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Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama

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Abstract In the lowland moist forest of Barro Colorado Island (BCI), Panama, larvae of four common species of odonates, a mosquito, and a tadpole are the major predators in water-filled tree holes. Mosquito larvae are their most common prey. Holes colonized naturally by predators and prey had lower densities of mosquitoes if odonates were present than if they were absent. Using artificial tree holes placed in the field, we tested the effects of odonates on their mosquito prey while controlling for the quantity and species of predator, hole volume, and nutrient input. In large and small holes with low nutrient input, odonates depressed the number of mosquitoes present and the number that survived to pupation. Increasing nutrient input (and consequently, mosquito abundance) to abnormally high levels dampened the effect of predation when odonates were relatively small. However, the predators grew faster with higher nutrients, and large larvae in all three genera reduced the number of mosquitoes surviving to pupation, even though the abundance of mosquito larvae remained high. Size-selective predation by the odonates is a likely explanation for this result; large mosquito larvae were less abundant in the predator treatment than in the controls. Because species assemblages were similar between natural and artificial tree holes, our results suggest that odonates are keystone species in tree holes on BCI, where they are the most common large predators.

Key words Odonata · Keystone predators · Neotropics · Mosquito control

Introduction

Predation significantly affects population dynamics and communities of prey species, especially in aquatic systems (Sih et al. 1985). Nevertheless, the interaction between 'top-down,' predator-mediated effects and 'bottom-up,' nutrient-driven effects on species composition is poorly understood (Hunter and Price 1992; Menge 1992). The relative importance of predators and nutrients may vary with the degree of disturbance and the time scale of the investigation (Wooton and Power 1993), and regional species diversity (Strong 1992). Testing predictions arising from the continuum of 'top down' and 'bottom-up' models of community organization poses significant methodological problems (Power 1992). Such problems may be easiest to surmount in discrete microhabitats such as phytolemata (water-filled plant containers), where each container is an independent replicate, the presence or absence of predators can be manipulated experimentally, prey density can be quantified, and seasonal drying is a distinct and predictable disturbance.

Studies of temperate tree holes, where mosquito predators are often absent (e.g., Kitching 1971; Hawley 1985; Woodward et al. 1988), underscore the importance of interspecific competition, parasitism, and seasonal drying for the population dynamics and community structure of the mosquito fauna (e.g., Fish and Carpenter 1982; Chambers 1985; Bradshaw and Holzapfel 1988; Hard et al. 1989; Livdahl and Willey 1991; Walker et al. 1991; Copeland and Craig 1992; Edgerly and Livdahl 1992). Predation is likely a more important determinant of species assemblages in tropical tree holes. For example, in tree holes of subtropical Florida, the predatory mosquito larva, *Toxorhynchites rutilus*, is the top predator whose presence reduces the populations of other mosquitoes below their carrying capacity (Bradshaw and Holzapfel 1983; Lounibos 1983). In this system, seasonal disturbance coupled with predation maintains species diversity in a nonequilibrium state. Species of *Toxorhynchites* have also been shown to reduce the emergence of the disease vectors, *Aedes aegypti* and *Culex quinquefasciatus* (Focks et al. 1982, Focks and Sackett, 1983). Although many tropical phytotelmata harbor an array of predators, including odonates

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(e.g., Corbet 1983; Kitching 1990; Fincke 1992a; Caldwell 1993), little is known of the effects of these large predators on the abundance of their mosquito prey.

In the lowland moist forests of Barro Colorado Island (BCI), Panama, four common odonates develop exclusively in water-filled tree holes. In order of size they are the aeshnid dragonfly *Gynacantha membranalis* (final instar = 33–42 mm in length) and the pseudostigmatid damselflies *Megaloprepus coerulatus* (24–34 mm), *Mecistogaster linearis*, and *Mecistogaster ornata* (both species 19–22 mm; Fincke 1984, and unpublished data). Newly hatched odonates feed on microinvertebrates and begin feeding on mosquito larvae within weeks. At least 34 species of mosquitoes are known from tree holes in Panama (Galindo et al. 1955; Heinemann and Belkin 1978), about a third of which were present in the current study. Odonates also feed on tadpoles and the larvae of syrphid flies, chironomid midges, and beetles, but these alternative prey are usually less common than mosquitoes.

Because one rarely sees many mosquitoes in tree holes that contain odonates, we suspected that these predators reduce tree hole mosquitoes below their carrying capacity. However, in this detritus-based community, any effect of odonates may be moderated by intraguild predation. Cannibalism and predation among odonate species reduce the density of odonates to low levels, perhaps too low to depress prey populations. For example, in 'large' holes, here defined as those ≥1 l, even well-fed *M. coerulatus* kill conspecifics until their density is reduced to one larva per 1–2 l. Predator density is typically higher in 'small' holes (i.e. < 1 l), which rarely contain more than a single odonate (Fincke 1992a). Tree holes on BCI also harbor predatory tadpoles of *Dendrobates auratus*, and larvae of the mosquitoes, *T. theobaldi* and, more rarely, *Trichoprosopon digitatum*. Newly hatched odonates are prey for these predators, which in turn are eaten by larger odonates (O.M. Fincke, unpublished manuscript). Thus, on a forest-wide scale, odonates may actually increase mosquito populations by depressing predator abundance.

Furthermore, any effect of odonates may be mitigated by high nutrient pulses. Because the surface area of tree holes on BCI is correlated with water volume (Fincke 1994), nutrient input is likely greater in larger holes, where odonate density is relatively low. When fruit falls or a monkey defecates into a hole, or a clutch of *Physalaemus pustulosus* tadpoles hatch, odonates may be swamped with prey and have little effect on the number of emerging mosquitoes as long as nutrients remain high.

