

Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority

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Abstract. 1. Water-filled tree holes in a lowland forest in Panama harbour an assemblage of large predators consisting of the larvae of five common species of Odonata, the mosquito *Toxorhynchites theobaldi*, and tadpoles of *Dendrobates auratus*. Odonate females oviposit in both large and small tree holes. However, the three largest species emerge from larger tree holes, on average, than do the two smallest species. Can assembly rules explain this and other patterns of predator distribution?

2. Past experiments suggested that fast growth of the largest, but later-colonizing odonates enabled them to out-compete the smaller, slower-growing *Mecistogaster* in large holes. In small holes, however, the first predator, regardless of species, should presumably kill any later arrivals. Priority effects in small holes were tested for their consistency across predator species. Two alternative explanations for differential odonate survivorship were also tested: abiotic conditions and the effect of non-odonate predators.

3. Diurnal fluctuations in oxygen content, pH, and temperature within holes were as great as the variation found between large and small tree holes; abiotic conditions were poor predictors of species occupancy.

4. Exchanging the largest and smallest odonate species from their original holes did not affect survivorship, suggesting that the observed patterns of emergence are unlikely to result from differential tolerance to abiotic factors that were not measured.

5. When larger and smaller predators were paired in 400-ml pots and provided with alternative prey, typically only the larger predator survived, regardless of species. The exception was *T. theobaldi*, which was often killed by odonates and tadpoles smaller than itself.

6. Between May and July, the occurrence of *Mecistogaster* in large tree holes declined, before larvae could have emerged. Neither abiotic effects nor differential predation by non-odonates could explain this habitat-specific decrease in survivorship. This temporal pattern is most consistent with the previous conclusion that in large holes, *Mecistogaster* suffer intraguild predation from later-colonizing, but faster-growing *Megaloprepus* and aeshnids. Whereas *Mecistogaster* can pre-empt guild members from small tree holes, they cannot do so in large holes where predators with fast initial growth realize a competitive advantage.

Key words. Assembly rules, *Dendrobates*, *Gynacantha*, interspecific competition, *Mecistogaster*, *Megaloprepus*, *Toxorhynchites*, *Triacanthagyna*.

Introduction

A major goal of ecology is to identify factors that predict species distribution and abundance, at both a geographical and a local scale. Within a given habitat, physical and chemical

characteristics often affect local insect distributions (e.g. Vepsäläinen, 1978; Streams, 1987; Witteveen & Joosse, 1987). Additionally, the organization of species assemblages may be affected by biotic factors such as predation, parasitism, interspecific competition, or by the interaction of abiotic and biotic factors (e.g. Resh & Barnby, 1987; Kingsolver, 1989; Dunson & Travis, 1991). Biotic factors, and interspecific competition in particular, may be especially important in tropical habitats that harbour high species diversity. However,

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the population and community dynamics of tropical insect populations are poorly understood. Evidence for on-going interspecific competition in shaping insect assemblages remains controversial (but see Denno *et al.*, 1995; Stewart, 1996). Parasitism apparently keeps the populations of herbaceous hispine beetles and other herbivores below the level at which interspecific competition occurs (Strong, 1977; Lawton & Strong, 1981). Similarly, predation apparently maintains some prey populations below their carrying capacity (e.g. Bradshaw & Holzapfel, 1983; Franks & Bossert, 1983; Fincke *et al.*, 1997). Finally, aggregation of the competitive dominants in dipteran assemblages permits coexistence of less competitive fugitive species (Shorrocks & Bingley, 1994; Sevenster & van Alphen, 1996).

Identifying the rules by which species may be assembled requires, among other things, an understanding of the mechanisms mediating species interactions, and how competitors are affected by the abiotic environment and by the order of microhabitat colonization (i.e. priority). Given the complexity of most habitats, and the difficulty of defining a *community* (Drake, 1990), it is not surprising that relatively simple aquatic habitats have been studied most intensely (e.g. Morin, 1984; Wilbur & Fauth, 1990; Wissinger & McGrady, 1993; Blaustein & Margalit, 1996). In the tropics, tree holes offer an excellent opportunity to investigate experimentally the determinants of community structure, because artificial holes are colonized readily by the same species assemblage that is found in natural holes (Fincke *et al.*, 1997). Moreover, the mechanism of competition within the predator guild can be observed directly; one competitor eliminates the other by killing it (Fincke, 1994). Finally, because tree holes are a limiting resource for some frogs as well as odonates, this system offers an opportunity to assess the impact of insects on vertebrates that occupy the same trophic niche (e.g. Lawler & Morin, 1993).

Past work on a guild of odonates that develop in water-filled tree holes in Panama suggested that competition, in the form of intraguild predation, plays an important role in organizing this community (Fincke, 1992a, 1994). Two aeshnid dragonflies (final instars = 35 and 45 mm, respectively) and the damselfly *Megaloprepus coerulatus* (final instar = 24–34 mm) are competitive dominants. They emerge from larger tree holes, on average, than either *Mecistogaster linearis* or *M. ornata* (final instars of both species = 19–22 mm), which most often emerge from *small* holes (i.e. < 1 litre of standing water). These two smaller species are the first to colonize holes early in the wet season, when they occupy both large and small tree holes. With the exception of the aeshnids, whose horizontally held wings prevent access to holes with slit openings, ovipositing females do not discriminate among holes on the basis of hole morphology, volume, or location in understorey versus light gaps (Fincke, 1992a). Vertical niche partitioning is limited; *Megaloprepus* is the only odonate not found in canopy tree holes (S. P. Yanoviak, unpublished data).

The largest species appear to exclude the smaller *Mecistogaster* from large holes, even when *Mecistogaster* are the first to colonize such holes. In large holes, *M. coerulatus*, and presumably aeshnids or any predator with fast initial

growth, finds sufficient food and hiding places to catch up with the slower-growing *Mecistogaster* in size, and eat them (Fincke, 1992a). In small pots, *Mecistogaster* was often able to maintain its initial size advantage, killing smaller *Megaloprepus*. If such priority effects occur across all of the predator species, then *M. coerulatus* and the aeshnids should be more successful in surviving in large holes than the two smaller *Mecistogaster*, or other relatively slow-growing species.

