The Macrofauna of Water-filled Tree Holes on Barro Colorado Island, Panama[1]

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ABSTRACT

The fauna of water-filled tree holes in Neotropical forests is not well documented. Cumulatively, 54 macroinvertebrate and 5 vertebrate taxa were found in artificial and natural tree holes censused over four wet seasons on Barro Colorado Island, Panama. Most of the species were in the insect order Diptera, occurred as aquatic larvae in tree holes, and were detritivore/omnivores. Half (49%) of the collected species are considered specialists in this and similar container habitats, and three invertebrate taxa were previously unknown from tree holes. Successional patterns were weak in tree holes, but some taxa predictably colonized holes shortly after they were filled. The mosquito *Culex urichii* was more common and abundant in artificial than in natural tree holes; occurrence frequencies and densities of most other taxa were similar between hole types.

RESUMEN

La macrofauna de reservorios de agua en los huecos de los árboles de bosques neotropicales no ha sido bien documentada. En total, 54 grupos de macroinvertebrados y 5 grupos de vertebrados fueron encontrados en huecos artificiales y naturales examinados durante cuatro estaciones lluviosas en la Isla Barro Colorado, Panamá. De las especies encontradas, la mayoría pertenecen al orden Diptera. También, la mayoría ocurren como larvas acuáticas y son detrívoros/omnívoros. Cerca de la mitad (49%) de las especies son consideradas como especialistas en este tipo de hábitat y reservorios similares, y tres grupos de invertebrados no han sido reportados en los huecos de los árboles. No existen patrones de sucesión fuertes en los huecos de los árboles, pero algunos grupos colonizan los reservorios poco tiempo después que están llenos. El mosquito *Culex urichii* fue la especie más común y más abundante en los huecos artificiales que en los huecos naturales; las frequencias y densidades de otras especies fueron similares entre los dos tipos de huecos.

TREE HOLES ARE PHYTOTELMATA (*i.e.,* plant-held waters; Varga 1928) formed by the collection of rainfall in rot holes or natural convolutions in the aboveground woody portions of trees (Kitching 1971). They are among the most abundant standing-water habitats in many tropical and temperate forests. A variety of macroorganisms use tree holes as breeding sites, and many species breed exclusively in this habitat. Larvae of true flies (Diptera) are generally the most common and diverse inhabitants of this system. Because they are primary breeding sites for many disease vectors, especially mosquitoes (Diptera: Culicidae) and biting midges (Diptera: Ceratopogonidae), tree holes are economically important habitats.

The macrofauna of water-filled tree holes is rel-atively well studied in North America (*e.g.,* Jenkins & Carpenter 1946, Snow 1949, Copeland 1989, Barrera 1996, Paradise 1997), Europe (Rohnert 1950, Kitching 1971), Asia (*e.g.,* Kitching 1987; Tsuda *et al.* 1994; Sota 1996, 1998), and Australia (*e.g.,* Kitching & Callaghan 1982, Kitching 1983). In Africa and the Neotropics, most tree hole surveys have focused on mosquitoes and other potential disease vectors (*e.g.,* Dunn 1927; Galindo *et al.* 1950, 1951; Vitale 1977; Lounibos 1981; Lounibos *et al.* 1987). Aside from the work of Snow (1949) in Guatemala and Fincke (1992a, 1998, 1999) in Panama and Costa Rica, the non-mosquito fauna of Neotropical tree holes is poorly known.

Water-filled tree holes are common in lowland, seasonally moist forests of central Panama. They are filled each wet season (May–December), and typically dry up completely by late dry season (*i.e.,* March; Fincke 1992b). Tree holes on Barro Colorado Island (BCI) range in volume from <0.05 to >50 liters (Fincke 1992b, Yanoviak 1999a) and
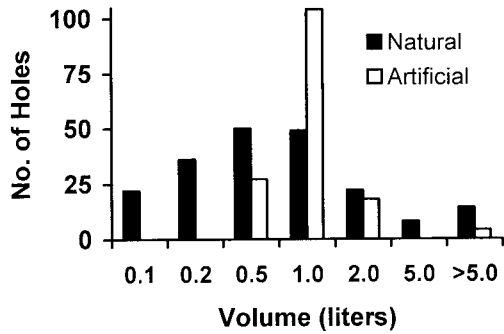
FIGURE 1.   Size (volume) distributions of natural and artificial tree holes examined in this study. $N = 201$ natural holes (5 of 206 holes not measured) and 153 artificial holes.

occur from ground level to the forest canopy (Yanoviak 1999b). The goal of this study was to catalog the common macroorganisms associated with water-filled tree holes on BCI and summarize their ecological roles within the tree hole ecosystem.

METHODS

This study was conducted in the lowland moist forest of BCI, Panama (site description in Leigh *et al.* 1996) and included several tree holes on the mainland (Gigante Peninsula and Pipeline Road in Parque Metropolitano). The same tree hole fauna occurred at all sites; hereafter, I will refer only to tree holes on BCI.

A total of 206 natural water-filled tree holes and 153 artificial tree holes (black plastic cups or pans tied to trees and containing leaf litter, rain water, and an emergent section of tree bark or balsa wood) were sampled on BCI during the wet seasons 1994–1997 (1995–1997 for natural holes). The size distributions of natural and artificial holes examined in this study are shown in Figure 1. Tree holes located >2 m above the ground were accessed using various modifications of the single-rope climbing technique (Perry 1978). I censused the macrofauna of most holes more than once in a year or in successive years; 657 censuses were from natural holes and 1684 from artificial holes. Each hole was censused by removing its contents to a plastic pan and recording the abundance of all species (or morphospecies) present. Except for subsamples needed to confirm species identifications, all contents were returned to the holes. Additional methodological details are summarized in Yanoviak (1999b).