The purpose of this study was to determine the general effects of odonates on the abundance of tree hole mosquito larvae and their survivorship to pupation. We specifically address four questions: (1) Can odonates depress mosquito populations in large holes (where predator density is low) as well as in small ones (where predator density is high)? (2) What are the effects of predators at high and low nutrient levels? (3) Are some sizes or species of odonates more effective predators? (4) On a forest-wide scale, how do odonates compare with *D. auratus* and *T. theobaldi* as potential control agents of tree hole mosquitoes?

Materials and methods

The study site was the lowland, moist forest of BCI, Panama (see Leigh et al. 1996 for a site description). Here, tree holes retain water from the beginning of the wet season rains in early May until they completely dry by March and are cleared of predators (Fincke 1992a, 1994). Work was done during the rainy season, in 1983–1984, 1990, and 1992–1996. We quantified mosquito abundance in natural tree holes, but because water volume varied considerably and very large holes were difficult to census, we also quantified mosquitoes in plastic pots (volume = 0.5, 2.5, 7, and 10 l) attached to trees in light gaps and forest understory as part of another experiment (see Fincke 1992b). Because these pots accumulated detritus naturally and were accessible to the full array of tree hole predators and prey, they were also used to compare macrofauna between artificial and natural holes.

At weekly intervals, we censused natural tree holes by removing leaves and other detritus to a plastic pan, and removing standing water with a turkey baster. Using a flashlight, we searched the empty hole and detritus for odonates and other macroorganisms. We poured the tree hole water through a fine mesh sieve to collect all mosquitoes, which were transferred to a white pan for counting. The contents of artificial holes were emptied directly into a pan. Mosquito larvae were scored by size as small (< 3 mm total length), medium (3–5 mm) or large (> 5 mm). Detritus, water, and organisms were returned to holes following censuses. In 1994, 1995, and 1996, subsamples of mosquito larvae and pupae were occasionally collected from artificial and natural tree holes and reared to adulthood for species identification.

We used artificial tree holes in all experiments in order to control for multiple variables and because it was not feasible to clear natural tree holes of odonates over an extended time. A single female inserts as many as 150 eggs into the bark above the water line where they are difficult to detect with the naked eye. Eggs require from 18 to 90 days to hatch (O.M. Fincke, unpublished data), and early instars (2–5 mm) typically hide in crevices where they are difficult to flush out with washing. The two *Mecistogaster* damselflies were pooled in this study because they are difficult to distinguish as larvae, and their growth rates and final instar sizes are similar (Fincke 1992a). Hereafter, we refer to the four odonate species by genus only.

In experiment 1, we determined the effect of odonates on mosquitoes that colonized holes in the large laboratory clearing. Forty-seven plastic bowls were filled with 0.8 l of water and clustered in the shade of a building, adjacent to mature forest. Each pot contained eight leaves from a single tree, and a small piece of bark. Twenty-eight of the pots also each contained a single *M. coerulatus* damselfly. Pots were checked daily for the presence of the odonate larvae and topped off with water as necessary. After 2 weeks, the mosquitoes present in each pot were counted.

In 1993 and 1994, we measured the effect of the three odonate genera on mosquitoes over a longer period of time and under more natural conditions. Pots with low nutrient input were placed in forest understory, adjacent to Snyder-Molino and T. Barbour trails. In experiment 2a, 450-ml pots of translucent plastic (8 cm in diameter and 10 cm deep) were painted black on the outside surface and attached singly to small trees at a mean height of 1.5 m. Each pot contained five leaves and a small piece of bark placed against the tree trunk to collect stem flow. We initially filled pots with filtered lake water, after which they collected rain water naturally. Nine pots each contained a single odonate larva (one with *Mecistogaster*, five with *Megaloprepus*, and three with *Gynacantha*), whereas no odonates were added to the nine controls. In this and all other single-odonate treatments, we used medium-sized larvae (10–18 mm) whenever possible because they experience the fastest subsequent growth. At weekly intervals for 4 weeks, we counted the number of mosquitoes present. Every 2 weeks, we measured the odonates from the head to the end of the abdomen, using calipers. In this experiment and in experiment 3, predator treatments were skewed towards *Megaloprepus* because it was the easiest odonate to collect; in 1993 we had only 2 months to conduct experiments.

Many of the pots lacked mosquitoes after one month, when experiment 2a was terminated. We thus repeated the experiment in 1994, but modified the protocol by adding the odonates only *after* mosquitoes were found in all of the pots (Experiment 2b, Table 1). At weekly intervals for 8 weeks, we counted the mosquitoes in three predator treatments (each with a different odonate genus) and one control pot at each of three sites. To ensure that no additional odonates colonized these holes over the course of the experiment, we enclosed the pots in chicken wire cages. The cages permitted colonization by mosquitoes and other potential prey, but prevented oviposition by odonates. They also prevented falling leaves and fruit from collecting in the pots. Although it was impossible to prevent colonization by *T. theobaldi*, we removed any that we found during the weekly censuses.

In experiment 3, we tested the effect of odonates in large artificial holes with low nutrient input. Twelve rectangular black plastic pans (77 × 14.5 × 8 cm) were modified with drain holes so the water volume never exceeded 3 l. To each pot we added a large piece of bark and 1.2 l of moderately packed leaves, such that the density of leaf detritus was similar between experiments 2 and 3. We placed 3–5 larvae of a single genus in each of six experimental pans (four with *Megaloprepus*, one with *Gynacantha*, and one with *Mecistogaster*). The larval size distribution was similar to that found in large natural holes (i.e., two to four smaller larvae, one to two larger ones). Each pan was secured (0.5–1.0 m, above the ground) to a different fallen log, at least 10 m, but typically >20 m, apart. The pans were censused weekly for only 3 weeks, too short a time for any odonate ovipositing in a pan to have a confounding effect on the treatments. Because the multiple larvae in a treatment were not individually marked, growth rates could be reliably measured only for the largest one in each replicate.

