

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

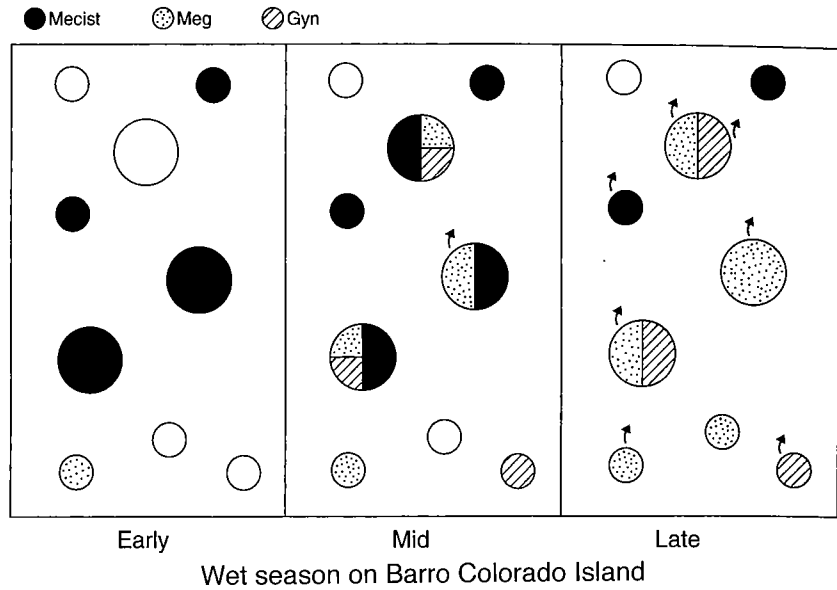


Fig. 17.1 Schema of seasonal changes in odonate occupancy of large and small tree holes on Barro Colorado Island. 'Early dry season' refers to less than 2 months from the first wet-season rains. Arrows indicate emergence of adults, which first occurs from large holes in mid-wet season, and continues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

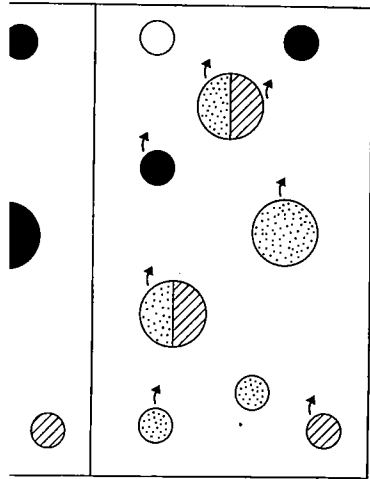
Table 17.1 Mean volume of tree holes by site and year that were occupied by predator genera. On Barro Colorado Island, sampling was at least 2 months after the start of rainy season

| 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 wet season. Meg: *Megaloprepus*; Gyn:

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

| | | <i>La Selva</i> | | |
|-----|---------|-----------------|---------|--|
| | 1992 | 1993 | 1991 | |
| | (92) | (97) | (64) | |
| 4 | 3.6±1.9 | 3.5±1.7 | 20.0* | |
| 3) | 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-

tive prey demonstrated a strong advantage to the larger individual (i.e. the first colonist). When *D. auratus* was paired with an odonate, or any two odonate genera were paired, the largest individual typically killed the smaller individual within 2 weeks. Occasionally however, small odonates co-existed with large tadpoles until the latter metamorphosed. *Toxorhynchites theobaldi* was the least competitive guild member. These mosquito larvae were killed in about half of the trials involving smaller odonates or *Dendrobates* (Fincke, in press).

