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Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying

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Abstract The relative importance of intraspecific, interspecific, and seasonal causes of larval mortality were investigated for aquatic larvae of the giant damselfly *Megaloprepus coerulatus* in Panama. These larvae live in water-filled holes in fallen and living trees, where they and three other common odonate species are the top predators. By mid wet season, *M. coerulatus* larvae were found in nearly half of all tree holes that harbored odonates. Although *M. coerulatus* were typically, but not always, eliminated from holes inhabited by larger heterospecifics, *M. coerulatus* were more likely to encounter conspecifics than other odonate species. Hole with less than 1 l of water rarely contained more than a single larva. In large holes where *M. coerulatus* was the only odonate species present, multiple larvae coexisted at a density of one larva per 1–2 l of water. There the absence of 2–4 of the 5 larval size classes, despite a continuous input of eggs, suggested that cannibalism was a common cause of mortality. The size of the final instar, which determined adult body size, was correlated positively with tree hole volume for male, but not female, larvae. Experiments showed that when two larvae were placed together in 0.4-l holes with abundant tadpole prey, the larger larva killed the smaller one. Often the larva that was killed was not eaten. Small larvae were more tolerant of each other than were pairs of medium or large larvae. Before killing occurred, the presence of larger larvae reduced the growth of smaller individuals, relative to controls. 'Obligate' killing was density-dependent. In 3.0-l holes with ad libitum prey, conspecific killing occurred until the larval density stabilized at one larva per 1–1.5 l, similar to the density found in large holes under field conditions, For *M. coerulatus*, cannibalism functions to reduce the number of potential competitors for food in addition to providing nutrition. When interactions between paired larvae in small holes were experimentally prevented, competition for food reduced the growth of one or both larvae relative to controls. Holes that were watered during the dry season supported larval densities similar to those in the wet season. Thus, dry season mortality could not be attributed to a decrease in available prey. Rather, *M. coerulatus* larvae could not survive more than 1 month of complete drying. Because the dry season typically lasts more than 6 weeks, habitat drying is a secondary source of mortality, affecting second- or third-generation larvae that fail to emerge before tree holes dry out completely.

Key words Density-dependent · Intraspecific competition Cannibalism · Intraguild predation · Odonata

Introduction

Both density-dependent and density-independent factors are thought to limit insect populations, although the relative importance of each type remains controversial (e.g. Price 1984; Strong et al. 1984). Whereas density-independent factors tend to be associated with weather, regulation occurs by means of biotic interactions such as inter or intraspecific competition, parasitism, and predation. Cannibalism is an extreme form of interference competition for food (see Dong and Polis 1992), and has been suggested as being an important source of larval mortality in odonates (Benke and Benke 1975; Thompson 1978; Merrill and Johnson 1984; Van Buskirk 1989, 1992; Wissinger 1989). Nevertheless, in natural populations of odonates, determining the importance of cannibalism relative to other regulating factors, such as fish predation, is difficult (e.g. Pierce et al. 1985). Although cannibalism is the mechanism thought responsible for density-dependent mortality in field enclosures (Benke et al. 1982; Johnson et al. 1985, 1987; Van Buskirk 1987), others (Folsom and Collins 1984; Baker 1989) failed to

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find evidence of it under field conditions. In fishless rock pools, Van Buskirk (1993) found density-dependent effects on the feeding activity and growth of larval dragonflies, but not on survivorship. Cannibalism is most likely to regulate populations of predaceous insect species whose larvae develop in confined areas where food is limiting (reviewed by Fox 1975). Water-filled plant containers such as bromeliads (e.g. Picardo 1913) and treeholes (e.g. Fincke 1992a) represent one such class of microhabitats that harbors a diversity of aquatic fauna in the tropics.

In the seasonally moist forests of Barro Colorado Island (BCI), Panama, larvae of the damselfly, *Megaloprepus coerulatus*, and three other common odonates develop in water-filled tree holes. *Megaloprepus coerulatus* adults live as long as 7 months, and feed on small web-building spiders (Fincke 1992 a). The high degree of overlap in the foraging heights of *Megaloprepus coerulatus* and two spider-eating *Mecistogaster* damselflies suggests that interspecific competition for food at the adult stage is low (Fincke 1992 a). During the breeding season from May to early March, male *Megaloprepus coerulatus* defend large tree holes usually located in tree-fall gaps. Adult territoriality cannot limit population growth because it does not limit the number of eggs laid by females. Multiple females visit both defended and undefended tree holes, with a single female laying up to 10 times as many eggs as the number of larvae emerging from a tree hole during a season (Fincke 1992b). Large males are more likely to obtain territories and to mate than are small males (Fincke 1992b). Because, as I show herein, final instar size is correlated with adult male body size, larval growth is critical to male fitness.

Tree holes are a limiting reproductive resource, and artificial holes are readily defended by adults and colonized by larvae (Fincke 1992 b, c). Population regulation apparently occurs at the larval stage. Differences among tree holes in pH, O_2, or temperature were not found to be a significnat source of mortality for the four odonate guild members (O.M. Fincke, unpublished manuscript). Odonate larvae are the top predators within water-filled tree holes. Young instars (i.e. <7 mm in length) can be killed by the predaceous larvae of the mosquito, *Toxorhynchites theobaldi*, and by tadpoles of *Dendrobates auratus*. More often than not, however, larvae ≥7 mm either eliminate both of these predators, or coexist with *D. auratus* (O.M. Fincke, unpublished manuscript). With ad libetum food, *Megaloprepus coerulatus* develops faster than the two smaller *Mecistogaster* species and the larger dragonfly guild member, *Gynacantha membranalis*. Under natural conditions, *Megaloprepus coerulatus* emerges in a minimum of 4 months after hatching (Fincke 1992 c). Its larvae are aggressive and display a dominance hierarchy based on relative size. However, individuals do not defend any specific area of a hole, even when food and/or leaf covers were experimentally limited (O.M. Fincke, unpublished manuscript).

