

VERTICAL DISTRIBUTION AND SPECIES COEXISTENCE OF TREE HOLE MOSQUITOES IN LOUISIANA¹

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ABSTRACT. Vertical distribution and species coexistence of mosquitoes inhabiting a deciduous forest in southern Louisiana were determined using 470 ml black jars for larval collections at ground level and 1, 3, 5, 7 and 9 m on selected trees. Specific preferences for discrete microhabitats by *Aedes triseriatus*, *Ae. hendersoni*, *Ae. vexans* and *Ae. albopictus* were not evident. Niche overlap indices, however, showed little overlap of these species and seemed to indicate that the mosquitoes partitioned the ovipositional/larval sites. Competition between the most abundant species, *Ae. triseriatus* and *Ae. albopictus*, was not apparent. The tree hole mosquito community structure appeared to be mediated by the predator, *Toxorhynchites rutilus septentrionalis*.

INTRODUCTION

Studies of the vertical distribution of mosquitoes have shown that behavior and preferences may cause specific vertical limits of oviposition. Several workers (Corbet 1961, Kitching 1971, Loor and DeFoliart 1969) demonstrated that ovipositional vertical distribution exists for tree hole mosquitoes. However, container preference rather than actual height was demonstrated by Mattingly (1969).

Aedes triseriatus (Say) had a strong preference for the basal level (Loor and DeFoliart 1969, 1970), and *Aedes hendersoni* Cockerell oviposited mainly in the canopy (Sinsko and Grinstad 1977, Scholl and DeFoliart 1977). Community structure of tree hole mosquitoes was found to be predator-mediated by *Toxorhynchites r. rutilus* (Coq.) and *Corethrella appendiculata* Grabham (Bradshaw and Holzapfel 1983). Habitat specialization (i.e., vertical distribution) apparently had not evolved via competition because populations were held below carrying capacity by predation. Furthermore, they state that unoccupied niches were available in the habitat.

Aedes albopictus (Skuse) was first discovered in the United States in Harris County, Texas (Sprenger and Wuithiranyagool 1986). Subsequently, the occurrence of *Ae. albopictus* in the southern and eastern United States has been extensively documented (Centers for Disease

Control 1986). Since its recent introduction, no work has been reported regarding its interactions with endemic species. This study sheds light on *Ae. albopictus* interaction with endemic tree hole species.

MATERIALS AND METHODS

In April 1986 the first infestation of *Ae. albopictus* in East Baton Rouge Parish, Louisiana, was recorded from a used tire disposal area in close proximity to a commercial tire recapping center. The first collection of *Ae. albopictus*, utilizing the forest area adjacent to the tires, was on July 19, 1986. The forest study site was a typical southern oak-beech-elm (*Quercus* sp. *Fagus* sp.-*Ulmus* sp.) ecotype with distinct understory. The ground and understory were composed of sapling oak, beech and elm trees with palmetto (*Sabel* sp.), poison ivy (*Rhus radicans*), and greenbriar (*Smilax* sp.) along the forest edges.

Eight trees were selected at random and used for ovipositional sampling. The height of the canopy in the study area exceeded 25 meters. On the exterior of each tree, 470 ml glass jars, sprayed with flat black enamel paint, were placed at ground level and vertical heights of 1, 3 and 5 m on July 26, 1986. The jars were supplemented with fallen leaves and 100 ml of tap water. Additional nutrients and water were a result of stemflow. Rainfall data revealed 1.93 cm in July, 4.88 cm in August, 6.55 cm in September, 11.63 cm in October and 31.42 cm in November. The jars at time of collection were never dry and many were completely filled with water and additional leaves and debris. Additional jars were placed at 7 m on September 3, and 9 m on October 10 to delineate the upper ovipositional limits of *Ae. albopictus*. The study was terminated after December 1 because of low larval recovery. Weekly larval collections were removed from the jars and taken to the

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laboratory for identification and counting. Identifications were made on 4th instar larvae utilizing taxonomic keys of Truman and Craig (1968), Darsie and Ward (1981) and Darsie (1986).

The extent to which each species interacted was estimated using a formula by Levins (1968) for niche overlap: $\alpha_{ij} = \sum p_{ih} p_{jh} (B_i)$, where α_{ij} is the niche overlap of species i over species j , p_{ih} and p_{jh} are the proportions of each species in the h^{th} of a resource set, (i.e., height) and B_i is the niche breadth of species i . For calculating a species niche breadth, we utilized Levins' (1968) niche breadth formula:

$$\beta = 1 / \sum_{i=1}^n p_i^2$$

where p_i is the proportion of a species found in the i^{th} unit of the resource set (height), and n is the number of the set (weeks). This niche overlap analysis was conducted on each species at each vertical stratum over the entire study.