Competitive asymmetries among odonates were revealed when prey abundance and/or hole size (and detritus) was increased. In small pots with superabundant prey, smaller *Megaloprepus* eventually eliminated larger *Mecistogaster* in about 50% of the trials (Fincke, 1992a). Similarly, in an experiment using large pots, smaller *Megaloprepus* often overtook larger but slower-growing individuals of *M. linearis* and *M. ornata* in size, and eventually killed them (Fincke, 1992a). In large, natural holes, *Mecistogaster* is found occasionally with smaller *Megaloprepus* or aeshnid individuals, but in these cases the *Mecistogaster* typically disappear before they have time to emerge. Based on their maximal growth rates, in large holes both the aeshnids and *Dendrobates* should also be able to overtake a larger *Mecistogaster*, as *Megaloprepus* was shown to do. However, *Dendrobates* tadpoles occupied less than 10% of available tree holes sampled well after the frogs began to breed, whereas by mid-wet season, odonates collectively occupied from 55–75% of the tree holes sampled (Fig. 17.2). Thus odonates pose the greatest threat to developing larvae. Asymmetrical competition among odonate guild members in large tree holes best explains the premature disappearance of *Mecistogaster* from these microhabitats.

17.5.3 Obligate siblicide

On Barro Colorado Island, where *Megaloprepus* is the dominant tree-hole predator (Fig. 17.2), its larvae are more likely to encounter a conspecific than another predator species. In the absence of other predators, possible factors limiting the abundance of *Megaloprepus* include (i) interference competition in the form of cannibalism; (ii) feeding inhibition; and (iii) exploitative competition for food. Field experiments demonstrated that all three phenomena occur, but that cannibalism is the most important proximal mechanism limiting the number of larvae in a tree hole (Fincke, 1994). In small pots supplied with *ad libitum* alternative prey (i.e. newly hatched *P. pustulosus* tadpoles) the larger individual of a pair of *Megaloprepus* typically killed the smaller one. Intermediate-sized *Megaloprepus* have the fastest growth rates, and were the quickest to kill conspecifics. In contrast, larvae less than ca 7 mm in size often did not kill until they grew to ≥ 10 mm. Final instars, which stop feeding about 10–14

repus coeruleus

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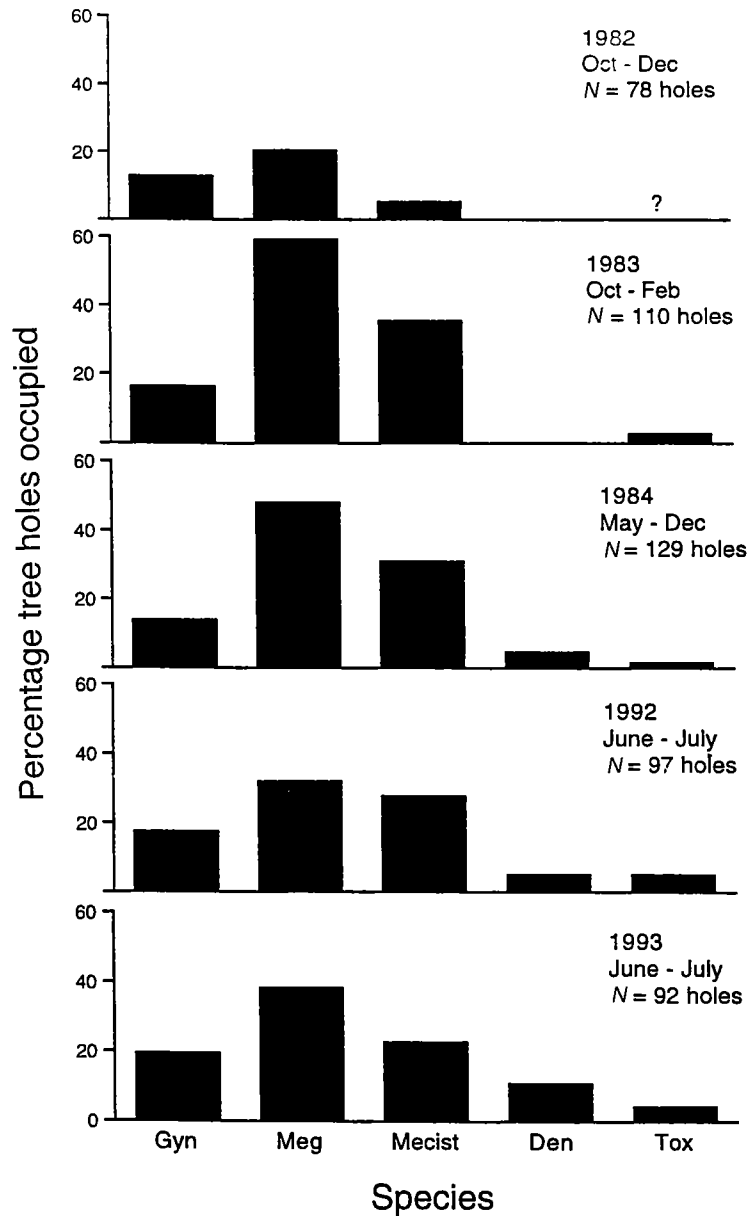