In experiment 4, we determined the effect of odonate predators in small pots after a high pulse of nutrients, using a protocol similar to that of experiment 2b. In addition to the initial leaf and bark detritus, we added half of a *Ficus* sp. fruit (collected from the same tree)

Table 1 Colonization by mosquitoes, and mean size and growth rate of odonate predators in holes censused in this study. The initial size range of odonates used is in parentheses. *n* refers to control plus predator replicates

Census type and year	*n*	Census span (weeks)	Holes never found with mosquitoes	Mean days for colonization by mosquitoes	Mean initial size of odonate (mm)	Mean growth of odonate (mm/week)
Natural tree holes 1993	47	3	6	–	–	–
Large and small pots colonized naturally 1983–1984	43	3–8	0	–	–	–
Experiment 1: small pots in lab clearing 1990	47	2	20	–	11.5 ± 0.6 (5.3–15.7)	1.3 ± 0.2
Experiment 2a: small pots low nutrients 1993	18	4	6	–	17.6 ± 6.6 (6.7–27.5)	0.1 ± 0.0
Experiment 2b: small pots low nutrients 1994	12	8	0	25	12.7 ± 2.3 (5–21)	0.9 ± 0.2
Experiment 3: large pots low nutrients 1993	12	3	0	<7	13.5 ± 4.5 (7.0–22.7)	2.0 ± 0.6
Experiment 4: small pots high nutrients 1995	20	16	0	<7	10.2 ± 0.6 (6–15)	1.8 ± 0.1[a]

[a] Rate calculated for first 8 weeks only for comparison with experiment 2b

and one fruit of *Protium tenuifolium* to each pot. All 20 pots (three predator treatments and one control, replicated at five sites) were colonized by mosquitoes within the first week. Thereafter, we counted mosquito larvae and pupae weekly for 16 weeks. To minimize the loss of predators due to emergence, we began the experiment using somewhat smaller odonates than in experiment 2b (Table 1). When an odonate reached the final instar or disappeared, it was replaced by a congener within the initial size range for that treatment. Most of the data that follow were generated by repeatedly censusing a given hole. Throughout, *F*-statistics refer to repeated-measures ANOVA, *t* statistics refer to two-tailed *t*-tests, and means are reported ± standard errors.

Results

Occurrence of predators and prey in holes colonized naturally

A total of 13 mosquito species in eight genera were found in holes (Table 2). All species were found both in natural and artificial holes with the exception of *Culex allostigma* and *Limatus durhamii*, which were rare occupants of pots but were never found in tree holes. Five of the 6 mosquitoes most likely to colonize a natural hole were also among the top 6 most likely to be found in pots. Similarly, other macrofauna found in natural holes also occurred in pots (Table 3). The relatively greater frequency of *Dendrobates*, *Megaloprepus*, and *Gynacantha* in pots likely reflected the longer time span over which they were censused. Tadpoles of *Agalychnis callidryas* were found in only one, 7-l artificial hole, but this species typically breeds in natural holes larger than those we sampled (Fincke 1992a).

The 47 natural tree holes used to quantify mosquito abundance in June and July 1993 ranged in volume from 10 to 4500 ml. The 41 holes containing mosquitoes were significantly larger ($\bar{x} = 997 \pm 162$ ml) than the 6 holes in which mosquitoes were never found on any of three weekly censuses ($\bar{x} = 312 \pm 78.7$ ml, $t = -3.8$, $P < 0.001$). The 36 holes in the sample that harbored at least one odonate by the end of July 1993 were larger on average ($\bar{x} = 1075 \pm 179.6$ ml) than the 11 holes lacking odonates ($\bar{x} = 367 \pm 91.0$ ml, $t = -3.5$, $P = 0.001$). Four tree holes contained neither mosquitoes nor odonates, more than expected if colonization was random across holes ($\chi^2 = 7.18$, $1\,df$, $P < 0.05$). Despite a potential bias caused by the control holes being relatively smaller, the density of mosquito larvae (but not pupae) was significantly lower in holes with odonates, although the effect was not consistent over time (Table 4). In large and small pots that were colonized naturally, the density of both mosquito larvae and pupae was lower if the pots contained at least one odonate than if odonates were absent (Fig. 1, Table 4). The sample of 'control' pots that lacked odonates on the first two censuses decreased over time because odonates continued to colonize some of them. Repeated-measures ANOVA required equal sampling of all treatments; hence statistics reported in Table 4 reflect only the first two censuses, though the trend was similar for the third and fourth censuses (Fig. 1).

Effects of odonates on mosquito abundance in small and large pots with low nutrient input

In experiment 1, after 2 weeks in the laboratory clearing, pots containing a single *Megaloprepus* larva had significantly fewer mosquitoes ($\bar{x} = 4.2 \pm 1.4$, $n = 28$ pots) than the controls ($\bar{x} = 27.0 \pm 8.5$, $n = 19$ pots, $t = 2.6$, $P < 0.02$). Although no mosquitoes were found in 14 of the predator replicates, this result could not be attributed to predation, because mosquitoes were also absent from 6 control pots, not a significant difference ($\chi^2 = 1.6$, $df = 1$, $P > 0.1$).

