

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

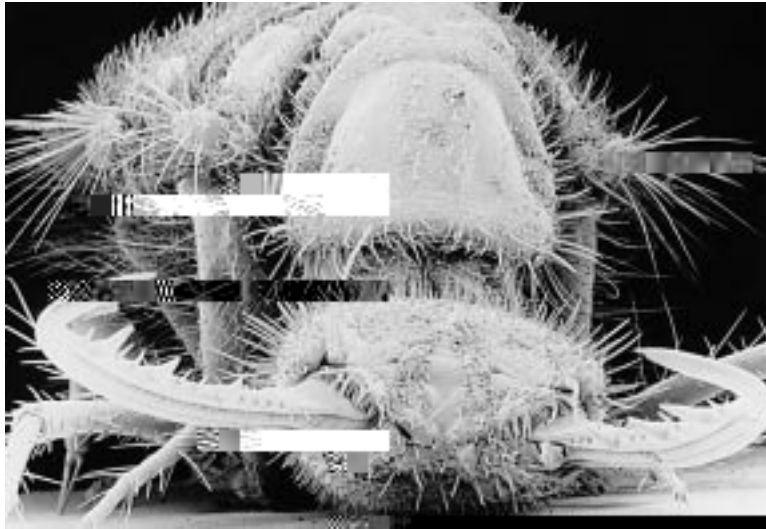


PLATE 1. Head and jaws of third-instar larva of *Myrmeleon immaculatus*. Photo courtesy of Dr. Kathleen Shields, USDA Forest Service.

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

TABLE 1. Summary of field and laboratory experiments.

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

Notes: Numerals and lowercase letters refer to instars and species. For example, *3Mi* 5 third-instar *M. immaculatus*; *1Mc* 5 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 5 Salyer East, SW 5 Salyer West, PC 5 Pugh Canyon, and NC 5 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

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

Number of <i>M. immaculatus</i> larvae	Number of <i>M. crudelis</i> larvae			
	0	1	2	4
0				
1	d			
2	e			
4				

Larvae were collected from the field on 30 June 1993. Larval density in this experiment varied from $\varnothing 90$ 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 \times four treatments \times two years \times four replicates) in the experiment.

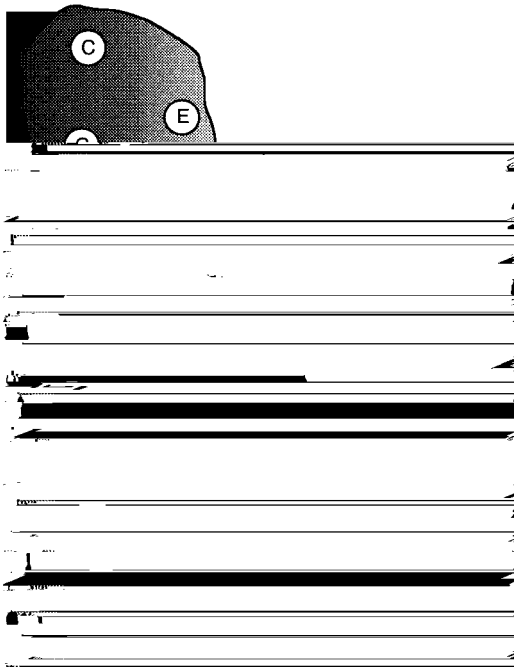


FIG. 1. Layout of field experiments to test for shadow competition (Experiment 6) and food supplementation (Experiment 7). The irregular polygon represents the ant lion zone, and the shading is proportional to natural ant lion density. The black bar represents the cliff ledge, and the arrow indicates 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.

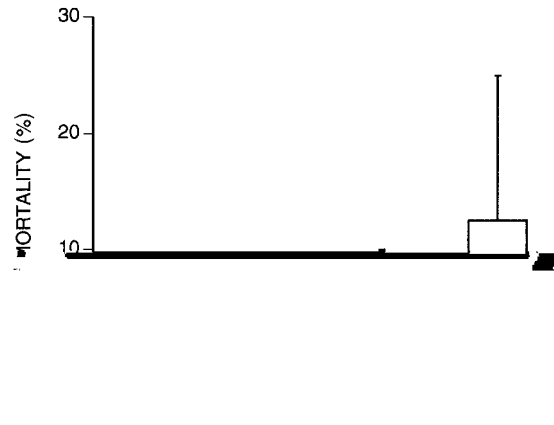


FIG. 2. Effects of density on mortality of second-instar *M. crudelis* (Experiment 1). Each bar is the average percentage mortality in a treatment. Vertical lines are 1 SD; $n = 5$ replicates per treatment (F).

