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MOSQUITO IMMATURES IN DROUGHT-PRONE AND DROUGHT-RESISTANT BAMBOO STUMPS IN FLORES, INDONESIA

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ABSTRACT. Mosquito species in water-filled bamboo stumps were compared with those emerged from dormant eggs in dry stumps. *Tripteroides* spp. was more abundant than *Aedes* (*Stegomyia*) spp. (mainly *annandalei* and *albopictus*) in water-filled stumps, whereas the latter was more abundant than the former in dry stumps. During 5 days after inundation, *Aedes* (*Stegomyia*) spp. developed faster than *Tripteroides* spp. Density of *Tripteroides* spp. was high in narrow and deep stumps. Both taxa of mosquitoes were at low densities in water-filled stumps with large detritivores (Tipulidae and Oligochaeta).

KEY WORDS *Aedes*, habitat segregation, mosquito community, species interaction, *Tripteroides*

INTRODUCTION

Several container-breeding mosquito species often co-occur in the same locality without competitive exclusion. Their coexistence can be attributed at least partially to habitat segregation, which results from differential specialization of mosquitoes under variable habitat conditions.

Drought susceptibility is one of the conditions that may result in habitat segregation of mosquitoes. Drought susceptibility varies among tree holes, bamboo stumps, and other artificial containers (Bradshaw and Holzapfel 1988, Sota et al. 1994, Sunahara and Mogi 1997a). Some mosquitoes, such as *Aedes* spp., whose eggs are highly resistant to desiccation, specialize on drought-prone containers, whereas others cannot breed successfully in these habitats. In tree holes in Florida, *Aedes triseriatus* (Say) uses drought-prone holes successfully, whereas breeding of other mosquitoes, such as *Orthopodomyia signifera* (Coq.) and predaceous *Toxorhynchites rutilus* (Coq.), is limited to drought-resistant holes (Bradshaw and Holzapfel 1983, 1988). In bamboo stumps in southwestern Japan, *Aedes albopictus* (Skuse) and *Tripteroides bambusa* (Yamada) are predominant in drought-prone and drought-resistant stumps, respectively (Sunahara and Mogi 1997a). Similar situations generally may occur in many localities where both drought-prone and drought-resistant containers exist.

This paper deals with mosquito communities in bamboo stumps in Flores Island, Indonesia. Although a high diversity of mosquitoes in bamboo stumps has been reported from Southeast Asia (Sota 1996b), their habitat segregation has not been investigated in detail. Our main purpose is to describe patterns of use of drought-prone and drought-resistant bamboo stumps by mosquitoes. We compared the mosquito species in stumps that retained water in the dry season with those that emerged from dormant eggs in dry stumps.

In addition to drought susceptibility, we examined effects of the stump morphology and presence of predators and large detritivores on habitat uses of mosquitoes. These habitat conditions vary among stumps and may affect the use of bamboo stumps by mosquitoes.

MATERIALS AND METHODS

Sampling was carried out in 7 sites near villages along the road from Ende City (8°48′S, 121°41′E) to Mount Keli Mutu, East Flores, in August 1997. Elevations of the 7 sampling sites were 70, 460, 700, 800, 960, 990, and 1,070 m. Wet months with rainfall more than 100 mm are from November to April in Ende (Monk et al. 1997). Although the sampling period was during the dry season, some rainfall occurred in the mountainous area. We found water-filled bamboo stumps at the 5 sites in the mountainous area (elevation, 700–1,070 m), but not at the 2 sites in the lowland (70–460 m).

Forty-five water-filled stumps (probably *Bambusa* spp.) were cut from the 5 sites in the mountainous area and brought to a laboratory in Ende City. For each stump, we measured the long (d_1) and the short (d_2) inner diameters (d_1 ranged from 2.3 to 11.0 cm), and calculated the opening area as $d_1 d_2 \pi / 4$. We measured depth of the stumps (from the cut to the bottom; ranged, 7.1–26.2 cm). Water volume in the stumps ranged from 5 to 402 ml (no data for 8 stumps). All insects and earthworms inside stumps were collected and preserved with 10% formalin, except for some mosquito larvae and pupae that were reared to adults for identification. The 3rd- and 4th-stage larvae and adults of mosquitoes were identified to species or genus. Identification followed Huang (1979) and Mattingly (1971, 1981). Individuals that died during rearing were not included in the number of individuals recorded for each species.

From 6 sites (elevation, 70–1,070 m), 38 dry bamboo stumps that were considered to have contained water (with black sediments in the bottoms) were cut and brought to the laboratory. There, we

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Table 1. Frequencies of occurrence and abundance of mosquito immatures in 45 water-filled bamboo stumps.