The occurrence frequency (percent of holes oc-

cupied) was determined for each species or higher taxon in natural holes. For holes censused more than once, I used data from the most species-rich census. Mean density (individuals per 0.5 liters where they occurred) was calculated for each species present in a subset of 100 natural holes ≥ 0.2 and ≤ 2.0 liters total volume. This range includes the mean (1.67 liters $\pm$ 0.34 SE) and median (0.46 liters) total volumes for the complete natural hole data set; holes outside this range were not used for density calculations due to problems associated with extrapolation.

The percent occurrence and mean density (as above) of each taxon were calculated in artificial holes using data from 20 repeated censuses of 40 containers used in a vertical stratification study (Yanoviak 1999b). Only data from small (0.65 liter) artificial holes were used for the density calculations ($N = 360$ censuses divided among 18 holes). I did not use the entire artificial tree hole data set (1684 censuses) for density and frequency calculations because many of the 153 containers were in place for relatively short periods of time (creating a bias for early successional species), or were manipulated for experiments. Artificial holes used in the vertical stratification experiment remained in place for more than three years and were not experimentally manipulated. The damselfly *Megaloprepus coerulatus* is a common tree hole inhabitant, but was found only in understory holes (Yanoviak 1999b); therefore, I calculated the frequencies for this species using data only from understory-level natural and artificial holes.

Insect larvae and pupae collected in tree hole subsamples were returned to the insectary or lab for rearing and identification. Immature organisms were fixed and stored in 70 percent ethanol, and adults were killed by freezing and mounted on pins or points. Larvae of chironomid midges and other non-mosquito Diptera were mounted on microscope slides. These specimens were cleared in warm 85 percent lactic acid for 15 to 30 min (Cumming 1992), rinsed in distilled water, dehydrated in ethanol (from 70 to 100 percent in three steps), and mounted in euparal.

Invertebrates were identified to genus and higher taxonomic levels with general references (Stehr 1987, 1991) and specialized references listed in Hurlbert and Villalobos-Figueroa (1982). Mosquito species were determined with keys of Darsie (1993) and an unpublished key to the mosquitoes of Panama (Gorgas Mem. Lab., Ancon, Panama). Taxonomic assistance was provided by H. P. Brown (Coleoptera), J. Gelhaus (Diptera: Tipulidae), P.

Gnaspini (Opiliones), D. Penney (Araneae), R. Pinto da Rocha (Opiliones), G. Poinar (Nematoda), J. Polhemus (Hemiptera), N. Powers (Diptera: Culicidae), A. S. Rand (Vertebrata), P. Spangler (Coleoptera), F. C. Thompson (Diptera: Syrphidae), S. A. Vanan (Coleoptera), and N. Woodley (Diptera: Stratiomyidae). Vouchers were deposited at the Smithsonian Tropical Research Institute, Panama, the U.S. National Museum, Washington DC, the Museu de Zoologia da Universidade de São Paulo, Brazil, and my private collection.

All taxa were classified based on their degree of association with the tree hole habitat following Rohnert's (1950) scheme as translated by Kitching (1971) and Fish (1983). In this system, "dendrolimnetoxene" refers to accidental species in tree holes; "dendrolimnetophile" denotes facultative tree hole inhabitants (*i.e.,* species that occur in a variety of other aquatic or semiaquatic settings); and "dendrolimnetobiont" describes species that occur only in tree holes or similar phytotelmata. For simplicity, I hereafter refer to these groups as "accidental," "facultative," and "specialist" tree hole inhabitants. When the assignment of a taxon to either the facultative or specialist class was uncertain, I used its occurrence frequency in natural tree holes as a deciding factor. These decisions were based on the assumption that species found infrequently in tree holes were using other breeding sites. Alternatively, some of these taxa may be tree hole specialists, but are rare on BCI.

The functional roles of tree hole taxa were determined from the literature (Pennak 1989, Merritt & Cummins 1996) and from observations of feeding behavior in the field and lab. For this study, "detritivores" consumed decaying leaf or woody material; "omnivores" filter fed in the water column or grazed indiscriminately on the surfaces of decaying litter; "predators" consumed other macroorganisms, sometimes conspecifics; and "scavengers" fed on dead macroorganisms trapped in the water surface film.

RESULTS AND DISCUSSION

Fifty-four macroinvertebrate and five vertebrate taxa were found in association with water-filled tree holes on BCI (Table 1). More than half of the species (56%) were in the insect order Diptera. Despite this large number of potential inhabitants, a typical water-filled tree hole on BCI contained five or six ($\bar{x}$ = 5.3; range = 0–14) species of macroorganisms on any wet season day. Multiple factors constrain diversity in individual tree holes on BCI,

including hole size and location, nutrient quality, nutrient quantity, and the presence or absence of top predators (Yanoviak 1999a, b, c, 2001).

Based on the association classes of Rohnert (1950), 15 percent of tree hole-inhabiting species on BCI are accidental, 36 percent are facultative, and 49 percent are tree hole specialists (Table 1). Some species (*e.g.,* of Chironomidae and Syrphidae) were tentatively classed as specialists, but too little is known of their habitat specificity to be certain of this designation.

As in temperate forests (Kitching 1971, Fish & Carpenter 1982), tree holes on BCI are detritus-based systems. Most (61%) species found in BCI tree holes function ecologically as omnivores, detritivores, or both (Table 1). A few species (discussed below) feed directly on decaying leaf or woody material. Omnivores and detritivores are the principal prey of predators in tree holes, although some predators also scavenge on dead or dying insects trapped in the surface film (Yanoviak 1999d; O. M. Fincke, pers. comm.). Unlike temperate tree holes, obligate and facultative predators are common and diverse in BCI tree holes (36% of the non-accidental fauna; Table 1). This pattern is consistent with other temperate–tropical tree hole comparisons (Kitching 1983).

Densities and frequencies of most taxa were similar between natural and artificial tree holes (Table 1); however, density values must be interpreted with caution. Hole size and macroorganism abundance are correlated (Yanoviak 1999a), but the relationship is not linear for many taxa. For example, two or more odonates (including neonates) were often found in 0.5-liter holes (Table 1), but their densities tended to be much lower in larger holes (*cf.* Fincke 1992b, 1998).