However, variation in pH has been shown to reverse competitive interactions (Dunson & Travis, 1991). Additionally, abiotic factors such as oxygen content may affect predator survivorship differentially. If small and large holes differed consistently with respect to abiotic factors, then non-random survivorship of odonates could result if the smaller *Mecistogaster* tolerated the abiotic conditions of small tree holes better than large tree holes. The size and shape of the hole opening affects the ease of accumulation of falling detritus such as leaves, fruits, and animal droppings, which in turn could affect water chemistry. The type of prey available may also vary with respect to tree hole size. Furthermore, predacious tadpoles of *Dendrobates auratus* and larvae of the mosquito *Toxorhynchites theobaldi* (maximum body length = 15 and 13 mm, respectively) might be distributed differentially between large and small holes, and affect some odonates more than others. Finally, priority effects, which depend on the order of colonization, may differ among competitors (e.g. Lawler & Morin, 1993).

The purpose of this study was to assess the role of abiotic factors and priority in determining species distribution among tree holes. Specifically: (1) Does variation in tree hole chemistry (i.e. O₂ content, pH, temperature) predict species occupancy? (2) Does prior colonization by one predator affect the survivorship of later-arriving predators, and, if so, are the effects equal among predators? The results support the conclusion that interspecific competition is a major determinant of predator assemblages in these microhabitats.

Materials and methods

Effect of abiotic factors on tree hole occupancy and larval survivorship

The work was conducted on Barro Colorado Island in the SORBERANIA National Park in the Republic of Panama. Here, the lowland forest experiences a wet season from May to December and a dry season from January to April (see Leigh *et al.*, 1996, for a site description). During the wet season, between June and August 1992 and 1993, natural tree holes were sampled repeatedly to determine the frequency distribution of macrofauna. At least eleven species of non-predatory mosquitoes were present (Fincke *et al.*, 1997), but were not identified to species in this study. Other tree hole occupants (e.g. the larvae of scirtid beetles and dipteran larvae in the families Chironomidae, Ceratopogonidae, and Tipulidae) are not included here because their presence was not noted consistently and, with the exception of the chironomids and scirtids, are not known to be eaten by the top predators.

Individuals of *Mecistogaster linearis* and *M. ornata* were pooled into a single treatment because their larvae are difficult to distinguish before the penultimate instar; their growth rates and final instar sizes are similar (Fincke, 1992a). Prior to 1995, any aeshnid encountered in a tree hole was assumed to be *Gynacantha membranalis*. Since then, most of the aeshnid larvae found in tree holes on Barro Colorado Island have been identified as *Triacanthagyna dentata*. Although similar in appearance, *T. dentata* has epiprocts and cerci of equal length, whereas *G. membranalis* has cerci that are about three-quarters the length of the epiprocts. Herein, these two aeshnids are pooled, and *aeshnid* refers to samples in which *G. membranalis* and *T. dentata* were not differentiated. For simplicity, species are referred to hereafter by generic names.

A tree hole was scored as being in a light *gap* if the canopy within 2 m of the hole was at least 10% open, as measured by a densiometer. The hole was classified as a *bowl* if it was deeper than it was wide, a *pan* if it was longer than it was deep, and a *slit* if its opening was ≤ 5 cm wide. Standing water was suctioned off with a turkey baster, and collected litter and water placed in a white plastic pan for inspection. The inside of the hole was searched with a torch. By checking hole contents several times over a few weeks, the presence of tadpoles and most other macroinvertebrates over about 6 mm in body length was determined. Insect larvae were measured with callipers, from the head to the end of the last abdominal segment. Tadpoles were measured from the head to the base of the tail. Water, detritus, and organisms were then returned to the hole. The maximum volume of standing water recorded for a given hole was used in analyses. *Species overlap* was calculated from sixty-three holes sampled in consecutive years, as the proportion of holes occupied by a given species in 1992 that were also occupied during the same time period in 1993. To determine whether *Mecistogaster* abundance in large holes declined seasonally, as would be predicted for a poor competitor, the distribution of odonates in the current study, 3 months after tree hole filling (i.e. late July 1992 and 1993) was compared with results of an earlier census, carried out within 1 month of tree hole filling (i.e. late May 1990, see Fincke, 1992a).

In 1992, abiotic features of sixty-two tree holes included in the above samples were measured three times during the day (08.30–11.00, 13.00–14.00 and 15.00–17.30 hours). The temperature and pH of tree hole water were measured using a portable electronic unit. Dissolved oxygen was measured using a portable OXAN O₂ analyser (Engineered Systems & Designs, Newark, U.S.A.). Because the oxygen probe was too large to fit into holes with openings < 4 cm in diameter, data on O₂ content were collected on only forty-five holes. Means were calculated for each time period, based on one to three censuses, roughly 2 weeks apart. Diurnal variation in pH, O₂, and temperature was analysed with repeated measures ANOVA. Discriminate function analysis of tree hole means was used to determine how well abiotic factors predicted species occupancy. Means are reported \pm SE throughout.

It is possible that some abiotic features other than those measured affected the survivorship of the odonate guild members significantly. This possibility was tested by an odonate switching experiment. *Megalopterus coeruleus* presumably

tolerates conditions of both small and large tree holes because it emerges from a wide range of holes (Fincke, 1992b). The experiment was thus limited to the two *Mecistogaster* species and the aeshnids. Thirty-three tree holes ranging from 0.04 to 3.2 litres in volume that were occupied by at least one odonate, were located. None of these holes contained *Toxorhynchites* or *Dendrobates*. The initial occupant(s) was replaced with a single, moderately large (10–20 mm) odonate. In the experimental treatments, the replacement genus differed from that of the original occupant, whereas in controls, replacements were the same genus as the original occupant. Although all of the original odonates found were removed, larvae less than about 6 mm in body length were easy to overlook. Nevertheless, any remaining small larvae should not have posed a threat to the much larger introduced individuals because predation is size-dependent (see results of the priority experiment below). Once a week for roughly 4 weeks, the holes were checked for the presence of the introduced odonate, which was measured every 2 weeks. If the odonate was not found, the hole was checked until the end of the experiment.

Effects of prior occupancy on predator survivorship

To determine how priority (i.e. arriving first) by one predator affected the survivorship of a subsequent predator, an individual of one species (analogous to a prior occupant) was paired with a smaller individual of another species (analogous to a later colonist) in a 0.45-litre plastic pot. Control pots contained a single individual. All pots contained five leaves for cover, a stick perch, and either five medium-sized non-predatory mosquito larvae, or five newly-hatched *Physalaemus pustulosus* tadpoles as alternative prey. Pots were checked daily for the presence of the predators. Individuals used in the experiment were field-collected, except for newly-hatched (hereafter, *neonates*) *Triacanthagyna* that were hatched from eggs. Before being used in a replicate, a predator was held for 1–7 days, during which time it was fed either mosquitoes or newly-hatched *Physalaemus pustulosus* tadpoles. An individual was used in only one test, with the exception of *Dendrobates auratus* and *Mecistogaster*. Because these predators were difficult to find, a few individuals were used twice, always in different treatments, at least 1 week apart.

