in alternating order. The response variables were larval growth during the first 2 wk, time to completion of the third-instar stage, duration of the pupal stage, pupal and adult body mass, and successful emergence rate from pupation. Data were analyzed with an ANCOVA, using $\log_{10}$ (initial body mass) as the covariate. Thirteen larvae escaped during the course of the experiment and were not included in the analysis.

## RESULTS

### Experiment 1. Intraspecific competition among second-instar M. crudelis

The ANOVA of density effects on mortality was nearly significant ($P = 0.072$), and a simple regression analysis of percentage mortality vs. larval density was highly significant ($N = 20$, $P = 0.007$). No mortality was recorded in the treatments with one or two larvae, but there was increasing mortality for the treatments
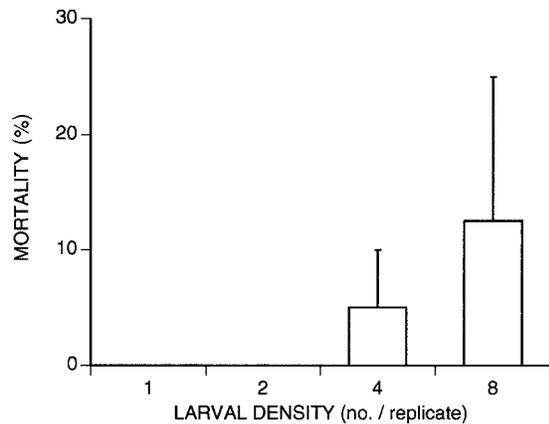


FIG. 2. Effects of density on mortality of second-instar *M. crudelis* (Experiment 1). Each bar is the average percentage mortality in a treatment. Vertical lines are 1 SD; $n = 5$ replicates per treatment ($F_{3,16} = 2.818$, $P = 0.072$; regression of mortality on $\log_{10}$ density $F_{1,18} = 9.259$; $P = 0.007$).

with four larvae (average percentage mortality $\pm$ 1 SD $= 5.0 \pm 12.5$) and eight larvae ($12.5 \pm 12.5$) (Fig. 2). The nominal regression revealed a significant effect of initial body size on larval fate ($P = 0.032$). As confirmed by ANOVA ($P = 0.004$), larvae that molted to the third instar by the end of the experiment were initially largest (average body mass $\pm$ 1 SD $= 7.89 \pm 2.32$ mg), and larvae that died were initially smallest ($5.32 \pm 1.87$ mg) (Fig. 3).

### Experiment 2. Intraspecific competition among fed second-instar M. crudelis

Both the ANOVA ($P = 0.0002$) and the regression ($N = 24$, $P = 0.0045$) of density effects on mortality were highly significant. Although all ant lions with pits were fed daily in this laboratory experiment, there was no mortality for solitary larvae, but increasing density-
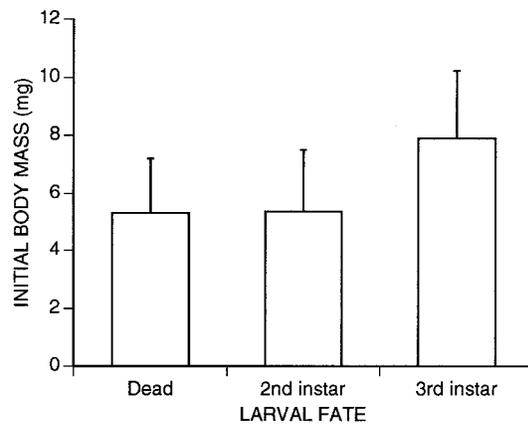


FIG. 3. Differences in initial body mass associated with larval fate at the end of Experiment 1. Each bar is the average initial body mass, pooled over all experimental treatments. Vertical lines are 1 SD. Dead $n = 6$; second-instar $n = 51$; third-instar $n = 13$ ($F_{2,67} = 6.132$; $P = 0.004$).
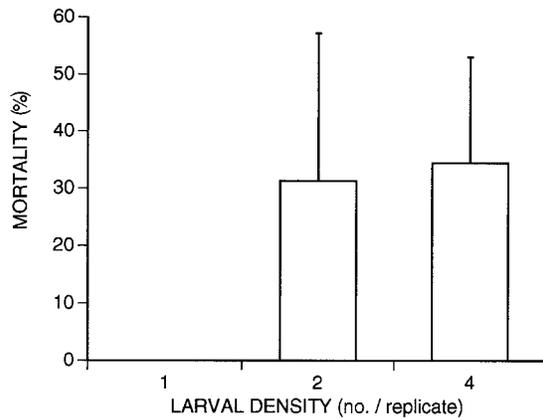
FIG. 4. Effect of density on mortality of fed *M. crudelis* (Experiment 2). Each bar is the average percentage mortality in a treatment. Vertical lines are 1 SD; $n = 8$ replicates per treatment ($F_{2,21} = 12.69$, $P = 0.0002$; regression of mortality on $\log_{10}$ density, $F_{1,22} = 15.64$, $P = 0.0007$).

dependent mortality for treatments with two (average percentage mortality $\pm$ 1 SD = 31.2 $\pm$ 25.9) or four (34.4 $\pm$ 18.6) larvae per replicate (Fig. 4).