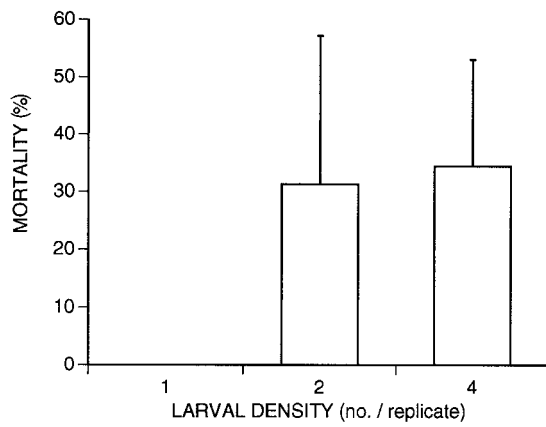


FIG. 4. Effect of density on mortality of fed *M. crudelis* (Experiment 2). Each bar is the average percentage mortality in a treatment. Vertical lines are 1 SD; $n = 8$ replicates per treatment ($F_{2,21} = 12.69$, $P = 0.0002$; regression of mortality on \log_{10}

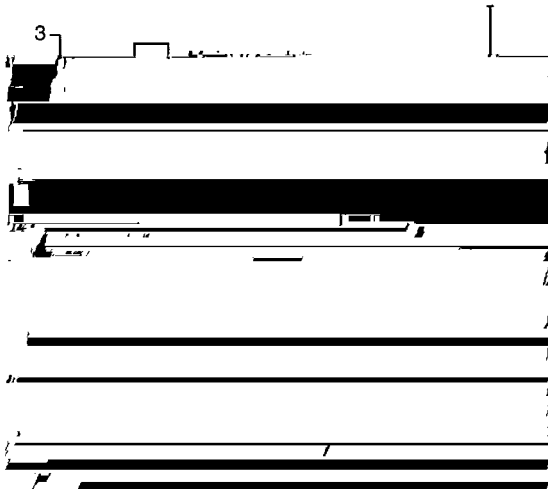


FIG. 6. Differences in initial body mass associated with larval fate at the end of Experiment 3. Each bar is the average initial body mass, pooled over all experimental treatments. Vertical lines are 1 SD. For *M. crudelis*, missing $n = 42$; first instar $n = 12$; second instar $n = 6$. For *M. immaculatus*, missing $n = 40$; first instar $n = 12$; second instar $n = 8$. (*M. crudelis* $F_{2,57} = 6.487$, $P = 0.003$; *M. immaculatus* $F_{2,57} = 6.237$, $P = 0.004$).

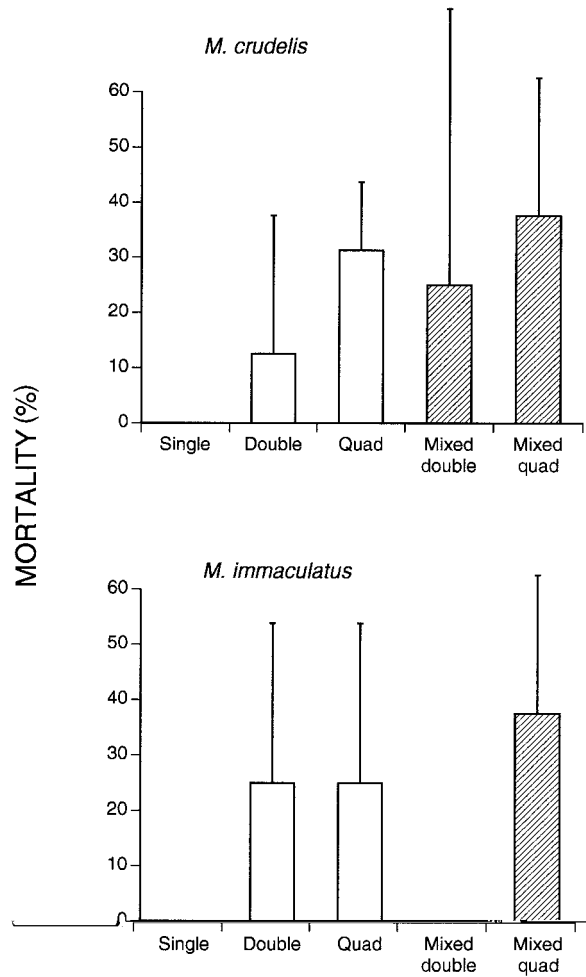


FIG. 7. Effects of density and species composition on mortality of third-instar larvae (Experiment 4). Each bar is the average percentage mortality for a particular treatment. Vertical lines are 1 SD. Single = 1 larva per replicate; Double = 2 larvae per replicate; Quad = 5