Intraguild predation (Polis et al. 1989) is a likely source of mortality for larval *Megaloprepus coerulatus*. On BCI, *Mecistogaster linearis* and *Mecistogaster ornata* damselflies are superior colonizers of tree holes, and their larvae occupy about half of both large and small tree holes within a month of the first rains of wet season (Fincke 1992c). An ovipositing female cannot detect the presence of odonate larvae in a hole, and females oviposit randomly with respect to tree hole volume (Fincke 1992 c). In a small hole, the first odonate larva to hatch is likely to kill later-hatching larvae, regardless of species, whereas tree holes over about 1 l in volume are more difficult for a single individual to patrol. Lab experiments with paired larvae in large artificial holes indicated that initally smaller *Megaloprepus coerulatus* individuals could outgrow and eventually kill *Mecistogaster* species before the latter larvae had time to emerge (Fincke 1992c).

In the absence of heterospecific odonate larvae, what kills larvae of *Megaloprepus coerulatus*? Potential sources of intraspecific mortality are exploitative competition for food, starvation resulting from feeding inhibition, and cannibalism. Larvae might also die from seasonal drying of tree holes, either from desiccation or from a lack of seasonal prey that disappear before tree holes dry out. Although there is no evidence from my studies (made during five wet seasons spanning a 10-year period) that parasitism contributes to larval mortality, I cannot rule out this possibility. Here I describe results of field surveys and lab experiments demonstrating that density-dependent conspecific killing effectively decreases exploitative competition for food. I argue that, ultimately, exploitative competition for food limits population size, and that cannibalism is a more pervasive source of larval mortality than is intraguild predation or tree hole drying.

Material and Methods

Field surveys and experiments were conducted during the wet and dry seasons of 1983 and 1984 and during the wet season (between June and August) of 1990, 1992, and 1993 at the field station of the Smithsonian Tropical Research Institute on BCI, Panama. Here, the lowland moist forest experiences roughly 2.6 m of rainfall per year, with less than 10% of the rainfall occurring during the dry season from January to April (Windsor 1990).

Field surveys

To determine the probability of *Megaloprepus coerulatus* larvae encountering conspecifics and other odonate guild members (i.e. *Gynacantha membranalis, Mecistogaster linearis*, and *Mecistogaster ornata*), I searched for odonate larvae in natural tree holes, in the early wet seasons of 1992 and 1993, by first removing leaves and other detritus from the hole. Using a hand operated pump, I then removed standing water. The leaves were washed to remove any larvae clinging to them. Larvae larger than about 15 mm body length often remained in tree holes after they were emptied of water. These larvae could be detected by carefully searching the hole with a flashlight. By these methods I could recover most larvae ≥6 mm in body length. In this paper, I ignore larvae less than 6 mm (newly-hatched *Megaloprepus coerulatus* are 2–3 mm). Because I could not differentiate between the two species of *Mecistogaster* larvae before the penultimate instar, I pooled the data for these species. After measuring the larvae, they were returned to the hole along with the detritus and water.

To determine the consequences of *Megaloprepus coerulatus* inhabiting a hole with conspecifics or other guild members, I followed, in the wet seasons of 1983 and 1984, the fate of larvae in 47 natural and 26 artificial holes that contained at least one odonate. Artificial holes were plastic tubs (2–15 l) lined with black plastic to which I added leaf litter and bark from the forest floor. Because the artificial holes could be completely emptied and sampled with minimum error, they served as a test of my ability to detect and extract odonate larvae from natural holes. I censused the holes as above, 1–2 times per month over a period of 3–8 months of the wet season. Final instar larvae (detected by their swollen wing pads) were held in an outdoor insectary until they emerged. Of these, only larvae that emerged within 10 days were used in the correlation of final instar size and tree hole volume. A larva that disappeared from a hole between censuses was considered to have emerged only if it could have grown to the minimum size necessary within that time, based on maximum growth rates (Fincke 1992c). Because species occupancy from year to year is highly variable (Fincke 1992c), I included in the data analysis 12 holes that were censused in each of the two wet seasons, resulting in a total of 85 season holes.

To determine if cannibalism was common in *M. coerulatus* under natural conditons, I measured, in the mid wet seasons of 1983–84, the size structure of larvae in 28 natural tree holes and 11 artificial holes in which I had never found odonate species other than *M. coerulatus*, nor either of the two potential non-odonate predators. The size distributions of *M. coerulatus* found in natural holes were compared with an expected size distribution of larvae. This was calculated from the proportion of total developmental time that a larva (fed ad libitum tadpole prey) spent in each size class (data from Fincke 1992c), and assumed a continual input of eggs and no mortality. Throughout, tree hole volume refers to the maximum volume of water that a hole contained. 'Large' holes are those holding more than 1 l of water, whereas 'small' holes held <1 l. I report density as the number of liters per larva to avoid reporting only a fraction of a larva in a small hole.