Fig. 17.2 Predator occupancy in Barro Colorado Island tree holes in five wet seasons. The presence or absence of *Toxorhynchites* was not noted consistently in 1982. *Dendrobates* was in only one hole in the 1983 census, and was absent in 1982; both censuses were at the end of the frog's breeding season. Mecist: *Mecistogaster*; Meg: *Megaloprepus*; Gyn: *Gynacantha* and *Triacanthagyna*; Den: *Dendrobates auratus*; Tox: *Toxorhynchites theobaldi*.

days before they emerge, often co-existed with smaller larvae. In 40% of the replicates in which killing occurred, the carcasses were not eaten, suggesting that large larvae kill potential competitors before they become a threat. Indeed, if cannibalism is prevented experimentally, exploitative competition for prey limits larval growth (Fincke, 1994), and under semi-natural conditions a single odonate significantly depresses the abundance of its mosquito prey (Fincke *et al.*, 1997).

Several lines of evidence suggest that cannibalism is the cause of the low larval density in tree holes, which rarely exceeds about one to two individuals per litre (Fig. 17.3). Territoriality by adult males results in an aggregation of *Megaloprepus* eggs in defended holes, with as many as 13 females known to oviposit in the same hole. Oviposition duration is positively correlated with tree-hole volume. A female may lay as many as 250 eggs in a large hole from which no more than 15 adults emerge in a season, and as many as 60 eggs in a small hole that subsequently produces only a single adult per season (Fincke, 1992b). Moreover, in tree holes that contained only *Megaloprepus* predators, small and intermediate larval size classes were often absent, despite recent known ovipositions by females. Finally, at such sites one also finds individuals missing caudal lamellae, legs, or most of their abdomen, damage which is caused by conspecifics in laboratory experiments (e.g. Fincke, 1994, 1995). Density-dependent regulation does not result from larval territoriality. Within holes, larvae exhibit size-dependent dominance. Larger individuals displace smaller ones as they move around in search of prey (Fincke, 1995). Small larvae often 'freeze' in the presence of a larger one, resulting in feeding inhibition.

Even though cannibalism occurs at relatively low densities, it is density dependent. When an excess of *Megaloprepus* larvae were placed in 3-litre artificial holes, individuals killed conspecifics until the density of larvae was reduced to 2–3 larvae (Fincke, 1994). Such densities permit maximum growth of at least the largest larvae in large holes, perhaps even when nutrient input is low. The fastest developmental rates in the field are similar to those with *ad lib* prey (Fincke, 1992a), and mean body size of adult *Megaloprepus* did not differ significantly between years (Table 17.2), despite a massive fruiting failure in 1994 (J. Wright, personal communication).