NOTES ON SELECTED GROUPS.—The autecology of many tree hole inhabitants is poorly known. Below, I summarize laboratory and field observations on the behavior and ecology of groups commonly encountered in tree holes on BCI.

Microfauna. The microorganism assemblages of water-filled tree holes have been largely ignored (*cf.* Lackey 1940). In addition to the bacteria and fungi responsible for litter decomposition, protists, rotifers, microturbellarians, and ostracods commonly occurred in BCI tree holes, and are considered accidental inhabitants. All were rare or nonexistent in artificial holes, including holes that remained in place for more than three years, suggesting that colonization is slow or requirements for their persistence were not met by the artificial

systems. Mites (Acarina) were never found in natural or artificial tree holes on BCI.

Most of the protists and rotifers encountered in this study were living in association with larval ptilodactylid beetles and larval odonates, especially mid-sized pseudostigmatids (>14 mm body length). Unidentified *Vorticella*-like protists and colonial rotifers successfully colonized virtually all exposed body surfaces of some ptilodactylid and odonate larvae (except the eyes and caudal lamellae of the latter). Accumulations of these groups were often sufficiently dense to make the insects appear as if infected with pathogenic fungi. At least one species of bdelloid rotifer also occurred in smaller numbers on odonate larvae. These solitary rotifers lived in gelatinous tubes (2–3 mm in length) attached to the larger body surfaces of odonates, especially the abdomen.

Two species of ostracods, tentatively identified as *Cypris* sp. (Cyprididae) and *Darwinula* sp. (Darwinulidae), commonly occurred in BCI tree holes. *Cypris* were always less abundant (<50/liter) than *Darwinula* (often >100/liter), and were typically seen swimming freely in the water column. *Darwinula* formed dense aggregations just below the water surface along the tree hole margins and on the edges of leaf litter. Both of these genera are also known from the oxygen-poor bottoms of lakes (Pennak 1989), which in terms of abiotic conditions, are probably very similar to tree holes (Yanoviak 1999b; *cf.* Fincke 1999).

A microturbellarian tentatively identified as *Microstomum* sp. (Platyhelminthes: Turbellaria: Microstomidae) was often very abundant in BCI tree holes; its densities were occasionally high enough (>20/ml) to cloud the tree hole water. At lower abundance, *Microstomum* formed yellowish aggregations on the edges of leaf litter and just below the water surface along the tree hole margin, where they fed on bacteria and other microorganisms (Pennak 1989).

Arachnida. Opilionids (*Cynorta* sp.) and the large ctenid spider *Cupiennius coccineus* often rested on the interior walls of tree holes. Opilionids appeared to use tree holes primarily for diurnal shelter and nesting habitat. Although they occasionally raised their forelegs as if to attack approaching mosquitoes, successful predation by *Cynorta* was not observed. *Cupiennius coccineus* generally perched head-down on the hole wall with their first two pairs of legs on the water surface. It is likely that they fed on adult pseudostigmatid damselflies (Fincke 1992a) and other relatively large insects visiting tree holes to oviposit. When disturbed, the spiders quickly crawled beneath the water surface and clung to detritus, and remained submerged for more than five minutes if necessary.

Pholcid spiders and various species of scorpions sometimes occurred in BCI tree holes. Pholcids typically constructed webs a few centimeters above the waterline and fed on mosquitoes and other small insects entering or exiting the hole. Scorpions used tree holes as diurnal refugia and were not important predators in this system. Scorpions were most often found in dry crevices of slit-type holes (see Fincke 1992b for hole classification), and like ctenid spiders, quickly crawled into the water when disturbed.

Odonata. The dragonfly *Libellula* sp. was a very rare occupant in natural tree holes on BCI; the only natural tree hole occurrence of *Libellula* sp. was in large, highly insolated holes of a recently fallen *Platypodium elegans* near a stream; however, this species sometimes colonized large artificial holes located in treefall gaps and was common in moats surrounding greenhouses.

Larvae of the remaining five species of odonates (along with larvae of the mosquito *Toxorhynchites theobaldi* and *Dendrobates auratus* tadpoles), were the top predators in tree holes. The behavior and ecology of these odonate species have been studied extensively (Fincke 1994, 1998, 1999; Fincke *et al.* 1997; Yanoviak 1999a, 2001).

Hemiptera. *Microvelia cavicola* and *Paravelia myersi* were neustonic predator/scavengers in tree holes. Laboratory experiments and field observations indicated that these species fed on mosquitoes emerging from holes as well as terrestrial insects trapped on the water surface (Yanoviak 1999d).

Coleoptera. Larvae of scirtid beetles were the most abundant and conspicuous coleopterans in natural and artificial tree holes. Adults were rarely seen. Scirtid larvae ate leaf detritus, submerged decaying wood, and associated decomposer microbes. When food was abundant, larvae became adults in about four weeks.

Adults and larvae of the dytiscid beetle *Copelatus* sp. occurred in both natural and artificial tree holes on BCI. Typically, a single adult beetle would colonize an artificial hole within two weeks of setup, and another adult beetle (usually the opposite sex) would appear one or two weeks later. The consistency of this pattern suggests that adult *Copelatus* use pheromones to attract mates to suitable breeding habitats. A second dytiscid, *Laccophilus* sp., was an occasional colonist of large artificial tree holes, especially those located in treefall gaps.

