

DISTRIBUTION AND ABUNDANCE OF *MICROVELIA CAVICOLA* POLHEMUS (HETEROPTERA: VELIIDAE) ON BARRO COLORADO ISLAND, PANAMA

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Abstract.—Data and observations from 1995, 1996 and 1997 wet season surveys of natural and artificial tree holes suggest that hole morphology and size are important predictors of the distribution and abundance of *Microvelia cavicola* Polhemus. The bugs occurred in 42% of the natural holes sampled and <3% of artificial hole censuses. The distribution of *M. cavicola* was not associated with holes in particular tree species or with hole height above the ground. Abundance increased with hole size and decreased with hole height. Analyses of presence/absence data showed significant within- and between-year microhabitat fidelity in this species. *Microvelia cavicola* reduced the emergence success of mosquitoes in a laboratory experiment, but their quantitative effect on mosquitoes in natural conditions is unknown.

INTRODUCTION

Tree holes are phytotelmata (i.e., plant-held water) formed by the collection of rainfall in rot holes or other cavities in the woody portions of trees (e.g., Kitching, 1971). A variety of macroorganisms use tree holes as breeding sites, and more than 50 invertebrate species are directly or indirectly associated with water-filled tree holes in Panama (Yanoviak, 1999a). The behavior and ecology of some of these taxa, such as odonates (Fincke, 1992a, 1992b, 1994, 1998) and mosquitoes (Galindo et al., 1950, 1951, 1955) are well documented. Aside from Snow's (1949) work in Guatemala, relatively little is known about the biology of the many other invertebrates that use this habitat.

Numerous biotic factors, including predation (e.g., Bradshaw and Holzapfel, 1983), competition (e.g., Fincke, 1992b; Juliano 1998), and nutrient availability (e.g., Srivastava and Lawton, 1998; Yanoviak, 1999b), may affect the presence or absence of invertebrate species in water-filled tree holes and similar habitats. In Panama, abiotic characteristics of tree holes, such as size, shape, disturbance frequency, and height above the ground additionally influence the distributions of some organisms (Galindo et al., 1951; Fincke, 1998, 1999; Yanoviak, 1999c).

Two genera of neustonic true bugs (Heteroptera: Veliidae), *Microvelia* Westwood and *Paravelia* Breddin, live and breed in neotropical phytotelmata (Drake and Hussey, 1954; Polhemus and Polhemus, 1991), including water-filled tree holes. The goals of this study were to: 1) describe the abundance, local distribution and behavior of a new *Microvelia* species, *M. cavicola* (Polhemus, 1999), discovered in water-filled tree holes of Panama; and 2) determine how the distribution of *M. cavicola* is related to factors such as tree species, hole volume, and hole height above the ground.

METHODS

This study was conducted in the lowland moist forest of Barro Colorado Island (BCI), Panama (see Leigh et al., 1996 and Leigh, 1999 for site description). Tree holes, the only known natural habitat of *M. cavicola*, are common and broadly distributed in the BCI forest. Most holes contain water throughout the wet season (May through December) and many (especially small or exposed holes) dry completely by March (Fincke, 1992b).

All individuals of *M. cavicola* used in this study were collected with an aspirator from the tree hole water surface and interior walls. Live specimens were transported to the laboratory for identification and behavioral observations. Only a portion of the population within a hole was removed on a collection date. Voucher specimens were killed in 80% ethanol, mounted on points, and deposited as allotypes (Polhemus, 1999).

Field. The abundance of *M. cavicola* in artificial and natural tree holes on BCI was recorded during three consecutive wet seasons: May–December 1995, May–August 1996, and July–December 1997. The same artificial holes (0.65 l and 1.5 l black plastic containers tied to trees at three different heights and filled with leaf litter, rain water, and an emergent piece of tree bark) were censused every year as part of a vertical stratification study (Yanoviak, 1999c). Natural holes were censused in a variety of tree species, but most sampled holes were in *Dipteryx panamensis* (Pitt.) Rec. and Mell (Fabaceae; 20%), two free-standing *Ficus* species (*F. insipida* Willd. and *F. yoponensis* Desv.; Moraceae; 16%), *Gustavia superba* (H.B.K.) Berg (Lecythidaceae; 8%), or *Platypodium elegans* J. Vogel (Fabaceae; 28%). Volumes of most of the natural holes were determined by removing water with a turkey baster into a graduated cylinder. Volumes of the largest holes and surface areas for all holes were estimated from dimensions of appropriately shaped polygons. Tree hole height and volume were not correlated ($R = 0.164$, $P = 0.13$, $N = 87$). Volume was used as a measure of overall hole size for analyses because volume and surface area were correlated (1996 natural hole data; $R = 0.803$, $P < 0.0001$, $N = 52$; also see Fincke 1994). Additional methodological details and summaries of tree hole characteristics are presented elsewhere (Yanoviak, 1999a, c).

