CONTAINER COLOR AND LOCATION AFFECT MACROINVERTEBRATE COMMUNITY STRUCTURE IN ARTIFICIAL TREEHOLES IN PANAMA

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ABSTRACT

I investigated the effects of habitat color and location on community structure in artificial water-filled treeholes in the forest of Barro Colorado Island, Panama. The macroinvertebrate fauna of 9 replications (5 in understory, 4 in tree-fall gaps) of black, blue, red, and green 650 ml plastic cups were censused weekly for 7 wks. Macroinvertebrate abundance and species richness were greater in understory cups than in gap cups. Seven species colonized black cups exclusively. Black cups in the understory, and red and black cups in gaps, attracted more species on average than other colors. Species richness and abundance were consistently lowest in green cups. Species were more broadly distributed among cup colors in the understory, suggesting that diffuse light conditions influenced color perception. There was no overlap in species composition between water in the artificial treeholes and water held by red *Heliconia* bracts or green tank bromeliads.

Key Words: color, microcosm, mosquitoes, phytotelmata, tree-fall gaps, tropics

RESUMEN

Investigué los efectos del color de hábitat y localidad en la estructura de la comunidad en huecos de árboles artificiales llenos de agua en el bosque de Isla Barro Colorado, Panamá. La fauna macro invertebrada de 9 replicaciones (5 en el “understory”, 4 en espacios abiertos de árboles caídos) de vasos plásticos de 650 ml de color negro, azul, rojo, y verde fueron observadas semanalmente por 7 semanas. La abundancia macro invertebrada y la riqueza de especies fueron mayor en vasos del “understory” que en los vasos de espacios abiertos. Siete especies colonizaron vasos negros exclusivamente. Los vasos negros en el “understory”, y los vasos rojos y negros en los espacios, atrajeron un promedio mayor de especies que otros colores. Riqueza y abundancia de especies fueron mas bajas consistentemente en vasos verdes. Las especies fueron distribuidas mas ampliamente entre colores de vaso en el “understory”, sugiriendo que condiciones de luz difusa influyen percepción de color. No hubo área común en composición de especies entre agua en los huecos de árbol artificiales y agua retenida por brácteas rojas de *Heliconia* o bromelias de tanque verde.

Container-breeding mosquitoes use a variety of physical and chemical cues when selecting oviposition substrates (Bates 1949; Bentley & Day 1989), and many species show preferences for specific habitat colors (Frank 1985, 1986, and references therein). Most investigations of mosquito response to habitat color have been lab-based, and color preferences have not been studied for other taxa that typically coexist with mosquitoes in the field. Although mosquitoes generally dominate the macrofauna of tropical phytotelmata, several other insect taxa are also common in these habitats (e.g., Fish 1983). The effects of habitat color on colonization by non-mosquito aquatic macroinvertebrates in tropical phytotelmata are not known.

Water-filled treeholes are common phytotelmata in many temperate and tropical forests (Snow 1949; Kitching 1971), and occur in both tree-fall gaps and forest understory. Artificial treeholes (plastic containers containing leaf litter and rain water) are often used for field-based population and community-level studies. These containers provide suitable mimics of the treehole habitat, and typically attract the same fauna found in the natural setting (e.g., Fincke et al. 1997; Yanoviak, in press). Artificial treeholes are usually clear (Pimm & Kitching 1987; Srivastava & Lawton 1998), black or brown (Fincke et al. 1997; Yanoviak 1999a), or blue (O. M. Fincke, Dept. Zoology, Univ. Oklahoma, pers. comm.). How such color differences may affect community structure in these experimental systems has never been investigated.