This study is the first to report the occurrence

TABLE 1. *The macrofauna associated with water-filled tree holes on BCI based on 1994–1997 wet season samples. Families and genera are listed alphabetically within higher taxa. Morphospecies are described in Yanoviak (1999a). Life stage = portion of life cycle typically found in tree holes. Functions: O = omnivore; D = detritivore; P = predator; and S = scavenger. Associations: A = accidental; F = facultative; and S = specialist. Frequencies: Nat = percent of 206 natural holes in which a taxon was found; and Art = percent of 800 artificial hole censuses (among 40 holes) in which a taxon was found. * = taxon occurred in some artificial holes, but not the subset used for frequency determination. Density = mean (SD) number of individuals per 0.5 liters where they occurred in 18 artificial holes (360 censuses) and 100 natural holes. [a] = maximum number of individuals per hole. NA = not present in the subset of holes used for density calculations. Frequencies for* Megaloprepus coerulatus *were based on understory censuses only. Density values for many taxa should not be extrapolated to larger holes (cf. Fincke 1998).*

Taxon	Life stage	Functions	Associations	Frequency		Density	
				Nat	Art	Nat	Art
NEMATODA							
Mermithidae	adult	NA	A	1.5	0.3	2[a]	2[a]
ANNELIDA							
Naididae							
Dero sp.	all	O	F	24.8	1.9	16.5 (24.5)	13.3 (8.0)
ARTHROPODA							
Arachnida							
Scorpiones	adult	P	A	1.5	0	1[a]	0
Araneae							
Ctenidae							
Cupiennius coccineus	adult	P	A	1.0	5.6	1[a]	1[a]
Pholcidae	adult	P	A	9.7	0	2[a]	0
Opiliones							
Cosmetidae							
Cynorta sp.	all	P	A	7.3	3.4	2[a]	2[a]
Crustacea							
Gecarcinidae							
Gecarcinus sp.	adult	P, S	A	0.5	0	1[a]	0
Insecta							
Odonata							
Aeshnidae							
Gynacantha membranalis and *Triacanthagyna dentata*	larva	P	S	13.1	16.6	1.4 (1.2)	NA
Libellulidae							
Libellula sp.	larva	P	F	0.8	0*	NA	NA
Pseudostigmatidae							
Mecistogaster linearis and *M. ornata*	larva	P	S	37.4	37.5	1.4 (1.0)	1.3 (0.9)
Megaloprepus coerulatus	larva	P	S	33.0	25.0	1.9 (1.2)	1.5 (0.7)
Hemiptera							
Microvelia cavicola	all	P, S	S	42.2	2.0	5.2 (5.8)	1.0
Paravelia myersi	all	P, S	S	4.4	1.3	0.9 (0.9)	2.0
Coleoptera							
Dytiscidae							
Copelatus sp.	all	P	F	2.4	13.3	1.4 (0.9)	1.2 (0.5)
Laccophilus sp.	all	P	A	0	0*	NA	NA
Ptilodactylidae	larva	D	S	14.6	0.9	3.2 (2.5)	1.0
Scirtidae (Helodidae)							
Prionocyphon sp. and *Scirtes* sp. 1 and 2	larva	D	S	45.1	42.1	8.9 (11.7)	6.6 (5.3)
Diptera							
Ceratopogonidae							
Bezzia snowi, Culicoides spp., and *Dasyhelea* sp.	larva	P D, O	S	33.0	20.4	11.7 (19.1)	10.9 (12.7)
Forcipomyia sp.	larva	O	F	8.3	7.4	9.8 (21.8)	9.7 (15.6)
Chaoboridae							
Corethrella appendiculata	larva	P	S	12.1	0.6	2.7 (1.6)	2.5 (0.7)

TABLE 1.   *Continued.*

Taxon	Life stage	Func-tions	Asso-cia-tions	Frequency		Density	
				Nat	Art	Nat	Art
Chironomidae							
Chironomus sp.	larva	O	S?	25.7	14.4	12.9 (9.0)	6.5 (6.3)
Tanytarsini	larva	O	F	1.0	0	NA	0
Culicidae							
Aedes septemstriatus	larva	O	F	5.3	0.4	3.1	1.7 (1.2)
A. terrens complex	larva	O	S	51.0	71.3	6.7 (7.9)	10.6 (11.2)
Anopheles eiseni	larva	O	F	31.1	15.0	3.8 (4.7)	2.4 (2.2)
Culex allostigma	larva	O, P	F	1.0	2.3	5.0	2.2 (0.8)
C. conservator	larva	O	S	19.9	3.1	4.7 (5.2)	3.7 (1.8)
C. corrigani	larva	O	S	20.4	9.8	12.3 (14.6)	13.6 (17.2)
C. mollis	larva	O	S	21.8	7.9	15.3 (29.4)	14.4 (10.1)
C. secundus and *C. urichii*	larva	O	F	16.0	84.8	4.4 (4.5)	14.6 (22.1)
Haemagogus equinus and *H. lucifer*	larva	O	S	37.9	7.4	5.4 (6.4)	4.3 (4.5)
H. leucotaeniatus	larva	O	S	6.3	2.4	3.9 (2.1)	3.0 (1.4)
Limatus assuleptus and *L. durhamii*	larva	O	F	1.0	1.6	NA	14.1 (12.8)
Orthopodomyia fascipes	larva	O	S	3.4	5.6	7.1 (2.9)	12.2 (18.3)
Toxorhynchites theobaldi	larva	P	S	8.3	1.5	2.0 (1.6)	1.0
Trichoprosopon digitatum	larva	O, P	F	1.0	3.4	2.1	2.3 (1.5)
Psychodidae							
Telmatoscopus sp. 1, 2, and 3	larva	O	F	15.5	4.8	6.0 (7.4)	3.6 (2.8)
Stratiomyidae							
Zuercheria bequaerti	larva	D, O	F	5.3	0.6	1.4 (1.6)	NA
Syrphidae							
Copestylum rafaelanum	larva	D, O	S?	5.8	7.0	1.4 (0.8)	5.3 (6.1)
Species 1	larva	D, O	S?	0.5	0	NA	NA
Tipulidae							
Sigmatomera amazonica, S. occulta, and *S. séguyi*	larva	D, P	S	42.2	36.3	3.4 (3.3)	1.5 (1.0)
VERTEBRATA							
Anura							
Dendrobatidae							
Dendrobates auratus	tadpole	P	F	6.3	3.9	1.8 (2.4)	1.6 (0.5)
Hylidae							
Agalychnis callidryas	tadpole	O	F	2.9	0*	1.0	NA
Leptodactylidae							
Eleutherodactylus spp.	adult	P	A	1.9	3.5	1[a]	1[a]
Physalaemus pustulosus	tadpole	O	F	1.5	0*	11.4	NA
Sauria							
Gekkonidae							
Sphaerodactylus lineolatus	adult	P	A	0.5	2.6	1[a]	2[a]