Host-tree specificity was analyzed with a chi-square test using *M. cavicola* presence/absence data for natural holes in the tree species listed above (*Ficus* spp. pooled for analysis). I only used data from the first occurrence of *M. cavicola* in each hole to prevent pseudoreplication (Hurlbert, 1984) and avoid possible effects of disturbance caused by hole sampling.

During 1996 field surveys, it appeared that a hole containing *M. cavicola* on the first sample date was more likely to contain this species on later sample dates than holes from which it was initially absent. Two separate chi-square analyses were used to address this site fidelity question. The first chi-square tested short term site fidelity with the null hypothesis of no association between presence of the bugs in the first sample of a hole and any of the four subsequent samples (pooled) for the 1996 natural hole data. In the same manner, the second chi-square tested for long term site fidelity among 25 holes sampled in both 1995 and 1996. The expected value for each cell in the contingency tables was the product of presence/absence probabilities determined from the total number of holes sampled in each census period. Data from

1997 censuses were excluded because some holes were frequently disturbed or manipulated for experiments.

Laboratory. I maintained several subpopulations of *M. cavicola* in clear glass or plastic dishes in the laboratory (24 ± 0.5 °C; irregular lighting conditions) for observations of feeding behavior and adult longevity. Each culture dish (ca. 10 cm diam., 1.5 cm deep) was filled to a depth of 0.5 cm with rain water and contained ≤ 30 bugs. Cork disks (10 mm diameter, 2 mm thick) served as perching sites and the dishes were kept covered except during observations. Live food (one dealated tortricid moth per dish) was supplied weekly. I removed prey remains after 24 hr and replaced the dish water every 7–10 d to prevent fungal growth. Lab populations of *M. cavicola* were maintained for up to 60 d before all cultures were terminated.

The effects of *M. cavicola* on mosquito emergence success were determined by placing 10 adult *M. cavicola* starved ≥ 3 d in a plastic cup (8.5 cm height, 5.5 cm diameter) containing 50 ml rain water, a stick perch, and four pupae of the tree hole mosquito *Culex urichii* (Coquillett). Control cups lacked *M. cavicola*. The experiment was replicated seven times, and new predators and prey were used in each replicate. Cups were individually covered with netting (0.5 mm mesh) to prevent escape of veliids and adult mosquitoes. Each cup was checked at least twice daily and the experiment was terminated when all mosquitoes emerged or were dead (ca. 2 d). The average number of mosquitoes surviving to adulthood was compared between treatments with a t-test assuming unequal variance.

RESULTS

Microvelia cavicola was found in 87 (42%) of the 206 different natural holes sampled over the three years. Their presence or absence was not significantly associated with tree species ($\chi^2 = 5.35$, $df = 3$, $P > 0.10$). The bugs occurred in 10 (1.9%) of the 520 artificial hole censuses in 1995, 3 (2.5%) of 120 censuses in 1996, and 3 (1.9%) of 160 censuses in 1997. Their abundance never exceeded 2 individuals per artificial hole.

Half (53%) of the natural holes in which *M. cavicola* was found contained 3 or more individuals. Where the bugs occurred, their mean (\pm SE) abundance was 10.5 ± 1.5 individuals per hole. The average density of *M. cavicola* (individuals per cm^2 surface area) was greater in highly shaded holes (0.13 ± 0.03 ; $N = 29$) than in more exposed holes (0.03 ± 0.01 ; $N = 25$, $t = 2.66$, $P = 0.01$). The largest number of individuals recorded in a census (70) occurred in a large, shaded, pan-shaped hole in the base of a mature *Pseudobombax septenatum* (Jacq.) Dug. (Bombacaceae).