In experiment 2a and subsequent experiments, odonate genus had no significant effect on mosquito abundance (Table 4), so species were pooled into a single predator treatment for analysis. With low nutrient input,

Table 2 Percentage of holes occupied by mosquitoes on at least one census. Sample sizes were 43 tree holes (mean volume = 770 ± 112 ml, range = 20–3400 ml) censused weekly for 5 weeks, and 20 450-ml pots censused weekly for 10 weeks. The mean frequency of occurrence was calculated only for species found at least once in a hole and refers to the proportion of total censuses for which a given species was present (data from 1995 and 1996)

	Natural tree holes		Pots	
	Occupied (%)	Occurrence ($\bar{x}$)	Occupied (%)	Occurrence ($\bar{x}$)
Aedes terrens	67.4	0.49 ± 0.04	60.0	0.19 ± 0.02
Anopheles eiseni	48.8	0.46 ± 0.04	40.0	0.17 ± 0.02
Culex allostigma	0.0	0.0	5.0	0.10 ± 0.00
Culex conservator	23.3	0.28 ± 0.2	55.0	0.21 ± 0.03
Culex corrigani	44.0	0.31 ± 0.18	90.0	0.29 ± 0.03
Culex mollis	20.9	0.22 ± 0.01	40.0	0.12 ± 0.10
Culex urichii	25.6	0.31 ± 0.04	70.0	0.32 ± 0.06
Haemagogus leucotaeniatus	11.6	0.24 ± 1.3	10.0	0.15 ± 0.02
Haemagogus lucifer	48.8	0.30 ± 0.02	20.0	0.22 ± 0.04
Limatus durhamii	0.0	0.0	5.0	0.10 ± 0.00
Orthopodomyia fascipes	2.3	1.00 ± 0.0	35.0	0.26 ± 0.04
Toxorhynchites theobaldi	7.4	0.36 ± 0.03	10.0	0.20 ± 0.00
Trichoprosopon digitatum	2.3	0.20 ± 0.00	10.0	0.10 ± 0.00

the number of mosquito larvae and pupae was significantly less in small pots with an odonate than in controls, but there was an interaction effect between treatment and time on the number of pupae present (Table 4). Six pots (33%) harbored no mosquitoes on any of the four weekly censuses. Five of these pots were predator treatments, more than expected if the absence of mosquitoes was simply due to a lack of colonization ($\chi^2 = 3.98$, 1 df, $P < 0.05$). Only one of the nine odonates grew more than 1 mm over the month period (Table 1).

Table 3 Mean percentage of holes occupied by macrofauna on at least one census in 98 and 92 natural tree holes sampled weekly for 6 weeks in 1992 and 1993, respectively (n = 128 total holes, mean volume = 1.7 ± 0.4 l, range = 0.01–4.5 l), and in 30 pots (mean volume = 5.6 ± 0.6 l, range = 0.5–10.0 l) sampled over 6 months in the 1983–1984 wet seasons. Data for *Toxorhynchites theobaldi* refer to only third-instar or later individuals. Syrphids colonized pots but their frequency was not systematically noted in 1983–1984

	Natural tree holes	Pots
Prey		
Mosquito larvae (except *Toxorhynchites*)	94.5	100.0
Physalaemus pustulosus	12.5	46.7
Syrphid fly larvae	7.6	–
Agalychnis callidryas	0.0	3.0
Predators		
Megaloprepus coerulatus	34.2	66.7
Mecistogaster	25.5	20.0
Gynacantha membranalis	17.4	26.6
Dendrobates auratus	7.0	23.3
Toxorhynchites theobaldi	7.0	6.6
Hemipteran, Veliidae (water surface dweller only)	7.0	6.6

In experiment 2b, two of the *Mecistogaster* larvae emerged and could not be replaced before the end of the experiment, so we excluded these replicates from the analysis. In this experiment, odonates were added only after the pots were known to be colonized by mosquitoes; hence the initial prey abundance was about six times higher than the maximum measured in experiment 2a. Nevertheless, by the first week, the odonates ($\bar{x}$ size = 14.9 ± 2.1 mm) had dramatically reduced mosquito abundance relative to controls (Fig. 2). Over the 2-month span, the number of mosquito pupae was significantly lower in the predator treatments, despite a precipitous drop in abundance of mosquito larvae in the controls by week 3 (Table 4). Mosquitoes were absent in eight of the nine odonate treatments on at least one census ($\bar{x} = 3.3 \pm 0.7$ censuses with no mosquitoes present). In contrast, mosquitoes were absent in only one of the three controls. In total, mosquitoes were absent in 47% of the experimental censuses, but were absent in significantly fewer (14%) of the control censuses ($\chi^2 = 10.4$, 1 df, $P < 0.005$). Although they often depleted their prey, the predators grew very slowly over the 2-month span (Fig. 3).

In experiment 3, all 12 large artificial holes with low nutrient input were colonized by mosquitoes within a week. By the 3rd week, the original five odonates in each predator replicate had been reduced by cannibalism to one to three per 3-l pan, typical of their natural density (see Fincke 1994). Even at these low densities, odonates significantly reduced the number of mosquito larvae and pupae, though the reduction of pupae was not consistent over time (Fig. 4, Table 4). Growth of the largest larvae in each treatment was similar to the mean larval growth under high nutrient conditions (Table 1).

Table 4 Statistics from repeated-measures ANOVA testing for the effect of the presence or absence of odonates (treatment) on the density of mosquito larvae and pupae over time. Sample sizes of larvae and pupae differed for natural holes because pupae were counted only after the first census

