

The population ecology of *Megaloprepus coerulatus* and its effect on species assemblages in water-filled tree holes

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17.1 INTRODUCTION

The role of competition, either in the form of intraspecific interactions that may lead to density-dependent population regulation, or in the form of interspecific interactions that may lead to niche differentiation, has recently come under renewed scrutiny from both theoreticians and empiricists (e.g. Cappuccino and Price, 1995; Denno *et al.*, 1995). Alternative explanations now abound for patterns of population persistence and species co-existence, and testing between these alternatives is a current challenge for insect population ecologists. Because many processes may lead to the same pattern, knowing the processes that give rise to population or community patterns is critical to understanding the dynamics of ecological assemblages. Too often, community ecologists infer process from pattern, whereas behavioural ecologists usually ignore the consequences of other species on individual fitness. The goal of my long-term research on tropical odonates is to bridge this gap.

Because they are discrete and relatively simple habitats, water-filled plant containers (phytotelmata), such as leaf axils, tank bromeliads, and tree holes, are particularly amenable to investigations into the processes controlling populations and structuring communities (e.g. Bradshaw and Holzapfel, 1983, 1988; Naeem, 1988; Mogi and Young, 1992). For the past

15 years, I have studied a guild of odonates whose larvae are top predators in tree holes. As a behavioural ecologist, my initial interest was in the adult reproductive behaviour of the three common pseudostigmatid damselflies, which were known primarily for their unusual habit of feeding on orb-weaving spiders (e.g. Calvert, 1911; Stout, 1983). I asked why males of *Megaloprepus coerulatus*, the world's largest damselfly, defend water-filled tree holes, whereas males of the two *Mecistogaster* species do not. One might think that all three species should be territorial, because they all use potentially defensible and limiting tree-hole oviposition sites (Fincke, 1992a). I then asked how larval dynamics affected adult fitness: for example, why do *M. coerulatus* lay as many as five times the number of eggs in a single tree hole as do *Mecistogaster* females, which oviposit a relatively small number of eggs in any hole, regardless of its size? Also, given that its larval offspring are cannibalistic, how long should a territorial *Megaloprepus* defend a tree hole, where progeny from later matings are likely to be consumed by their older half-sibs? Such questions could not be answered by focusing only on adults, or on a single species. Because intraguild predation (*sensu* Polis and McCormick, 1987) is a major source of mortality for tree-hole predators, studying the community dynamics at the larval stage was required to understand how guild members, especially *M. coerulatus*, are regulated. Thus I have come to population and community ecology through the back door, so to speak. My initial goal was not to test theoretical hypotheses about population regulation or community assemblages, but rather to understand adult reproductive behaviour. I hope to show that regulation of *M. coerulatus* is best understood in terms of competition between larvae. In the first part of this chapter, I summarize population data on *M. coerulatus* collected over an 11-year period from the tropical moist forest of Barro Colorado Island, Panama. I identify life-history characteristics of larval and adult guild members, which enable *Megaloprepus* to dominate tree holes, and suggest that seasonal tree-hole drying prevents it from excluding less-competitive species. I then test this hypothesis by comparing the Barro Colorado guild with the tree-hole assemblage at La Selva Biological Station in Costa Rica, where tree holes retain water throughout the year.

17.2 NATURAL HISTORY

Tree holes that collect water form in rotting burls, branch break-offs, or convolutions in the trunk of fallen trees. Those harbouring odonates range in volume from 0.01 to over 50 litres. This system lends itself to controlled field experiments, because artificial tree holes are colonized by a fauna nearly identical to that of natural holes (Fincke *et al.*, 1997). Tree holes on Barro Colorado Island harbour a more complex array of top predators than at previously studied tropical sites (e.g. Kitching, 1990).

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The major macropredators, from the largest to the smallest (as measured by maximal larval size), are two aeshnid dragonflies, *Gynacantha membranalis* and *Triacanthagyna dentata*, and the pseudostigmatid damselflies *Megaloprepus coerulatus*, *Mecistogaster linearis* and *Mecistogaster ornata*, tadpoles of *Dendrobates auratus*, and the mosquito *Toxorhynchites theobaldi*. Another pseudostigmatid, *Pseudostigma accedens*, is extremely rare on Barro Colorado Island: during my 14-month stay on the island in 1983–84 I found two larvae, each in a small tree hole, and since then I have seen only five adults, so this species is ignored here. In past work, I referred only to the aeshnid *G. membranalis*, but I recently discovered that most of the aeshnids in Barro Colorado Island tree holes are the smaller and more abundant species *T. dentata*.