### Experiment 3. Effects of intraspecific competition and presence of third-instar M. crudelis *on first instars of* M. crudelis *and* M. immaculatus

For both species, there were no significant effects of either density (*M. immaculatus, P* = 0.999; *M. crudelis, P* = 0.200) or presence of third instars (*M. immaculatus, P* = 0.652; *M. crudelis, P* = 0.491) on persistence of first instar larvae. For *M. crudelis,* the pattern was one of inverse density dependence: none of the first-instar larvae in the single-larva treatment persisted to the end of the experiment, whereas persistence was higher in the high-density treatments (Fig. 5). For *M. immaculatus,* the logistic regression revealed that initial body mass had a significant effect on larval fate (*P* = 0.038); the effect was marginal for *M. crudelis* (*P* = 0.084). A separate ANOVA for each species also confirmed that initial body mass differed significantly among larval fates (*M. crudelis, P* = 0.003; *M. immaculatus, P* = 0.004). For both species, larvae that molted to second instars were initially larger than those that did not molt or were missing at the end of the experiment, irrespective of treatment (Fig. 6).

### Experiment 4. Effects of inter- and intraspecific competition on third-instar M. crudelis *and* M. immaculatus

For *M. crudelis,* there was no mortality in the single-larva treatment, but significantly higher mortality (*P* = 0.020) in the two- and four-larvae treatments (Fig. 7). Patterns were similar for intraspecific density treatments of *M. immaculatus,* although the results were not statistically significant (*P* = 0.274).

The interspecific analysis failed to reveal any sig-

nificant effect of species identity or density (two or four larvae) on the mortality of either species (*P* > 0.10, all main effects and interactions). For *M. crudelis,* mortality was somewhat higher in mixed vs. single-species treatments (Fig. 7). For *M. immaculatus,* there was no mortality in the mixed two-larvae treatment (Fig. 7). However, there was considerable variance about the means, and these differences were not statistically significant.

The nominal regression analysis also confirmed that larval fate was not influenced by experimental treatment (*P* > 0.10, all treatment effects). However, for
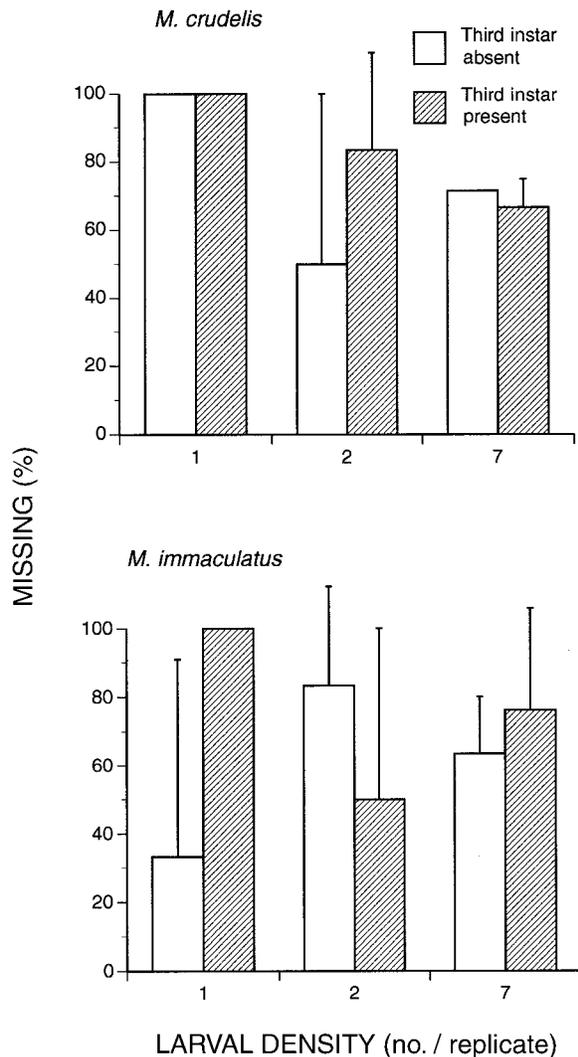