Interference competition

In 1983, to determine if killing or cannibalism occurred in the presence of abundant alternative prey, I observed pairs of larvae in small artificial holes with ad libitum tadpole prey. 'Tadpole prey' refers to newly hatched *Physalaemus pustulosus* tadpoles which were obtained by collecting the foam egg nests that regularly appeared in two artificial ponds and concrete moats in the lab clearing. I placed two individuals of *Megaloprepus coerulatus* in 400 ml of water in plastic jars (surface area=100 cm^2). Each jar contained a stick for a perch and leaves for cover. I paired combinations of small (6–9 mm, $\bar{x}$=7.6 mm), medium (10–19 mm, $\bar{x}$=14.6 mm), or large (≥20 mm, $\bar{x}$=25.3 mm) *M. coerulatus*, resulting in a total of six size treatments. Control jars were identical to experimental jars except that they contained only a single small ($\bar{x}$=7.9±0.3 mm) medium ($\bar{x}$=13.1±0.7) or large ($\bar{x}$=24.1±0.2 mm) individual. Body length (from the head to final abdominal segment, excluding the caudal lamellae) was used as a measure of size because it allowed me to measure larval growth within molts. Body length of *M. coerulatus* larvae was highly correlated with head width (r=0.96, n=53, P<0.0001). I checked the odonate larvae daily to record any deaths or injuries (i.e. missing caudal lamellae, legs, or holes in the thorax) and to add extra tadpoles to ensure that at least five tadpoles were always present. Once a week, I measured the larvae using calipers. I calculated growth rate as the difference in the initial and final body length divided by the number of days between the measurements. Because the growth curve is sigmoidal (Fincke 1992c), I report rates for small, medium, and large size classes separately. Experimental larvae were monitored for 14–21 days or until the emergence or death of one of the pair, whichever occurred first. Control larvae were monitored over a 30-day span. To determine if feeding inhibition occurred, I compared growth rates of individuals reared in the presence of larger or smaller individuals with growth rates of the solitary controls. For solitary larvae reared with ad libitum prey, size increase over a 4-day span was minimal. I thus limited comparisons of growth rates to larvae that persisted for ≥5 days. Throughout, means are presented with their standard errors, and t-tests are two-tailed.

The results of the above experiment using small hole suggested that medium and large larvae obligately killed conspecifics. In 1993, to determine whether such obligate killing also occurred in large holes, I placed one small, three medium, and one large *M. coerulatus* (range 6.3–21 mm, $\bar{x}$=11.5±1.4 mm) in each of two, panlike artificial holes (77×14.5×8 cm). The holes were filled to a volume of 3 l. I supplied one hole with ad libitum mosquito prey by adding egg rafts of the mosquito, *Trichoprosopon digitatum*, once every 2–3 days. Each raft contained about 50 eggs. Two days before the start of the experiment, I added three foam nests of *P. pustulosus* to a second hole. Within 2–4 days, such nests produced 100–225 tadpoles 2–3 mm in size, which, after a month, were still ≤8 mm. I checked both holes daily for the presence of *M. coerulatus* larvae. Once every 2 weeks, I measured the odonate larvae and counted the number of prey. Difficulty in obtaining sufficient numbers of *M. coerulatus* larvae in the desired size range prevented me from using a larger sample size for this experiment.

Exploitative competition

To determine the effect of exploitative competition for food on larval growth, I compared the growth of paired larvae that were not allowed to interact directly with the growth of solitary controls. In the experimental treatments, I placed two *M. coerulatus* larvae of nearly equal size ($\bar{x}$ difference=0.63±0.2 mm) on either side of a polyurethane-coated screen mesh that equally divided a 400 ml plastic jar (surface area=100 cm^2). The openings of the wire mesh were small enough (3.2×3.2 mm) to prevent passage of odonates larger than 9 mm in body length. Newly-hatched tadpoles and mosquito larvae prey that were placed on one side of the mesh dispersed across the mesh within seconds. Each side contained a stick perch and three leaves for cover. In 1990, I added three tadpoles per side, 3 times per week. This level of caloric input is much higher than that normally found in a 400-ml tree hole (O.M. Fincke and R.D. Hanschu, unpublished data). In the control jars, the wire mesh lined rather than divided the jar. 'A' controls contained 200 ml of water, a single *M. coerulatus* larva (10–15 mm), three leaves, a stick perch, and three tadpoles provided 3 times per week. In these controls, the density of both odonates and prey was identical to the experiments. 'B' controls contained a single odonate in 400 ml of water, to which was added six tadpoles 3 times per week. In these controls, prey density per container was identical to that of the experimental jars, but the density of *M. coerulatus* was half that of the experimental jars. I checked the jars daily to insure that no *M. coerulatus* had switched sides or died. I measured *M. coerulatus* larvae once every 2 weeks. The jars were kept in an outdoor insectary, where they were protected from rain and direct sun by a partial tin roof and shade cloth covering a lower screened ceiling.

A second experiment using naturally colonizing mosquito prey was done in 1992. The protocol was similar to that above, except that instead of adding tadpole prey, I placed the jars on a table outside a lab building. The mean difference in the size of the paired experimental larvae was 1.5±0.4 mm, marginally greater than in the above experiment (t=1.95, P>0.06). Four jars that only contained leaves and water were colonized by mosquito larvae within a week, and none of the jars ever contained a *P. pustulosus* egg nest or tiny odonates. Although I did not measure prey density, mosquito larvae were often observed in both treatment and control jars. Both experiments ran for 3–4 weeks. In both experiments, the *M. coerulatus* larvae used varied from 9 to 29 mm, although only a single size class of larva was used per set of one experimental jar and control jars A and B.

Habitat drying

To determine how well *M. coerulatus* larvae could withstand dry conditions, I did a drying experiment in an outdoor insectary under natural photoperiod and temperature. Ten larvae ($\bar{x}$=22.7±1.1 mm) were individually placed between two layers of leaves (six each) in a 200-µl (60-mm-diameter) plastic tub. Each tub was filled with water and allowed to stand for 30 min for thorough soaking of the leaves. The standing water was then poured off and the tubs were placed under ambient temperature in a screened lab, protected from rain and direct sunlight. Once a week, until the first dead larva was found, larvae were removed and placed in water for 30 s. Live larva moved within that time. Surviving larvae were blotted dry and returned to their position in the leaf pack. After the first dead larva was found, larvae were checked every 2 days until all had died.