Because a male *Megaloprepus* defends a given hole for as little as a day or for as long as 3 months, and will mate with several females that then lay in the same hole, full sibs, half sibs and unrelated larvae may all occur together. Although kin recognition should be adaptive in this situation, it has not evolved in *Megaloprepus*. In experimental holes seeded with one larger sib and an equal number of smaller sibs and unrelated individuals, the larger sib displayed to, and killed, conspecifics closest to themselves in size, regardless of kinship (O.M. Fincke, unpublished data). Thus can-

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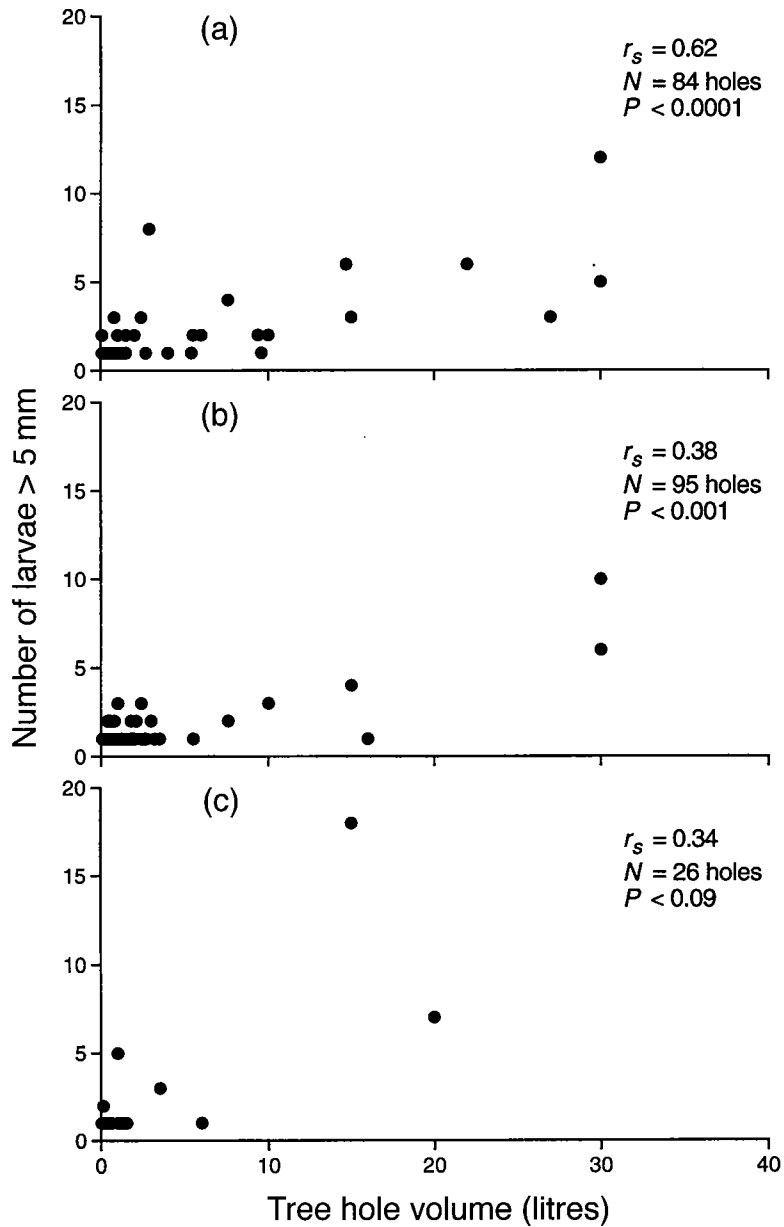


Fig. 17.3 Maximum number of odonate larvae found during a single check of natural tree holes as a function of tree-hole volume. (a) Barro Colorado Island, 1983 data; (b) Barro Colorado Island, 1984 data; (c) La Selva, 1991 data. Many holes were <1 litre, and single points for each hole sampled are not always distinguishable at the scale shown. r_s , Spearman rank coefficient.