To delineate the effect of predation in our artificial tree holes (jars), 2×2 contingency tables were constructed as shown in Bradshaw and Holzapfel (1983). The protocol was as follows:

1. To be selected, a jar must have had standing water in both the previous and current census (week) and must have had the prey species during the previous census.
2. These jars with prey present in the previous census were divided into two categories according to the presence or absence of *Toxorhynchites septentrionalis* (Dyar and Knab), hereafter referred to as *Toxorhynchites*.
3. a = No. of jars where *Toxorhynchites* was present in the previous census and prey were present in the current census.
b = No. of jars where *Toxorhynchites* was present in the previous census and prey were absent in the current census.
c = No. of jars where *Toxorhynchites* was absent in the previous census and prey were present in the current census.
d = No. of jars where *Toxorhynchites* was absent in the previous census and prey were absent in the current census.

χ^2 = Chi-square corrected for continuity (Pielou 1977)

$\chi^2 = (ad - bc - (a + b + c + d)/2)^2 / (a + b + c + d)(a + b)(c + d)(a + c)(b + d)$. If the overall χ^2 was significant (1 degree of freedom), we would then perform single degree-of-freedom comparisons for each census. If the χ^2 row and column totals were less than 15, we utilized Fisher's exact test (Steel and Torrie 1980).

In addition to a direct effect on each species, *Toxorhynchites* may influence intraspecific interactions among the prey themselves. To investigate this possibility, the method of Bradshaw and Holzapfel (1983) was used again by constructing 2×2 contingency tables with the following protocol:

1. To be selected, a jar must have had standing water in both the previous and current census and must have had the prey species being affected (species B) in it during the preceding census.
 2. These jars were then subdivided into two categories according to the presence or absence of species pairs, A (the impinging species) and B (the affected species).
 3. Then,
 - a = The number of jars where species A was present during the previous census and species B persistent in the current census.
 - b = The number of jars where species A was present during the previous census and species B was absent in the current census.
 - c = The number of jars where species A was absent during the previous census and species B persisted in the current census.
 - d = The number of jars where species A was absent during the previous census and species B was absent in the current census.
- χ^2 = Was calculated as above.

RESULTS

A total of 3,804 mosquito larvae were collected and identified to species. The sampling procedure collected all of the common species of mosquitoes associated with woodland habitats in East Baton Rouge Parish as noted by Chapman and Johnson (1986). This study recorded a new parish record for *Ae. hendersoni*. *Aedes vexans* (Meigen), *Psorophora ferox* (Humbolt) and *Culex restuans* Theobald, are normally considered freshwater pool mosquitoes in woodland habitats (Horsfall 1972). These species were collected in our study, and are considered accidentals.

Three species commonly found by Bradshaw and Holzapfel (1983) were not recovered in this study. *Orthopodomyia signifera* (Coq.) plus *An. barberi* Coq. are insignificant relative to species composition and relative abundance in East Baton Rouge Parish, Louisiana (M. Yates, unpublished data). *Corethrella appendiculata* was not recovered either nor has it been recovered in the state (Chapman and Johnson 1986).

The most prevalent species collected during the study was *Ae. triseriatus* (68.5% of the mosquitoes collected), followed by *Toxorhynchites* (15.8%), *Ae. albopictus* (14.6%), *Ae. aegypti* (Linn.) plus *Ae. hendersoni* with (<1%). The remainder of the species accounted for 0.003%.

The distribution of tree hole mosquito species collected at each of the elevations is given in Table 1. *Aedes triseriatus* is generally distributed evenly from the ground level containers up to 5 m, with the species percentages ranging from 20 to 26% at these levels. At 7 and 9 m, the percentages of *Ae. triseriatus* decrease sharply. Similar findings have been obtained by Sinsko and Grimstad (1977) and Scholl and DeFoliart (1977). *Aedes albopictus* was evenly distributed from ground level to the 3 m interval with the species percentages ranging from 24 to 26% at these levels.

Toxorhynchites, the only insect predator collected in our jars, was evenly distributed from ground level to 5 m. *Aedes aegypti*, although not prevalent, was collected from the ground to 5 meters. *Aedes hendersoni* had its greatest proportion at the higher elevations. The accidental species had 100% of their numbers col-

lected at the lowest strata (ground or 1 m in height).

Niche overlap is a relative measure of ecological similarity, resource partition, and competition between two species (Thornhill 1977). Values can range from 1.00 to 0. Low values (such as 0.05) are indicative of a low amount of ecological similarity, high resource partitioning with respect to habitats, and lack of competition whereas, high values (0.40) are indicative of high ecological similarity, low resource partitioning, and species competition. Values above 1.00 are indicative that the species major habitat is outside the area being analysed (tables 2 and 3). These values were observed with respect to *Ae. aegypti* and *Ae. hendersoni*. A small amount of overlap at each height level is revealed in this study (Tables 2 and 3). Thus, there appears to be a substantial partitioning of height and low amounts of competition among the tree hole species occurring in the study site.