An alternative reason why larvae might fail to survive the dry season is a scarcity of prey during this time. I compared larval densities and growth rates in six large (9–15 l) artificial holes sampled during the wet season, with those of the same holes that were watered during the dry season. During the dry season, I kept holes full by periodically adding previously collected rain water (see Fincke 1992 b for details). Because any mark applied to the cuticule would be shed during a molt, I did not try to identify individual larvae from one census to the next but rather assumed that the rank size order of larvae did not change from one census to the next. I calculated growth rate from the size increase of a larva over a span of 20–44 days. I report data from only those cases where several larvae in the same size class did not disappear between censuses, which made identification of those remaining ambiguous.

Results

Field evidence for intraguild predation and cannibalism

In 1992, 69.7% of the holes in which I eventually found odonate larvae were discovered after the first search, 15% after a second search, 11% after the third search, and 3% after the fourth. If I had not detected any larvae by the fourth census, three additional searches did not improve my detection rate. By the end of July 1992, I found odonates in 79% of the 82 tree holes whose contents were emptied at least 3 times. Of these occupied holes, *M. coerulatus* occupied 70.5% of the 17 large holes and were the largest occupants in 35% of the small holes. *M. coerulatus* overlapped with the dragonfly *Gynacantha membranalis* in 23% of the large occupied holes. Similarly, by the end of July 1993, I had detected odonate larvae in 77% of the 70 tree holes emptied at least 3 times. Of these occupied holes, *M. coerulatus* were in 48% of the large holes, and were the largest occupants of 44% of the small holes. In this year, *M. coerulatus* co-occured with *G. membranalis* in only 7% of the large occupied holes. In both years, the probability of *M. coerulatus* being found with another guild member was about half that expected if its presence in a hole was random with respect to occupancy by any other guild member (1992: χ^2=11.2, 1 *df*, P<0.005; 1993: χ^2=7.95, 1 *df*, P<0.005).

In 57 (67%) of the 85 season holes censused repeatedly throughout the wet seasons of 1983–84, I never detected more than a single species present. *Megaloprepus coerulatus* remained the dominant guild member throughout the wet season, accounting for 68.4% of the monospecific holes, whereas *Mecistogaster* and *G. membranalis* accounted for 19.3 and 12.3%, respectively. Table 1 summarizes the outcome of 28 cases where larvae of two species were found in the same hole on at least one census (more than two species were never found in the same hole on a given census). The combination of species was random with respect to large and small holes ($F_{2,22}$=0.53, P>0.58). At the last census in which both species were still found in a given hole, most holes harbored a single individual of each species, except for eight holes (28%) that had multiple individuals ($\bar{x}$=1.4 individuals, range 1–6) of one species. In two cases, both involving large holes (≥9 l), *Megaloprepus coerulatus* coexisted with another guild member until one emerged. The relative size difference between the largest larvae of each species present, before one was eliminated, was not significantly different among the three species combinations ($F_{1,22}$=0.41, P>0.65) nor between large or small holes ($F_{1,22}$=0.08, P>0.78). In nearly all of the 26 cases in which a species disappeared before it could have emerged, the largest missing heterospecific individual was smaller than the surviving larva. The exception was a 14-mm *Megaloprepus coerulatus* larva found with a 17-mm *Mecistogaster* in a 3-l hole. At the next census 3 weeks later, the *Megaloprepus coerulatus* was 25 mm, and the *Mecistogaster* larva was gone. Because none of these holes contained *Dendrobates auratus* tadpoles, I assumed that the disappearance of at least the largest missing heterospecific resulted from intraguild predation. In no case did both species of

Table 1 Outcome of 28 co-occurrences of two species in 11 natural and 17 artificial holes. Size refers to body length of the largest individual of a species present, measured on the last census in which both species were observed. Mean size of the ultimate survivor (mm) is in parentheses. (*Gyn Gynacantha membranalis, Meg Megaloprepus coerulatus, Mecist Mecistogaster linearis* or *Mecistogaster ornata*)

Species pair	$\bar{x}$ size difference (mm)	Sole remaining species:			Coexisted until emergence
		Gyn	*Meg*	*Mecist*	
Gyn × *Meg*	11.4±2.0	11 (22.9±2.6)	2 (14.4±5.3)	–	1
Gyn × *Mecist*	10.5±3.2	5 (22.0±1.4)	–	0	0
Meg × *Mecist*	6.9±1.1	–	6[a] (19.7±1.8)	2 (18.7±3.2)	1

[a] One of these was the only case where the larva remaining was initially smaller than the larva that disappeared

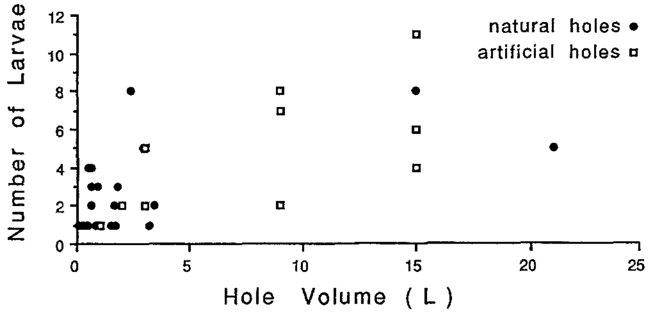

Fig. 1 Number of total *Megaloprepus coerulatus* larval occupants (>6 mm) as a function of volume of holes containing no other odonate species. *Squares* refer to artificial holes, *circles* to natural tree holes (r=0.67, n=39, P<0.0001)

larva disappear, as might be expected if a non-aquatic predator was causing the elimination.