Table 17.2 Mean size of adult males and females marked, and the relative abundance of adults on Barro Colorado Island and La Selva. Other than 1994, when sampling was biased towards the end of the year, sampling was throughout the rainy season

| Year | Males | | | Females | | | Encounter rate (Individuals/ observer day) |
|-----------------------|-------|----------|----------|---------|----------|----------|--|
| | N | Wing | Abdomen | N | Wing | Abdomen | |
| Barro Colorado Island | | | | | | | |
| 1983-84 | 115 | 67.4±0.4 | 80.6±0.5 | 78 | 61.2±0.6 | 72.0±0.6 | 2.0 |
| 1994 | 83 | 66.9±0.6 | 79.5±0.6 | 49 | 61.7±0.5 | 72.6±0.6 | |
| 1995 | 140 | 68.4±0.5 | 81.3±0.5 | 77 | 61.8±0.5 | 72.3±0.6 | |
| 1996 | 238 | 66.0±0.4 | 80.5±0.4 | 82 | 61.7±0.5 | 73.2±0.5 | 1.3 |
| La Selva | | | | | | | |
| 1991 | 38 | 75.9±1.0 | 87.9±1.0 | 5 | 67.2±2.0 | 77.5±2.6 | 1.9 |

On Barro Colorado Island, body size did not differ among years ($F_{3,612}=1.29$, $P>0.27$ for male wing length, $F_{3,281}=0.67$, $P>0.55$ for female wing length). Males and females at La Selva were larger than the pooled sample from Barro Colorado Island ($t=-8.4$, $P<0.001$, $t=-2.77$, $P<0.005$ for male and female wing length, respectively).

nibalism in this species is often siblicide, promoted by females which lay an excess of eggs.

Are *Megaloprepus* mothers promoting cannibalism or simply trying to swamp any predator already in the hole? The latter is unlikely, because the timing of hatching rather than clutch size *per se* is the variable critical to survivorship. When single clutches of *Megaloprepus* (each producing about 80 hatchlings) were added to large pots seeded with five aeshnid larvae, *Megaloprepus* rarely survived unless the initial aeshnids were very small, or very large and soon to emerge (O.M. Fincke, unpublished data). Moreover, under field conditions, some holes known to receive multiple clutches of *Megaloprepus* over an 8-month span produced only aeshnid adults (Fincke, 1992b). Finally, in large pots with a staggered input of *Megaloprepus* clutches, offspring survivorship was not correlated with the mother's clutch size (Fincke and Hadrys, unpublished data).

I hypothesized that laying excess eggs is an adaptive response by *Megaloprepus* to sexual selection for large male size or fast developmental time. Even among larvae hatching on the same day, slight differences in prey capture early in life result in a size hierarchy among sibs. Because tiny sibs feed on cladocerans and other prey too small for larger individuals to catch easily, harvesting smaller sibs may be an efficient way for the largest larva to exploit all of the prey available in a hole. I am currently testing this 'multiple mouths' hypothesis by determining whether cannibals emerge faster, or at a larger size, than individuals reared singly.

emales marked, and the relative land and La Selva. Other than 1994, and of the year, sampling was

| Females | | Encounter rate (Individuals/ observer day) |
|----------|----------|--|
| Wing | Abdomen | |
| 61.2±0.6 | 72.0±0.6 | 2.0 |
| 61.7±0.5 | 72.6±0.6 | |
| 61.8±0.5 | 72.3±0.6 | |
| 61.7±0.5 | 73.2±0.5 | |
| 67.2±2.0 | 77.5±2.6 | 1.9 |

ffer among years ($F_{3,612}=1.29, P>0.27$ for wing length). Males and females at La Selva Colorado Island ($t=-8.4, P<0.001, t=-2.77$, ectively).