Size ratios of the final developmental stages among the common macropredators are *Gynacantha:Triacanthagyna*, 1.2; *Triacanthagyna:Megaloprepus*, 1.3; *Megaloprepus:Mecistogaster*, 1.2; *Mecistogaster:Dendrobates*, 1.4; *Dendrobates:Toxorhynchites*, 1.2. Although it has been suggested that such ratios indicate that these predators partition the feeding niche (e.g. Hutchinson, 1959; but see Lawton and Strong, 1981), the two *Mecistogaster* species contradict this pattern, being nearly identical in final instar size and growth rate (Fincke, 1992a).

Mosquito larvae are the most abundant and ubiquitous prey in tree holes (Fincke *et al.*, 1997). Syrphid fly larvae, chironomid midge larvae, tadpoles of *Physalaemus pustulosus*, and smaller individuals of the predator guild are also taken if available. In large holes, newly hatched *Megaloprepus* and *Mecistogaster* can emerge within 3.5 and 4 months, respectively, whereas the aeshnids require at least 5.5 months. In small holes, odonates may take 8 months or more to emerge as adults (Fincke 1992a; Fincke *et al.*, 1997). *Dendrobates auratus* eggs hatch within 11 days, after which the male carries the tadpoles to tree holes where they metamorphose after 1–3 months (Summers, 1990). *Toxorhynchites* develop within a month (Lounibos *et al.*, 1987).

The tropical moist forest on Barro Colorado Island receives an average of 2600 mm of rainfall annually, but experiences a dry season that lasts from January to late April (Rand and Rand, 1982). Most tree holes dry out by mid-March, and larvae that have not emerged by this time usually die because they cannot withstand more than 3 weeks of totally dry conditions (Fincke, 1994). For example, in one year only 5% of the tree holes contained larvae (either *Megaloprepus* or aeshnids) that survived the dry season. Because two to three cohorts of *M. coerulatus* can emerge over a wet season, tree-hole drying affects only the last generation. *Megaloprepus* and aeshnid adults are reproductive throughout the year except late in the dry season (i.e. March–April), when they aestivate. They reappear in May or June to produce the first wet-season generation of the year. In contrast, *Mecistogaster linearis* and *M. ornata* seem to produce only one

generation per year. Adults of both species emerge in late wet or early dry season, and forage throughout the dry season. *M. linearis* begins mating in mid-December and apparently lays diapause eggs until the following wet season. This is the only species seen to oviposit regularly into holes with little water that soon thereafter dry out completely. *M. ornata* adults remain in reproductive diapause from the time they emerge until shortly before or after the first wet-season rains. The onset of reproduction in *M. ornata* is indicated by sexually dimorphic changes in wing pigmentation. The ventral side of the yellow wing tips of the male turn black, whereas those of females remain yellow (Fincke, 1984).

Of the odonates, *M. coerulatus* and *T. dentata* (possibly *G. membranalis*) males defend tree holes, usually large ones in light-gap areas where females can be reliably found (Fincke, 1992b; O.M. Fincke, unpublished data). Males of both species typically defend a hole for 2 weeks, although *Megaloprepus* may stay as long as 3 months, mating with any female before permitting her to lay eggs in the defended hole. *Megaloprepus* is one of the few odonates whose males are significantly larger than females. Sexual selection favours large males. Although females also oviposit in undefended holes, they mate only at defended sites. Because body size rather than prior residency best predicts the winner of territorial disputes, mated males are larger than males not seen to mate. Small males defend large holes until displaced by a larger male; they also play a satellite role at very large territories. Body size of males, but not females, is correlated with the volume of their larval habitat (Fincke, 1992b).

17.3 METHODS

During five wet seasons, the distribution of tree-hole organisms was quantified by repeatedly checking the contents of natural holes. Detritus and standing water were first removed, and emptied into white pans for inspection. The inside of the hole was then searched with a torch to detect odonate larvae, which typically are not sucked out with the water. A total of 331 unique tree holes were censused. Of the tree holes sampled in 1983, 52% were included in the 1984 sample. Similarly, 65% of holes sampled in 1992 were also sampled in 1993. However, of the holes sampled in 1992 and 1993, only 21 and 27%, respectively, were sampled in 1984. These yearly censuses can be considered independent for the present purpose because they are cleared of odonates in the dry season, and prior colonization of a hole by a predator was not predictive of its colonization by that predator in subsequent years (Fincke, 1992a; in press).

The distribution of tree holes from which odonates successfully emerged was determined by collecting final instars and allowing them to emerge in an outdoor insectary. To determine whether tree-hole predators used alternative habitats on Barro Colorado Island, the contents of freshly

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fallen, water-filled fruit husks of the liana *Tontelea ovalifolia (richardii)* were sampled repeatedly between 2 May and 10 July 1990. Fallen palm fronds were also censused irregularly during the wet seasons of 1983, 1984 and 1997.

