

## Larval behaviour of a giant damselfly: territoriality or size-dependent dominance?

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(Received 23 November 1994; initial acceptance 6 March 1995;  
final acceptance 18 May 1995; MS. number: A7171R)

**Abstract.** Behavioural interactions and habitat use by larvae of the giant damselfly, *Megaloprepus coerulatus*, were studied in Panama. These larvae live in water-filled holes in fallen and living trees. Despite potential advantages for larval territoriality in this species, *M. coerulatus* did not exhibit exclusive use of resources, probably because their prey were not spatially clumped. Both well-fed and starved larvae initiated agonistic displays typical of other damselfly species, and even small differences in relative size affected their behaviour towards conspecifics. Habitat use in *M. coerulatus* varied with levels of food and cover. When cover was abundant, as it is in natural holes, larvae were hyper-dispersed. A larva rarely showed exclusive use of a given area from one day to the next, however, even when both cover and motile prey were experimentally limited. The ability of larger individuals to displace smaller ones as they move around the habitat is best described as size-dependent (and site-independent) dominance rather than territoriality. The results suggest that it is premature to characterize an animal as 'territorial' on the basis of its behaviour in the laboratory, unless the abundance and distribution of resources that are provided are realistic, and the experimental design is sufficient to differentiate between size-dependent dominance and site-specific exclusion of conspecifics from a critical resource.

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Territoriality may be defined as occupancy of a defended area that is used exclusively by the defending individual (e.g. Brown 1975; Morse 1980; Wittenberger 1981). This type of interference competition should evolve if limiting resources are spatially, but not temporally, clumped, such that the benefits gained from a territory outweigh the energetic costs of its defence (Emlen & Oring 1977). In contrast to territoriality, dominance implies 'priority acquired by past or present aggressive behaviour' (Brown 1975, page 85), and is often found in species in which the home ranges of individuals overlap. Distinguishing between territoriality and dominance is not easy, particularly if the behaviour of individuals is difficult to observe under field conditions. Both types of competition are often established by agonistic behaviour, and the criteria that determines successful competitors in each case

may be identical (e.g. size and/or age). For example, several authors have demonstrated that larval odonates use agonistic behaviour to exclude conspecifics from a resource and concluded that larval odonates exhibit territoriality (Rowe 1980; Harvey & Corbet 1985; Convey 1988). Nevertheless, their results are equally consistent with dominance of some individuals over others.

Although resource defence is widespread among adult vertebrates and invertebrates as a means of competing with conspecifics for mates (reviewed by R. R. Baker 1983), territoriality has rarely been well documented among juvenile vertebrates or larval invertebrates. Where it has been found, territoriality typically functions in defence of food resources (e.g. Hart 1987; Stamps & Eason 1989). Hart (1987) predicted that territoriality should evolve in aquatic insect larvae that are resource-limited when (1) body size is large relative to the available foraging area and (2) standing crop is large or readily renewable. Furthermore, because variation in larval growth of insects may result in considerable variation in adult body size

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(e.g. Fincke 1994), selection for agonistic and/or territorial behaviour might be stronger in species for which there is directional rather than stabilizing selection on size with respect to some fitness component.

Larvae of the largest extant damselfly, *Megaloprepus coerulatus*, meet all of the above conditions. On Barro Colorado Island in Panama, this species is one of three pseudostigmatid damselflies, in addition to an aeshnid dragonfly, that are top predators in holes in upright or fallen trees containing from 0.1 to 50 litres of water (Fincke 1992a). Within these microhabitats, odonate larvae are found at low densities, typically hiding under leaves, fruits, pieces of bark or other detritus along the sides and bottom of tree holes. Mosquito larvae are their most ubiquitous and dependable prey, but medium and large odonates also feed on tadpoles, fly larvae and other odonates. The latter are the largest prey available in tree holes. The abundant detritus found in natural holes probably protects *M. coerulatus* from intra-guild predation and cannibalism, and may also reduce feeding inhibition that otherwise occurs in the presence of conspecifics (e.g. Fincke 1994).

Within tree holes, food ultimately limits the size and number of emerging adults. Exploitative competition for food is reduced, however, because larger larvae obligately kill smaller conspecifics (i.e. even with ad libitum prey) until the density stabilizes at one larva per 1–2 litres (Fincke 1994). Consequently, in the absence of intra-guild predators, tree holes with 1 litre or less of water (hereafter 'small' holes) are typically occupied by a single larva (Fincke 1992a, b). The first larva to hatch in a small hole can maintain exclusive use of the resource by eating all potential competitors. Because this ability results from a priority effect resulting from the timing of oviposition by adult females, and not from differential competitive ability of the larva per se, the killing that occurs in small holes should not be considered territoriality unless larvae similarly exclude conspecifics from portions of holes that support multiple larvae to emergence.