In the 39 holes that contained only *Megaloprepus coerulatus*, the maximum number of larvae found during a given census was positively correlated with the volume of water in the hole (Fig. 1). Of the 16 natural holes with ≤1 l of water, only 4 (25%) contained more than a single *M. coerulatus*, whereas 7 of the 11 holes (64%) with more than 1 l of water contained multiple *M. coerulatus*. In these large holes, the average density of larvae was one per 1.6±0.30 l, not significantly different from the density of larvae in the 11 large artificial holes ($\bar{x}$=one larva per 2.0±0.4 l, t=0.79, P>0.4).

All of the 22 large holes that contained only *M. coerulatus* larvae were defended by adult male *M. coerulatus*, visited by ovipositing females, and thus had a continual input of eggs during the wet season (see Fincke 1992b). In 8 (30%) of the 37 total monthly samples, the observed distribution of larvae differed from the expected (P<0.05, χ^2 tests). However, the low larval densities resulted in expected values of less than five larvae per size class, usually even when two of the 5 size classes were combined. Conclusions drawn from such comparisons are thus questionable. Nevertheless, of the 22 holes sampled once in mid-late wet season, 95% had at least one size class missing, and 82% had two or more missing classes ($\bar{x}$=2.6±0.4 size classes, n=11 natural holes; $\bar{x}$=2.2±0.2 missing size classes, n=11 artificial holes). The median percentage of larvae per size class was generally lower than that expected (Table 2). In 5 (23%) of the large holes with multiple larvae, I found larvae missing caudal lamellae, legs, or parts or their abdomen, injuries identical to those known to be caused by conspecifics under lab conditions. Four of the artificial holes were sampled repeatedly once per month for 2–7 months ($\bar{x}$=4.8 months). In 20% of these 19 total samples, recruitment into the two smallest size categories did not occur until individuals had left the intermediate or larger size classes.

The size of final instar larvae taken from natural and artificial holes under field conditions was positively correlated with wing and abdomen length, respectively, of the emerging adults (males: r=0.99, r=0.92, n=29, P <0.0001; females: r=0.71, r=0.80, n=30, P<0.0001). The size of the final instar was correlated positively with tree hole volume for male larvae (r=0.50, n=29, P<0.01) but not for female larvae (r=0.31, n=30, P>0.09).

Interference competition

The results of the interferance experiment are presented in Table 3. Within the 30-day period, 2 of the 30 (6%) control larvae died during molting. In contrast, in 40 of

Table 2 The observed median proportion of the *Megaloprepus coerulatus* larvae in each size class found in 22 large holes that were sampled in mid wet season (1983–1984 data). Ranges are in parentheses. The expected distribution refers to the percentage of total developmental time a larva spends in a given size class

	Larval size class (mm):				
	>5–10	>10–15	>15–20	>20–25	>25
Natural holes	0	0.13	0	0.13	0.20
(n=11)	(0–0.6)	(0–0.5)	(0–1.0)	(0–0.5)	(0–1.0)
Artificial holes	0.	0.13	0	0.07	0.25
(n=11)	(0–0.62)	(0–0.5)	(0–0.67)	(0–1.0)	(0–0.64)
Expected	0.21	0.13	0.09	0.24	0.33

Table 3 Mean differences in larval size and the outcome of the cannibalism experiment. Days until larva killed refers only to cases where just one of the pair survived. (*L* larger individual of pair survived, *S* smaller individual of pair survived, *B* both survived, *N* neither survived)

Treatment	n	Initial size difference (mm)	Final size difference (mm)	Days until larva killed	Survivors			
					L	S	B	N
Large-large	9	1.1±0.3	1.1±0.4	5.2±3.0	5	–	4	–
Large-medium	9	10.3±1.4	10.46±1.5	4.0±1.5	5	–	4	–
Large-small	9	17.7±1.0	16.8±0.8	5.6±0.7	7	–	2	–
Medium-medium	9	2.4±0.6	2.5±0.6	3.8±0.7	6	2	–	1
Medium-small	8	4.9±1.3	7.5±1.3	8.5±2.4	5	1	2	–
Small-small[a]	10	0.6±0.2	2.9±0.9	9.9±2.1	9	–	–	1

[a] All but two of the survivors entered the medium size class before they killed conspecifics

Table 4 Growth rates (mm/day) of individuals in the interference competition experiment that persisted at least 5 days before killing occurred (sample size in parentheses). *F* values from ANOVAs

Larval size class	Treatment			*F*
	Control	With smaller individual	With larger individual	
Large	0.21±0.02 (10)	0.18 (13)	–	0.44
Medium	0.41±0.03 (9)	0.48±0.09 (6)	0.18±0.05 (5)	5.55*
Small	0.50±0.05 (11)	0.40±0.08 (4)	0.26±0.07 (14)	3.78*