FIG. 5. Effects of larval density and presence of a third-instar *M. immaculatus* larva on the disappearance of first-instar larvae of each species (Experiment 3). Each bar is the average percentage of larvae missing in a treatment at the end of the experiment. Vertical lines are 1 SD; $n = 3$ replicates per treatment per species. (*M. immaculatus* density effect, $F_{2,2} = 0.000$, $P = 1.000$; third-instar effect, $F_{1,2} = 0.275$, $P = 0.652$; *M. crudelis* density effect, $F_{2,2} = 4.020$, $P = 0.200$; third-instar effect, $F_{1,2} = 0.700$, $P = 0.491$).
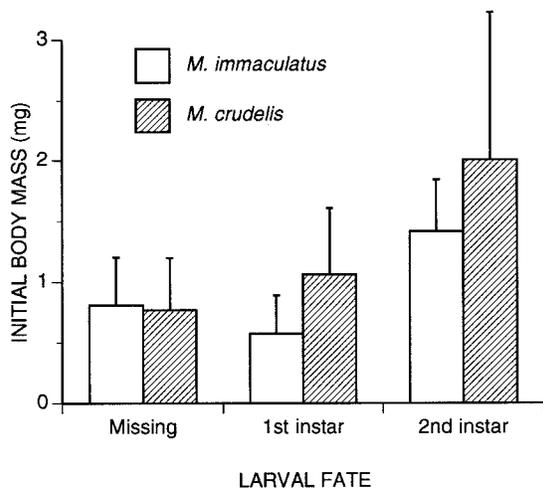
FIG. 6. Differences in initial body mass associated with larval fate at the end of Experiment 3. Each bar is the average initial body mass, pooled over all experimental treatments. Vertical lines are 1 SD. For *M. crudelis,* missing $n = 42$; first instar $n = 12$; second instar $n = 6$. For *M. immaculatus,* missing $n = 40$; first instar $n = 12$; second instar $n = 8$. (*M. crudelis* $F_{2,57} = 6.487$, $P = 0.003$; *M. immaculatus* $F_{2,57} = 6.237$, $P = 0.004$).

both species, larval fate was influenced by the initial body mass of the larva at the start of the experiment (*M. immaculatus, P = 0.032; M. crudelis, P = 0.035*). Irrespective of treatment, large larvae tended to survive better than small larvae (Table 3). A two-way ANOVA also revealed significant differences in initial larval body mass between species ($P < 0.001$) and among larval fates ($P < 0.001$). For both species, larvae that died during the course of the experiment were initially small, larvae that pupated were initially large, and larvae that survived as third instars were initially of intermediate body mass (Fig. 8).

### Experiment 5. Effects of year, site, third-instar larvae, and sham ant lion pits on recruitment of first-instar M. crudelis and M. immaculatus

The MANOVA did not reveal significant effects of site, year, or treatment on the recruitment of ant lion larvae ($P > 0.10$, all main effects and interactions). The contrast of the control (Treatment 1) vs. the average of the other treatments (2, 3, and 4) was marginally nonsignificant ($P = 0.06$; Fig. 9). The contrast of the average of the treatments with no third instars (Treatments 1 and 3) vs. the average of the treatments with third instars present (Treatments 2 and 4) was not significant ($P = 0.32$).

### Experiment 6. Effects of spatial position within the ant lion zone on growth and emergence of third-instar M. crudelis larvae

Life history traits varied significantly for larvae reared in the edge vs. the center of the ant lion zone. Initial growth was significantly higher for the edge lar-

vae than for the center larvae (Fig. 10). However, this growth was not accompanied by significant changes in length of the larval or pupal life or adult body mass (Table 4). Although mortality did not occur while larvae were reared in the field, the probability of successful adult emergence in the laboratory was significantly greater for larvae reared in the center of the ant lion zone than for those reared on the edge (Table 4).

### Experiment 7. Effects of food supplementation on growth, pupation, and adult body size of third instar M. immaculatus

Food supplementation had dramatic effects on ant lion life history. Compared to controls, animals fed an
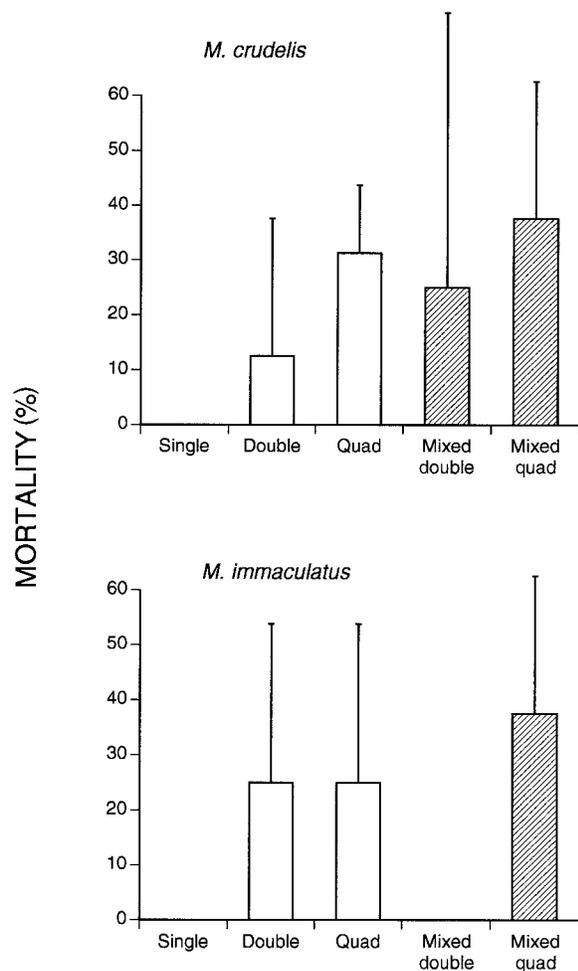