Larvae require 4–6 months after hatching to emerge as adults from 'large' tree holes (i.e. greater than 1 litre), whereas they take up to 8 months to emerge from small holes (Fincke 1992b). Under field conditions, larvae grow more slowly and typically reach a smaller size at emergence than they do at similar densities with ad

libitum prey in the laboratory (Fincke 1992a, 1994). For both sexes, adults emerging from small holes are smaller than those emerging from large holes, and for males, but not females, the size of final instars and emerging adults is correlated with tree hole volume (Fincke 1992b, 1994). Larger adult males are superior in defending tree holes, and consequently enjoy greater mating success than smaller males (Fincke 1992b). Thus, the behavioural ecology of this species offers a potential selective advantage for larval territoriality in large holes if, by defending a portion of a hole, a larva enjoys greater survivorship and/or feeding efficiency.

Here I describe agonistic behaviour of larval *M. coerulatus* and quantify it as a function of hunger state. I conducted a laboratory experiment to determine the effects of resource abundance (cover and food) and relative larval size on habitat use. Finally, I discuss the implications of my results for the behaviour of other aquatic insects.

## METHODS

I conducted the study during early dry season, in January and February 1986, at the field station of the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama. The lowland moist forest there has a dry season lasting from December to May. I collected *M. coerulatus* larvae from natural tree holes before they dried out (Fincke 1992a, b). Although *M. coerulatus* larvae range from 2 to 33 mm in size, I limited individuals in this study to intermediate-sized larvae to minimize variation in behaviour due to developmental stage. For example, no final instars were used, because these larvae typically stop feeding 7–10 days before emergence (personal observation), and larvae under about 9 mm are less likely than larger ones to interact aggressively (Fincke 1994). Because larvae inhabiting the same tree hole were not put together in the same replicate, I assumed that interacting larvae were unrelated. All larvae were individually marked with enamel paint on the legs, and the two that moulted during the study were re-marked a day later. Using callipers, I measured larvae from the head to the end of the final abdominal segment, excluding the caudal lamellae (three leaf-shaped structures used in respiration). So measured, body length was highly correlated with head width, and

the size of final instars was correlated with the size of the emerging adult (Fincke 1994). Hereafter 'size' refers to body length. In any replicate, the largest individual was only 16–24% larger than the smallest individual. I therefore assumed that a larva perceived smaller conspecifics as competitors rather than prey. In all experiments, 'food' refers to newly hatched *Physalaemus pustulosus* tadpoles (3–4 mm body length), a natural prey (Fincke 1992a, unpublished data). Throughout, means are presented with their standard errors.

To determine the effect of hunger on agonistic behaviour, I quantified interactions between six pairs of fed and unfed larvae (18–23 mm). No food, cover or perches were provided during the observation periods. I fed 'starved' larvae ad libitum for 1 day, then not at all for 3 days before the start of the observations; they received no additional food over the course of the 3-day experiment. Between observation periods, I maintained each larva individually in 0.15 litres of water, and provided 'fed' larvae with food ad libitum. Four of the starved larvae were slightly larger than the fed larvae with which they were paired, and two were slightly smaller. Nevertheless, the average difference between paired larvae was only  $2.5 \pm 0.9$  mm, and the mean size of the larger larvae in the pairs did not significantly differ from the mean size of the smaller larvae ( $t=1.6$ ,  $P>0.3$ ). Once or twice on each of 3 consecutive days, I placed each pair in a container measuring  $9 \times 9$  cm (in 0.15 litres of water), and recorded all interactions that occurred during each of five, 30-min observation periods.

To measure the effect of resource abundance on habitat use by individuals, I noted the position of a triad of larvae in artificial holes with two levels of food and cover. I scored the bottom of rectangular pans ( $29 \times 23$  cm) into six equal sections ( $9.7 \times 11.5$  cm) using an indelible marker. The volume of natural tree holes is highly correlated with surface area ( $r=0.89$ ,  $N=29$ ,  $P<0.001$ ). Although each shallow pan held only 1 litre of water, the 667-cm<sup>2</sup> surface area was characteristic of tree holes that harboured as many as six larvae at a time (Fincke 1994). In tree holes, *M. coerulatus* larvae do not typically occupy the water column. Thus, these artificial holes were functionally 'large' holes whose shallowness allowed me to easily score the position of larvae.