The potential importance of habitat color extends beyond artificial treeholes; there is considerable variation in color among natural phytotelmata. Common phytotelmata in the lowland forests of Panama include water-filled treeholes, tank bromeliads (e.g., *Vriesia* spp., *Guzmania* spp.), fallen palm petioles and spathes (e.g., of *Astrocaryum standleyanum* Bailey), and exocarps of fallen *Tontelea ovalifolia* (Miers) A. C. Smith fruits. Treehole interiors typically appear black or brown; bromeliads are generally green; palm spathes and *T. ovalifolia* husks are initially cream-colored, but gradually become orange, reddish, and eventually dark brown as they age (pers. obs.). In addition, the red and green bracts of *Heliconia* spp. often contain sufficient water to support aquatic macroinvertebrate assemblages (e.g., Seifert & Seifert 1979; Naeem 1988; Lounibos & Machado-Allison 1993).

This study examined the effects of container color and location (tree-fall gap or forest understory) on colonization of artificial treeholes by macroinvertebrates under field conditions. Specifically, I hypothesized that container location and color would affect macroinvertebrate species composition, species richness, and abundance. Earlier work on this system showed that highly exposed treeholes (in forest canopy) contained fewer species than holes in the understory (Yanoviak 1999b). Thus, I predicted that macroinvertebrate species richness and abundance would be lower in gap holes of this study. Based on field observations and other studies showing oviposition preference for dark containers (e.g., McDaniel et al. 1976), I predicted that black cups would attract more species than other colors. Finally, because color is a potentially important cue for species colonizing bromeliads (Frank 1985, 1986), I expected that green cups would attract some taxa (e.g., *Wyeomyia* spp. mosquitoes) that normally inhabit tank bromeliads in Panama.

MATERIALS AND METHODS

In mid-July 1997, I established 9 replications of four colored plastic cups (black, blue, green, and red; 650 ml, 8.5 cm diameter × 12 cm height - Churchill Container Corp., Shawnee, KS, USA) in the seasonally wet tropical forest of Barro Colorado Island (BCI), Panama (see Leigh et al. 1996 for a site description). Four replicates were located in tree-fall gaps and 5 in forest understory. I secured each cup to a pole-sized (10-20 cm diameter) tree approximately 1 m above the ground (as described in Yanoviak 1999a). Cups initially contained ca. 400 ml rain water and a strip of balsa wood (0.2 × 4 × 16 cm) as an oviposition site for insect colonists (Novak & Peloquin 1981). The balsa strip was small enough relative to the cup that it had little effect on general color appearance of the habitat. Holes drilled in the cup rims maintained water levels ca. 100 ml below capacity. Thus, any insect entering to oviposit was exposed to the cup color from all sides and from below. Cups within a replication were separated by > 5 m and the distance between replicates was > 100 m. I allowed rain water and detritus to accumulate naturally.

The macroinvertebrate fauna (organisms > 0.5 mm) of all cups was censused weekly for 7 wks beginning 26 July 1997. I occasionally collected subsamples of pupae and late-instar larvae to confirm field identifications. Water temperatures were measured at irregular intervals with a Corning® modular electronic probe. The experiment was terminated after 7 wks because detritus accumulations and fungal or algal growth changed the interior color of some cups to dark brown.

In addition to the fauna of artificial treeholes, I qualitatively sampled macroinvertebrates living in nearby water held by 14 tank bromeliads, 20 *T. ovalifolia* exocarps, 12 fallen palm spathes, and 12 *Heliconia latispatha* Benth. bracts (from 12 different plants) for comparison with the species composition of communities in the plastic cups. Taxa that could not be identified in the field were collected and reared in the lab.

Differences in macroinvertebrate species richness and abundance in the artificial tree holes were analyzed with 2-way repeated-measures ANOVAs using location (gap or understory) and color as main effects. When significantly different, means were compared with Ryan-Einot-Gabriel-Welsch multiple range tests (SAS 1989). Abundance data were log(x+1) transformed prior to analysis to correct variance heterogeneity (Sokal & Rohlf 1981), but all means presented in results were calculated from untransformed data. Sørensen's (1948) coefficient of similarity [$C_s = 2j \cdot (a + b)^{-1}$, where j = number of species common to two treatments, and a and b = the number of species in each treatment] was used to quantify overlap in species composition (all replicates pooled within gap or understory locations) among the four cup colors.