It soon became clear that the smaller predator had little chance of surviving when size differences were very large. Thus, in order to detect any subtle asynchrony in the priority effect, the pairings were biased to mimic a relatively short time lag between colonists. Mean sizes of individuals used in the pairings were, from largest to smallest predators: aeshnids, 14.8 ± 0.8 mm ($n = 78$, range 2–35 mm), *Megalopterus*, 11.7 ± 0.6 mm ($n = 88$, range 3.1–30 mm), *Mecistogaster*, 10.7 ± 0.5 mm ($n = 67$, range 3.4–21.8 mm), *Dendrobates*, 11.2 ± 0.3 mm ($n = 96$, range 5.7–17 mm), and *Toxorhynchites*, 9.5 ± 0.2 mm ($n = 81$, range 5–13.4 mm). Because of time constraints and the difficulty of collecting sufficient individuals in any given year, the experiment was conducted in multiple years, between May and November 1990, 1992, 1993, 1996 and 1997. Prior to 1996, pots were kept in an outdoor insectary

Table 1. Number of tree holes containing macrofauna at some time during the 2-month sampling period ($n = 97$ and 92 in 1992 and 1993, respectively). Based on the sixty-three holes sampled in both years, overlap is the percentage of the holes occupied in 1992 that were also occupied in 1993. Data for *T. theobaldi* refer only to ≥ 3 rd instar individuals.

	1992	1993	% overlap	Mean volume (litres)	Range (l)
Anura:					
<i>Agalychnis callidryas</i>	2	1	100	28.87 ± 5.6	21.60–40.0
<i>Dendrobates auratus</i>	5	10	25	2.31 ± 1.6	0.02–25.0
<i>Physalaemus pustulosus</i>	9	15	60	3.23 ± 1.6	0.04–40.0
Culicidae:					
Prey species (pooled)	92	87	98	1.40 ± 0.3	0.01–40.0
<i>Toxorhynchites theobaldi</i>	5	4	20	0.61 ± 0.1	0.08–1.1
Odonata:					
<i>Gynacantha membranalis</i>	17	18	38	3.56 ± 1.3	0.01–32.0
<i>Triacanthagyna dentata</i> (pooled)					
<i>Mecistogaster</i> (<i>linearis</i> , <i>ornata</i> pooled)	27	21	38	0.66 ± 0.1	0.01–5.0
<i>Megaloprepus coeruleus</i>	31	35	54	2.30 ± 0.8	0.05–40.0
Syrphidae					
	10	2	0	0.49 ± 0.1	0.01–1.2
Veliidae:					
<i>Paravelia myersi</i>	5	3	0	2.60 ± 0.5	0.50–5.0

and additional alternative prey were added weekly. In 1996 and 1997, pots were placed outside, on a shaded platform in the laboratory clearing, and in addition to the initial five mosquitoes, 0.05 g of yeast was added to facilitate natural colonization by mosquitoes.

Results

Species distribution and abiotic effects on occupancy

Table 1 lists the frequency of occurrence of the common large tree hole predators and their most obvious potential prey. Odonates have been observed to eat all of the prey listed with the exception of the veliid bugs, which skate on the water surface, preying on insects trapped at the air–water interface. Odonates may occasionally take veliids or other insects on the water surface (O. M. Fincke, pers. obs.). Collectively, mosquito larvae, found in over 90% of the tree holes sampled, were the most ubiquitous prey available. Although clutches of *Physalaemus pustulosus* typically contain over 200 eggs and are a rich source of prey, these tadpoles occurred in less than 16% of the tree holes sampled. Syrphid fly larvae were among the largest prey, but were also rare.

Toxorhynchites and *Dendrobates* were relatively rare predators; each was found in less than 10% of the holes sampled. Odonates were the most common predators, collectively occupying about 75% of the holes by the end of July, 3 months from the first hole-filling rains of the wet season. By then, *Mecistogaster* was found in about a quarter of the holes, whereas this genus occupied 48% of holes sampled

within a month of the first rains in 1990 (Fincke, 1992a). Early in the wet season of 1990, it was found in larger holes (mean = 2.1 ± 0.4 l, $t = 3.3$, $P < 0.01$) than it occupied by July in the current study (Table 1). These results suggest that *Mecistogaster* disappeared prematurely from large holes as the rainy season progressed. Its disappearance cannot be confounded with emergence, because a minimum of 4 months is required for eggs to develop into adults (Fincke, 1992a).

Individual tree holes differed significantly with respect to temperature ($F_{82,206} = 5.4$, $P < 0.001$), pH ($F_{82,206} = 35.1$, $P < 0.001$), and O_2 content ($F_{59,137} = 28.2$, $P < 0.001$). Tree hole water temperature and pH, but not O_2 content, varied significantly over the course of a day (Fig. 1). However, large (≥ 1 litre) and small (< 1 litre) tree holes did not differ in temperature, pH, or O_2 content, and none of these variables was significantly correlated with tree hole volume ($r = -0.04$, -0.08 , and -0.18 , for temperature, pH, and O_2 content, respectively). Oxygen content was positively correlated with water temperature ($r = 0.35$, $P < 0.05$). Small and large holes in gaps were warmer ($F_{1,64} = 9.0$, $P < 0.01$) and had higher oxygen content ($F_{1,41} = 5.7$, $P < 0.05$) than those in forest understorey, but they did not differ in pH ($F_{1,41} = 1.2$, $P = \text{NS}$).