I provided cover by tying a thread around a leaf petiole and taping it to the side of the container so

that each leaf remained in only a single section. 'High cover' treatments had one similar-sized leaf in each of the six sections. All leaves were collected from a single tree. 'Low cover' treatments contained a single leaf, the position of which varied among the replicates. In 'high food' treatments, tadpoles were added once or twice per day such that at least 10 were always present. Prey motility prevented me from quantifying the effect of prey density on larval movement within these treatments. In the 'low food' treatment, I added five tadpoles once, on the second day of the experiment, and none thereafter. Because all of these tadpoles were eaten within a day, no food was available in this treatment on 3 of the 4 days of a trial.

The mean difference between largest and smallest larvae in each replicate ranged between 3.1 and 4 mm. For a given triad, 'rank 1' refers to the largest individual ( $\bar{X} \pm \text{SE} = 20.9 \pm 0.6$  mm), 'rank 2' to the intermediate-sized larvae ( $18.7 \pm 0.4$  mm), and 'rank 3' to the smallest ( $17.0 \pm 0.3$  mm) individual. If two larvae were identical in body length, the one with the wider head was deemed larger. In two cases individuals shared the same rank. Prior to the experiment, I maintained larvae individually and fed them ad libitum for 1–2 days. Each larva was introduced to a section of pan that shared no side with another occupied section, and, in the low cover treatments, did not contain cover. Larvae were given 2–3 h to acclimate and their positions were then checked daily, usually once in the morning and once in the afternoon, for 4 days (i.e. eight samples/replicate). I first scanned the sections for larvae, which were usually under leaves. I identified hidden larvae by holding a small mirror adjacent to the leaf and gently lifting it until I could identify the individual. This procedure did not result in larvae moving to another section.

Because of difficulty in obtaining sufficient numbers of medium-sized larvae, I subjected each replicate to three or four of the treatments (once only). The two treatments with high food had seven replicates, whereas the other two treatments had eight replicates. A total of 32 individuals were used. I limited each treatment to 4 days to minimize reduction in larval density by conspecific killing. Nevertheless, three larvae, one of each rank, in two replicates of low food/high cover and one replicate of low food/low cover were killed before the end of the experiment. I did not use

these replicates in the analysis of larval distributions or in calculating treatment means. I replaced dead larvae or those missing two or more caudal lamellae by another of similar size before starting the subsequent treatment. The entire experiment ended after 16 days.

To minimize any carry-over effect of the high-food treatment on a subsequent low-food treatment, I subjected each replicate to a high-food treatment followed by two low-food treatments, and ending with a high-food treatment. For the second and third treatments (low-food), high cover was the second treatment in four cases, and the third treatment in three cases. I assumed that there was no carry-over effect of cover because a larva that moves away from cover is likely to be immediately aware that it is not under cover.

I used the following features of larval behaviour to quantify habitat use. (1) Movement: the number of moves/larva check. (2) Site Use: the proportion of the six sections occupied by an individual over the 4-day span. (3) Exclusive use of cover: the proportion of checks in which an individual found under a leaf was the only larva using the leaf. (4) Limited cover use: for the two low-cover treatments, the proportion of total checks that an individual was found in the section with the leaf cover.

A larva was credited with a 'move' if it was in a different section than it was on a previous check. Both a territorial individual and a dominant individual should exhibit exclusive use of cover and high limited cover use. If larvae are territorial, however, they should exhibit low movement and site use, whereas an individual that is dominant, independent of site, might exhibit moderate to high movement and site use. For analysis of individual means, I arcsine-transformed the above variables and used a repeated-measure ANOVA model with replicates as the error term.

To determine whether the spacing of larvae was non-random, I calculated the expected probability that individuals would be found in the same section of pan if a larva's position was independent of the position of the other individuals. These probabilities were 0.555 (i.e. 1(5/6) (4/6)), 0.417 (i.e. 3(1) (1/6) (5/6)), and 0.028 (i.e. 1(1/6) (1/6)) for one, two and three larvae in the same section, respectively. Because the latter probability generated expected values of less than 5, I pooled the latter two distributions for analysis. I calculated separate chi-squared tests for each sampling

period per treatment, because the distributions of larvae within a replicate measured repeatedly were not independent of each other. I then calculated a chi-squared value on the pooled  $\ln P$ -values from each sampling period within a treatment (i.e.  $-2 \ln P$  is distributed as  $\chi^2$ ,  $df=2$ ; see Sokal & Rohlf 1969). Non-random distributions might result by chance if, after an initial random move, larvae remained in the same section from one sampling period to another. To control for this possibility, I calculated chi-squared values on the subset of periods (66 of the total 218 samples) in which all three larvae in a replicate moved between time periods. A maximum of three such samples existed for any given replicate, and I assumed that these moves were independent of each other.