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i eggs is an adaptive response by arge male size or fast developmen- ng on the same day, slight differ- sult in a size hierarchy among sibs. s and other prey too small for larg- ing smaller sibs may be an efficient ll of the prey available in a hole. I ouths' hypothesis by determining at a larger size, than individuals

17.6 TEMPORAL AND SPATIAL REFUGIA

Although it is possible that over a wet season, all members of the predator guild could emerge from the same large tree hole, more commonly, one or two eliminate the others (Fincke, 1992a). The behaviour and life-history traits of these predators appear to be adapted to their asymmetrical competitive ability and the uncertainty of tree-hole occupancy. Egg-laying odonate females do not discriminate between holes known to contain odonate larvae and those that do not (Fincke, 1992a), as if they cannot detect larvae already present. Because small odonates can be found in holes with large *Dendrobates*, females apparently do not avoid holes occupied by tadpoles. However, *Dendrobates* adults typically repeatedly swim about in tree holes before transporting their tadpoles to them (Summers, 1989). On Barro Colorado Island, the infrequent overlap of *Dendrobates* and larger odonates suggests that an adult frog rejects a hole if it encounters an odonate predator (Fincke, in press; see also Caldwell, 1993). Similarly, of 14 tree holes frequented by adult *Dendrobates pumilio* at La Selva, only three contained *Megaloprepus* larvae, fewer than expected based on the frequency of odonates in holes at this site ($\chi^2=4.6, 1 \text{ d.f.}, P<0.05$).

On Barro Colorado Island, *Mecistogaster*, *Dendrobates* and *Toxorhynchites* begin breeding earlier in the wet season than either *Megaloprepus* or the aeshnids, resulting in an initial temporal refugium from the dominant competitors. All tree holes, even those at territorial sites, must be rediscovered by *Megaloprepus* and the aeshnids the following wet season. Thus, *Mecistogaster* might emerge from large tree holes before any later-colonizing heterospecifics get too big (Fincke, 1992a). This may explain why *Mecistogaster linearis* and *M. ornata* do not totally ignore large oviposition sites. They lay a few eggs in any hole encountered, thereby spreading their risk across a large number of holes.

Megaloprepus has evolved a unique way of coping with the unpredictable presence of predators in large tree holes. *Megaloprepus* eggs take a minimum of 18 days to hatch. The time span between first- and last-hatched *Megaloprepus* eggs, all laid within 2 h of each other and kept submerged in water, is as great as 184 days (O.M. Fincke, unpublished data). Such extreme hatching asynchrony, unique among odonates, increases the chances of at least some of a female's offspring encountering a predator-free window of opportunity. In contrast, egg hatch in a few *Triacanthagyna* clutches occurred over a span of less than 2 weeks. The 5-6-month developmental time of the aeshnids means they must hatch quickly to have time to develop before tree holes dry out. Similarly, once tree holes fill in the wet season, *Mecistogaster* should benefit from fast egg hatching because the earlier in the wet season they enter a hole, the greater their chance of surviving. Because of their slower growth rate,

even if they successfully 'invaded' a large hole in mid-season, it is likely that they would be overtaken by later colonists of *Megaloprepus* or aeshnids. *M. ornata* eggs hatch in as little as 12 days and over a span of 78 days. Unfortunately, *Mecistogaster* rarely oviposits in captivity, and I have been unable to collect eggs from *M. linearis*.

Dendrobates and *Toxorhynchites* also have spatial refugia from tree-hole odonates, whose larvae have not been found in other phytotelmata on Barro Colorado Island. Only on one occasion, in July 1990, did I see a *Mecistogaster ornata* oviposit in a water-filled *Tontelea* husk that harboured a 11-mm *Dendrobates* tadpole. However, I assume this was a case of confusion, because the husk was adjacent to a live *Platypodium elegans* tree that contained several holes near ground level, where the female subsequently laid eggs. Furthermore, *Tontelea* husks decomposed rapidly, leaking water after about 2 months, which is barely enough time for a *Dendrobates* to develop, much less a tree-hole odonate. By early June 1990, 44% of the nine *Tontelea* fruit husks sampled contained *D. auratus* tadpoles, and two (22%) harboured *Toxorhynchites*. The largest tadpole found at that time had a snout-vent length of 10 mm; it metamorphosed a month later, in early July. Although some husks lost all of their water to evaporation between rains (Table 17.3), a drying experiment demonstrated that tadpoles could withstand 7–20 days of completely dry conditions (O.M. Fincke, unpublished data).