Reflectance data for the red, blue, and green cups were obtained with an Ocean Optics® S2000 spectrophotometer. Measurements were taken under dim illumination to reduce the variance attributable to environmental lighting. The probe was dark-spectrum calibrated by placing it into a black plastic bag, and a reference spectrum was obtained by measuring an Ocean Optics reflectance standard (a white piece of plastic). Three separate recordings, each resulting in 1570 data points between 360 and 860 nm, were taken from each cup. Reflectance spectra for the red, blue, and green cups are shown in Fig. 1.

RESULTS

Artificial treeholes located in the understory were colonized by more individuals and more species than cups in tree-fall gaps (Tables 1 and 2; compare Figs. 2 and 3). Conditions in the cups differed dramatically between locations. Temperatures in gap cups exceeded 40°C on sunny days, and all gap cups contained abundant filamentous algae by Week 5. In understory cups, temperatures never exceeded 32°C and algae were virtually nonexistent. There were no significant inter-

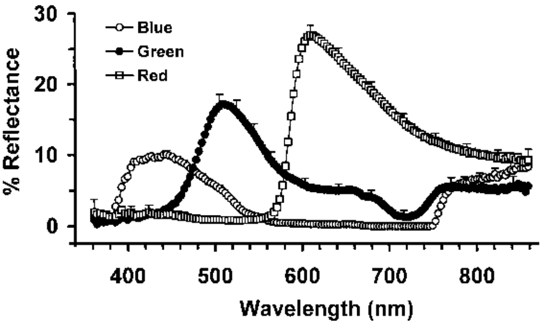

Fig. 1. Reflectance spectra for the red, blue, and green cups used in this study. Each point is the mean of 30 data associated with 10 wavelength measurements (3 replicates × 10 adjacent wavelengths), and each mean was plotted against its median wavelength value. Variance was very low; error bars (±1 SD) are shown only for a subset of the means.

actions between treehole color and location for both macroinvertebrate species richness and abundance (Table 1), so effects of color were tested separately for gap and understory locations.

Average species richness and abundance differed among cup colors in both gaps and understory (Table 1), but significant effects did not occur in either location until Week 4 (based on Ryan post-hoc tests). Species richness was greatest in black cups in the understory (Fig. 2a) and black and red cups in gaps (Fig. 3a) after 7 wks of colonization. Macroinvertebrate abundance was significantly lower in green cups in forest understory, but did not differ among black, blue, and red cups on Weeks 6 and 7 (Fig. 2b). Black and red cups in gaps contained more individuals than did green cups by the end of the study (Fig. 3b). The significant time*treatment interaction for understory species richness, but not for abundance (Table 1), reflects the early successional status of the artificial treeholes (Yanoviak, in press). Species richness in understory cups increased over time whereas abundance remained relatively constant (Fig. 2). The lack of a similar time interaction in gaps is attributed to high variance (Fig. 3).

Black cups were colonized by the most taxa overall, whereas green cups attracted the fewest species (Table 2). Seven species, including four non-mosquito taxa, occurred exclusively in black cups. Overlap in species composition among different colors was marginally greater in the understory than in gaps (Wilcoxon 2-sample test using Sørensen's coefficients obtained for each location, P = 0.077), and assemblages in understory black cups showed higher similarity to assemblages in red and blue cups than to those in green cups (Table 3). Several species that avoided blue and/or green cups in gaps colonized one or both of those colors in the understory (Table 2).

There was no overlap between the species composition of water held by bromeliads or *H. latispatha* bracts on BCI and the cups used in this experiment. However, several treehole species were found in water held by palm spathes and *T. ovalifolia* exocarps; both were dominated by the mosquitoes *Trichoprosopon digitatum* (Rondani) and *Limatus* spp.