Abiotic factors were poor indicators of species occupancy (Table 2). Holes occupied by different predators did not differ in temperature ($F_{4,64} = 1.1$), oxygen content ($F_{4,44} = 0.4$), pH ($F_{4,64} = 1.1$), or volume ($F_{4,64} = 2.0$; $P > 0.05$ for all four analyses). Discriminate function analysis using these four variables misclassified 54–75% (mean = 65.9%) of the five predator genera. *Mecistogaster* and *Toxorhynchites*, the two smallest predators, collectively occupied smaller holes on average than the group of the largest predators (aeshnids,

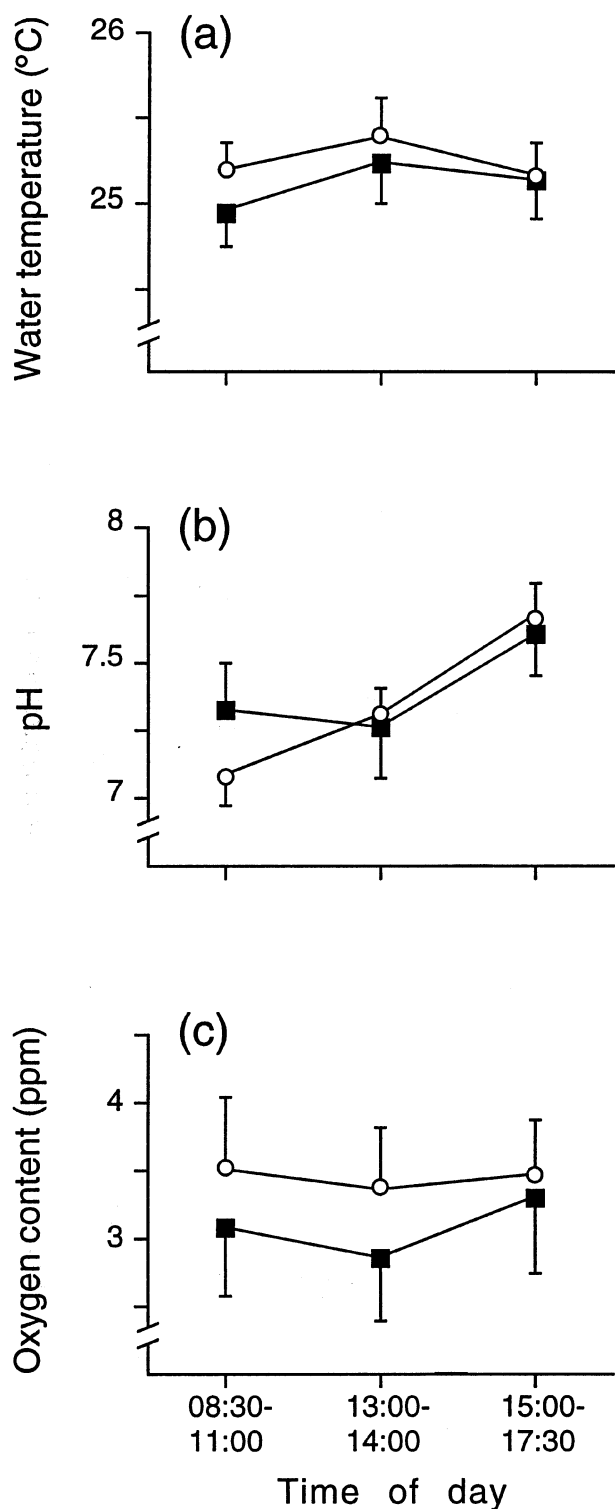


Fig. 1. Daily variation in (a) water temperature, (b) pH, and (c) O_2 content of natural tree holes. Large (≥ 1 litre) holes (■) did not differ from smaller holes (○) with respect to temperature ($F_{1,82} = 0.13$), pH ($F_{1,82} = 0.23$), or oxygen ($F_{1,59} = 0.01$) (all $P > 0.05$).

Megaloprepus, *Dendrobates*, $F_{1,172} = 5.3$, $P < 0.05$). *Physalaemus* tadpoles typically occupied pan holes in fallen trees (all were ≤ 1.5 m in height), usually in light gaps. Thus, their holes were warmer than those occupied by *Dendrobates* ($F_{1,11} = 15.5$, $P < 0.001$), which were found only in shaded, understorey holes. *Physalaemus* also occupied holes whose oxygen content was significantly higher (mean = 6.0 ± 0.0 p.p.m.) than holes without these tadpoles (mean = 3.3 ± 0.4 , $t = -2.0$, $P < 0.05$). The few data on *Agalychnis callidryas*, the largest tadpole in Barro Colorado Island tree holes, suggest that this tree frog develops in very large holes, where predation by odonates should be minimized. Sample sizes for the other species were small and none of the abiotic factors measured was predictive of their occupancy. Syrphids, however, were typically found in holes with abundant, and often fruity, detritus.

The overlap in odonate occupancy between years was not greater than expected if colonization of tree holes was random ($\chi^2 = 2.4$, 3.1, and 0.7 for aeshnids, *Megaloprepus*, and *Mecistogaster*, respectively, d.f. = 1, $P > 0.05$). The frequency of other macrofauna was too low to test for random colonization. Pooling the data on anurans indicated that they occupied collectively the same holes from one year to the next at greater frequency than expected ($\chi^2 = 7.8$, d.f. = 3, $P = 0.05$).

Results of the odonate switching experiment supported further the conclusion that abiotic factors did not affect odonate survivorship significantly. Two *Mecistogaster* larvae that disappeared from two holes that also contained large aeshnids (22 and 23 mm, respectively) that were not detected during the initial clearing, were excluded from the analysis. In all other replicates, no odonates other than the introduced ones were found. Two *Mecistogaster* controls (8 and 11 mm, respectively) were missing after 2 weeks, and were not found on two subsequent checks. These larvae tended to be smaller than the *Mecistogaster* that survived, but not significantly so ($t = -2.0$, $P = 0.06$). All other larvae survived for the entire 4-week period. As shown in Table 3, there was no difference between the growth rates of the experimental and control *Mecistogaster* ($t = -0.6$, $P > 0.5$), even though the experimental larvae were in larger tree holes than the controls ($t = -3.6$, $P < 0.01$). In contrast, the experimental aeshnids grew more slowly than control individuals ($t = 2.4$, $P < 0.05$), probably because they tended to be in smaller holes than the controls. The sample was small and the difference was not significant ($t = 2.1$, $P = 0.06$).

None of the holes sampled simultaneously contained both *Toxorhynchites* and *Dendrobates*. Of the fifteen holes occupied by *Dendrobates*, six also contained one or more odonates (mean volume = 4.6 ± 4.0 l), fewer than expected based on the proportion of tree holes that contained odonates ($\chi^2 = 7.2$, d.f. = 1, $P < 0.05$). In five of the six holes, tadpoles were medium-sized, whereas the odonates were less than 5 mm, indicating that the odonates hatched after tadpoles were deposited. As many as five tadpoles were found in a 1.3-litre hole. In five of the thirteen holes in which *Toxorhynchites* was found, this predator co-occurred with odonates (mean volume of co-occupied hole = 0.89 ± 0.26 litres). Two of the mosquito larvae were smaller, and three were larger than the odonate

Table 2. Mean temperature, pH, O₂, and volume of tree holes with macrofauna by mid wet season. Ranges are in parentheses. The smaller *n* refers to sample size for oxygen content. Here, volume refers only to the subset of total holes for which water chemistry was measured. Aeshnids refer to pooled samples of *G. membranalis* and *T. dentata*.