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	C
	2	C	C	C	C	C
	3	C	C	C	C	C
	4	C	C	C	C	C
e	3	I	I			
	4	I	I			
f	2	I	I	I	I	I
	3	I	I	I	I	I
g	2	C	I			
h	1	C	C	I	I	I
	2	C	C	I	I	I
	3	I	I	C	C	C
	4	C	C	I	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.

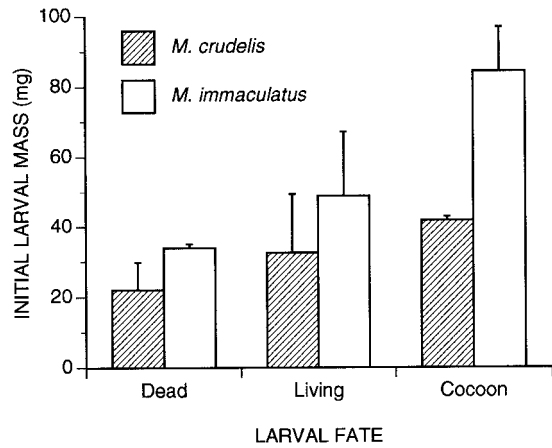


FIG. 8. Differences in initial body mass associated with

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 \pm 2.00	39.80 \pm 1.80
Length of third instar stage (d)	29.59 \pm 4.75	42.14 \pm 4.75
Length of pupal stage (d)	35.76 \pm 1.93	33.34 \pm 2.32
Adult mass (mg)	21.31 \pm 1.56	23.37 \pm 2.03
Adult emergence (%)*	83.3	42.9

Notes: Least squares adjusted means \pm 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

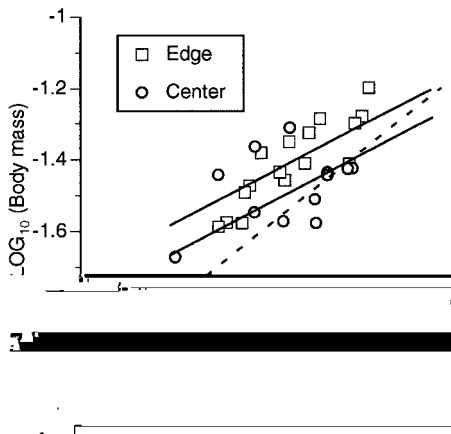


FIG. 10. Initial growth of third-instar *M. crudelis* reared in the edge and center of the ant lion zone (Experiment 6). The y axis is larval mass on 5 October 1992 and the x axis is larval mass on 25 June 1992. Each point is a different larva. The solid lines indicate the ANCOVA regression for each 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.

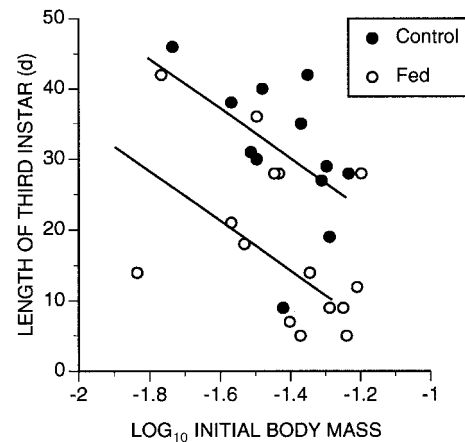


FIG. 11. Effects of food supplementation on length of the third instar of *M. immaculatus* (Experiment 7). Larvae were reared in individual containers in the center of the ant lion zone (see Fig. 1 for layout). Control larvae experienced ambient prey, and fed larvae were hand fed an additional three *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 \pm 2.51	55.44 \pm 2.81
Length of larval life (d)**	31.22 \pm 2.87	18.35 \pm 2.57
Length of pupal life (d)*	20.34 \pm 1.40	24.38 \pm 1.24
Pupal mass (mg)**	223.49 \pm 12.44	267.44 \pm 11.12
Adult mass (mg)*	9.75 \pm 0.98	12.54
Mortality (%)	20	

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 extinction

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