FIG. 7. Effects of density and species composition on mortality of third-instar larvae (Experiment 4). Each bar is the average percentage mortality for a particular treatment. Vertical lines are 1 SD. Single = 1 larva per replicate; Double = 2 larvae per replicate; Quad = 4 larvae per replicate; Mixed double = 2 larvae, 1 of each species, per replicate; Mixed quad = 4 larvae, 2 of each species, per replicate. Open bars = single-species treatments; hatched bars = mixed-species treatments. (*M. crudelis*: density, $F_{1,1} = 9.000$, $P = 0.205$; mixture, $F_{1,1} = 1.000$, $P = 0.500$. *M. immaculatus*: density, $F_{1,1} = 1.000$, $P = 0.500$; mixture, $F_{1,1} = 0.111$, $P = 0.795$).

TABLE 3. Effects of initial body size on mortality in a competition experiment (Experiment 4).

| Treatment† | Replicate number | Larvae | | | |
|---|---|---|---|---|---|
| b | 4 | **C** | C | | |
| c | 1 | **C** | C | C | C |
| | 2 | C | **C** | **C** | C |
| | 3 | **C** | C | C | C |
| | 4 | **C** | C | C | C |
| e | 3 | **I** | I | | |
| | 4 | **I** | I | | |
| f | 2 | **I** | I | **I** | I |
| | 3 | **I** | I | **I** | I |
| g | 2 | **C** | I | | |
| h | 1 | C | C | **I** | I |
| | 2 | **C** | C | I | I |
| | 3 | **I** | I | C | C |
| | 4 | **C** | C | I | **I** |

*Notes:* Each row represents a replicate in which mortality was recorded. Within a replicate, individual third-instar larvae are ordered by mass, with the smallest initial body mass on the left. Symbols indicate species identity: C = *M. crudelis*; I = *M. immaculatus*. If a symbol is bold, the individual died during the course of the experiment. Note the tendency for higher mortality among smaller individuals, regardless of the experimental treatment.

† See Table 2.

additional three ants per week pupated in an average of 18 d, compared to 31 d for controls (Fig. 11). In addition to the shorter length of the larval life, fed larvae gained significantly more mass, spent less time before pupation, formed larger pupae, spent longer in the pupal stage, and emerged with significantly greater adult body mass. Mortality rates were slightly lower for fed larvae, but the differences were not significant (Table 5).

### DISCUSSION

#### Body size and intraguild predation

My results are consistent with other community studies that document the effects of intraguild predation and cannibalism on species coexistence (reviews in Fox 1975, Polis 1981, Polis et al. 1989). However, there are two novel features of ant lion coexistence that are atypical of previous work. First, many examples of intraguild predation and cannibalism involve size-related habitat shifts (Werner and Gilliam 1984, Polis et al. 1989). In aquatic systems, in particular, predation and competition often lead to habitat segregation that can be predicted on the basis of body size (Power et al. 1989, Osenberg et al. 1992, Diehl and Eklöv 1995). For larval ant lions, however, there is no opportunity for habitat segregation, because both species are limited by rainfall and high temperatures to a spatially restricted microhabitat (Gotelli 1993).

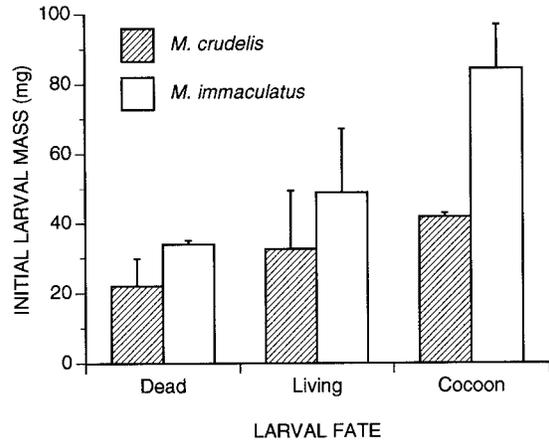A second feature of intraguild predation (and cannibalism) is that predation commonly occurs between