Occupant	<i>n</i>	Temperature (°C)	pH	O ₂ (p.p.m.)	Volume (litres)
Anura:					
<i>Dendrobates auratus</i>	3,5	24.9 ± 0.3 (23.9–25.4)	7.9 ± 0.2 (7.5–8.6)	2.5 ± 1.1 (0.8–4.7)	5.46 ± 4.9 (0.1–25.0)
<i>Physalaemus pustulosus</i>	4,7	26.3 ± 0.2 (25.4–26.8)	7.8 ± 0.1 (7.3–8.1)	6.0 ± 0.9 (4.8–8.8)	0.89 ± 0.3 (0.2–2.4)
Culicidae:					
<i>Toxorhynchites theobaldi</i>	4,6	25.4 ± 0.3 (24–26.5)	7.7 ± 0.2 (7.3–8.3)	2.8 ± 1.2 (0.8–4.9)	0.88 ± 0.3 (0.16–2.4)
Odonata:					
Aeshnids	11,14	25.4 ± 0.3 (23–26.8)	7.7 ± 0.2 (6.6–9.0)	3.8 ± 0.8 (0.8–8.8)	2.9 ± 1.9 (0.18–25.0)
<i>Mecistogaster lineariz & ornata</i>	13,20	24.7 ± 0.4 (20.8–28.3)	7.9 ± 0.2 (5.8–9.0)	2.8 ± 0.7 (1–11.0)	1.9 ± 1.1 (0.06–5.0)
<i>Megaloprepus coerulatus</i>	18,25	24.9 ± 0.1 (23–26.8)	7.4 ± 0.2 (5.1–9.0)	3.9 ± 0.7 (0.6–11.0)	1.1 ± 0.3 (0.12–5.0)
Syrphidae	6,8	24.5 ± 0.6 (20.8–26.8)	7.7 ± 0.3 (5.9–8.7)	4.0 ± 1.7 (0.9–11.0)	0.44 ± 0.1 (0.08–0.9)
Veliidae:					
<i>Paravelia myersi</i>	3	24.9 ± 0.3 (24.4–25.5)	7.4 ± 0.6 (6.3–8.0)	4.3 ± 1.7 (1.1–6.6)	3.03 ± 1.3 (0.6–5.0)

Table 3. Survivorship and growth over a 4-week period of individuals introduced into natural tree holes that were cleared of previous odonate occupants. Experimental larvae were placed in holes originally occupied by a different odonate genus, whereas control larvae were individuals that replaced the original congeneric occupants. Aeshnids refer to pooled samples of *G. membranalis* and *T. dentata*. * $P < 0.05$ (*t*-tests).

Treatment	<i>n</i>	Number surviving	Mean hole volume (litres)	Mean initial size (mm)	Mean growth (mm/day)
<i>Mecistogaster</i>:					
Control larvae	5	3	0.4 ± 0.1 *	11.8 ± 1.8	0.15 ± 0.1
Experimental larvae	12	12	1.5 ± 0.3	15.5 ± 1.0	0.17 ± 0.0
Aeshnids:					
Control larvae	5	5	0.5 ± 0.1	11.8 ± 1.7	0.36 ± 0.1*
Experimental larvae	10	10	0.3 ± 0.1	17.1 ± 2.1	0.15 ± 0.0

larvae with which they occurred, suggesting that females of neither species discriminated against holes already occupied by a predator.

Two or more odonate genera were found in sixteen holes (mean volume = 3.4 ± 1.9 litres). Only 6% of the 130 small holes contained two or more predator genera, whereas 23% of the 59 holes ≥ 1 litre contained multiple predator genera, a significant difference ($\chi^2 = 9.4$, d.f. = 1, $P < 0.01$). Excluding prey mosquitoes that were not identified to species, the number of macrofauna species (see Table 1) that occupied a hole at some time during the 2-month sampling period was correlated

with tree hole volume ($r = 0.21$, $n = 189$ holes, $P < 0.01$), although the number of predator genera was not ($r = 0.08$, $n = 189$, $P = \text{NS}$).

Priority effects on predator survivorship

In the priority experiment, none of the six *Toxorhynchites* and nine *Dendrobates* controls died over the time they were observed (mean = 17.8 ± 2.6 and 21 ± 2.2 days, respectively). Of the *Toxorhynchites* (initial size 7–9 mm), 83% emerged

Table 4. Differences in initial size and time to outcome, as a function of outcome in the priority experiment. Size differences are expressed as the size of the first predator listed minus the size of the second predator listed. Letters indicate means that are not significantly different ($P > 0.05$, Bonferroni tests). ** $P < 0.01$, *** $P < 0.001$.

Treatment	<i>n</i>	Mean initial size difference (mm)	Mean days to outcome
<i>Dendrobates</i> vs. odonates:			
<i>Dendrobates</i> wins	30	2.1 ± 0.8 ^a	7.3 ± 1.0 ^d
Odonate wins	26	-7.5 ± 1.2	2.8 ± 0.6 ^d
Coexist	17	1.9 ± 0.9 ^a	14.1 ± 2.3
		$F_{2,72} = 22.3^{***}$	$F_{2,72} = 13.7^{***}$
<i>Toxorhynchites</i> vs. odonates:			
<i>Toxorhynchites</i> wins	14	4.4 ± 0.7 ^b	2.3 ± 0.3 ^e
Odonate wins	37	-0.5 ± 0.7	4.3 ± 0.0 ^e
Coexist	7	5.9 ± 1.8 ^b	8.4 ± 0.7
		$F_{2,55} = 12.3^{***}$	$F_{2,55} = 7.1^{**}$
<i>Dendrobates</i> vs. <i>Toxorhynchites</i> :			
<i>Dendrobates</i> wins	15	1.4 ± 0.7	3.8 ± 1.2
<i>Toxorhynchites</i> wins	4	-4.3 ± 0.4 ^c	3.0 ± 1.0
Coexist	4	-3.4 ± 1.5 ^c	8.3 ± 0.6
		$F_{2,20} = 6.7^{**}$	$F_{2,20} = 1.9$ NS