Larval *Toxorhynchites* were the only tree-hole predator also found in water-filled fallen palm fronds, occupying 6% of those checked at least twice. Palm fronds often have a large, exposed surface area and thus can collect more detritus than fruit husks and even tree holes of comparable volume. The macrofauna of fronds included scirtid (heliodid) beetle larvae and adults, occasionally syrphid fly larvae, and chironomids, in addition to mosquito larvae, particularly *Trichoprosopon*, which were often very abundant. However, between wet-season rains, fronds dried out more frequently than fruit husks, which might be why none was found harbouring *Dendrobates* or odonates.

17.7 STABILITY OF THE TREE-HOLE GUILD ON BARRO COLORADO ISLAND

Cannibalism and priority effects play important roles in stabilizing and organizing the assemblage of tree-hole predators on Barro Colorado Island. This conclusion is supported by consistently low larval densities within tree holes, and the remarkable year-to-year similarity in species occupancy over an 11-year period (Table 17.1; Fig. 17.2). Population stability attributed to cannibalism has also been documented in a lake dragonfly (Crowley and Johnson, 1992; Hopper *et al.*, 1996). The apparent stability of tree-hole odonate populations contrasts with many herbivo-

loprepus coerulatus

ge hole in mid-season, it is likely colonists of *Megaloprepus* or aeshas 12 days and over a span of 78 y oviposit in captivity, and I have *iris*.

ave spatial refugia from tree-hole found in other phytotelmata on occasion, in July 1990, did I see a filled *Tontelea* husk that harboured I assume this was a case of confu- a live *Platypodium elegans* tree that vel, where the female subsequent- sks decomposed rapidly, leaking rely enough time for a *Dendrobates* ite. By early June 1990, 44% of the ined *D. auratus* tadpoles, and two rgest tadpole found at that time netamorphosed a month later, in all of their water to evaporation periment demonstrated that tad- completely dry conditions (O.M.

tree-hole predator also found in ing 6% of those checked at least xposed surface area and thus can nd even tree holes of comparable luded scirtid (helioidid) beetle lar- larvae, and chironomids, in addi- *Trichoprosopon*, which were often et-season rains, fronds dried out h might be why none was found

BUILD ON BARRO COLORADO

mportant roles in stabilizing and le predators on Barro Colorado / consistently low larval densities year-to-year similarity in species ≥ 17.1 ; Fig. 17.2). Population stabil- en documented in a lake dragon- pper *et al.*, 1996). The apparent ns contrasts with many herbivo-

Table 17.3 Comparison of abiotic characteristics of phytotelmata

| Habitat | N | Volume (litre) | Persistence | O ₂ (p.p.m.) | pH | Temperature (°C) |
|-----------------------|-----|--------------------------------------|-------------------------|------------------------------------|-----------------------------------|--------------------------------------|
| Bromeliads | 20 | 0.19±0.1 (0.05-0.6) | 0.9 (0.66-1) | - | - | - |
| Palm fronds | 13 | 0.26±0.5 ^a (1.8-0) | 0.4±0.2 (0-0.8) | 4.9±1.3 (2.7-6.5) | 5.6±0.7 (4.4-6) | 27.8±0.1 (27.3-28.3) |
| Barro Colorado Island | 17 | 0.31±0.1 ^a (0.0-5-0.9) | 0.2±0.2 (0-1.0) | - | - | - |
| Fruit husks | | | | | | |
| <i>Lecythis</i> | 14 | 0.60±0.1 ^b (0.1-0.9) | 0.69±0.2 (0-0.9) | 0.51±0.2 (0.1-2.5) | 6.3±0.3 ^a (4.7-7.2) | 26.0±0.0 (24-29) |
| Fresh | 17 | 0.50±0.0 ^b (0.1-1.2) | 0.22±0.1 (0-0.4) | 1.41±0.2 ^c (0.1-3.1) | 5.0±0.4 ^a (1.4-7.2) | 25.7±0.1 (24-29) |
| Old | 9 | 0.08±0.0 (0.04-0.17) | 0.11±0.01 | - | - | - |
| <i>Tontelea</i> | | | | | | |
| Tree holes | | | | | | |
| La Selva | 64 | 1.5±0.4 ^e (0.01-20) | 0.76±0.03 (0.11-1.0) | 1.1±0.1 ^c (0.3-2.0) | 4.6±0.07 (3.4-6.0) | 25.1±0.2 ^f (24.3-29.7) |
| Barro Colorado Island | 331 | 1.9±0.3 ^e (0.01-40) | - | 3.4±0.4 (0.6-11) | 7.7±0.0 (5.1-9.0) | 25.0±0.1 ^f (20.1-29.6) |