Over the course of this experiment, I opportunistically observed larval interactions and habitat use over a short time on 6 days. During 12 periods of 5–60 min (240 min total), I recorded all larval interactions that occurred in a replicate. These observations were biased in that I focused on replicates in which larvae were moving or interacting when I first scanned the pans.

## RESULTS

### Larval Behaviour

The pair-wise larval interactions consisted of the following patterns of behaviour, listed in the order they normally occurred in an encounter that ended in a tossel (i.e. in order of increasing aggression): (1) approach: larva approaches within 5 cm of another; (2) orient: head is turned towards conspecific, caudal lamellae are lifted; (3) tremor: caudal lamellae are held together and vibrated at low amplitude; (4) slow wave: abdomen is swung in a wide arc, on the same plane as, or slightly above, the body, with caudal lamellae displaced 90° or more; (5) strike: labium is extended and struck at conspecific; (6) tossel: one larva grabs the other with its labium while the other larva tries to pull away; (7) retreat: after any of the above behaviour patterns, one larva moves more than 5 cm away from the other.

'Slow wave' and 'labial strike' were similar to behaviour patterns described for some coenagrionid damselflies (Harvey & Corbet 1985 and Baker 1981, respectively). Strikes and tossels, which involved both individuals, were credited only to

**Table I.** Means  $\pm$  SE of mutually exclusive behaviour patterns (retreats excepted) initiated by fed and starved individuals of six pairs of similar-sized *M. coeruleus* larvae during six 30-min observations per pair (36 total observations)

	Fed	Starved
Approach	3.2 $\pm$ 1.4 (0–9)	3.0 $\pm$ 1.6 (0–8)
Orient	4.2 $\pm$ 1.9 (0–12)	5.0 $\pm$ 1.8 (2–11)
Tremor	0.8 $\pm$ 0.6 (0–4)	1.5 $\pm$ 1.3 (0–8)
Slow wave	2.2 $\pm$ 1.1 (0–6)	2.0 $\pm$ 0.9 (0–6)
Strike	2.8 $\pm$ 1.7 (0–9)	4.8 $\pm$ 2.4 (0–14)
Tossel	0.5 $\pm$ 0.5 (0–3)	1.7 $\pm$ 1.7 (0–10)
Total acts	13.7 $\pm$ 6.5 (2–35)	18.0 $\pm$ 6.8 (5–47)
Retreat	0.5 $\pm$ 0.3 (0–2)	4.0 $\pm$ 2.1 (0–11)

Ranges are in parentheses. Total acts include all behaviour patterns but retreats. No difference was significant at  $P < 0.05$ , with either Mann–Whitney  $U$ -tests or  $t$ -tests.

the individual that initiated them. An encounter was considered terminated after one or both individuals retreated. I credited retreats to an individual only if it was clear that one individual, rather than both, moved away from the area of an encounter.

Starved individuals tended to retreat more often than did well-fed larvae of similar size, but that difference, and any other between the two groups was not significant (Table I). A two-way ANOVA using relative size (i.e. larger or smaller) and hunger level as treatments revealed significant interaction effects between relative size and hunger for number of approaches ( $F_{1,11} = 5.2$ ,  $P < 0.05$ ) and number of spars initiated ( $F_{1,11} = 12.0$ ,  $P < 0.05$ ).

During the experiment on habitat use, larvae occasionally walked over immobile larvae without either larva reacting to the other. In contrast, larval interactions were always initiated only after one larva oriented to the other. When interactions occurred, they ranged in frequency from one per 3 min to one per 50 min ( $N = 9$  replicates). Change of section by an individual varied from one per 3 min to one per 18.5 min. In all cases that I saw, interactions were initiated either by individuals of

rank 1 or 2. Twice I saw a rank-3 individual lose a tibia, once resulting from a spar and once from a tossel. One rank-2 individual lost a caudal lamellae during a spar.

Leaves were used as retreats. When a larger individual went under an occupied leaf, the smaller individual usually exited, although larvae that were under leaves did not typically react to an individual moving onto the top of the leaf. One response to an approach was to move slowly under a leaf. Sometimes a larva would display to a conspecific that was under a leaf; the latter usually was not seen to react. One large larva that I saw kill a smaller conspecific in a low-food treatment first pulled the carcass under a leaf before consuming it.