Adults and immatures of *M. cavicola* were found at all heights and in all size classes of holes censused except those < 100 ml in volume (Fig. 1). Natural holes containing *M. cavicola* were larger than holes lacking the bugs ($t = 5.86$, $P < 0.0001$). Abundance of *M. cavicola* in natural holes increased with hole volume and weakly declined with hole height (Fig. 1, Table 1). However, exclusion of data from holes > 17 m above the ground ($N = 4$) nullified the significant slope of the height-abundance relationship ($t = -1.70$, $P > 0.05$).

Of the 43 natural holes repeatedly sampled in 1996, 15 (35%) contained one or more bugs on the first sample date and 22 (51%) never contained *M. cavicola*. The association between their presence in a hole on the first sample date and any sub-

Table 1. Multiple regression output for effects of tree hole volume and height on *Microvelia cavicola* abundance. $N = 87$ natural holes containing one or more individuals. Data were log-transformed before analysis to correct variance heterogeneity (Sokal & Rohlf 1981). Model: $F_{2,84} = 20.02$, $P = 0.0001$, $R^2 = 0.323$. ** = $P < 0.01$

Variable	Estimate	SE	t
y-intercept	-1.324	0.334	-3.97**
Height	-0.221	0.074	-2.97**
Volume	0.656	0.109	6.00**

sequent sample date was significantly different from random ($\chi^2 = 10.95$, $df = 1$, $P < 0.001$). Of the 25 natural holes censused in both 1995 and 1996, 11 contained *Microvelia* in 1995. Nine (82%) of these 11 again contained *M. cavicola* in 1996. This association was also significantly different from random ($\chi^2 = 15.62$, $df = 1$, $P < 0.001$).

Mosquito emergence success was significantly reduced by *M. cavicola* in the laboratory-based predation experiment (Fig. 2). The density of veliids used in the experiment (0.42 cm^{-2} surface area) was greater than the mean (\pm SE) density for small natural holes (area $< 200 \text{ cm}^2$; 0.14 ± 0.04 , $N = 15$), but was still less than the maximum density (0.46 cm^{-2}) of *M. cavicola* observed in the field. This artificially high predator abundance was balanced by the experimental prey density (0.08 ml^{-1}), which was greater than the average mosquito density (0.02 ± 0.006 ; $N = 15$, including larvae and pupae) observed in small natural holes.

Examination of mosquito remains indicated that most were attacked shortly after exposure of the thorax during emergence. On several occasions, I observed *M. cavicola* probing the thoracic horns of mosquito pupae visiting the surface, and in every case the pupae responded by immediately descending into the water column. Six pupae in the predator treatment (none in controls) were found dead with no evidence of an emergence attempt.

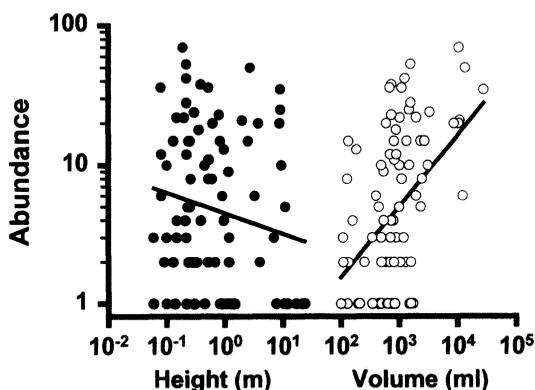


Fig. 1. Effect of tree hole height (filled circles) and volume (open circles) on *Microvelia cavicola* abundance in the 87 natural holes where it occurred. Mean (\pm SE) height = 2.6 ± 0.5 m and volume = 1992 ± 425 ml.