* $P<0.05$

Table 5 Mean growth of paired experimentals and solitary control larvae in the exploitative competition experiment (see text for details). Although experimental larvae initially were similar in size, one typically grew faster than the other during the experiment. Means within each experiment with the same *superscript* are not significantly different (Bonferroni tests, $P>0.05$)

	n	$\bar{x}$ growth rate (mm/day)
I. Tapole prey (1990)		
Experimental larvae	20	0.13±0.02
Faster growing larva	10	0.21±0.03^{a}
Slower growing larva	10	0.05±0.02
Controls	24	0.28±0.03
A (200 ml)	12	0.25±0.04^{a}
B (400 ml)	12	0.30±0.05^{a}
II. Mosquito prey (1992)		
Experimental larvae (400 ml)	20	0.06±0.02
Faster-growing larva	10	0.07±0.03^{b}
Slower-growing larva	10	0.05±0.02^{b}
Control	10	0.12±0.02
A (200 ml)	4	0.13±0.05^{c}
B (400 ml)	6	0.12±0.02^{c}

the 54 (74%) experimental holes, one larva of the pair was dead within 2 weeks. In all but three of these trials, the larger individual killed the smaller one. Each of the dead larvae either had a hole in the ventral portion of the thorax, or was missing part of the abdomen. Eighteen (45%) of the 40 dead individuals were wounded but had not been partially consumed. The average time to death was 7.9±0.78 days. The size of the surviving larva was negatively correlated with the number of days until killing occurred ($r=-0.32$, $n=40$, $P<0.05$). In 7 of the 9 small-small pairings, the survivors had entered the medium-size category before killing the other larva, which in all cases remained in the 'small' size class. In contrast, all but 1 of the 13 medium-sized larvae that killed conspecifics did so prior to entering the 'large' size category ($\chi^2=16.4$, 1 *df*, $P<0.001$).

Both individuals of a pair survived in 12 (22%) of the trials. All of these pairs involved at least one final instar larva, of which three emerged during the experiment. In two trials (3%) both larvae died. In both of these trials, one of the pair died during a molt whereas the cause of death of the other could not be determined.

Even before killing occurred, larger conspecifics inhibited the growth of smaller individuals (Table 4). When paired with larger larvae, medium-sized individuals grew slower than controls. However, the initial size of the medium larva ($\bar{x}=18.9\pm0.4$ mm) that were paired with large larvae was significantly greater than the size of the medium larva in the other treatments ($\bar{x}=13.1\pm1.4$, $F_{2,18}=5.4$, $P<0.05$). Even though maximum growth of larvae of size 10–20 mm is fairly constant (Fincke 1992 c), reduced growth of the medium larvae in the presence of larger larvae might be explained by the larger initial size of medium larvae used in this treatment, rather than by feeding inhibition. There was no difference among treatments in the initial size of small larvae used ($F=1.16$, $P>0.3$). Nevertheless, small larvae in the presence of larger larvae grew significantly more slowly than the controls. In contrast, the growth rates of large individuals paired with smaller individuals did not differ from the controls.

In the 3-l artificial hole with ad libitum tadpole prey, the number of *M. coerulatus* was reduced from five to three individuals within 9 days. The remaining three larvae coexisted for the remaining 2 weeks of the experiment (i.e. 1 larva/l). Similarly, in the artificial hole with ad libitum mosquito prey, two larvae were killed within the first 4 days. After 9 days, only two larvae remained, stabilizing at the density of one per 1.5 l for the remaining 2 weeks. In both of the holes, survivors were the largest of the original five larvae.

Exploitative competition

When larval interactions were prevented, growth rates of paired experimental larvae were significantly less than those of the solitary controls in both the experiment with tadpole ($F_{1,42}=14.17$, $P<0.0005$) and mosquito prey ($F_{1,18}=4.47$, $P<0.05$, Table 5). There were no differences in the initial size of larvae used among treatments (tadpole prey: $F_{1,42}=2.9$, $P>0.1$; mosquito prey: $F_{1,18}=0.33$, $P>0.5$). With tadpole prey, one member of the experimental pair grew faster than the other. In this experiment, although growth of the slower-growing larva was less than that of the faster-growing larva, there was no difference in the growth rate of the latter and either of the two controls (Bonferroni *t*-test, $P>0.05$). In contrast, with naturally colonizing mosquito prey, growth rates were very low, and did not differ either between individuals in the experimental pairs or between the two controls, although the experimentals grew only about half as fast as the controls.

Resistence to seasonal drying

Most of the ten *M. coerulatus* larvae survived at least 2 weeks of drying, but none survived more than a month

Table 6 Mean comparisons of *Megaloprepus coerulatus* occupants in 6 large artificial holes that were watered during the dry season (12 samples) versus the same holes during the wet season (10 samples). Growth rates were measured only once per individual (sample size in parentheses)

	Dry season (watered)	Wet season	*t*	*P*
Total larvae	8.0±1.0	7.2±1.3	−0.49	0.63
Density of larvae (l/larva)	1.9±0.3	2.6±0.4	1.37	0.19
Growth rate of larvae (mm/day):				
Large	0.10±0.03 (6)	0.21±0.02 (10)	−3.0	0.01
Medium	0.27±0.02 (18)	0.30±0.02 (16)	−1.1	0.28
Small	0.33±0.03 (15)	0.27±0.04 (4)	1.4	0.19

without water (mean survival time=23.9±1.3 days). The first larva died between the 2nd and 3rd week. Of the remaining larvae, seven survived 18–25 days, two survived more than 25 days, and all were dead by 32 days. All larvae moved to the bottom of the leaf pile, which was the last portion to dry out.

As seen in Table 6, the larval density in artificial holes that were watered during the dry season did not differ significantly from larval density in the same holes during the wet season. Growth rates of medium and small larvae also did not differ between the treatment and control holes, although large larvae grew significantly slower in holes watered during the dry season than in the same holes in the wet season.