In the high-food treatments, at any given time, about half of the tadpoles rested in groups of two to three along the edges of the container or under leaves. They spent most of the time on the bottom of the pan, moving up to the surface to take air and then re-submerging, sometimes to a different section. Tadpoles moved frequently and swam forward if approached by a *M. coeruleus* larva. The behaviour of *M. coeruleus* towards a tadpole differed from behaviour directed towards a conspecific, in that slow waves and tremors did not precede strikes, and tossels were not seen. Larvae oriented to moving tadpoles, approached, and then remained motionless, usually striking as soon as the tadpole moved again.

### Spacing and Habitat Use

Spacing patterns of *M. coeruleus* larvae on multiple checks were non-random for three of the four treatments in the territoriality experiment (Table II). Even when the data were reduced to only those cases in which all three larvae in a replicate moved between sampling periods, spacing patterns were still non-random in two of the four treatments (Table III). With abundant cover and low food, the treatment that was most similar to natural conditions, larvae were more regularly spaced than expected if spacing was independent of the position of conspecifics. In the low-cover treatment when food was abundant, larvae were more clumped than expected. When cover was high, larvae were more hyper-dispersed than expected by chance (Table III), whereas low food caused larvae to clump only when cover was also low. Thus, food as well as cover affected the spacing of larvae.

**Table II.** Distributions of three larvae between the six sections in the four treatments of the territoriality experiment

Treatment (cover/food)	Larval distribution	Number of observed distributions in sampling period								$-2\sum \ln P$
		1	2	3	4	5	6	7	8	
HH	1 1 1 0 0 0	5	5	6	4	6	5			14.5
	2 1 0 0 0 0	1	2	1	2	1	2			$df=12$
	3 0 0 0 0 0	1	0	0	1	0	0			
HL	1 1 1 0 0 0	5	6	7	7	7	3	5	6	37.8*
	2 1 0 0 0 0	2	1	0	0	0	4	2	1	$df=16$
	3 0 0 0 0 0	0	0	0	0	0	0	0	0	
LH	1 1 1 0 0 0	1	2	2	2	0	0	1	2	52.8**
	2 1 0 0 0 0	2	3	3	3	5	4	4	2	$df=16$
	3 0 0 0 0 0	4	2	2	2	2	3	2	3	
LL	1 1 1 0 0 0	5	4	2	4	1	2	0	4	28.6*
	2 1 0 0 0 0	2	2	4	2	6	5	6	3	$df=16$
	3 0 0 0 0 0	0	1	1	1	0	0	1	0	

Sampling periods are repeated measures on the same replicate. The expected frequency of a larval distribution was 0.555 for one larva per section, 0.417 for two larvae in any given section, and 0.028 for all three larvae in any given section. H: High; L: low. HH and HL had a leaf cover in each of six sections; LH and LL had a leaf cover in only one of the six sections.

\* $P<0.05$ ; \*\* $P<0.001$ .

**Table III.** Distribution of larvae in cases when all three larvae moved between checks

Treatment (cover/food)	Larval distribution	Number of observed distributions	Expected	$\chi^2$ , $df=2$
HH	1 1 1 0 0 0	18	11.10	9.6*
	2 1 0 0 0 0	2	8.30	
	3 0 0 0 0 0	0	0.56	
HL	1 1 1 0 0 0	14	11.10	2.4
	2 1 0 0 0 0	5	8.30	
	3 0 0 0 0 0	1	0.56	
LH	1 1 1 0 0 0	2	5.00	4.1*
	2 1 0 0 0 0	2	3.75	
	3 0 0 0 0 0	5	0.25	
LL	1 1 1 0 0 0	10	9.44	0.07
	2 1 0 0 0 0	7	7.08	
	3 0 0 0 0 0	0	0.47	

Categories with expected values less than 5 were pooled.

\* $P<0.05$ .