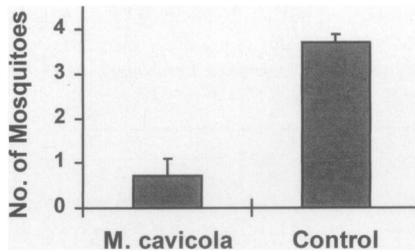


Fig. 2. Mean (+SE) number of mosquitoes successfully emerging from cups containing *M. cavicola* and control cups lacking *M. cavicola*. $t = 8.82$, $df = 10$, $P < 0.001$

In field and lab feeding trials, *M. cavicola* rapidly attacked prey struggling in the surface film. Prey were quickly subdued and their activity typically stopped <1 min after arrival of the first bug. In the lab, more than 20 *M. cavicola* were observed to feed simultaneously on a single moth by initially aggregating side to side and then climbing over one another as foraging space became limited. The last few individuals to arrive at a prey item were often denied access by interference from those already feeding. Although aggressive interactions among individuals were frequent in the lab and the field, there was no evidence of cannibalism, even during prolonged periods (i.e., >10 d) of food limitation. Only one of the >200 *M. cavicola* kept in captivity died during the 60 d study period.

DISCUSSION

Hole morphology, exposure, and size appear to be important factors limiting the distribution of *M. cavicola* in the BCI forest. Their greatest density occurred in slit-type natural holes (see Fincke, 1992b for classification) or bowl-type holes with steep sides and a shaded or concealed water surface. The low occurrence (and abundance) of veliids in artificial tree holes was probably because the water surface in the containers was more exposed than in natural holes. Where *M. cavicola* did occur, its abundance increased with hole size (Fig. 1). Mosquitoes, which are potential prey for veliids (Frick, 1949; this study), also tend to increase in abundance with hole volume (e.g., Lounibos, 1983). Although larger holes are often more exposed, the greater (in absolute terms) availability of prey and spatial resources probably facilitates the coexistence of large numbers of *M. cavicola*, which interact aggressively when food is scarce.

The distribution of *M. cavicola* in the BCI forest differs markedly from that of the Old World veliid *Cylicovelia kenyana* Polhemus and Copeland, the only other tropical tree hole species for which local occurrence and abundance data have been collected. Polhemus and Copeland (1996) found a significant positive association between hole height and the presence of *C. kenyana*, but only sampled holes to a maximum height of 6.4 m. My results showed a weak negative relationship between tree hole height and *M. cavicola* abundance on BCI. *Cylicovelia kenyana* also differs from *M. cavicola* in that it does not occur in shaded tree holes and its presence or absence is independent of hole volume (Polhemus and Copeland, 1996).

There are at least two explanations for the short-term and long-term site fidelity

exhibited by *M. cavicola* in BCI tree holes. First, the bugs may be highly microsite-selective both within and between years such that consistency in their occurrence reflects non-random annual recolonization of "preferred" holes. A second possibility is that current *M. cavicola* distributions represent many years of population persistence in certain holes, i.e., holes that are sufficiently large or sheltered to resist complete drying. The local distribution of *M. cavicola* is probably limited by both availability of suitable tree holes and habitat disturbance frequency, but detailed investigations of dispersal, colonization, and possible dry season diapause are needed to determine the degree to which each of these (or other) explanations are applicable.

The feeding behavior of *M. cavicola* is similar to that described for other members of the genus (Bueno, 1910, 1917; Frick, 1949; Travers, 1993). Adult mosquitoes and other mobile insects visiting tree holes (e.g., to oviposit) are not typically eaten by *M. cavicola* (pers. obs.); the most common sources of food appear to be dead and dying invertebrates that become trapped in the water surface film (Bueno, 1910, 1917), and insects in the process of emerging from the water. The rapid and direct movement of *M. cavicola* to struggling prey suggests that they locate food by detecting water surface vibrations (Travers, 1993). Although not observed in this study, Hoffmann (1924) noted that *Microvelia* can also capture prey occurring just beneath the water surface. This sort of predation may explain the apparent drowning deaths of mosquito pupae in the lab experiment. The effect of *M. cavicola* on mosquito survivorship under completely natural circumstances is not known, but may be important when abundance of the bugs in a hole is high relative to mosquito abundance.

Growth rates of *M. cavicola* in the lab were similar to those described for temperate (Bueno, 1910, 1917) and tropical (Frick, 1949) congeners (pers. obs.). The longevity of individuals in the lab suggests that ≥ 2 generations are produced each wet season and that adults are relatively long-lived.

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