Mosquito	No. positive stumps	Proportion	Density per cm^2 (mean ± SE)	Total no. immatures
Detritivore				
Aedes (Stegomyia) annandalei	10	0.222	0.054 ± 0.029	43
Aedes (Stegomyia) albopictus	9	0.200	0.024 ± 0.011	32
Aedes (Stegomyia) scutellaris	1	0.022	0.001 ± 0.001	1
Aedes (Finlaya) sp. 1	1	0.022	0.003 ± 0.003	4
Aedes (Finlaya) sp. 2	1	0.022	0.002 ± 0.002	4
Tripteroides sp. 1	18	0.400	0.247 ± 0.090	168
Tripteroides sp. 2	14	0.311	0.078 ± 0.035	71
Armigeres sp.	3	0.067	0.113 ± 0.072	198
Ficalbia sp.	3	0.067	0.014 ± 0.004	21
Culex (Culiciomyia) sp.	1	0.022	0.004 ± 0.004	6
Orthopodomyia sp.	1	0.022	0.001 ± 0.001	2
Carnivore				
Toxorhynchites sp.	9	0.200	0.008 ± 0.004	12

filled them with well water and placed them under eaves. The stumps were covered with mesh sheets to prevent the entry of mosquitoes. Five days later, 13 of these stumps retained water but the rest had lost water due to leaks. For each stump with water, we measured d_1 (range, 3.2–8.0 cm) and depth (range, 9.6–23.8 cm). Water volume ranged from 4 to 145 ml (no data for 1 stump). All insects in the 13 stumps were collected and mosquito larvae were identified according to genus. The number of larvae in each developmental stage was counted for each mosquito genus. Some of the larvae of each genus found in each stump were allowed to develop to the 3rd instar or further for identification. The remainder were fixed with 10% formalin. We estimated the number of individuals of each species of a genus assuming that the proportion of each species in the identified samples was equal to that in the total individuals on the 5th day after inundation.

RESULTS

Comparison of wet and dry stumps

From water-filled stumps, 12 species of 7 genera of mosquitoes were identified (Table 1). These included 1 carnivore, *Toxorhynchites* sp. Detritivorous immature mosquitoes were found in 36 stumps (80%). In addition to *Armigeres* sp., which occurred in high densities in 3 stumps (27–137 individuals per stump), the 2 species of *Tripteroides* were predominant in frequency of occurrence and density (number/cm^2). The combined density of immature *Tripteroides* spp. was significantly higher than that of immature *Aedes* (*Stegomyia*) spp. (Wilcoxon's signed rank test, $Z = -2.763$, $P < 0.01$). In addition to mosquitoes, detritivorous insect larvae such as Tipulidae (10 stumps), Helodidae (6 stumps), Ceratopogonidae (18 stumps), Chironomidae (14 stumps), and Psychodidae (8 stumps) were collected. Of these, Tipulidae were the largest in body length (maximum length, 38 mm). Other unidentified dipteran larvae were found in 10 stumps. In addition, large individuals of Oligochaeta (maximum length, 50 mm) were found in 8 stumps.

Mosquito larvae emerged from dormant eggs in all of the 13 stumps that retained water for 5 days. From these stumps, 5 mosquito species of the genera *Aedes* and *Tripteroides* were collected (Table 2). In addition to the mosquito larvae, larvae of Ceratopogonidae (5 stumps), Helodidae (1 stump), and Tipulidae (1 stump) were collected. The 2 species of *Aedes* (*Stegomyia*) were predominant in terms of frequency of occurrence and the density. The combined density of *Aedes* (*Stegomyia*) spp. larvae was significantly higher than that of *Tripteroides* spp. larvae (Wilcoxon's signed rank test, $Z =$

Table 2. Frequencies of occurrence and abundance of mosquito larvae that emerged from dormant eggs in 13 dry bamboo stumps.

Mosquitoes	No. positive stumps	Proportion	Density per cm^2 (mean SE)	Total no. larvae
Aedes (Stegomyia) annandalei	8	0.615	1.243 ± 0.460	229
Aedes (Stegomyia) albopictus	9	0.692	0.460 ± 0.179	135
Aedes (Finlaya) sp.	1	0.077	0.020 ± 0.020	12
Tripteroides sp. 1	6	0.462	0.426 ± 0.258	57
Tripteroides sp. 2	5	0.385	0.266 ± 0.207	31

Table 3. Number of immatures in each developmental stage in dry stumps at the 5th day from inundation.