	Treatment	Time	Interaction	Difference due to genus
Natural tree holes				
Larvae	$F_{1,30}$ = 5.0*	$F_{2,60}$ = 7.6*	$F_{2,60}$ = 6.0 **	
Pupae	$F_{1,13}$ = 0.2	$F_{2,26}$ = 1	$F_{2,26}$ = 0.1	
Large and small pots colonized naturally				
Larvae	$F_{1,41}$ = 18.0**	$F_{1,41}$ = 0.7	$F_{1,41}$ = 0.32	
Pupae	$F_{1,41}$ = 5.1*	$F_{1,41}$ = 1.8	$F_{1,41}$ = 4.2*	
Experiment 2a: small pots low nutrients				
Larvae	$F_{1,16}$ = 8.1*	$F_{3,48}$ = 0.7	$F_{3,48}$ = 1.3	$F_{2,6}$ = 0.7
Pupae	$F_{1,16}$ = 12.8**	$F_{3,48}$ = 3.0*	$F_{3,48}$ = 3.3*	
Experiment 2b:				
Larvae	$F_{1,8}$ = 5.1*	$F_{7,56}$ = 6.7**	$F_{7,56}$ = 2.9*	$F_{2,4}$ = 0.2
Pupae	$F_{1,8}$ = 7.9*	$F_{7,56}$ = 1.8	$F_{7,56}$ = 0.4	
Experiment 3: large pots low nutrients				
Larvae	$F_{1,10}$ = 6.4*	$F_{2,20}$ = 3.6	$F_{2,20}$ = 1.3	$F_{2,3}$ = 2.0
Pupae	$F_{1,10}$ = 6.2*	$F_{2,20}$ = 9.2*	$F_{2,20}$ = 5.7*	
Experiment 4: small pots high nutrients				
Larvae	$F_{1,18}$ = 0.01	$F_{15,270}$ = 13.1*	$F_{15,270}$ = 0.97	$F_{2,12}$ = 1.0
Pupae	$F_{1,18}$ = 18.4**	$F_{15,270}$ = 2.0	$F_{15,270}$ = 1.2	

*$P < 0.05$, **$P < 0.01$

Effects of odonates on mosquito abundance in small holes with high nutrient input

In experiment 4, the addition of fruit quickly increased mosquito density of controls to nearly three times the highest level found in the controls of experiment 2b, when only leaves and bark were added (compare Fig. 5a with Fig. 2a). Prior to week 5, odonates did not significantly depress the number of mosquito pupae present $(F_{1,18,} = 0.4, P > 0.4)$. After the first 6 weeks when their mean size was 21.8 ± 1.0 mm, they consistently depressed the number of pupae relative to the controls (Fig. 5b, Table 4). However, the number of mosquito larvae did not differ between predator treatments and the controls, a result likely explained by preferential predation by odonates on the largest mosquito larvae available. Holes with odonates contained fewer large mosquito larvae than the controls $(F_{1,18} = 6.0, P = 0.02$, Fig. 6C). In contrast, the number of small and medium larvae did not differ between predator treatments and controls $(F_{1,18} = 0.08, P = 0.8$, and $F_{1,18} = 0.12, P = 0.7$ for small and medium larvae, respectively; Fig. 6A, B). Moreover, *T. theobaldi*, the largest mosquito present at this site, was never found in pots with odonates, although one to two *T. theobaldi* per pot were found (and removed) on 20 censuses of the controls.

As in experiment 2b, the abundance of mosquito larvae, but not pupae, decreased over time, even in the controls. Although the odonate genera grew at different

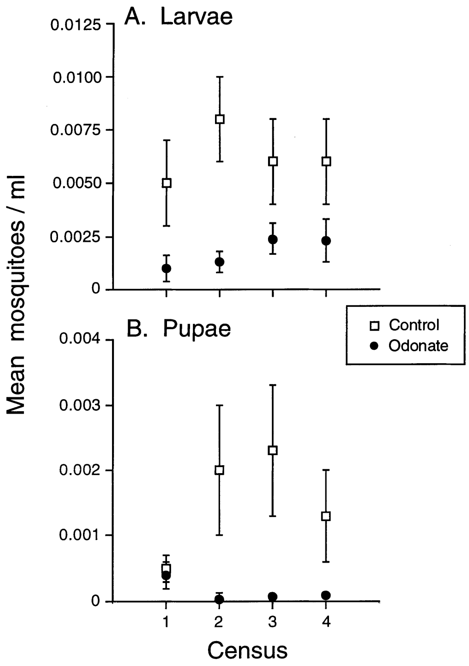

Fig. 1A,B Mean mosquito density in pots of four sizes (0.5, 2.5, 7, and 10 l) that were colonized naturally and censused once every 1–2 weeks, 4–8 weeks after being placed in the field. During the first two censuses, 23 pots harbored odonates (mean volume = 3.3 ± 0.7 l) and 20 did not (mean volume = 5.2 ± 0.8 l). By census 4, only 14 pots still lacked odonates. *Bar* indicates SE

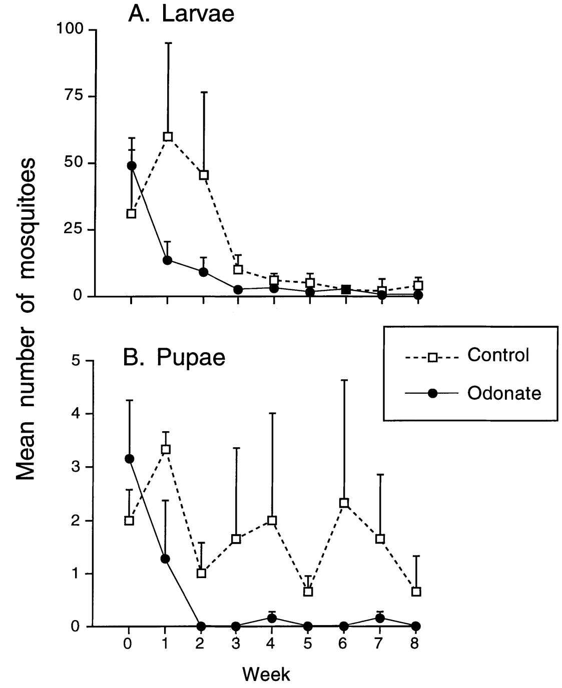

Fig. 2A,B Mean mosquito abundance in small pots with low nutrients (experiment 2b). *Week* 0 indicates the first time mosquito larvae were found in all pots. *Bar* indicates 1 SE