Habitat use by individuals is summarized in Table IV. In none of the treatments did a larva demonstrate exclusive use of a portion of the habitat over the 4-day span. The longest exclusive use of a site was in the high-cover and low-food treatment, by a rank-1 larva that remained alone in the same section for 3 days. Another rank-1 larva was always found alone in the same section over a 2-day span. The mean proportion of sites used by an individual in this treatment was the

highest among the four treatments, however, and most of the larvae changed their positions at least once per day. Larvae in the low-cover, high-food treatment changed their position the least, but rarely were both conspecifics excluded from a leaf cover. In this treatment, 16 of the 21 individuals occupied the single leaf in their replicate on at least half of the checks, but shared the leaf with at least one conspecific, for 89% of the checks on average (range 28–100%). When food was also

**Table IV.** Replicate means of behaviour of individuals (3 individuals per replicate, 7–8 replicates per treatment)

Treatment (cover/food)	Larval behaviour				Proportion	
	Moves/ check	Proportion of sites used	Exclusive use of cover	Use of limited cover	Missing caudal lamellae	Killed
HH	0.52 ± 0.04	0.58 ± 0.03	0.68 ± 0.07	—	0.25	0
HL	0.52 ± 0.04	0.69 ± 0.04	0.87 ± 0.02	—	0.08	0.08
LH	0.35 ± 0.10	0.41 ± 0.04	0.10 ± 0.04	0.68 ± 0.07	0.33	0
LL	0.53 ± 0.05	0.51 ± 0.03	0.22 ± 0.05	0.52 ± 0.06	0.29	0.08
	$F_{3,7}=5.2^*$	$F_{3,7}=12.13^*$	$F_{3,7}=22.4^{**}$	$F_{3,7}=8.5^*$		

H: High; L: low. *F*-values refer to repeated measures, one-way ANOVAs.

\* $P<0.05$ ; \*\* $P<0.001$ .

limited, the 13 individuals that occupied a single leaf shared it with a conspecific for more than half of the total checks, significantly less ( $\bar{X}=72.5\%$  of the checks) than when food was abundant (Table IV).

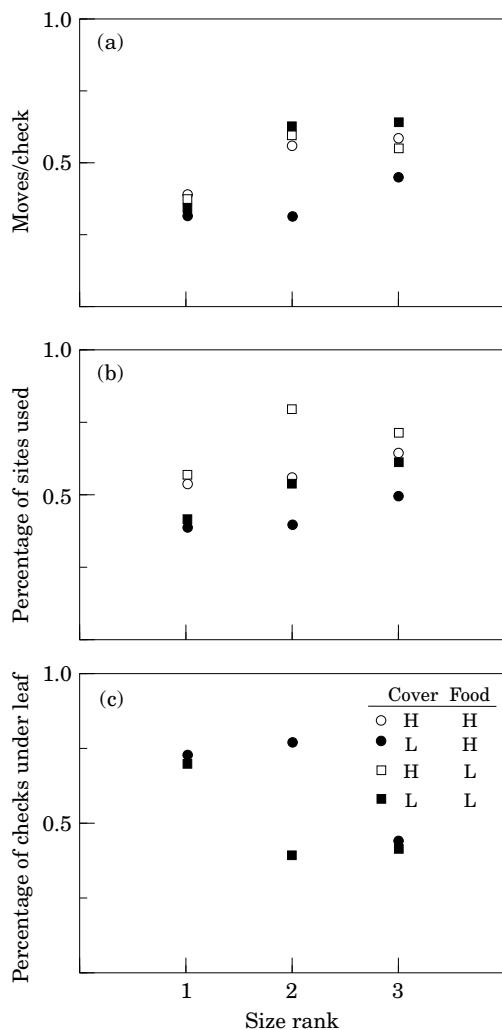
Results of a two-way ANOVA with cover and food as treatment effects revealed a significant interaction effect with respect to larval movement ( $F_{1,7}=6.9$ ,  $P<0.04$ ). There was no significant interaction effect between cover and food with respect to the percentage of sites used ( $F_{1,7}=0.4$ ,  $P>0.54$ ), or exclusive use of sites ( $F_{1,7}=1.5$ ,  $P>0.25$ ). Excess cover increased the percentage of sites used ( $F_{1,7}=25.6$ ,  $P<0.01$ ) and increased the exclusive use of leaves by individuals ( $F_{1,7}=62.1$ ,  $P<0.0001$ ). When food was limited, larvae used more sites ( $F_{1,7}=11.1$ ,  $P<0.02$ ) and were less likely to use limited cover ( $F_{1,7}=8.5$ ,  $P<0.05$ ) than when food was not limiting. Limited food did not affect the exclusive use of cover ( $F_{1,7}=3.4$ ,  $P>0.15$ ).