Mosquitoes	Instar I	Instar II	Instar III	Instar IV	Pupa
Tripteroides spp.	1	72	15	1	0
Aedes (Stegomyia) spp.	0	58	137	162	0

−2.197, $P < 0.05$). Except for *Aedes* (*Finlaya*) sp., which occurred only in 1 stump collected at 990 m, these mosquitoes occurred both in low-elevation (70–460 m) and high-elevation (700–1,070 m) sites. Their rank order in terms of the density of larvae was the same as that in Table 2 both in the low- and high-elevation sites.

By the 5th day after inundation of the dry stumps, development of larvae of *Aedes* spp. was more advanced than that of *Tripteroides* spp. (Table 3). The proportion of the 3rd- and 4th-stage larvae of *Aedes* spp. was significantly higher than that of *Tripteroides* spp. (Fisher's exact probability, $P < 0.001$). The 4th-stage larvae of *Aedes* spp. were found in 9 of 11 *Aedes*-positive stumps, whereas only 1 4th-stage larva of *Tripteroides* sp. was found in 1 stump out of 9 *Tripteroides*-positive stumps (difference in the proportion of stumps with 4th instars: Fisher's exact probability, $P < 0.01$).

Stump morphology

The relationship between stump morphology and density (number per area) was different between *Aedes* (*Stegomyia*) spp. and *Tripteroides* spp. (Table 4). Both in water-filled and dry stumps, density of *Tripteroides* spp. was negatively correlated with the area of the opening. In water-filled stumps, density of *Tripteroides* spp. was positively correlated with the depth of the stump. Density of *Aedes* (*Stegomyia*) spp. was not correlated significantly with either area or depth in both water-filled and dry stumps.

Presence of predators and large detritivores

Densities of the immature mosquitoes were smaller in stumps with 4th instars of *Toxorhynchites* sp. than in stumps without them, although the difference was significant only when all detritivorous mosquitoes were pooled (Table 5). The number of immature mosquitoes was significantly smaller in stumps with large detritivores (Tipulidae or Oligochaeta) than in stumps without them (Table 5). The difference in densities between stumps with and without the large detritivores was significant for *Tripteroides* spp. and *Aedes* (*Stegomyia*) spp.

DISCUSSION

The predominance of aedine mosquitoes in drought-prone sites has been reported previously (Bradshaw and Holzapfel 1988; Sunahara and Mogi 1997a, 1997b). The greater abundance of *Aedes* (*Stegomyia*) spp. than *Tripteroides* spp. in dry stumps in our results is due to the greater input rate and/or higher survival rate of *Aedes* (*Stegomyia*) spp. eggs. *Aedes* (*Stegomyia*) spp. lay eggs on container walls above the water line. Their desiccation-resistant eggs survive in dry containers and hatch immediately after flooding. On the other hand, *Tripteroides* spp. lay eggs mainly on the water surface and eggs hatch without delay (Miyagi 1973, Okazawa et al. 1985). *Tripteroides* eggs have been reported to have some degree of desiccation resistance (Miyagi 1973, Okazawa et al. 1985, Sunahara and Mogi 1997c). However, Okazawa et al. (1985) showed that no eggs of *Tripteroides aranoides* (Theobald) survived more than 40 days at 80% relative humidity and 20°C. The relative predominance of *Aedes* (*Stegomyia*) spp. to *Tripteroides* spp. in drought-prone stumps might be due to the difference in desiccation resistance of eggs, as well as in preference of oviposition sites between the 2 groups.

In addition to their predominance in abundance, *Aedes* (*Stegomyia*) spp. had a faster rate of larval development in the dry stumps 5 days after inundation. *Aedes albopictus* (Skuse) develops faster than *Tr. bambusa* (Sunahara and Mogi 1997b). Probably the difference in the stage structure at the 5th day after inundation between *Stegomyia* spp. and *Tripteroides* spp. was due to the difference in growth rate. However, hatching times may also have been different between the 2 groups. Rapid hatch and/or development after flooding can enhance the probability of completing larval development before the stump dries up. Moreover, fast

Table 4. Spearman's coefficient of rank correlation (r_s) between densities of mosquitoes and morphologic characteristics of bamboo stumps.[1]

	Water-filled stumps		Dry stumps	
Mosquitoes	Area	Depth	Area	Depth
Tripteroides spp.	−0.537***	0.395**	−0.767**	0.119 NS
Aedes (Stegomyia) spp.	−0.225 NS	0.199 NS	−0.278 NS	−0.438 NS

[1] Levels of significance: **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

Table 5. Comparison of the density (no./cm^2) of mosquito immatures (mean ± SE) in water-filled stumps with or without the 4th instar of *Toxorhynchites* sp. and large detritivores (Tipulidae or Oligochaeta).