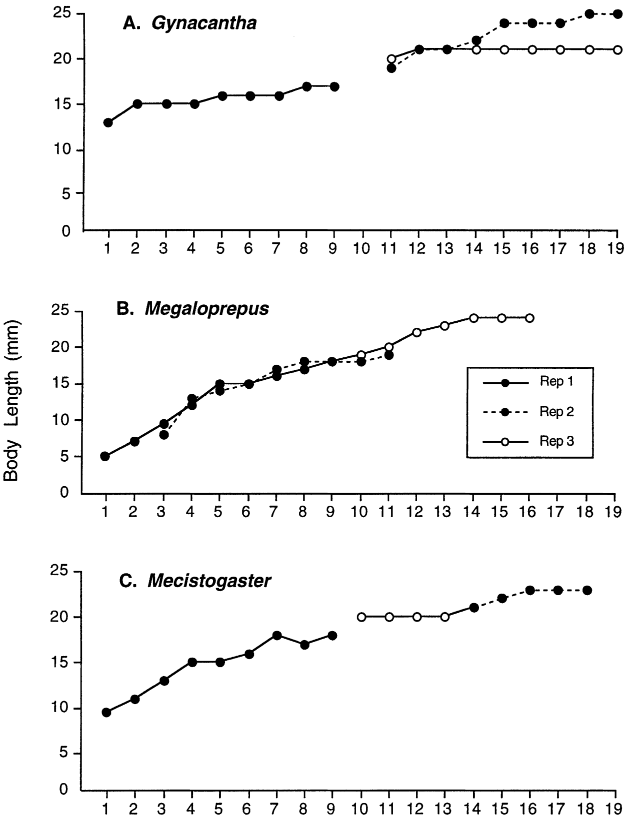

Fig. 3A-C Growth of the odonate genera in small pots with low nutrient input (experiment 2b). Replicates are overlapped to project estimated growth of an individual over a longer period of time rates ($F_{2,11} = 4.6$, $P < 0.04$), with high nutrient input, individuals grew twice as fast as in the low nutrient treatment (Table 1), such that a small *Mecistogaster* or *Megaloprepus* could emerge in about 4 months (Fig. 7).

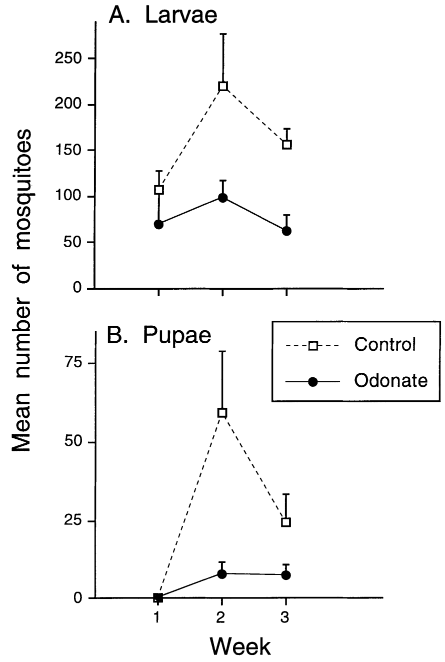

Fig. 4A,B Mean mosquito abundance in large pots with low nutrient input (experiment 3). *Bar* indicates 1 SE

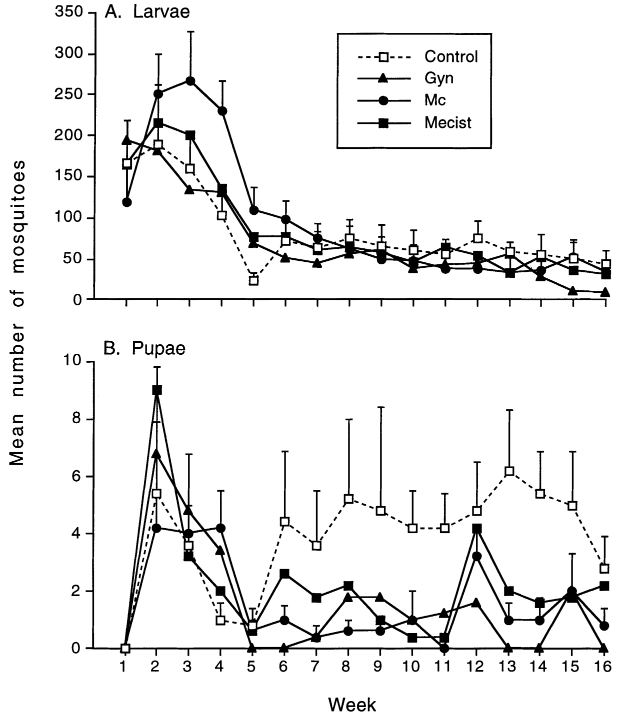

Fig. 5A,B Mean mosquito abundance in small pots with high nutrient input (experiment 4). *Bars* indicate 1 SE. Variance did not differ significantly among genera (*Gyn Gynacantha*, *Mc Megaloprepus*, *Mecist Mecistogaster*)