FIG. 8. Differences in initial body mass associated with larval fate at the end of Experiment 4. Each bar is the average initial body mass, pooled over all experimental treatments. Vertical lines are 1 SD. For *M. crudelis,* dead $n = 10$; living $n = 23$; pupa $n = 7$. For *M. immaculatus,* dead $n = 9$; living $n = 26$; pupa $n = 5$. (Species, $F_{1,74} = 19.82$, $P < 0.0001$; fate, $F_{2,74} = 32.28$, $P < 0.0001$.)

animals of dissimilar size, while competition occurs between animals of similar size. For example, Hopper et al. (1996) found that cannibalism in dragonfly larvae was uncommon between the same instars (2.4%), frequent between larvae with a one-instar difference (53%), and certain between larvae with a two-instar difference (100%). Wissinger (1992) constructed indices of competition that were based on the frequency with which dissimilar size classes encounter one an-
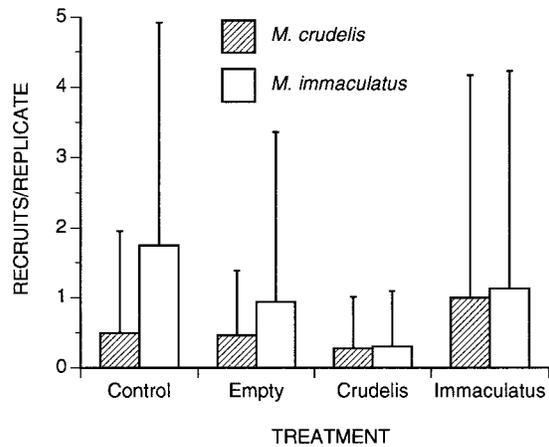


FIG. 9. Effects of experimental treatments on recruitment of first-instar ant lion larvae (Experiment 5). Bars represent average number of recruits per replicate. Vertical lines are 1 SD. Replicates are averaged over 2 yr and four sites; $n = 32$ replicates for each bar. Control = container with sand; Empty = container with sand and a sham ant lion pit; Crudelis = container with sand and one third-instar *M. crudelis*; Immaculatus = container with sand and one third-instar *M. immaculatus*. (MANOVA terms for main effects: year, $F_{2,95} = 0.052$, $P = 0.950$; site, $F_{6,190} = 1.473$, $P = 0.189$; treatment, $F_{6,190} = 1.663$, $P = 0.132$).

TABLE 4. Effects of spatial microhabitat on life history of *M. crudelis* (Experiment 6).

| Life history trait | Control | Edge |
|---|---|---|
| Larval mass at 14 d (mg)* | 33.54 ± 2.00 | 39.80 ± 1.80 |
| Length of third instar stage (d) | 29.59 ± 4.75 | 42.14 ± 4.75 |
| Length of pupal stage (d) | 35.76 ± 1.93 | 33.34 ± 2.32 |
| Adult mass (mg) | 21.31 ± 1.56 | 23.37 ± 2.03 |
| Adult emergence (%)* | 83.3 | 42.9 |

*Notes:* Least squares adjusted means ± 1 SE are given for control larvae ($n = 18$) raised in the center of the ant lion zone and edge larvae ($n = 19$) raised on the outermost edge of the ant lion habitat. Means are estimated from an analysis of covariance with initial larval mass as the covariate. Symbols indicate strength of the difference between treatment groups.

* $P < 0.05$.

other. For larval ant lions, body size was correlated with survival in several density experiments (Figs. 3, 6, and 8). However, these results only held for comparisons within the same instar. Between-instar experiments revealed no significant effect of third instars on either the persistence (Fig. 5) or the recruitment (Fig. 9) of first-instar larvae.

For damselfly larvae that coexist in tree holes, Fincke (1994) also found that predation was most severe between similar-sized larvae, with the larger individual of a pair usually winning in experimental contests. Coexistence of damselfly species depended on differential colonization ability due to differences in behavior of adult females (Fincke 1992). For ant lions, little is known of adult behavior or oviposition preferences, but these may well contribute to species coexistence, particularly since larval interactions do not indicate any obvious niche partitioning.

Why wasn't predation pressure evident for first-instar larvae? One reason is that the circular pits of third instars, even if they are packed at maximum density, create interstitial space that can be used by smaller instars. Indeed, first-instar larvae in the field sometimes construct pits within the inner walls of established third-instar pits (N. J. Gotelli, *personal observation*). Brown (1995) and others have speculated that body size differences create fractal patterns of niche segregation, and this idea seems to be confirmed for the spatial geometry of ant lion pits. The other reason is that multiple sources of migration and mortality may have obscured the effects of third instars on the survival of first instars. However, the statistical power of Experiment 3 was 0.56, so it is more likely that the results reflect a lack of third-instar effects than a Type II error.