DISCUSSION

My results show that the location and color of artificial treeholes can influence species richness, abundance, and composition in container communities. As predicted, macroinvertebrate species richness and abundance were lower in artificial treeholes located in gaps. This result is likely due to oviposition preferences for shaded vs. exposed sites. Prior work on this system showed that some species are more common in shaded holes (Yanoviak 1999c) and that highly exposed canopy tree holes contain fewer species than understory holes (Yanoviak 1999b). It is also probable that extremely high water temperatures in gap cups depressed richness and abundance through larval mortality. Larvae of several mosquito species cannot survive temperatures above 40°C for more than a few minutes (Bates 1949). Finally, abundant algae in gap cups may have deterred oviposition by chemical or other means, and occasionally caused larval mortality by restricting their movements within the cups (pers. obs.).

TABLE 1. REPEATED-MEASURES ANOVA OUTPUT. SS = TYPE III SUM OF SQUARES. TIME = P-VALUE FOR UNIVARIATE TEST OF TIME*TREATMENT INTERACTION. * = P < 0.05, ** = P < 0.005.

	Abundance				Richness			
Treatment	SS	df	F	Time	SS	df	F	Time
Location	10.45	1,28	16.83**	0.71	31.74	1,28	26.07**	0.02
Color	16.21	3,28	8.70**	0.07	66.94	3,28	18.32**	<0.01
Location*Color	0.36	3,28	0.20	0.68	4.21	3,28	1.15	0.13
Color, Gap	5.64	3,12	7.72**	0.19	17.21	3,12	11.61**	0.40
Color, Underst.	11.59	3,16	4.27*	0.35	58.54	3,16	11.08**	<0.01

TABLE 2. DISTRIBUTION OF INVERTEBRATE TAXA AMONG DIFFERENT COLORED CUPS IN FOREST UNDERSTORY AND TREE-FALL GAP LOCATIONS. VALUES ARE MAXIMUM NUMBER OF INDIVIDUALS OBSERVED IN A CUP WITHIN A TREATMENT. MINIMUM ABUNDANCE WAS ZERO IN MOST CASES. MEAN ABUNDANCE AND MEAN RICHNESS ARE THE AVERAGE (±1 SD) NUMBER OF INDIVIDUALS AND SPECIES WITHIN A TREATMENT, ALL CENSUS DATES COMBINED.

	Understory				Gap			
Taxon	Black	Blue	Green	Red	Black	Blue	Green	Red
Annelida: Naididae								
Dero sp.	115	7	0	0	0	0	0	0
Odonata: Pseudostigmatidae								
Mecistogaster spp.	1	0	0	0	1	0	0	0
Coleoptera: Scirtidae								
Prionocyphon sp.	16	0	0	0	4	0	0	0
Diptera: Ceratopogonidae								
Bezzia snowi Lane	5	2	0	5	4	0	0	0
Forcipomyia spp.	26	0	0	1	3	0	37	0
Diptera: Chironomidae								
Chironomus sp.	0	0	0	0	1	0	0	0
Diptera: Culicidae								
Aedes terrens (Walker) complex	35	1	2	35	9	0	0	15
Anopheles eiseni Coq.	4	0	0	0	0	0	0	0
Culex conservator D. & K.	8	5	0	0	5	0	0	0
C. corrigani D. & K.	33	0	0	18	2	0	0	0
C. urichii (Coq.)	21	59	10	58	12	2	0	44
Haemagogus equinus Theobald	7	6	1	9	8	4	0	23
H. leucotaeniatus (Komp)	0	0	0	1	0	0	0	0
H. lucifer (Howard, Dyar & Knab)	0	0	0	15	0	9	0	0
Limatus assuleptus (Theobald)	16	15	15	38	6	5	1	32
Orthopodomyia fascipes (Coq.)	0	0	0	0	1	0	0	0
Toxorhynchites theobaldi (D. & K.)	1	0	0	0	1	0	0	0
Diptera: Psychodidae								
Telmatoscopus spp.	0	0	0	0	8	0	3	0
Diptera: Syrphidae								
Copestylum rafaelanum (Townsend)	69	0	0	0	0	0	0	0
Diptera: Tipulidae								
Sigmatomera spp.	0	0	0	0	0	0	5	0
Total no. of taxa represented	14	7	4	9	14	4	4	4
Mean abundance	22.3 (31.20)	10.5 (16.18)	3.0 (4.87)	19.1 (14.89)	4.8 (4.80)	1.3 (2.10)	2.1 (6.95)	11.3 (13.41)
Mean richness	2.5 (1.71)	1.2 (1.10)	0.7 (0.77)	2.0 (1.17)	1.3 (1.00)	0.4 (0.56)	0.2 (0.55)	0.9 (0.80)