Larval *Mecistogaster linearis* and *M. ornata* are not easily distinguished; data refer to pooled samples of the two species. Similarly, *G. membranalis* and *T. dentata* larvae were pooled. The term 'aeshnid' is used when no distinction was made between the two genera. Newly hatched odonates range from 2–3 mm in size, and no effort was made to detect very tiny odonate larvae or first-instar larvae of *Toxorhynchites*. Thus, species' occupancies may be underestimated, especially for the mosquito. Throughout, mean numbers are reported \pm s.e. 'Small pots' refers to 400-ml plastic pots; 'large pots' were 7-litre tubs that usually contained 4–5 litres of water. All pots also contained leaves and a stick perch. Detailed methods for studies summarized here are described elsewhere (Fincke, 1984, 1992a, b, 1994; Fincke *et al.*, 1997).

17.4 PATTERNS OF EMERGENCE AND OVIPOSITION ON BARRO COLORADO ISLAND

The largest odonate species consistently dominate large tree holes within 2 months of the first rains of wet season (Table 17.1). The aeshnids and *Megaloprepus* begin to emerge about September, and continue to do so until tree holes dry up in March. The two smaller *Mecistogaster* species, which emerge from relatively small holes, have a single, peaked emergence from late wet season to early dry season (Fig. 17.1, Fincke, 1992a). These patterns suggest that *Mecistogaster* preferentially oviposits in smaller tree holes than either *Megaloprepus* or the aeshnids. However, a field experiment designed to detect very early wet-season colonization demonstrated this was not the case. Loosely covering tree holes with netting a month after the first rains of the wet season, prevented any subsequent oviposition by odonates, but not by their mosquito prey. When the larvae had grown large enough to identify, it was found that *Mecistogaster* had occupied about half of both large and small holes, significantly more than had been colonized by *Megaloprepus* or the aeshnids (Fincke, 1992a). Thus ovipositing *Mecistogaster* females do not preferentially use small tree holes. I have seen both *M. linearis* and *M. ornata* oviposit in large, defended holes. *Megaloprepus* males inspect the females but do not chase them away. Moreover, any female can oviposit when territorial males are absent, as they often are in late afternoon.

Indeed, the only niche partitioning by odonate females that was detected, was an absence of aeshnid larvae from holes with slit openings. Because of their short abdomens and inability to hold their wings together vertically, the aeshnids are prevented access to these holes (tree-hole

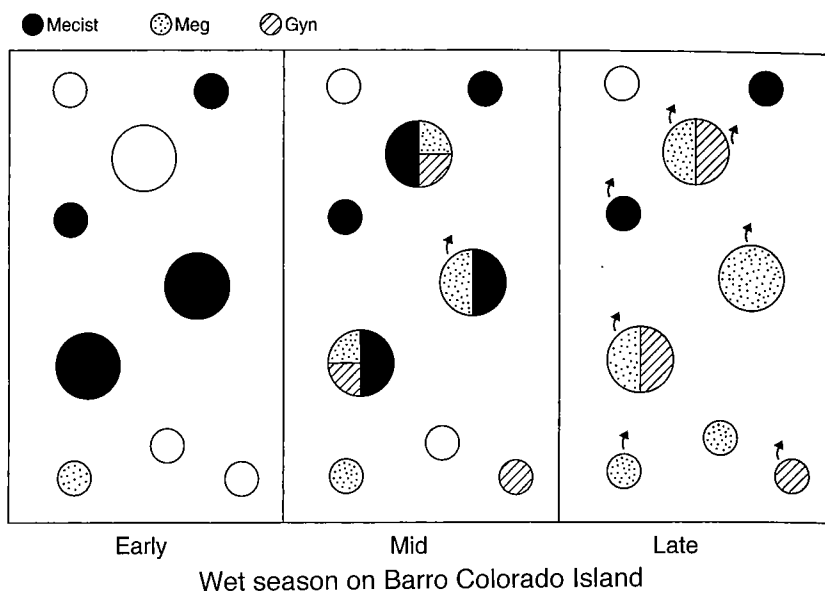


Fig. 17.1 Schema of seasonal changes in odonate occupancy of large and small tree holes on Barro Colorado Island. 'Early dry season' refers to less than 2 months from the first wet-season rains. Arrows indicate emergence of adults, which first occurs from large holes in mid-wet season, and continues until the holes dry out in March. Mecist: *Mecistogaster*; Meg: *Megaloprepus*; Gyn: *Gynacantha* and *Triacanthagyna*.