of ptilodactylid beetles in neotropical water-filled tree holes (P. J. Spangler, pers. comm.). Ptilodactylid larvae were relatively common in natural tree holes on BCI (Table 1), where they fed on submerged decaying wood. Larvae also readily consumed decaying *Ficus yoponensis* leaf litter in the lab. These insects created vertical tunnels in the woody interior of natural holes as they fed, gradually increasing the size and physical heterogeneity of the habitat.

Ptilodactylid larvae appeared to be the longest-lived inhabitants of BCI tree holes, and were highly resistant to desiccation. Their growth was very slow, even when food was provided *ad libitum* in the laboratory, and field observations suggested that two wet seasons are required for development to adulthood. None of the larvae successfully pupated in the lab, and the adults are unknown. Ptilodactylid larvae desiccated in the lab became dormant and appeared dead within 48 hours, but all individuals resumed normal activity when rehydrated (even after three weeks in the air-conditioned en-

vironment). This suggests that these beetles can survive the repeated or persistent drying that occurs in many holes during the dry season on BCI.

Diptera: Culicidae. Mosquitoes of tropical tree holes are relatively well studied because of their role as disease vectors (*e.g.,* Galindo *et al.* 1951). The biology of *Toxorhynchires,* a top predator in tree holes, is especially well known (review in Steffan & Evenhuis 1981), largely due to its potential use as a biological control agent. Bates (1949) and Clements (1992) have thoroughly reviewed the general biology of mosquitoes.

A few of the tree hole mosquito species found in Panama by Galindo *et al.* (1950) and Trapido *et al.* (1955) were not encountered in this study. The absence of these species (*e.g., Sabethes cyaneus*) was due primarily to their ovipositional preference for concealed aquatic habitats with small lateral openings (Galindo *et al.* 1951, 1955). This type of habitat occurs on BCI (*e.g.,* hollow branches of *Pseudobombax septenatum* with 1- to 2-cm exterior openings), and female mosquitoes were often seen ovipositing in them; however, this study focused exclusively on tree holes with exposed water, which explains the absence of *Sabethes* spp. and some *Haemagogus* species from Table 1.

Limatus spp. and *Trichoprosopon digitatum* were rare in natural tree holes on BCI, but colonized almost any recently formed pool of water within 1 m of the ground. These species were found most often in water collected by fallen fruit husks (*e.g.,* of *Tontelea ovalifolia*) and palm spathes, which are their typical breeding sites (Zavortink *et al.* 1983). The few natural tree holes containing *Limatus* spp. and *T. digitatum* were either newly formed (see Succession below) or at ground level.

Diptera: Ceratopogonidae. Ceratopogonid midge larvae (*Bezzia snowi*) frequently swam near the surface of the tree hole water and at the waterline, but were most often encountered partially embedded in the sediment at the bottom of holes. Although *Culicoides* spp. are common inhabitants of temperate tree holes (Snow 1949, Pappas *et al.* 1991), they were rare in my collections. Larvae of *B. snowi* and *Culicoides* spp. fed both singly and gregariously upon mosquito larvae and other small aquatic macroinvertebrates in BCI tree holes. They rapidly advanced toward struggling prey, and as many as 12 *B. snowi* fed on a single mosquito larva. *Bezzia snowi* larvae are also cannibalistic, more so at high densities. The quantitative effects of these secondary predators on the abundance and diversity of other organisms in BCI tree holes are unknown.

Diptera: Chaoboridae (Corethrellidae). *Corethrella appendiculata* was found only in relatively small natural holes, and generally occupied the same individual holes in successive years. These midges are predators of small invertebrates, especially early-instar mosquito larvae (Petersen & Chapman 1969). Although *C. appendiculata* can significantly reduce the abundance of *Aedes triseriatus* in tree holes of Florida (Lounibos 1983, 1985; *cf.* Bradshaw & Holzapfel 1983), their effect on mosquito abundance and invertebrate community structure in tree holes of Panama is unknown.

Diptera: Chironomidae. Larvae of *Chironomus* sp. lived in small (1 cm) vertically orientated silken tubes on the bottom and interior walls of tree holes. Examination of gut contents showed that the larvae fed omnivorously on decomposer microbes and fine particulate matter. *Chironomus* densities were occasionally >50/liter in both natural and artificial holes. Larvae of Tanytarsini also were found in two natural holes, and are presumed accidental colonists of this system. Generic identification of these individuals was not possible because only females were reared.

Diptera: Syrphidae. At least two species of syrphid flies developed in water-filled tree holes on BCI; *Copestylum rafaelanum* was the most common (Table 1). Adult female syrphids were apparently attracted to volatile compounds released when a hole was disturbed. On several occasions, up to three female *C. rafaelanum* landed and began ovipositing as a hole was being sampled. Adult males were never seen in the field, and adult females were never encountered at undisturbed holes. A female preparing to oviposit perches head-downward on moist bark 5–25 cm above the tree hole water surface and probes the bark with its ovipositor. Eggs are inserted singly into separate bark crevices and development to adulthood requires about six weeks in the field.

Adults of a second syrphid species visited a large hole 17 m above the ground in a *Dipteryx panamensis* tree while it was being sampled. Attempts to collect these adults and to rear larvae were unsuccessful. This species was never found in artificial tree holes.