Cup color significantly affected macroinvertebrate species richness and abundance in both locations and, as predicted, black cups attracted the most species overall. Although many taxa colonized more than one color of cup, the general distribution of species among colors suggests that most prefer to oviposit in dark containers or avoid green oviposition sites. This pattern is well documented for several mosquito species (e.g., Williams 1962; Wilton 1968; McDaniel et al. 1976; Hilburn et al. 1983; Beehler et al. 1992; Jones & Schreiber 1994; also reviewed by Frank 1985), and at least partly explains why the green cups of this study contained few species and individuals.

Differences in distributions of species among cup colors between gap and understory locations most likely reflect differences in how colors are perceived in these light environments. (One exception among the taxa found in this study is the annelid *Dero* sp., which is primarily dispersed by phoresy.) Most insects are unable to see red (Chapman 1998), thus red containers probably appear dark gray to potential colonists. Wavelengths of incident light in forest understory are shifted toward the blue/green end of the spectrum by the surrounding vegetation and toward red under overcast conditions (Endler 1993), thus blue and green cups in forest understory may also

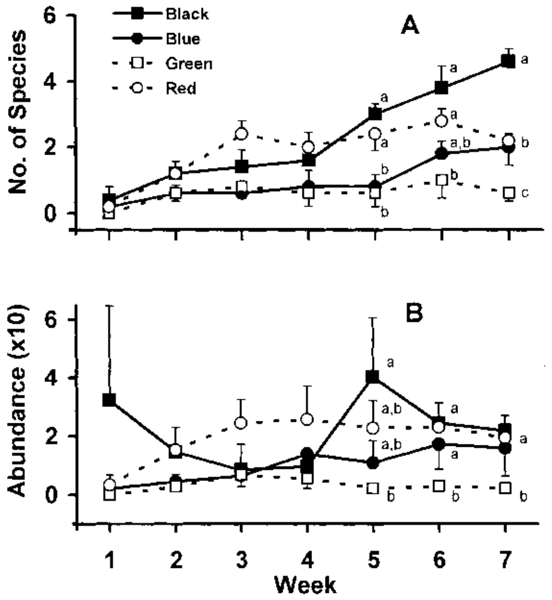

Fig. 2. Mean (±SE) macroorganism species richness (A) and abundance (B) in different colored cups located in forest understory. N = 5 for each mean. Within a week, means followed by the same letter do not differ based on post-hoc tests (only noted where differences occurred; a single letter was used for overlapping means). Some error bars were omitted for clarity.