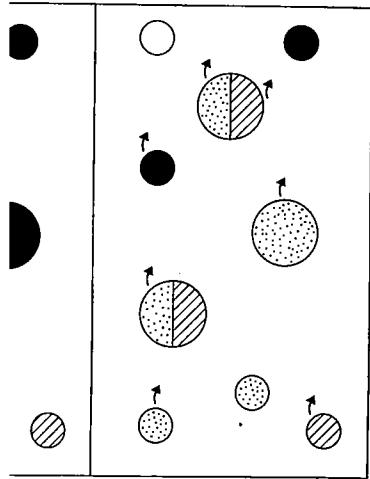
Table 17.1 Mean volume of tree holes by site and year that were occupied by predator genera. On Barro Colorado Island, sampling was at least 2 months after the start of rainy season

Predator	Barro Colorado Island					La Selva
	1982 (78)	1983 (110)	1984 (129)	1992 (92)	1993 (97)	1991 (64)
Tree-hole aeshnids	6.3±2.6	7.4±2.1	5.8±2.1	3.6±1.9	3.5±1.7	20.0*
<i>Megaloprepus</i>	7.4±2.1	3.2±0.4	2.4±0.7	1.5±0.4	3.0±1.4	2.3±0.8
<i>Mecistogaster</i>	0.2±0.0	0.8±0.2	0.6±0.1	0.7±0.2	0.6±0.1	0.2*
<i>Dendrobates</i>	-	5.4*	6.7±4.7	5.4±4.9	0.7±0.3	3.5±2.8
<i>Toxorhynchites</i>	-	0.3±0.1	1.8±1.3	0.5±0.2	0.7±0.2	0.8±0.2

Number of holes sampled is in parentheses.

*, Larvae found in only a single hole.

Volume of tree holes occupied by odonate genera did not differ across years on Barro Colorado Island ($F_{3,68}=1.1, P>0.3$; $F_{3,194}=0.8, P>0.4$, $F_{4,133}=0.4, P>0.7$, for aeshnids, *Megaloprepus* and *Mecistogaster*, respectively).



Late

Barro Colorado Island

Occupancy of large and small tree holes during the 'late wet season' refers to less than 2 months after emergence of adults, from the start of the wet season, and continues until the end of the dry season. Meg: *Megaloprepus*; Gyn:

and year that were occupied by *Megaloprepus* was at least 2 months after sampling

	La Selva		
	1992	1993	1991
4	(92)	(97)	(64)
2.1	3.6±1.9	3.5±1.7	20.0*
0.7	1.5±0.4	3.0±1.4	2.3±0.8
0.1	0.7±0.2	0.6±0.1	0.2*
4.7	5.4±4.9	0.7±0.3	3.5±2.8
1.3	0.5±0.2	0.7±0.2	0.8±0.2

did not differ across years on Barro Colorado Island. $F_{4,133}=0.4, P>0.7$, for aeshnids,

odonates on Barro Colorado Island insert their eggs into bark just above the water line). Because all the sampled tree holes were below about 4 m above ground, niche partitioning by height is a possibility. Sampling of tree holes and pots in the forest canopy on Barro Colorado Island failed to find any *Megaloprepus* larvae, although *Mecistogaster* and aeshnids were found there (S.P. Yanoviak, unpublished data). The absence of *Megaloprepus* larvae in canopy holes does not seem to result from an inability of adults to reach such holes, as on several occasions I watched a territorial *Megaloprepus* male fly from the hole it was defending in the lower trunk of a *Ceiba pentandra* tree, to the top of the tree, where there was a very large tree hole occupied by *D. auratus* tadpoles (R. Wirth, personal communication). Moreover, when foraging for spiders, *Megaloprepus* flies at least as high as *Mecistogaster* (Fincke, 1992c).

I argue below that differential survivorship of larvae with respect to tree-hole volume, rather than niche partitioning by adults, is the most likely explanation for the observed changes in tree-hole occupancy by mid wet season (Fig. 17.1). I systematically eliminate alternative explanations for differential survivorship and conclude that observed patterns of emergence are most likely to be the result of competition among odonate larvae.

17.5 CAUSES OF LARVAL MORTALITY DURING THE WET SEASON ON BARRO COLORADO ISLAND

17.5.1 Tree-hole chemistry

Differential survivorship of species with respect to tree-hole volume might result from physiological differences in larval tolerance of abiotic factors characteristic of large and small holes. However, although oxygen content, pH, and temperature varied significantly among tree holes on Barro Colorado Island, these factors did not differ consistently between large and small tree holes, nor were they predictive of species occupancy. Moreover, switching an odonate from its original hole to one previously occupied by another odonate genus did not affect its survivorship, contrary to what would be expected if tree-hole odonates were differentially adapted to the physical conditions of tree holes (Fincke, in press).

17.5.2 Priority effects and intraguild predation

If intraguild predators are equal in their competitive ability, then the species that is the first to colonize a tree hole should have an advantage over latecomers. This is typically the case for small tree holes, where the first colonist can patrol the entire hole and nutrient input is typically low. Experiments using pairs of predators in small pots provided with alterna-