Across treatments, body size was negatively correlated with mean movement ( $r=-0.48$ ,  $N=26$ ,  $P<0.02$ ), site use ( $r=-0.40$ ,  $N=26$ ,  $P<0.05$ ) and was positively correlated with use of limited cover ( $r=0.50$ ,  $N=24$ ,  $P<0.02$ ). Relative size as measured by rank mimicked these trends (Fig. 1). The larger individuals in the triads moved less, used fewer sites, and used limited cover more often than the smallest individuals in the triad. Exclusive use of limited cover was not significantly correlated with body size ( $r=0.14$ ,  $N=22$ ,  $P>0.5$ ) or rank ( $r=-0.36$ ,  $P>0.09$ ). Larvae lost caudal lamellae in all treatments, but rank-3 individuals were no more likely to lose lamellae than those of rank 1 or 2 ( $\chi^2=1.3$ ,  $df=2$ ,  $P>0.5$ ).

## DISCUSSION

Agonistic behaviour of *M. coerulatus* included orienting to conspecifics, raising and swinging the caudal lamellae, and striking, which are type of behaviour similar to those described for coenagrionid damselflies (Rowe 1980; Baker 1981; Harvey & Corbet 1986). Unlike many species whose larvae cannibalize rarely, or only when food-stressed (e.g. Dong & Polis 1992; Johansson 1992; Rowe 1992), even well-fed *M. coerulatus* were aggressive towards conspecifics. In contrast with another damselfly (Anholt 1990), and other aquatic insects (Walde & Davies 1984; Hart 1987), agonistic behaviour of *M. coerulatus* carried high costs, resulting in larvae losing tibia, caudal lamellae, and even their lives. Such innate aggressiveness might be adaptive under natural conditions because prey abundance is typically low (Fincke 1994). Given that, as adults, large size is more advantageous for males than females (Fincke 1992b), male larvae might be more aggressive than females, possibly accounting for some of the unexplained behavioural variation in Table I. Sex of larvae is only apparent in late instars and was thus not considered in the current study.

Agonistic behaviour was used to displace others from an area. When cover was abundant, such behaviour resulted in more regular spacing of larvae than expected by chance. Nevertheless, when cover was limited to a single leaf, at least two larvae were nearly always found using it (see also McPeck & Crowley 1987; Anholt 1990). For *M. coerulatus*, possession of cover appears important in avoiding predation by both



**Figure 1.** Mean behaviour of individuals by rank in the four treatments of the territorial experiment. Size ranks of 1 and 3 refer to the largest and smallest individual, respectively, in each replicate. H: High; L: low. Use of limited cover (i.e. percentage of checks where a larva was under a leaf) was relevant only for the low-cover treatments. (a)  $r=0.49$ ,  $N=26$  individuals,  $P<0.02$ , (b)  $r=0.47$ ,  $N=26$  individuals,  $P<0.02$ , (c)  $r=-0.46$ ,  $N=24$ ,  $P<0.03$ .

conspecific and heterospecific odonates. In the two cases where larvae were killed, both lacked cover. Given more time in the low-cover/low-food treatment, one of the larger larvae would be likely to eventually kill others that persisted in sharing the leaf (see Fincke 1994). In large natural holes,

young instars ( $\leq 5$  mm) of *M. coeruleatus* are typically found on leaves close to the water surface, or in the shallow areas of the hole, whereas larger larvae are intermittently spaced in deeper areas (Fincke 1992c). Such spacing is likely to result, as it did in the experimental holes, from smaller larvae actively avoiding larger conspecifics and larger individuals expelling smaller ones from cover.

*Megaloprepus coeruleatus* larvae should not be described as territorial, even though their behaviour was similar to that of larval odonates described as such (i.e. Rowe 1980; Harvey & Corbet 1985, 1986; Convey 1988). Most *M. coeruleatus* moved between leaf sites at least once per day, and used multiple sections over a 4-day span. The longest exclusive use of a leaf accounted for only 1.6–2.5% of a larva's lifespan. Moreover, the two daily checks greatly underestimated habitat use, at least for many of the larvae that were observed between the daily checks. When food was abundant, larvae moved less but they still used a variety of sites, probably because their prey did not remain clumped in any particular area. Because larger *M. coeruleatus* moved less, used fewer sites, but were more likely than small larvae to use limited cover, their behaviour most closely corresponds to site-independent dominance based on relative size.

In contrast with my results, Rowe (1980) and Harvey & Corbet (1985) found that prior occupancy rather than size was a better predictor of which larva retreated during an encounter, but neither study gave data on the size difference between interacting larvae. Differences in our results might be explained if the range of larval sizes in their experiments was less than in mine. In my study, surprisingly small differences in body size resulted in a significant interaction effect of size and hunger state on levels of agonistic encounters.