Because both predation and competition are more severe between similar-sized larvae, there is little opportunity for size-based resource partitioning between *M. crudelis* and *M. immaculatus.* Although third-instar larvae of *M. immaculatus* are larger than third instars of *M. crudelis,* both species overlap considerably in
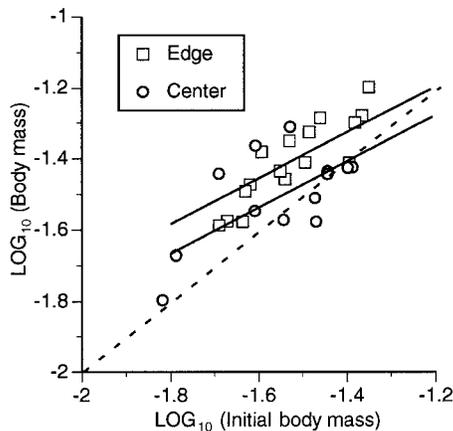


FIG. 10. Initial growth of third-instar *M. crudelis* reared in the edge and center of the ant lion zone (Experiment 6). The *y* axis is larval mass on 5 October 1992 and the *x* axis is larval mass on 25 June 1992. Each point is a different larva. The solid lines indicate the ANCOVA regression for each treatment group, and the dashed line is the expected curve if no increase in body mass had occurred (treatment effect, $F_{1,26} = 5.260$, $P = 0.030$). Results were not affected by deletion of either of the two points in the lower left-hand corner of the graph.
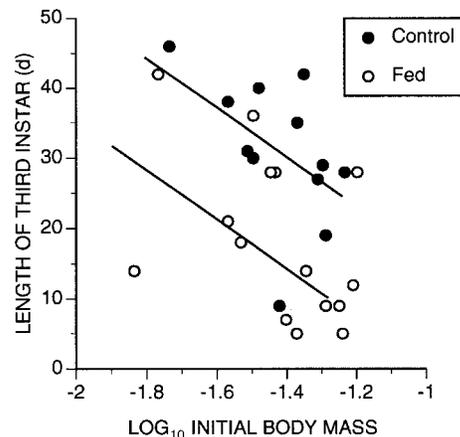


FIG. 11. Effects of food supplementation on length of the third instar of *M. immaculatus* (Experiment 7). Larvae were reared in individual containers in the center of the ant lion zone (see Fig. 1 for layout). Control larvae experienced ambient prey, and fed larvae were hand fed an additional three *Camponotus modoc* major workers per week. After controlling for differences in initial larval mass, length of the larval life was significantly reduced for fed larvae (see Table 5; treatment effect, $F_{1,24} = 11.110$, $P = 0.003$).

TABLE 5. Effects of food supplementation on life history of *M. immaculatus* (Experiment 7).

| Life history trait | Control | Food supplement |
|---|---|---|
| Larval mass at 14 d (mg)** | 42.05 ± 2.51 | 55.44 ± 2.81 |
| Length of larval life (d)** | 31.22 ± 2.87 | 18.35 ± 2.57 |
| Length of pupal life (d)* | 20.34 ± 1.40 | 24.38 ± 1.24 |
| Pupal mass (mg)** | 223.49 ± 12.44 | 267.44 ± 11.12 |
| Adult mass (mg)* | 9.75 ± 0.98 | 12.54 ± 0.87 |
| Mortality (%) | 20 | 16.7 |

*Note:* Least squares adjusted means ± 1 SE are given for control larvae ($n = 12$) and larvae whose diets in the field were supplemented with 3 *Camponotus modoc* major workers per week ($n = 15$). Adjusted means are estimated from an analysis of covariance with initial larval mass as the covariate. Symbols indicate strength of the difference between treatment groups.
\* $P < 0.05$; \*\* $P < 0.01$.

body size during most of their development, and traditional explanations of size-based resource partitioning probably cannot account for their coexistence. The statistical power of Experiment 4 was low (0.34), so the differences in Fig. 7 could be statistically significant, but obscured by small sample size and large variance. On the other hand, the nominal logistic regression, which had good sample sizes, also suggested no difference in inter- and intraspecific effects. Body size does predict larval fate, so differences in body size of cohorts of two competing species could translate into species-specific responses.

### Evidence for intraspecific resource limitation

Before analyzing the importance of interspecific competition in natural communities, it is necessary to document that resources limit population growth intraspecifically. I increased intraspecific density in enclosures and found that mortality of both *M. crudelis* and *M. immaculatus* increased. However, the effect varied with larval instar. Intraspecific competition for space was evident for second- and third-instar larvae (Figs. 2, 3, and 7), but not for first-instar larvae (Fig. 5). Their small size makes it unlikely that space is a limiting resource, even when densities are experimentally elevated well above those observed in nature.