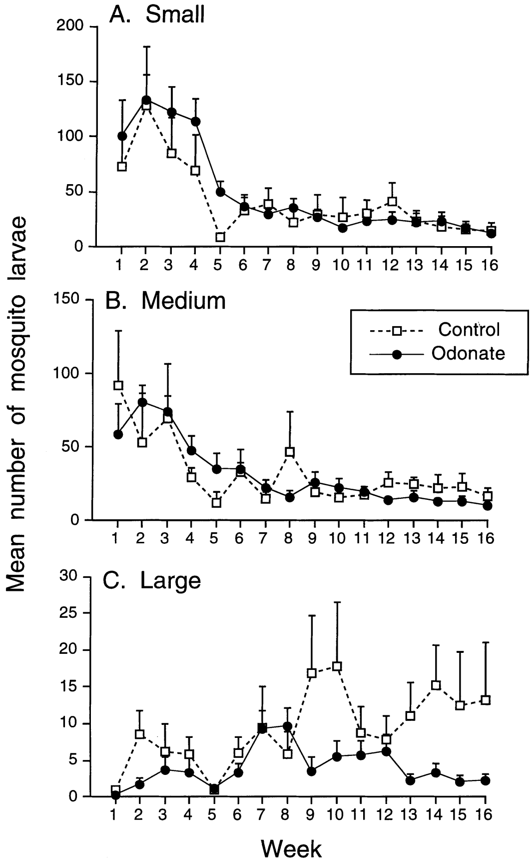

Fig. 6A-C Mean abundance of small (**A**), medium (**B**), and large (**C**), mosquito larvae in small pots with high nutrient input (experiment 4). *Bar* indicates 1 SE

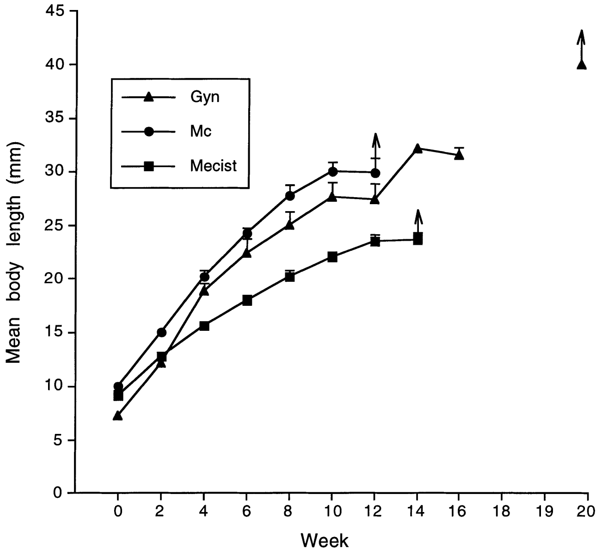

Fig. 7 Mean growth of odonate genera in small pots with high nutrient input (experiment 4). $n = 5$ for each treatment. *Bar* indicates 1 SE. The variance was too low to indicate for some censuses. *Arrows* indicate the size and approximate time at which adults emerge; no *Gynacantha* reached such a size (*Gyn Gynacantha*, *Mc Megaloprepus*, *Mecist Mecistogaster*)

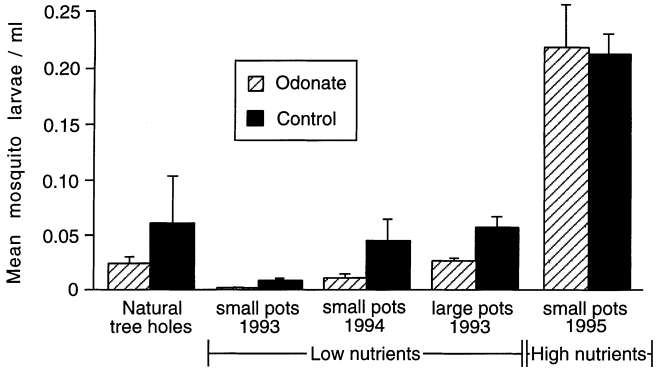

Fig. 8 Comparison of the mean density of mosquito larvae in natural tree holes and experimental pots with and without odonates. *Bar* indicates 1 SE

Discussion

This is the first study demonstrating that odonate predators depress the abundance of mosquitoes in water-filled tree holes in tropical forests. Tree holes and artificial holes that were colonized naturally generally harbored fewer mosquitoes when at least one odonate larva was present than when these predators were absent. This result was corroborated and the effect of odonates was more accurately demonstrated in our experiments with artificial tree holes which controlled water volume, nutrient input, and predator species and number (summarized in Fig. 8). Because of the close similarity between species assemblages in artificial and natural holes, results from our experiments are relevant to mosquito populations in tree holes on BCI. Because of the complexity of food web interactions, specific effects of tree hole predators cannot be known without experiments (Estes 1995). Do odonates play a similar role in other phytotelmata? In Kenya, Copeland et al. (1996) noted that tree holes with odonates tended to have fewer mosquitoes than holes lacking odonates. In contrast, Lounibos et al. (1987a) found mosquitoes more abundant in bromeliads with odonates than in those lacking them. Finally, Louton et al. (1996) reported no statistically significant effect of predators on mosquito abundance in bamboo internodes. However, none of these studies quantified mosquito density, controlled for the number and size of odonate predators, or measured the survivorship of mosquitoes to pupation. As we have shown, the abundance of mosquito larvae in a hole is not always well correlated with the number of mosquitoes that eventually emerge (Fig. 5).

In our study, the effect of odonate predators was not always easy to demonstrate. Mosquitoes were more likely to be absent in natural tree holes that also lacked odonates, and natural 'controls' were considerably smaller than natural 'predator treatments.' Even when volume was standardized by using artificial holes under otherwise natural conditions, long-term comparisons between predator-occupied holes and 'controls' were problematic because continued odonate colonization reduced the sample size of the controls over time. When we experimentally manipulated the presence and absence of odonates, the effect of predators was not always consistent over time due to variation in mosquito colonization, decline in nutrient levels, and growth of the odonates. Scattered small pots required about 3 weeks to be colonized whereas mosquitoes cued quickly to small pots clustered in the laboratory clearing, and in the field to large pots, and small pots with fruit detritus. When our experimental design prevented additional colonization of odonates, few additional nutrients could enter the holes. Then, mosquito density decreased over time, as expected in a detritus-based system (see also Leonard and Juliano 1995), making a predator effect harder to detect. High nutrient input resulted in levels of mosquito abundance about four times that found in natural holes (Fig. 8), initially mitigating the effect of medium-sized predators. Nevertheless, after 5 weeks of near-maximum growth, odonates >18 mm were able to depress the number of mosquitoes surviving to pupate, even though the abundance of mosquito larvae remained high. Finally, some variation in mosquito abundance in predator treatments inevitably resulted from the fact that odonates stop feeding during and shortly after molting, and about a week before they emerge as adults (personal observation).