Discussion

Intraspecific killing and cannibalism of larval *Megaloprepus coerulatus* was a more pervasive source of mortality in this species than was intraguild predation. Despite the superior colonizing ability of *Mecistogaster* in the early wet season (Fincke 1992 c), by the end of July in 1992 and 1993 *Megaloprepus coerulatus* was the dominant species in large holes, and had successfully colonized most of the small holes that had not been previously colonized by *Mecistogaster*. Given that oviposition is random with respect to tree hole morphology and volume (save for *Gynacantha membranalis*, whose females cannot access holes with slit openings, Fincke 1992c), *Megaloprepus coerulatus* co-occurred with heterospecifics less than expected by chance. Evidence for intraguild predation stems from this finding, coupled with the observation that the largest larva in a hole, regardless of species, was usually the only one ultimately surviving when two species co-occurred. Nevertheless, because smaller *Megaloprepus coerulatus* sometimes eliminated a larger *Mecistogaster* from large holes (see also Fincke 1992c), and *Megaloprepus coerulatus* remained the dominant tree hole occupant throughout the wet season, the potential for *Megaloprepus coerulatus* to prey on other guild members was greater than the reverse. In holes previously colonized by heterospecifics, the potential for intraguild predation on *Megaloprepus coerulatus* is less in small than in large holes, because female *Megaloprepus coerulatus* lay fewer eggs in small holes than large ones (Fincke 1992b). Nevertheless, in large holes, the overlap between *Megaloprepus coerulatus* and the dragonfly *G. membranalis* was less than 25%, and in 7% of these, at least some individuals of the two species coexisted until emergence. Unlike *Mecistogaster*, whose adults are scarce by September, *Megaloprepus coerulatus* and *G. membranalis* continue to oviposit for the remainder of the wet season (Fincke 1992c). Thus, *Megaloprepus coerulatus* hatching out after July (i.e. during the remaining two thirds of its reproductive season) are more likely to encounter conspecifics than they are to encounter other guild members.

A surprising result of the interference competition experiment was that individuals killed conspecifics even with a superabundance of tadpole prey, as naturally occurs when *Physalaemus pustulosus* oviposits in an occupied tree hole. The obligate killing exhibited by *Megaloprepus coerulatus* differs strikingly from the behavior of odonate species that inhabit ponds or lakes. Larvae of the latter that have been maintained at densities higher than in my experiment, with or without abundant prey, experienced low or no mortality (Pierce et al. 1985; Crowley et al. 1987a; Convey 1988; Gribbin and Thompson 1990). Johansson (1992) Found that although the degree of cannibalism varied among three lake species, in all three it increased as alternative prey became scarc (see also Dong and Polis 1992). In contrast, well fed *M. coerulatus* in large holes obligately reduced larval density to roughly one larva per 1–2 l, similar to the larval densities that I found in large holes in the field. Under natural conditions, the lack of entire size classes of *M. coerulatus*, despite a continuous input of eggs, suggested that cannibalism was a common cause of mortality. Natural tree holes with less than 1 l of water typically had multiple early instar larvae in May and June (Fincke 1992c), whereas by July in 1992 and 1993 in this study, the small holes rarely harbored more than two larvae over 6 mm. In the absence of other odonate species, intraspecific killing or cannibalism explains why only one *M. coerulatus* adult emerged from small holes, and why large holes produced no more than 15 adults per reproductive season (Fincke 1992b). In the current study, I attributed larval disappearance to the action of odonate predation, but a few *M. coerulatus* may have been preyed on by non-aquatic predators. I repeatedly noted ground spiders at a few of the tree holes. Twice these spiders submerged when I disturbed them, suggesting that spiders may prey on larvae under water or close to the surface.

In addition to a density threshold effect, conspecific killing depended on the developmental stage of the larvae. In the small experimental holes, the larvae most tolerant of conspecifics were either final instars, which typically stop feeding 7–10 days before emergence (personal observation), or small larvae that had yet to enter the period of most rapid growth. Medium-sized larvae were those most likely to kill each other. This is in contrast with findings by Wissinger (1988) that similar-sized *Libellula* larvae rarely attacked each other. In *M. coerulatus*, small larvae were the most likely to coexist, probably because food is least likely to be limiting to small larvae. Obligate killing that is dependent on developmental stage is also known for the tree hole mosquito *Toxyrhinchites* (Corbet and Griffiths 1963). In these mosquitoes, a final instar larva kills its predacious conspecifics prior to pupating in order to protect itself from being eaten as a vulnerable pupa. In contrast with *Toxyrhinchites*, final instars of *M. coerulatus* were less likely to kill conspecifics than were younger instars. Although molting is a vulnerable time for *M. coerulatus*, the larvae that killed conspecifics in the interference competition experiment did not molt immediately afterwards.

In addition to providing additional prey, conspecific killing in *M. coerulatus* functions to prevent exploitative competition for food, which is the resource that ultimately limits the population size of this insect. When killing was prevented in small holes, exploitative competition for naturally colonizing mosquito prey decreased the growth rates of both of the experimental larvae relative to the controls. In addition, for male larvae, the size of the final instar was positively correlated with tree hole volume, suggesting that exploitation competition for food is greater in smaller holes. In contrast with studies showing that the presence of odonate larvae have little or limited effect on prey populations (Johnson et al. 1987; Van Buskirk 1993), *M. coerulatus* larvae significantly reduced the number of moquitoes surviving to pupate in tree holes (Fincke and Hanschu, in preparation). In small holes (about 70% of the avalable habitats, Fincke 1992c), the minimum time required for larvae to emerge was nearly 3 weeks longer than that of large holes (Fincke 1992b), and the density of mosquitoes per odonate larvae is greater in large holes (Fincke and Hanschu, in preparation). Large holes are more likely than small holes to attract ovipositing frogs (Fincke 1992c).