Diptera: Tipulidae. All three *Sigmatomera* species occurred in natural and artificial tree holes, and were found in holes at all heights in the forest. *Sigmatomera séguyi* was the most commonly encountered species (*ca* 70% of collected individuals). Adult female *Sigmatomera* spp. laid their eggs in the moist margins of tree holes. A female preparing to oviposit would perch 2–10 cm above the water

surface in the shade and out of plain view. It then curled its abdomen ventrad (more or less forming an S-shape) and inserted its bladelike ovipositor into a bark crevice. Oviposition was rarely observed during daylight hours (*i.e.,* only under dark overcast skies), and probably occurs more often at night, or at dawn or dusk.

Each *Sigmatomera* larva lived in a tube constructed of silken material secreted from the mouthparts. Feces and debris were incorporated into the tube, which was ≥4 times the length of the larva. Tubes typically were constructed in a U-shape with two openings at or above the water surface on the interior sides of the hole. Second instar larvae required six to eight weeks to complete development in the lab, pupation occurred at an exposed end of the silk tube, and adults emerged in five to seven days.

Sigmatomera larvae fed on decaying leaf material and the attached decomposer microfauna, but also preyed on mosquito larvae (Alexander 1930, Snow 1949, Fish 1983) and presumably ate other insects browsing the surfaces of detritus in natural holes. Passing mosquitoes were subdued either by contacting the tipulid mouthparts, or by becoming entangled in additional tipulid silk secreted in their immediate vicinity. Fresh silk appeared to be more effective at prey capture than older silk (which the tipulid larvae often consumed; *cf.* Fish 1983). As noted by Shannon (in Alexander 1930), the sticky silk is a very attractive food source for mosquito larvae.

Vertebrates. The frogs *Agalychnis callidryas, D. auratus,* and *Physalaemus pustulosus* used water-filled tree holes as breeding sites. *Dendrobates auratus* tended to colonize holes in the early part of the wet season (Fincke 1999) and generally were found in the same holes year after year (Yanoviak, pers. obs.). *Agalychnis callidryas* and *P. pustulosus* breed in a variety of aquatic habitats (Rand 1983, Scott 1983) and were less common than *D. auratus* in natural holes on BCI (Table 1). Although they sometimes occurred in large understory holes (Fincke 1998), *A. callidryas* tadpoles were most often found in large holes >2 m above the ground, especially holes in freestanding *Ficus* spp. Adult *P. pustulosus* are poor vertical climbers; their egg masses and tadpoles occurred only in understory holes. All three amphibian species also colonized artificial holes (Table 1), and *D. auratus* tadpoles were occasionally found in water collected by fallen palm spathes.

Adult *Eleutherodactylus* spp. frogs and the gecko *Sphaerodactylus lineolatus* did not breed in tree holes, but used the habitat as a source of shelter and probably fed opportunistically on emerging or colonizing insects. *Sphaerodactylus lineolatus* was most often encountered in the forest canopy, where it was also associated with vascular epiphytes (G. Zotz, pers. comm.). Male and female *S. lineolatus* were sometimes found in the same hole, and juveniles occurred with adults on several occasions. I never found more than one *Eleutherodactylus* in a hole. Like some of the arachnids, the frogs and geckos quickly crawled beneath the water surface and hid among the detritus when disturbed.

Miscellaneous taxa. *Dero* sp. (Annelida) were common in natural tree holes on BCI, where they sometimes formed conspicuous, dense, reddish-brown aggregations on detritus and at the waterline. They fed on decaying litter and decomposer microbes. The lower frequency of *Dero* in artificial holes (Table 1) may have been due to their limited dispersal ability.

This study is the first to report the presence of mermithid nematodes in Neotropical water-filled tree holes. Their occurrence in this habitat may have resulted from infected spiders or terrestrial insects visiting tree holes in search of water (Poinar 2000); however, the possibility that certain tree hole specialist taxa are occasionally infected cannot be completely dismissed.

Land crabs (*Gecarcinus* sp.) were infrequently found in natural tree holes at or near the ground, where they were a significant source of disturbance. *Gecarcinus* commonly redistributed the detritus in a hole (or removed it completely) over a period of days, probably in search of invertebrate prey. In addition, *Gecarcinus* occasionally foraged in the moist detritus of dry tree holes. Other visitors, such as coatis (*Nasua narica*) and spider monkeys (*Ateles geoffroyi*), similarly disturbed wet and dry tree holes on BCI (Fincke 1992b; Yanoviak, pers. obs.).

SUCCESSION.—Most facultative and specialist macroorganism species could be found in BCI tree holes at any time during the wet season, but several taxa colonized holes primarily during the first several weeks after filling. This was most evident in small holes that dried and refilled frequently, and new holes created when large trees with fluted trunks (*e.g., P. elegans* and *Quararibea astrolepis*) fell and collected rain water. The mosquitoes *Culex corrigani, C. mollis, C. urichii,* and sometimes *Limatus* spp., were generally the most abundant macroorganisms in newly filled tree holes on BCI. If the new hole was within 1 m of the ground, the mosquito *T. digitatum* was sometimes present. Psy-

chodidae, Chironomidae, Ceratopogonidae, and the syrphid *C. rafaelanum* were additional early colonists. Whereas many of the species listed above may continue to colonize holes for several weeks or months, *Limatus* and *T. digitatum* generally stopped colonizing two to four weeks after a hole filled, and the density of *C. rafaelanum* larvae declined from >100 to <3/liter (Yanoviak 1999c).

Taxa appearing later in a hole (≥4 weeks after filling) included pseudostigmatid damselflies, aeshnid dragonflies, ptilodactylid beetles, the mosquito *Aedes terrens,* and scirtid beetles. Some of these taxa can survive periodic desiccation (Fincke 1994) and may pass the dry season by burrowing into the litter or sediment accumulated in the bottom of a hole. As a consequence, these "late" species sometimes appeared in older holes (*i.e.,* with substantial sediment accumulations) less than 24 hours after they were refilled.