My conclusions are most consistent with those of R. L. Baker, who documented size-dependent dominance under laboratory conditions for the coenagrionids *Coenagrion resolutum* (1981) and *Ischnura cervula* (1983). Larger individuals of both species repelled others from perches or artificially clumped food (Baker 1980). Because familiarity with an area offered a larva no advantage in excluding other individuals, whereas a dominant individual continued to displace conspecifics regardless of location,



Baker (1980) concluded that his study species were not territorial.

The lack of territoriality in *M. coerulatus* counters several conclusions drawn from past laboratory studies on larval behaviour of odonate species for which the natural abundance and distribution of critical resources were unknown. Rowe (1980) and Harvey & Corbet (1985) suggested that by defending a perch, a larva has greater access to food, and consequently emerges as a larger adult than larvae without perches. In a 2-month study, Rowe (1980) marked eight *Xanthocnemis zealandica* larvae, provided them with eight perches and abundant food, and found that two final-instar larvae remained on the same perch for 50 days. Those larvae may have been in diapause however, or food may have been sufficiently abundant that they did not have to search for it. Unfortunately, the mean length of time a larva spent on a given perch was not provided, nor the number of perches an individual occupied over the course of study. Despite the 1:1 ratio of perches to larvae, in 82% of the 375 observations, half or more of the individuals shared perches, and thus did not exhibit exclusive use of the resource. Although Harvey & Corbet (1986) demonstrated exclusive use of a perching surface by one larva of pairs of *Pyrrhosoma nymphula*, their design prevented the possibility for larva to move between multiple perch sites.

Neither of the above studies examined the consequences of perch possession with respect to larval growth. Although Harvey & Corbet (1985) argued that large size of adult males was favoured by sexual selection, their data confounded natural and sexual selection, as Gribbin & Thompson (1991) subsequently demonstrated (there was weak natural selection on size).

In an extensive study, Convey (1988) found that larger *C. puella* used agonistic behaviour to displace smaller larvae from perches (see also McPeck & Crowley 1987), and larvae were more regularly spaced than expected by chance. He also showed that larvae with perches were less susceptible to fish predation, but did not grow faster, than those without perches. Because the larvae were not individually marked, however, Convey could not document exclusive use of perches by individuals over time. Indeed, on average, larvae moved once or twice per h. His results are as consistent with size-dependent dominance as they are with territoriality.

My experiment with *M. coerulatus* demonstrated that larval behaviour depends on the availability of cover, analogous to perch sites in the above studies, and food. These results emphasize the need to understand natural resource conditions before concluding that behaviour observed under laboratory conditions is relevant to what occurs in the field. For example, when cover was unnaturally limiting, larvae were more clumped than expected, and larger individuals displaced smaller ones from cover. Despite the evolution of a behavioural repertoire that could enable *M. coerulatus* to defend its limited food resources, they do not do so. Larvae actually moved more, not less, when food was artificially limited, suggesting that active searching for motile prey is a more profitable foraging strategy than defence of a given area. Lack of defence of limited food resources is best explained by the motility of their prey (i.e. mosquitos, beetle and fly larvae, and tadpoles), which do not remain clumped in any given area (see also Baker 1986). Comparison of behaviour of *M. coerulatus* with that of caddisflies, which also feed on motile prey (Hart 1985), suggests that territoriality is lacking in *M. coerulatus* but is present in caddisflies, because food renewal rates relative to optimal intake are lower for *M. coerulatus* than they are for caddisflies. Caddisflies may obtain all the food they need by defending a given area. For *M. coerulatus*, even when mosquito prey were abundant under natural conditions, larvae grew more slowly than they did with ad libitum tadpole prey (Fincke 1994).

Collectively, data from field studies also fail to provide evidence for larval territoriality in odonates. Baker (1989) found no evidence of density-dependent growth and mortality in *I. verticalis*, even though, under laboratory conditions, another *Ischnura* species excluded others from patches of prey (R. L. Baker 1983). He also failed to find evidence that dispersing larvae of either species were disproportionately small, as might be expected if small larvae were excluded from feeding territories in the field (Baker 1987). Where density-dependent effects have been noted for odonate larvae, either in field enclosures or under natural conditions, interference competition appears to be mediated by size-dependent feeding inhibition and/or cannibalism rather than territoriality (e.g. Johnson et al. 1985, 1987; Van Buskirk 1989, 1992; Wissenger 1989; Fincke 1994).

## ACKNOWLEDGMENTS

I am indebted to George Rüppell, who generously funded this work in exchange for my help in filming pseudostigmatids on BCI. I thank the Smithsonian Tropical Research Institute for logistical help, C. McCallister for figures and two anonymous referees for comments on an early draft of the manuscript.

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