after 20.4 ± 0.6 days. Of the *Dendrobates* controls (initial size 10–15 mm), 55% metamorphosed after 25.4 ± 1.7 days. Of the eighteen odonate controls, fifteen remained alive over the time they were monitored (mean = 11.1 days). Three of the nine controls that were < 5 mm disappeared after 1, 3, and 7 days, respectively. Of the twenty-two experimental odonate larvae that were < 5 mm, thirteen (59%, nine paired with *Dendrobates* and four paired with *Toxorhynchites*) disappeared before they grew to > 5 mm in size. These were excluded from the analysis because predation could not be distinguished unambiguously from natural mortality. However, *Toxorhynchites* have been observed to spear odonate neonates, and *Dendrobates* consume them easily. Any experimental predator ≥ 5 mm that disappeared was assumed to have been eaten. When *Dendrobates* or odonates ≥ 7 mm were killed, the outcome was usually unambiguous because parts of the dead individual remained. Although *Toxorhynchites* larvae often disappeared without trace, their absence could not be confounded with emergence, which is preceded by an aquatic pupal stage.

In the experimental treatments, a predator that disappeared did so after 4.2 ± 0.3 days ($n = 175$), whereas predators that coexisted did so for a longer time (mean = 11.7 ± 1.6 days, $n = 29$, $t = 4.3$, $P < 0.001$). In eleven of the latter cases, *Toxorhynchites* or *Dendrobates* emerged from the holes after a mean of 7.1 days. Thus, coexistence did not result simply because one of the predators left the hole after a shorter time than that over which predation typically occurred. Initial size difference had a significant effect on the outcome of predator pairings (Tables 4 and 5). There was no significant difference among odonate species in their fate when paired with larger *Dendrobates* (Fig. 2, $\chi^2 = 2.5$, d.f. = 2, $P > 0.1$). In 59% of the cases when *Dendrobates* was paired with a smaller odonate, the odonate was killed. In 30% of such pairings, the predators co-existed until the tadpole metamorphosed. *Dendrobates* was killed only 11% of the time. In pairings of odonates with

smaller tadpoles, 61% of the tadpoles were killed. In 22% of the pairings, *Megaloprepus* or *Mecistogaster* larvae were killed by smaller tadpoles, but none of the aeshnids was killed, a significant difference ($\chi^2 = 8.4$, d.f. = 2, $P < 0.05$, Fig. 2). Of damselfly larvae paired with tadpoles, 24% were missing one or more caudal lamellae (i.e. breathing structures on the tail), and 8% were missing one or more legs, before they were found dead. Aeshnid larvae have no caudal lamellae; 4% of them were found with missing legs.

Similarly, none of the aeshnids was killed by smaller *Mecistogaster* or *Megaloprepus*, whereas 37 and 20% of the latter genera, respectively, were killed by smaller heterospecifics ($\chi^2 = 6.9$, d.f. = 2, $P < 0.01$, Figs 3–5). In contrast, smaller aeshnids were able to kill larger damselfly larvae in 32% of cases. In 14% of the trials, damselfly larvae lost one or more caudal lamellae and 8% of the odonates lost legs.

A pre-emptive advantage of early colonization was much less pronounced for *Toxorhynchites* (Figs 6 and 7). The mosquito larvae killed smaller predators only 30% of the time. In 54% of those trials, mosquitoes were killed by a smaller predator. As the larger of the two predators, the mosquito was killed significantly more often than were tadpoles or odonates in similar trials ($\chi^2 = 26.9$, d.f. = 2, $P < 0.01$). Only one mosquito killed a predator larger than itself.

Discussion

Although oxygen content, water temperature, and pH differed among individual tree holes, these variables did not differ consistently between large and small tree holes, nor did they predict predator occupancy. These results concur with other studies of tropical phytotelmata (i.e. water-filled plant containers), which also vary widely in abiotic conditions (e.g. Laessle, 1961; Kitching & Callaghan, 1982). Given that tree

Table 5. Differences in initial size and time to outcome, as a function of outcome in the priority experiment. Size differences are expressed as the size of the first predator listed minus the size of the second predator listed. Coexistence occurred only once. Aeshnids: *G. membranalis* and *T. dentata* pooled, *Mecistogaster*: *M. linearis* and *M. ornata* pooled. Letters indicate means that are not significantly different ($P > 0.05$, Bonferroni tests). * $P < 0.05$, *** $P < 0.001$.

Treatment	<i>n</i>	Mean initial size difference (mm)	Mean days to outcome
<i>Aeshnid vs. Mecistogaster</i> :			
Aeshnid wins	12	5.2 ± 2.0	2.8 ± 0.4
<i>Mecistogaster</i> wins	7	-5.2 ± 1.2	3.1 ± 0.6
		$F_{1,17} = 6.4^*$	$F_{1,17} = 0.8$ NS
<i>Aeshnid vs. Megaloprepus</i> :			
Aeshnid wins	10	7.8 ± 2.2 ^a	3.9 ± 1.7
<i>Megaloprepus</i> wins	8	-4.9 ± 0.9	2.0 ± 0.2
Coexist	1	20.5 ^a	9.0
		$F_{2,16} = 9.1^{***}$	$F_{2,16} = 0.9$ NS
<i>Megaloprepus vs. Mecistogaster</i> :			
<i>Megaloprepus</i> wins	8	4.2 ± 1.7	3.4 ± 0.5
<i>Mecistogaster</i> wins	5	-4.5 ± 1.9	11.5 ± 2.9
		$F_{1,10} = 6.2^*$	$F_{1,10} = 13.5^*$

holes are a scarce resource and holes support relatively few individual predators (Fincke, 1992a, 1994), broad tolerance ranges would be advantageous for their unique fauna. Indeed, the only significant abiotic effect (other than volume) found was that *Physalaemus* occupied holes with higher than average oxygen content. Not surprisingly, this frog is not a tree hole specialist, but also breeds commonly in streams, where oxygen content is relatively much higher than in tree holes.