The screen mesh enclosing each replicate prevented migration, which might have been a behavioral response to locally high densities. Ant lions throw considerable quantities of sand during pit construction and maintenance (Lucas 1982), and larvae will abandon patches if their pits are frequently filled with sand (Gotelli 1993). However, in the limited microhabitat of sheltered cliff ledges, larvae will not be able to permanently escape high density by movement.

The increase in mortality in the high-density treatments for second- and third-instar larvae (Figs. 2, 4, and 7) was due exclusively to cannibalism and interspecific predation. This result is probably not an artifact caused by the screen mesh reducing prey availability. In Experiment 2, larvae were fed daily, but density-dependent cannibalism was found as in Experiment 1 (see Figs. 2 and 3). Thus, cannibalism and interspecific predation are direct responses to increased density, not indirect responses to reduced food resources.

Ambient food levels may be chronically reduced because of effective avoidance behavior by ants (Gotelli 1996). The supplementation experiment (Experiment 7) demonstrates that food limitation is important, but its effects are more subtle than those of space limitation. Food limitation does not cause direct mortality, but induces shifts in ant lion life history. Increased food levels reduce the length of the larval life and increase adult body size (Table 5). However, there may be increased mortality from density-independent sources with increased larval life-span, and shifts in adult body size may have consequences for mating success, fecundity, and adult survivorship (Fincke 1992).

Given that both food and space are limiting resources, we would expect to see animals conform to an ideal free spatial distribution in which the costs of crowding are balanced by the availability of food (Fretwell and Lucas 1970). But this is not observed in nature. Instead, density is lowest in the front of the aggregation (Fig. 1; see also Fig. 2 in Gotelli 1993), where food is most abundant. The transplant experiment (Experiment 6) reveals why. Animals transplanted to the front of the ant lion aggregation do initially gain more mass (Fig. 10), so the potential exists for shadow competition (Linton et al. 1991) between larvae in the front and the rear of the ant lion zone. However, larvae reared in the front of the ant lion aggregation suffered greater mortality in the pupal stage (Table 4).

Although pupae were not reared in the field, there is unlikely to have been any additional mortality from cannibalism in the center vs. the edge of the ant lion zone. Ant lion larvae only feed on small, struggling prey. They will not feed on pupae, which are large and quiescent. By moving away from the front of the aggregation, ant lion larvae may sacrifice short-term gains in feeding to avoid greater mortality in the pupal stage. Although there is good evidence that animal foraging is constrained by current risks of mortality (Lima and Dill 1990), the results presented here suggest that the risk of future mortality dictates short-term feeding behavior and controls intraspecific density gradients.

### Mechanisms of species coexistence

In spite of the evidence for intraspecific competition for food and space (see also Lucas 1989, Matsura and Takano 1989, Griffiths 1991), both ant lion species coexist in the same microhabitat. The field experiments suggest that three mechanisms enhance the coexistence of these competitors. The first factor is that intra- and interspecific competitive effects did not differ statistically for third-instar larvae (Experiment 4). In terms of a simple Lotka-Volterra competition model, this would mean that the competition coefficients are similar, so that the isoclines would be parallel. Carrying capacities for both species are probably also similar, so the isoclines may be almost congruent. Under these circumstances, the time to competitive exclusion is long, and both species may persist indefinitely if there is any temporal variation in carrying capacity (Hutchinson 1961, Gallagher et al. 1990). Competition may also be mediated by shifts in habitat association (Abramsky et al. 1991). However, this mechanism is not available for ant lions, which are limited by abiotic factors to sheltered microhabitats (Gotelli 1993). Although there are apparently gradients in survivorship and food availability within the ant lion zone (Fig. 10 and Table 4), there is little evidence of spatial segregation among species (Gotelli 1993).

The second factor that promotes coexistence is that neither recruitment (Fig. 9) nor persistence (Fig. 5) of first-instar larvae is affected by the presence of third-instar larvae. Consequently, if either species were driven to local extinction, it would always be able to reinvade in the presence of third-instar larvae.

This ability to invade in the presence of other species is an important element of coexistence (Rummel and Roughgarden 1983, Milligan 1986). For larval ant lions, coexistence is enhanced because the presence of third-instar larval pits generates interstitial habitat for first-instar larvae, and because density-dependent mortality among first-instar larvae is weak (Fig. 5). Third-instar larvae may cannibalize first instars, but if so, there are compensatory sources of mortality, because there was no significant effect of third instars on either the disappearance (Fig. 5) or the recruitment (Fig. 9) of first-instar larvae.

Finally, variation in recruitment may contribute to species coexistence. There were no effects of microhabitat on recruitment of either species. Instead, recruitment was patchy and varied among identical replicates. However, there were not significant differences among either years or sites, which may be necessary for a storage effect (Warner and Chesson 1985) to enhance species coexistence.