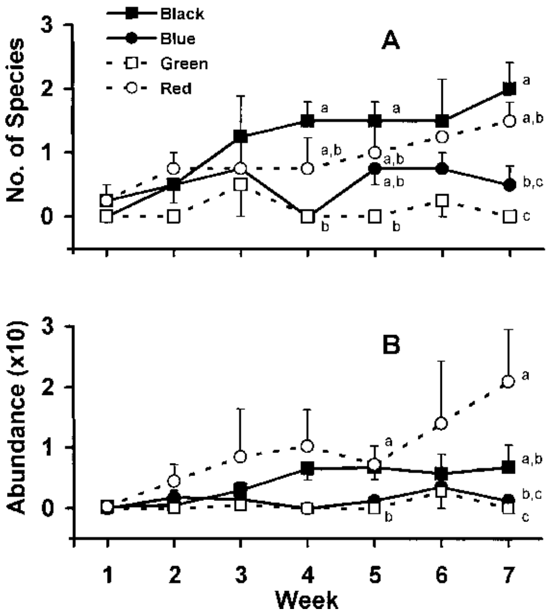

Fig. 3. Mean (±SE) macroorganism species richness (A) and abundance (B) in different colored cups located in tree fall gaps. N = 4 for each mean. Within a week, means followed by the same letter do not differ based on post-hoc tests (only noted where differences occurred; a single letter was used for overlapping means). Some error bars were omitted for clarity.

have been perceived as gray or reddish. Results of this study support such a conclusion. Blue and red cups attracted more species overall in the understory than in gaps, and species that colonized three or more colors tended to be more abundant in red and black. The mosquitoes *Culex urichii* (Coquillett) and *Limatus assuleptus* (Theobald) are exceptions to the latter, but both are also habitat generalists and will colonize water in almost any container (pers. obs.).

Five of the 7 species found only in black cups occurred in very low abundance. The midge *Chironomus* sp. and the mosquito *Orthopodomyia fascipes* (Coquillett) are normally more abundant in artificial treeholes than was observed here (Yanoviak, in press), so their distribution in this study may not reflect color preferences. Despite its low abundance, the presence of *Anopheles eiseni* Coquillett only in black cups probably reflects a color preference; several other *Anopheles* species prefer to oviposit in dark containers (reviewed by Frank 1985). *Mecistogaster* spp. and *Toxorhynchites theobaldi* (Dyar & Knab) are top predators in this system, and typically exist in low abundance due to competition and cannibalism (Fincke 1999). Treeholes are a limiting reproductive resource for pseudostigmatids (Fincke 1992a), and the species occurring on BCI avoid other phytotelmata, including bromeliads (Fincke 1992b). Lab studies showed that some *Toxorhynchites* species prefer to oviposit in black containers (Hilburn et al. 1983; Jones & Schreiber 1994). Therefore, it is reasonable to conclude that the presence of these two taxa only in black cups reflects a habitat color preference.

TABLE 3. SØRENSEN'S SIMILARITY COEFFICIENTS FOR MACROINVERTEBRATE ASSEMBLAGES OCCURRING AMONG THE FOUR CUP COLORS IN UNDERSTORY AND TREE-FALL GAP LOCATIONS.

	Understory			Gap		
	Black	Blue	Red	Black	Blue	Red
Blue	0.667	—	—	0.333	—	—
Red	0.609	0.625	—	0.444	0.750	—
Green	0.444	0.727	0.615	0.333	0.250	0.250

The lack of species overlap between the colored cups and similarly colored phytotelmata on BCI can be explained by physical attributes of these systems other than color. First, the general form of a container may influence colonization. For example, Frank (1986) used artificial bromeliads to show that ovipositing mosquitoes are sensitive to the general shape of plant containers. Second, macroinvertebrate colonization is influenced by the vertical position of phytotelmata. Fallen fruit husks and palm spathes occur at ground level, whereas all of the containers used in this study were ca. 1 m above the ground. Some mosquito species in the BCI forest (e.g., *Limatus* spp., *T. digitatum*) are sensitive to this difference in height (Yanoviak 1999b, in press). Finally, many species respond to chemical cues when selecting oviposition sites (Bentley & Day 1989), and these cues may complement or exceed the effects of color (Lounibos & Machado-Allison 1993).

CONCLUSIONS

My results suggest that differential colonization and harsh environmental conditions in treefall gaps tend to reduce the abundance and diversity of macroinvertebrates in artificial tree holes. Container color appears to play a role in habitat selection for several species in this system, but perception of color may be confounded by variable light conditions in forest understory. Additional studies under controlled laboratory conditions are needed to determine oviposition preferences of the many non-mosquito colonists of tropical phytotelmata.

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