ARTIFICIAL VERSUS NATURAL TREE HOLES.—Although the fauna of natural and artificial tree holes was similar in overall composition and density, a few species differed in their frequency of occurrence between hole types (Table 1). Some of these differences could be attributed to the size, location, and physical characteristics of artificial holes relative to natural holes. For example, the absence of the frog *A. callidryas* from the artificial tree hole censuses was due to the relatively small size of containers used in the vertical stratification study; only 14 percent were more than three liters in volume (Fig. 1; Yanoviak 1999b). In addition, all of the artificial tree holes were secured to trees ≥1 m above ground level, which prevented them from being visited by the crab *Gecarcinus* sp. or colonized by the frog *P. pustulosus.*

The greater frequency of *C. urichii* (and to a much lesser extent, *C. secundus*) in artificial holes versus natural holes was perhaps the most important faunistic difference between hole types. Unlike natural holes, *C. urichii* was often the most abundant mosquito species in artificial tree holes (Table 1). This difference, as well as differences in frequencies of *Haemagogus* spp., other *Culex* spp., and the hemipteran *M. cavicola,* was attributable to the greater exposure of artificial holes versus natural holes. *Culex urichii* was a common inhabitant of water collected by fallen palm spathes (Bates 1949; Yanoviak, pers. obs.), and may have oviposited preferentially in habitats with highly exposed surfaces. The opposite was probably true for some *Haemagogus* spp. (Galindo *et al.* 1951, 1955) and *M. cavicola* (Yanoviak 1999d).

Water-filled tree holes on BCI (and other forested sites in central Panama) are occupied or visited by a diverse macrofauna that is dominated by detritivorous and omnivorous insect larvae, especially Diptera. Aside from Snow's (1949) study, this is the most comprehensive investigation of organisms using tree hole habitats in the Neotropics. More intensive collections of larvae and adults are needed to complete the species list for some (*e.g.,* non-mosquito) groups. Detailed ecological information remains sparse for most tree hole species, especially secondary and facultative predators.

ACKNOWLEDGMENTS

LITERATURE CITED

ALEXANDER, C. P. 1930. The genus *Sigmatomera* Osten Sacken with observations on the biology by Raymond C. Shannon. Encycl. Entomol. 5: 155–162.

BARRERA, R. 1996. Species concurrence and the structure of a community of aquatic insects in tree holes. J. Vector Ecol. 21: 66–80.

BATES, M. 1949. The natural history of mosquitoes. Macmillan, Gloucester, Massachusetts.

BRADSHAW, W. E., AND C. M. HOLZAPFEL. 1983. Predator-mediated, non-equilibrium coexistence of tree-hole mosquitoes in southeastern North America. Oecologia 57: 239–256.

CLEMENTS, A. 1992. Biology of mosquitoes. Vol. 1. Development, nutrition, and reproduction. Chapman and Hall, New York, New York.

COPELAND, R. S. 1989. The insects of treeholes of northern Indiana with special reference to *Megaselia scalaris* (Diptera: Phoridae) and *Spilomyia longicornis* (Diptera: Syrphidae). Great Lakes Entomol. 22: 127–132.

CUMMING, J. 1992. Lactic acid as an agent for macerating Diptera specimens. Fly Times 8: 7.

DARSIE, R. F., JR. 1993. Keys to the mosquitoes of Costa Rica. International Center for Disease Control, Columbia, South Carolina.