The abiotic factors measured could not account for the apparently premature disappearance of *Mecistogaster* from large holes as the season progressed. Although the difference in the distribution of *Mecistogaster* in May 1990 compared with July 1992 might simply reflect yearly variation in tree hole occupancy, this is unlikely. In repeated censuses made 2 months and more after the start of the rainy season during 5 years spanning a 15-year period, *Mecistogaster* were rarely found in holes over 1 litre (Fincke, 1998). Moreover, the non-random emergence of *Mecistogaster* from small holes is unlikely to be due to its ability to tolerate some unmeasured abiotic characteristic of small holes. When *Mecistogaster* were switched to relatively large holes whose original aeshnid occupants were placed in holes occupied by *Mecistogaster*, both groups survived as well as the controls. The slower growth of aeshnid larvae in the experimental treatment relative to the controls is unlikely to have resulted in higher larval mortality, had larvae been followed until emergence. In another field experiment using 0.45-litre holes with low nutrient input, aeshnids persisted for a 9-week period, during which they grew very slowly or not at all (Fincke *et al.*, 1997).

Results from the priority experiment indicated that size-dependent, intraguild predation accounts for the pattern of small holes being occupied by a single predator. The effect of priority was weakest for *Toxorhynchites*, which was more susceptible to attack by smaller predators (see also Caldwell, 1993). *Toxorhynchites theobaldi* may be found more commonly in smaller holes either because *Megaloprepus* and aeshnids

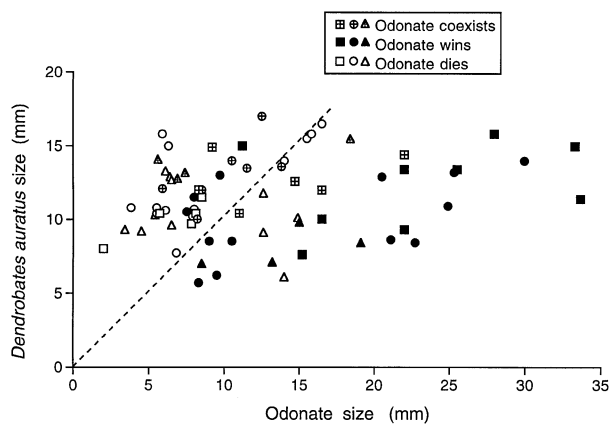


Fig. 2. Outcome of pairings of *Dendrobates auratus* and odonates. Dotted line denotes equal-sized pairs. Maximum size of the tadpole is about 15 mm. Aeshnids (*Gynacantha membranalis* and/or *Triacanthagyna dentata*) are represented by squares, *Megaloprepus coeruleus* by circles, and *Mecistogaster* by triangles.

eliminate it from large holes, or because adult mosquitoes oviposit preferentially in small holes. Other studies also report *Toxorhynchites* from small plant containers, where it is rarely found with any other predator (Lounibos *et al.*, 1987; Kitching, 1990). *Dendrobates* and all four odonate genera were easily able to exclude later-arriving heterospecifics from small holes; even a small positive size difference often predicted a favourable outcome. Aeshnids had a slight advantage over damselfly larvae whose caudal lamellae could be removed by smaller *Dendrobates* and odonates, forcing larvae to spend more time near the water surface. Loss of caudal lamellae also reduces swimming speed, which would also increase predation (Robinson *et al.*, 1991).

Thus, differential priority effects by non-odonate predators could not explain the preponderance of *Mecistogaster* in small

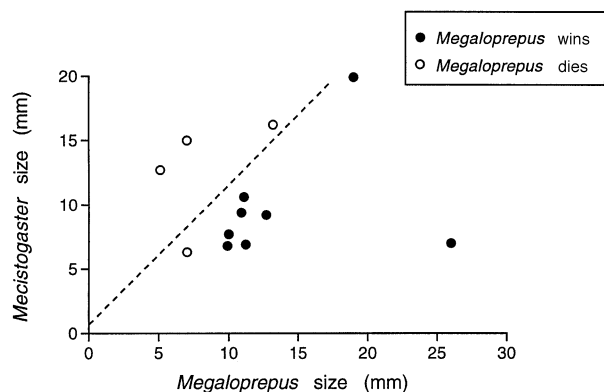


Fig. 3. Outcome of pairings of *Mecistogaster* and *Megaloprepus coerulatus*. Dotted line denotes equal-sized pairs.

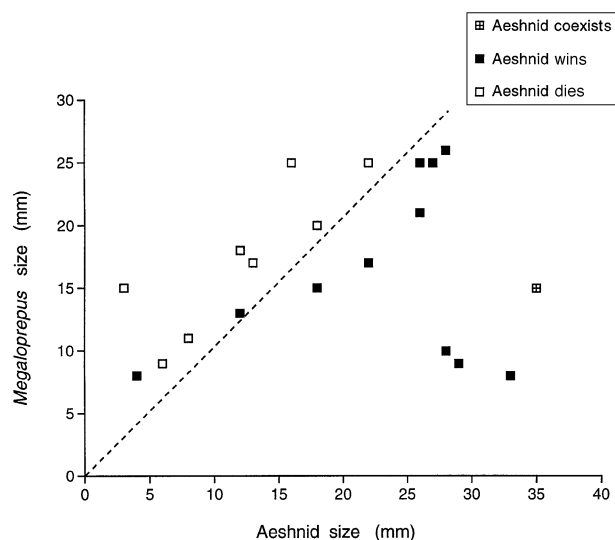


Fig. 4. Outcome of pairings of *Megaloprepus coerulatus* and aeshnids (i.e. *Gynacantha membranalis* and/or *Triacanthagyna dentata*). Dotted line denotes equal-sized pairs.

holes. The most plausible explanation for the apparently premature disappearance of *Mecistogaster* from large tree holes, therefore, is that *Mecistogaster*'s ability to pre-empt later arrivals is limited to small tree holes. Results of the current study are consistent with past experiments and observations of species' changes in natural holes, indicating that in large holes, *Megaloprepus* and aeshnids survive long enough to surpass *Mecistogaster* in size and eliminate them (Fincke, 1992a). Given the relatively fast initial growth of *Dendrobates*, this predator should also contribute to the premature seasonal decline of *Mecistogaster* in large holes.