Mosquitoes	*Toxorhynchites* sp.			Large detritivores		
	Absent (n = 38)	Present (n = 7)	Mann–Whitney U-test	Absent (n = 28)	Present (n = 17)	Mann–Whitney U-test
All detritivorous mosquitoes[1]	0.621 ± 0.154	0.095 ± 0.066	$P < 0.05$	0.810 ± 0.197	0.093 ± 0.047	$P < 0.001$
Tripteroides spp.[2]	0.374 ± 0.120	0.058 ± 0.049	NS[3]	0.513 ± 0.155	0.016 ± 0.010	$P < 0.001$
Aedes (Stegomyia) spp.[2]	0.093 ± 0.038	0.034 ± 0.019	NS	0.114 ± 0.048	0.035 ± 0.027	$P < 0.05$

[1] 1st through 4th instars and pupa.
[2] Not including 1st through 2nd instars.
[3] NS, not significant.

developers have an advantage over slow developers in exploiting competition within a single generation because the greater body size of fast developers is associated with higher feeding rates (Chambers 1985, Sunahara and Mogi 1997b). *Tripteroides* spp. or other mosquitoes possibly colonize drought-prone stumps after rain water fills them. However, because of the time lag between oviposition and hatching, *Aedes* (*Stegomyia*) spp. larvae that emerge from dormant eggs should have an advantage in the use of new aquatic sites, at least initially. Thus, the greater abundance and more rapid development suggests that *Aedes* (*Stegomyia*) spp. use drought-prone stumps more efficiently than do *Tripteroides* spp.

In water-filled stumps, *Tripteroides* spp. were predominant to *Aedes* (*Stegomyia*) spp. in frequency of occurrence and density. Because we did not check the egg pools in water-filled stumps, it is not clear whether the relative predominance is the same in the rainy season, when water levels increase and dormant eggs above the water line hatch.

The genus *Tripteroides* is distributed widely in the Oriental region (Mattingly 1981). The result of the present study is similar to that of Sunahara and Mogi (1997a) who found that *Tr. bambusa* was predominant in drought-resistant bamboo stumps in southwestern Japan. *Tripteroides* spp. are also the main constituents of mosquito communities in water-filled bamboo stumps in North Sulawesi, Indonesia (Sota 1996b). Predominance of *Tripteroides* spp. in drought-resistant containers may be observed generally in the Oriental region.

Aedine mosquitoes have been reported to be inferior to others in using permanent aquatic sites because of their high susceptibility to predation (Bradshaw and Holzapfel 1983, Chambers 1985), and low survival and growth rates under limited food conditions (Sunahara and Mogi 1997b). These disadvantages might partially contribute to the low frequency and density of *Aedes* (*Stegomyia*) spp. in water-filled stumps.

Although *Tripteroides* spp. seem to use water-filled stumps more efficiently than other mosquitoes, they did not use all stumps evenly. The density of *Tripteroides* spp. immatures was positively correlated with depth of the stump, and negatively correlated with opening area. *Tripteroides* spp. were suggested to prefer narrow and deep stumps. Such a preference of *Tripteroides* has been reported previously (Sota 1996a, Sunahara and Mogi 1997a). The opening area and depth of the stump may be correlated with habitat quality, such as persistence of the water body.

The use of water-filled stumps by *Tripteroides* spp. and other mosquitoes also seemed to be limited by presence of predators and large detritivores. *Toxorhynchites* is the most important predator in container habitats. The density of mosquito immatures was lower in *Toxorhynchites*-positive stumps than in stumps without *Toxorhynchites*. The differences in mosquito densities was greater between stumps with and without large detritivores. These differences might be the result of exploiting competition between large detritivores and mosquitoes, or interference. Recent studies have reported the positive effects of shredders on mosquitoes or midges via the processing chain (Bradshaw and Holzapfel 1992, Heard 1994, Paradise and Dunson 1997). The present study suggests the possible negative effect of the large detritivores on mosquitoes.

To summarize, the present study showed that use of bamboo stumps by mosquitoes was limited by drought susceptibility, stump morphology, and possibly interactions with predators and large detritivores. Use of bamboo stumps by *Aedes* (*Stegomyia*) spp. and *Tripteroides* spp. was differentially limited by these factors. Such variable responses of mosquito species to habitat conditions can result in habitat segregation and enhance coexistence of mosquitoes in bamboo stumps.

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