For bromeliads, N is the number of leaf axils sampled in five individuals (ranges). Persistence is the minimum volume during wet season/maximum volume. Letters a-f indicate means are not significantly different (Bonferroni tests, P>0.05). Phytotelmata differed in volume (F_{3,124} = 2.9, P<0.04), O₂ (F_{2,70} = 112.5, P<0.0001), pH (F_{2,83} = 11.8, P<0.001) and temperature (F_{1,46} = 61.2, P<0.001).

rous insects on Barro Colorado Island whose populations fluctuated over a 14-year period in a seemingly unregulated way (Wolda, 1992; but see Ray and Hastings, 1996).

On Barro Colorado Island, co-existence of tree-hole odonates appears to be mediated by trade-offs between larval competitive ability and colonization efficiency among adult guild members, coupled with a predictable disturbance in the form of a dry season, which clears the holes of predators. Tree-hole drying provides the opportunity for *Mecistogaster* to realize its colonization advantage over *Megaloprepus* and the aeshnids, whose larvae would otherwise be predicted to exclude the two smaller species. Seasonal drying results in the wholesale, but temporary loss of larval habitats, a disturbance that is less than total destruction of the forest, but more serious than intermittent drying. Thus my data support Hutchinson's (1959) multiple-niche hypothesis and Connell's (1978) intermediate-disturbance hypothesis for species co-existence. Another relevant hypothesis is that of Shorrocks (1990), who explained co-existence of competitors that use the same temporally and spatially patchy resources. If the eggs of superior competitors are aggregated, they cannot swamp all sites, providing refugia for the less-competitive species, as occurs in the *Drosophila* community on Barro Colorado Island (Sevenster and Van Alphen, 1996). Tree holes are a temporally and spatially patchy resource used by all odonates, and both the aeshnids and *Megaloprepus* aggregate eggs in large, defended holes in light gaps, which are easier to find than holes in understorey (Fincke, 1992b). However, because *Megaloprepus* and, to a lesser extent, the aeshnids also colonize small holes, it seems only a matter of time before they would exclude the two smaller species. Marked *Megaloprepus* adults have been re-sighted after 8 months, can travel a kilometre in less than a week, and disperse over the entire island. Large pots that were kept watered during the dry season (see Fincke, 1992b) contained only *Megaloprepus* or aeshnid larvae the following wet season, suggesting that continuous occupancy by dominants precludes establishment of *Mecistogaster*. I predict that seasonal drying, rather than egg aggregation, maintains odonate diversity in tree holes on Barro Colorado Island.

17.8 COMPARATIVE STUDY AT LA SELVA: A TEST OF THE ROLE OF COMPETITION

To test the role of tree-hole drying on species co-existence, and to determine if *Megaloprepus* retains its dominant position in a different forest type, I examined the distribution of tree-hole predators at La Selva Biological Station in Costa Rica. This lowland forest receives an average of 3900 mm of rain annually (1.5 times the rainfall on Barro Colorado Island). The driest months are February and March, which commonly have a 12-