Large odonates depressed mosquito abundance better than smaller ones. Despite generic differences in growth rates and the size of final instars, odonate genera did not differ in their ability to depress mosquito abundance in our experiments, a conclusion best supported by results from the small, low-nutrient pots. In the large-pot experiment which ran for a relatively short time, *Megaloprepus* was the predominant predator, and the maximum size differences among genera were never realized. In the high-nutrient treatment, early instars of all the odonate species could be swamped by prey. By the time the predators grew large enough to affect prey abundance, it was too low to demonstrate any statistically significant difference in odonate satiation levels, although the *Mecistogaster* treatments often had the most mosquitoes (Fig. 5). Over their larval lives, *Megaloprepus* and *Gynacantha* should consume more prey than the smaller and slower-growing *Mecistogaster*. The latter spends the shortest amount of time at its maximal potential as a predator (i.e. >18 mm), and would be the first to emerge under low nutrient conditions (Fig. 3). Under natural conditions, *Mecistogaster* is rarely found in large natural tree holes two months after the beginning of wet season because it is eaten by later-colonizing, but faster-growing, *Gynacantha* and *Megaloprepus* (Fincke 1992a). Although we lacked a large-hole treatment with high nutrient input, in another experiment using 8-l artificial holes, cohorts of medium to large *Megaloprepus* and *Gynacantha* regularly reduced the density of mosquito larvae to one to two per liter, despite bimonthly additions of yeast (O.M. Fincke, unpublished data).

Odonates tended to crop the largest larvae available, a habit also found in predatory *Toxorhynchites* (Lounibos et al. 1987b). Consequently, odonates may disproportionately affect large mosquito species, such as *T. theobaldi* and *Orthopodomyia fascipes*. Indeed, in our experiments, *T. theobaldi* colonized pots rather frequently but were never found in the predator treatments. A similar negative correlation between odonates and *Toxorhynchites* was found in water-filled fruit husks (Caldwell 1993) and bamboo internodes (Louton et al. 1996), but not in bromeliads (Lounibos et al. 1987a). Because most odonates frequent the sides and bottom of a tree hole, they may also have a greater impact on benthic prey than on mosquitoes such as *Anopheles eiseni* or *Culex conservator* which feed near the water surface. Finally, mosquito pupae appear less susceptible to odonate predation than mosquito larvae, which are more mobile and less compact in form. Differences among prey species in their susceptibility to odonate predators are currently being investigated.

Mosquitoes are also conspicuously rare in tree holes occupied by two nonodonate predators, *D. auratus* and *T. theobaldi*; both species depress mosquito abundance in experiments analogous to those reported here (O.M. Fincke, unpublished data). However, over an entire wet season and on a forest-wide scale, these nonodonate predators should have less impact on prey species than odonates, which frequent holes for a longer period of time, both as individuals and as species. With low nutrients, odonates would require 7 months or more to emerge as adults (Fig. 3). Although the near-maximum growth rates experienced by the largest *Megaloprepus* larvae in the large pots with low nutrients would minimize individual occupancy time, hatching asynchrony and the continual egg input to large tree holes insure high occupancy throughout the wet season (Fincke 1992b, 1994).

In contrast with odonates, *Toxorhynchites* develops in as little as 3 weeks (Lounibos et al. 1987b), and although it is found in tree holes on BCI throughout the wet season, it can be eliminated from holes occupied by odonates. *D. auratus* requires 2–3 months to metamorphose (Summers 1990), but it is rarely found in tree holes on BCI from September to May. Even at their peak abundance, these two nonodonate predators each occupied less than 10% of tree holes sampled in this study, whereas odonates were found in over three quarters.

Mosquitoes should have the greatest chance of escaping odonate predation (1) early in wet season before odonate eggs have hatched or before odonates have colonized tree holes, (2) immediately after a tree hole is created, as when some trees fall and collect water in trunk depressions, and (3) when odonates are relatively small and/or when nutrients are very high. Because we found odonates persisting in as little as 10 ml of water, very small holes are not necessarily predator-free refugia. Moreover, odonates inhabit tree holes from the forest floor to the canopy (S.P. Yanoviak, unpublished data). On BCI and in the wetter forest of La Selva Biological Station, Costa Rica, water-filled fallen palm fronds and fruit husks are not colonized by odonates, but these phytotelmata are not predator-free sites because *Toxorhynchites*, *Trichoprosopon*, and *Dendrobates* breed there (Fincke 1992a, and personal observation).

Tree hole odonates inhabit mature and secondary forests in aseasonally wet and seasonally dry lowlands of the neotropics (see Corbet 1983), and are also found in Africa (Pinhey 1962; Corbet and McCrae 1981) and Asia (Orr 1994). Because they are often the largest and most common predators in tree holes and smaller phytotelmata (e.g., Calvert 1911; Lounibos et al. 1987a; Caldwell 1993; Louton et al. 1996), which may also harbor disease vectors, odonates merit more attention by ecologists and medical entomologists. For example, the tree hole-breeding *Aedes albopictus*, an effective vector of dengue, and possibly yellow fever and encephalitis viruses (Mitchell 1991; Savage et al. 1992), moves freely between sylvan and urban habitats in tropical regions (Miller and Ballinger 1988). The spread of such disease vectors is inevitably exacerbated by forest clearing, which destroys the habitat of a guild of their most efficient natural predators.

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