Prey availability may not always be sub-optimal for all larvae in large holes, simply because *M. coerulatus* reduce their density below that which occurs in small holes with a single occupant. The minium time required for *M. coerulatus* to emerge from the largest natural tree holes was only slightly greater than the developmental time of the larva reared with ad libitum food (Fincke 1992b, unpublished data). However, the variance in size of emerging adults increased with tree hole volume (Fincke 1992b), suggesting that the density of alterantive prey is sub-optimal for many *M. coerulatus* that survive to emerge. Indeed, in the current study, growth rates in large artificial holes under natural conditions (Table 6) were considerably less than those of larvae reared singly in small holes with ad libitum prey (Table 4). Because odonate larvae forage on a two-dimensional surface, whereas their mosquito prey are often found in the water column, prey capture rates per larva may be lower in large holes than in small ones, despite greater prey density of the former. In addition, larger larvae may supress the growth of smaller conspecifics even in the presence of abundant food.

Such feeding inhibition was documented in the interference competition experiment before any killing occurred. This type of interference has been documented in other damselflies (Baker 1981; Pierce et al. 1985; McPeek and Crowley 1987; Crowley et al. 1987a, 1988), but may have little effect on population regulation (Crowley et al. 1987b). In *M. coerulatus*, smaller larvae are often preyed upon by larger ones, and therefore avoidance of movement in the presence of a larger larvae is likely adaptive. This type of visual feeding interference may explain why, in the exploitation experiment with tadpole prey, the slightly larger experimental larva in a pair grew faster than the other. Feeding inhibition would also explain why, under field conditions, recruitment into the small size classes sometimes occurred only after intermediate or large size classes were vacated.

Because the density of *M. coerulatus* did not differ between holes watered in the dry season and those same holes in wet season, larval death during the dry season cannot be attributed to starvation resulting from a paucity of prey as the dry season progresses. Rather, *M. coerulatus* larvae died after 2–3 weeks of total desiccation. Tree holes on BCI typically remain dry for 6 weeks or more (Fincke 1992c). My current results explain why holes that contained *M. coerulatus* larvae too small to emerge by the time tree holes dried up were not found again the following wet season (Fincke 1992b). Because emergence of adults is staggered over the wet season, seasonal drying would affect only larvae hatching after December in most years. Seasonal drying shrinks the larval habitat, thereby increasing the risk of cannibalism before larvae die of dehydration. Results from the watering experiment suggest that in habitats with less seasonal rainfall, *M. coerulatus* should dominate tree holes year around, as they do in a lowland site in Costa Rica where the dry season is limited to a month or less (O.M. Fincke, unpublished data).

Factors limiting population growth of most animals, particularly tropical ones, are poorly known. The small, discrete habitat and relatively simple larval ecology of *M. coerulatus* allowed me to experimentally tease apart multiple sources of larval mortality and to document the first clear case of resource limitation in an odonate under field conditions. Field researchers working on temperate odonates in complex pond or lake habitats have often concluded that food is not limiting to larval odonates (Lawton 1971; Thompson 1982; Pierce et al. 1985), although enclosure experiments suggest otherwise, at least for some prey species (Johnson et al. 1987; Anholt 1990). Fish or inter-odonate predation may keep odonate densities below the level at which inter or intraspecific competition becomes important (e.g. Pierce et al. 1985; Crowley et al. 1987a; Wissenger 1989). Nevertheless, many studies have documented density-dependent effects on growth or survivorship, attributing these effects to some form of interference competition, either cannibalism or feeding inhibition (e.g. Benke 1978; Benke et al. 1982; Johnson et al. 1985, 1987; Anholt 1990; Van Buskirk 1993). Intraspecific competition implies that some resource is limiting, but the resource as well as the mechanism of the interference has been difficult to identify. If food is not limiting, why should larvae cannibalize each other? Although food may not be limiting, feeding on smaller conspecifics may be a more efficient foraging strategy in the presence of fish. Alternatively, some have suggested that agonistic behavior of odonate larvae might be explained by competition for perch sites, either because they allow increased feeding efficiency or enable larvae to avoid predators (e.g. Convey 1988). As yet, however, perch sites have not been shown to be limiting under natural conditions (but see Macan 1977).

Comparison of my results with those of two other studies suggests that both the population dynamics and the behavior of odonates are best viewed from an evolutionary perspective. Because selection at the level of the individual has been shaped by environmental conditions over evolutionary time, the intensity of individual interactions should reflect the importance of intraspecific competition. For example, *M. coerulatus* exhibits the most extreme form of interference competition of any odonate for which data are available, and exists at natural densities well below those reported for other species (see Benke and Benke 1975). In contrast, *Libellula* larvae are less likely to kill each other (Wissenger 1988), and the degree of exploitative competition for food varies seasonally (Wissenger 1989). The density at which conspecific killing occurs should optimize some function of the mean size and number of a female's offspring that survive to emergence. I predict that, given strong selection on adult body size, over evolutionary time the number of emerging larvae will be sacrificed at the expense of offspring size. Consequently, the threshold density at which cannibalism occurs should be lowest in species under the strongest selection for large adult body size. Unlike *M. coerulatus*, where larger males have higher mating rates than smaller males, size has not been found to be important for mating efficiency of dragonflies generally (e.g. Koenig and Albano 1987; McVey 1988; but see Miller 1983). For example, Van Buskirk (1993) Found that in *Aeshna juncea*, a rock-pool inhabitant, growth rates and the size of final instars decreased with increasing density, but survivorship did not. Unlike *M. coerulatus, A. juncea* did not seem to affect the density of its prey. This comparison suggests that both exploitative competition for food and selection for large adult size is weaker in *A. juncea* than it is in *M. coerulatus*. Although Van Buskirk suggested that larger adult *A. juncea* may live longer than smaller ones, evidence is lacking. The above comparisons suggest that, by understanding factors contributing to the fitness of individuals at *both* the larval and adult stage, we can begin to make sense of the contrasting ecological patterns among odonates and other insects with complex life histories.

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