In summary, field experiments demonstrate that both space and food limit ant lion populations intraspecifically. In contrast to most other assemblages, intraguild predation is most severe among instars of similar body size. As a consequence, inter- and intraspecific effects are similar, and first-instar larvae are not excluded from recolonization. These interactions among different larval instars, as well as interactions among adults and female oviposition choices, may contribute to the coexistence of ant lion larvae that experience limited food and space resources.

### LITERATURE CITED

Abramsky, Z., M. L. Rosenzweig, and B. Pinshow. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. Ecology **72**:329–340.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Case, T. J., and J. M. Diamond. 1986. Community ecology. Harper and Row, New York, New York, USA.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Diehl, S., and P. Eklöv. 1995. Effect of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology **76**:1712–1726.

Fincke, O. M. 1992. Interspecific competition for tree holes: consequences for mating systems and coexistence in neotropical damselflies. American Naturalist **139**:80–101.

———. 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia **100**:118–127.

Fox, L. 1975. Cannibalism in natural populations. Annual Review of Ecology and Systematics **6**:87–106.

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

Gallagher, E. D., G. B. Gardner, and P. A. Jumars. 1990. Competition among the pioneers in a seasonal soft-bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model. Oecologia **83**:427–442.

Goldberg, D. E., and S. M. Scheiner. 1993. ANOVA and ANCOVA: field competition experiments. Pages 69–93 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

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

———. 1996. Ant community structure: effects of predatory ant lions. Ecology **77**:630–638.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, DC, USA.

Griffiths, D. 1991. Intraspecific competition in larvae of the ant-lion *Morter* sp. and interspecific interactions with *Macroleon quinquimaculatus*. Ecological Entomology **16**:193–201.

Hanski, I. 1983. Coexistence of competitors in patchy environment. Ecology **64**:493–500.

Hopper, K. R., P. H. Crowley, and D. Kielman. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. Ecology **77**:191–200.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist **95**:137–145.

Keough, M. J., and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia **54**:348–352.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619–640.

Linton, M. C., P. H. Crowley, J. T. Williams, P. M. Dillon, H. Aral, K. L. Strohmeier, and C. Wood. 1991. Pit relocation by antlion larvae: a simple model and laboratory test. Evolutionary Ecology **5**:93–104.

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

———. 1989. Differences in habitat use between two pit-building antlion species: causes and consequences. American Midland Naturalist **121**:84–98.

Lucas, J. R., and L. A. Stange. 1981. Key and descriptions to the *Myrmeleon* larvae of Florida (Neuroptera: Myrmeleontidae). Florida Entomologist **64**:208–216.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, New York, USA.

Marsh, A. C. 1987. Thermal responses and temperature tolerance of a desert antlion larva. Journal of Thermal Biology **12**:295–300.

Matsura, T., and H. Takano. 1989. Pit-relocation of antlion larvae in relation to their density. Researches on Population Ecology **31**:225–234.

Milligan, B. G. 1986. Invasion and coexistence of two phenotypically variable species. Theoretical Population Biology **30**:245–270.

Moran, M. D. 1995. Intraguild predation between sympatric species of mantids (Mantodea: Mantidae). Proceedings of the Entomological Society of Washington **97**:634–638.

Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology **73**:255–267.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics **12**:225–251.

———. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? American Naturalist **123**:541–564.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interaction. Trends in Ecology and Evolution **7**:151–155.

Polis, G. A., and S. J. McCormick. 1987. Intraguild predation and competition among desert scorpions. Ecology **68**:332–343.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics **20**:297–330.

Power, M. E., T. L. Dudley, and S. D. Cooper. 1989. Grazing catfish, fishing birds, and attached algae in a Panamanian stream. Environmental Biology of Fishes **26**:285–294.

Rummel, J. D., and J. Roughgarden. 1983. Some differences between invasion-structured and coevolution-structured competitive communities: a preliminary theoretical analysis. Oikos **41**:477–486.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353–391.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Topoff, H. 1977. The pit and the antlion. Natural History **86**:65–71.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist **125**:769–787.

Werner, E., and J. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393–425.

Wheeler, W. M. 1930. Demons of the dust. Norton, New York, New York, USA.

Wiens, J. A. 1982. On size ratios and sequences in ecological communities: are there no rules? Annales Zoologici Fennici **19**:297–308.

Wilbur, H. M. 1988. Interactions between growing predators and growing prey. Pages 157–172 *in* B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, Berlin, Germany.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. American Naturalist **109**:769–784.

———. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology **73**:1984–2000.

Wissinger, S. A. 1989. Seasonal variation in the intensity of competition and predation among dragonfly larvae. Ecology **70**:1017–1027.

———. 1992. Niche overlap and the potential for competition and intraguild predation between size-structured populations. Ecology **73**:1431–1444.