DUNN, L. H. 1927. Tree-holes and mosquito breeding in west Africa. Bull. Entomol. Res. 18: 139–144.
FINCKE, O. M. 1992a. Interspecific competition for tree holes: consequences for mating systems and coexistence in Neotropical damselflies. Am. Nat. 139: 80–101.
———. 1992b. Behavioural ecology of the giant damselflies of Barro Colorado Island, Panama. *In* D. Quintero and A. Aiello (Eds.). Insects of Panama and Mesoamerica, pp. 102–113. Oxford University Press, Oxford, England.
———. 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation, and habitat drying. Oecologia 100: 118–127.
———. 1998. The population ecology of *Megaloprepus coerulatus* and its effect on species assemblages in water-filled tree holes. *In* J. P. Dempster and I. F. G. McLean (Eds.). Insect populations in theory and in practice, pp. 391–416. Kluwer Academic, Dordrecht, The Netherlands.
———. 1999. Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority. Ecol. Entomol. 24: 13–23.
———, S. P. YANOVIAK, AND R. D. HANSCHU. 1997. Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. Oecologia 112: 244–253.
FISH, D. 1983. Phytotelmata: flora and fauna. *In* J. H. Frank and L. P. Lounibos (Eds.). Phytotelmata: terrestrial plants as hosts for aquatic insect communities, pp. 1–27. Plexus, Medford, New Jersey.
———, AND S. R. CARPENTER. 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. Ecology 63: 283–288.
GALINDO, P., S. J. CARPENTER, AND H. TRAPIDO. 1951. Ecological observations on forest mosquitoes of an endemic yellow fever area in Panama. Am. J. Trop. Med. 31: 98–137.
———, ———, AND ———. 1955. A contribution to the ecology and biology of tree hole breeding mosquitoes of Panama. Ann. Entomol. Soc. Am. 48: 158–164.
———, H. TRAPIDO, AND S. J. CARPENTER. 1950. Observations on diurnal forest mosquitoes in relation to sylvan yellow fever in Panama. Am. J. Trop. Med. 30: 533–574.
HURLBERT, S. H., AND A. VILLALOBOS-FIGUEROA (Eds.). 1982. Aquatic biota of Mexico, Central America, and the West Indies. San Diego State University, San Diego, California.
JENKINS, D. W., AND S. J. CARPENTER. 1946. Ecology of the tree hole breeding mosquitoes of Nearctic North America. Ecol. Monogr. 16: 31–47.
KITCHING, R. L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. J. Anim. Ecol. 40: 281–302.
———. 1983. Community structure in water-filled treeholes in Europe and Australia—comparisons and speculations. *In* J. H. Frank and L. P. Lounibos (Eds.). Phytotelmata: terrestrial plants as hosts for aquatic insect communities, pp. 205–222. Plexus, Medford, New Jersey.
———. 1987. A preliminary account of the metazoan food webs in phytotelmata from Sulawesi. Malay. Nat. J. 41: 1–12.
———, AND C. CALLAGHAN. 1982. The fauna of water-filled tree holes in box forest in south-east Queensland. Aust. Entomol. Mag. 8: 61–70.
LACKEY, J. B. 1940. The microscopic flora and fauna of tree holes. Ohio J. Sci. 40: 186–192.
LEIGH, E. G., JR., A. S. RAND, AND D. M. WINDSOR (Eds.). 1996. The ecology of a tropical forest, 2nd edition Smithsonian Institution, Washington, DC.
LOUNIBOS, L. P. 1981. Habitat segregation among African treehole mosquitoes. Ecol. Entomol. 6: 129–154.
———. 1983. The mosquito community of treeholes in subtropical Florida. *In* J. H. Frank and L. P. Lounibos (Eds.). Phytotelmata: terrestrial plants as hosts for aquatic insect communities, pp. 223–246. Plexus, Medford, New Jersey.
———. 1985. Interactions influencing production of treehole mosquitoes in south Florida. *In* L. P. Lounibos, J. R. Rey, and J. H. Frank (Eds.). Ecology of mosquitoes: proceedings of a workshop, pp. 65–77. Florida Medical Entomology Laboratory, Vero Beach, Florida.
———, J. H. FRANK, C. E. MACHADO-ALLISON, P. OCANTO, AND J. C. NAVARRO. 1987. Survival, development, and predatory effects of mosquito larvae in Venezuelan phytotelmata. J. Trop. Ecol. 3: 221–242.
MERRITT, R. W., AND K. W. CUMMINS (Eds.). 1996. An introduction to the aquatic insects of North America, 3rd edition Kendall-Hunt, Dubuque, Iowa.
PAPPAS, L. G., S. MOYER, AND C. D. PAPPAS. 1991. Tree hole *Culicoides* (Diptera: Ceratopogonidae) of the Central Plains in the United States. J. Am. Mosq. Control Assoc. 7: 624–627.
PARADISE, C. J. 1997. Abiotic and biotic factors controlling the structure of insect treehole communities. Ph.D. dissertation. Pennsylvania State University, College Park, Pennsylvania.
PENNAK, R. W. 1989. Fresh-water invertebrates of the United States. John Wiley and Sons, New York, New York.
PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.
PETERSEN, J. J., AND H. C. CHAPMAN. 1969. Chemical factors of water in tree holes and related breeding of mosquitoes. Mosq. News 29: 29–36.
POINAR, G. JR. 2000. *Heydenius araenus* n. sp. (Nematoda: Mermithidae), a parasite of a fossil spider, with an examination of helmiths from extant spiders (Arachnida: Araneae). Invert. Biol. 119: 388–393.
RAND, A. S. 1983. *Physalaemus pustulosus. In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 412–415. University of Chicago Press, Chicago, Illinois.
ROHNERT, U. 1950. Wassererfüllte Baumhöhlen und ihre Besiedlung. Ein Beitrag zur Fauna dendrolimnetica. Arch. Hydrobiol. 44: 472–516.

Scott, N. J. 1983. *Agalychnis callidryas. In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 374–375. University of Chicago Press, Chicago, Illinois.

Snow, W. E. 1949. The Arthropoda of wet tree holes. Ph.D. dissertation. University of Illinois, Urbana, Illinois.

Sota, T. 1996. Effects of capacity on resource input and the aquatic metazoan community structure in phytotelmata. Res. Popul. Ecol. 38: 65–73.

———. 1998. Microhabitat size distribution affects local difference in community structure: metazoan communities in treeholes. Res. Popul. Ecol. 40: 249–255.

Steffan, W. A., and N. L. Evenhuis. 1981. Biology of *Toxorhynchites.* Annu. Rev. Entomol. 26: 159–181.

Stehr, F. W. (Ed.). 1987. Immature insects. Vol. 1. Kendall-Hunt, Dubuque, Iowa.

———. 1991. Immature insects. Vol. 2. Kendall-Hunt, Dubuque, Iowa.

Trapido, H., P. Galindo, and S. J. Carpenter. 1955. A survey of forest mosquitoes in relation to sylvan yellow fever in the Panama isthmian area. Am. J. Trop. Med. Hyg. 4: 525–542.

Tsuda, Y., M. Takagi, and Y. Wada. 1994. Ecological study on mosquito communities in tree holes in Nagasaki, Japan, with special reference to *Aedes albopictus* (Diptera: Culicidae). Jpn. J. Sanit. Zool. 45: 103–111.

Varga, L. 1928. Ein interessanter Biotop der Biocönose von Wasserorganismen. Biol. Zentralbl. 48: 143–162.

Vitale, G. 1977. *Culicoides* breeding sites in Panama. Mosq. News 37: 282.

Yanoviak, S. P. 1999a. Community ecology of water-filled tree holes in Panama. Ph.D. dissertation. University of Oklahoma, Norman, Oklahoma.

———. 1999b. Community structure in water-filled tree holes of Panama: effects of hole height and size. Selbyana 20: 106–115.

———. 1999c. Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in neotropical tree hole microcosms. Oecologia 120: 147–155.

———. 1999d. Distribution and abundance of *Microvelia cavicola* Polhemus (Heteroptera: Veliidae) on Barro Colorado Island, Panama. J. New York Entomol. Soc. 107: 38–45.

———. 2001. Predation, resource availability, and community structure in Neotropical water-filled tree holes. Oecologia 126: 125–133.

Zavortink, T. J., D. R. Roberts, and A. L. Hoch. 1983. *Trichoprosopon digitatum*—morphology, biology, and potential medical importance. Mosq. Syst. 15: 141–149.