Because the maximum size of a *D. auratus* tadpole is considerably less than that of even the smallest odonate species, the survival of *Dendrobates* in either small or large holes requires early colonization. *Dendrobates* tadpoles are found in tree holes shortly after the first rains of the wet season, and require 1–3 months to metamorphose (Summers, 1990; O. M. Fincke, pers. obs.). The tadpoles are rarely found after October,

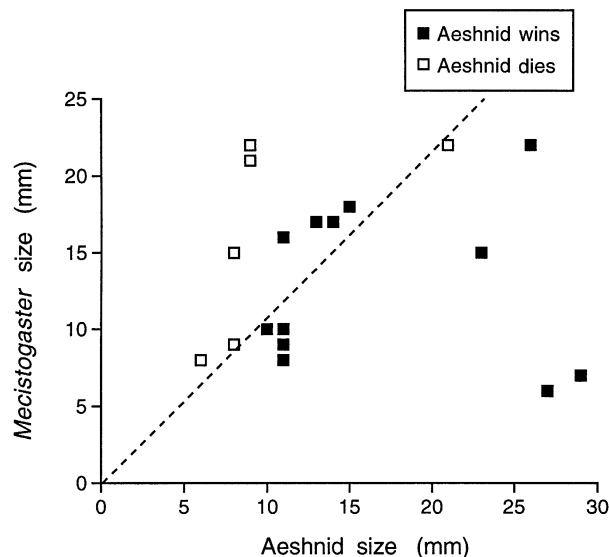


Fig. 5. Outcome of pairings of *Mecistogaster* and aeshnids (i.e. *Gynacantha membranalis* and/or *Triacanthagyna dentata*). Dotted line denotes equal-sized pairs.

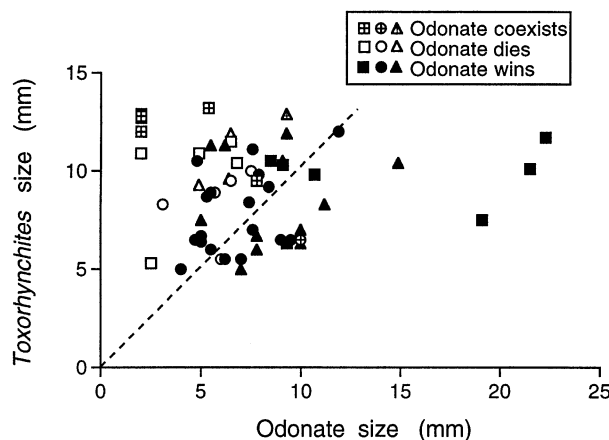


Fig. 6. Outcome of pairings of *Toxorhynchites theobaldi* and odonates. Dotted line denotes equal-sized pairs. Aeshnids (*Gynacantha membranalis* and/or *Triacanthagyna dentata*) are represented by squares, *Megaloprepus coerulatus* by circles, and *Mecistogaster* by triangles.

by which time most holes contain odonates (Fincke, 1998). Newly-deposited tadpoles are about 5 mm in size, more than twice the size of newly-hatched odonates or *Toxorhynchites*. The lack of overlap between *Dendrobates* and larger odonates suggests that the frogs, which swim around in holes before depositing their tadpoles, reject holes containing predators (see also Caldwell, 1993; Fincke, 1998).

Not surprisingly, *Mecistogaster* and *Toxorhynchites* are also among the first to colonize tree holes early in the wet season (Fincke, 1992a), thereby optimizing their chances of encountering tree holes free of the dominant predators. *Toxorhynchites* emerge in as little as 3 weeks, and before pupating, a final instar kills any conspecific larvae (Corbet &

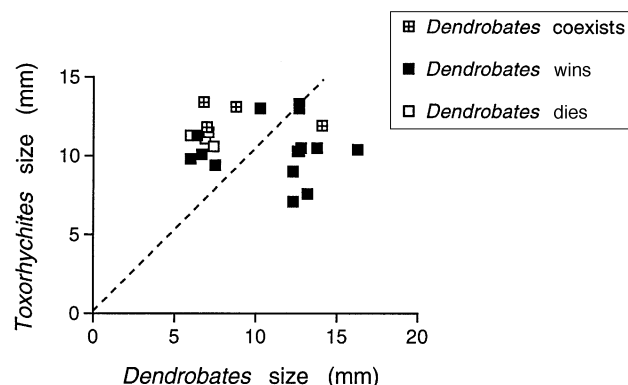


Fig. 7. Outcome of pairings of *Toxorhynchites theobaldi* and *Dendrobates auratus*. Dotted line denotes equal-sized pairs.

Griffiths, 1963). *Mecistogaster* could occupy a small hole for as long as 8 months. Small tree holes vacated by these predators are subsequently occupied by *Megaloprepus* or aeshnids, which breed until holes dry up completely, usually by mid-March (Fincke, 1992a,b).

Their large size, long developmental time, and extended breeding season may explain why odonates are often the most abundant predators in phytotelmata, where intraguild predation and priority effects appear to be common. Caldwell (1993) found three top predators in water-filled fruit husks in a lowland Brazilian forest: the pseudostigmatid damselfly *Microstigma anomalum*, tadpoles of *Dendrobates castaneoticus*, and *Toxorhynchites* sp. No two predators coexisted in the husks, which were similar to small tree holes in volume (mean = 101 ml). Similarly, in Peru, Louton *et al.* (1996) found almost no overlap between *Toxorhynchites* and a *Mecistogaster* sp. that occupied 50 to 60% of bamboo internodes sampled. In Borneo, three species of odonates occupied 91% of large tree holes but rarely co-occurred in the same hole (Orr, 1994). However, in Papua New Guinea, a top odonate predator was found in only 4% of the holes sampled (Kitching, 1990). Its low reported frequency may be due to the sampling method used, a relatively short sampling period, or significantly different community dynamics.

Tree holes in the seasonally moist forest of Barro Colorado Island have a more complex array of top predators than found previously in any type of phytotelmata. Based on colonizations pooled over a 6-week sampling period, diversity of macrofauna in tree holes on Barro Colorado Island increased with water volume (which is correlated with surface area, Fincke, 1994). Although predator diversity did not increase linearly with volume, holes over 1 litre in volume were more likely to harbour multiple predator species than smaller holes. Predator diversity within holes is likely to be constrained because large holes support a very low density of predatory individuals, regardless of species (Fincke, 1992a, 1998; see also Orr, 1994). Because *Megaloprepus* and the aeshnids also colonize small holes and breed until the end of the wet season, persistence of the less competitive *Mecistogaster* appears to depend on seasonal drying, which clears holes of all predators (i.e. an intermediate disturbance, see Connell, 1978). *Toxorhynchites*

and *Dendrobates* are less dependent on seasonal drying because both species also breed in microhabitats other than tree holes (Fincke, 1998). In forests where tree holes do not dry up seasonally, relatively few top predators coexist (e.g. Kitching, 1990; Orr, 1994; Fincke, 1998), tentatively supporting the habitat drying hypothesis. Field experiments are needed to determine how priority effects interact with predator life history characteristics to mediate species coexistence in aseasonally wet forests.

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