The χ^2 analysis to determine the effect of predation of *Toxorhynchites* on the two most abundant prey species, *Ae. triseriatus* and *Ae. albopictus*, revealed a significant effect on *Ae. triseriatus* (overall $\chi^2 = 4.63$, $df = 1$, number of jars = 340, $P < 0.05$) and no significant ef-

Table 1. Percentages of vertical distribution for tree hole mosquito larvae in East Baton Rouge Parish, Louisiana.

Species	N	Ground	Vertical height (in meters)				
			1	3	5	7 ¹	9 ²
<i>Ae. triseriatus</i>	2,607	26	20	20	23	6	1
<i>Ae. albopictus</i>	555	26	24	24	11	2	<1
<i>Tx. rutilus septentrionalis</i>	601	11	19	33	27	6	0
<i>Ae. aegypti</i>	20	20	20	15	40	3	0
<i>Ae. hendersoni</i>	11	18	0	18	36	6	3
<i>Ae. vexans</i>	6	1	0	0	0	0	0
<i>Ps. ferox</i>	1	1	0	0	0	0	0
<i>Cx. quinquefasciatus</i>	3	0	0	0	0	0	0
<i>Cx. restuans</i>	3	1	0	0	0	0	0
Total	3804	17	25	24	23	7	1

¹ Weighted percentages for 13 of 19 weeks.

² Weighted percentages for 8 of 19 weeks.

Table 2. Niche overlap (α_{ij}) for tree hole mosquito larvae at ground level and vertical heights of 1 and 3 m using 470-ml jars as ovipositional containers.

Height		<i>Ae. triseriatus</i>	<i>Ae. albopictus</i>	<i>Tx. rutilus septentrionalis</i>
Ground	<i>Ae. triseriatus</i>	1.00	0.013	0.006
	<i>Ae. albopictus</i>	0.13	1.00	0.09
	<i>Tx. r. septentrionalis</i>	0.045	0.008	1.00
1 m	<i>Ae. triseriatus</i>	1.00	0.009	0.006
	<i>Ae. albopictus</i>	0.15	1.00	0.02
	<i>Tx. r. septentrionalis</i>	0.05	0.01	1.00
3 m	<i>Ae. triseriatus</i>	1.00	0.01	0.02
	<i>Ae. albopictus</i>	0.14	1.00	0.05
	<i>Tx. r. septentrionalis</i>	0.10	0.02	1.00

Table 3. Niche overlap (α_{ij}) for tree hole mosquito larvae at vertical heights of 5, 7, and 9 meter level using 470-ml glass jars as ovipositional containers.

Height (m)		<i>Ae. triseriatus</i>	<i>Ae. albopictus</i>	<i>Tx. r. septentrionalis</i>
5	<i>Ae. triseriatus</i>	1.00	0.004	0.01
	<i>Ae. albopictus</i>	0.17	1.00	0.04
	<i>Tx. r. septentrionalis</i>	0.12	0.01	1.00
7	<i>Ae. triseriatus</i>	1.00	0.05	0.02
	<i>Ae. albopictus</i>	0.08	1.00	0.0004
	<i>Tx. r. septentrionalis</i>	0.10	0.03	0.0005
9	<i>Ae. triseriatus</i>	1.00	0.007	—
	<i>Ae. albopictus</i>	0.03	1.00	—

fect on *Ae. albopictus* (overall $\chi^2 = 0.05$, $df = 1$, number of jars = 130, $P > 0.05$). A vertebrate predator was found to occur in the ovijars, a southern grey tree frog, *Hyla* sp., but had no effect on either species ($\chi^2 = 1.79$, $df = 1$, number of jars = 100, $P > 0.05$).

In Fig. 1, the effect of *Toxorhynchites* on *Ae. triseriatus* through 17 weekly censuses is given. Only census 8 (September 17–26), census 10 (October 3–10), and census 16 (November 14–21) showed significant effects ($P < 0.05$) on *Ae. triseriatus* *Toxorhynchites* predation. However, the presence or absence of *Toxorhynchites* on intraspecific competition between the two major species, *Ae. triseriatus* and *Ae. albopictus*, was not indicated, $\chi^2 = 0.18$, 1.15, 0.37 and 0.01 respectively ($P > 0.05$).

DISCUSSION

The opportunity for competition between species, especially *Ae. triseriatus* and *Ae. al-*

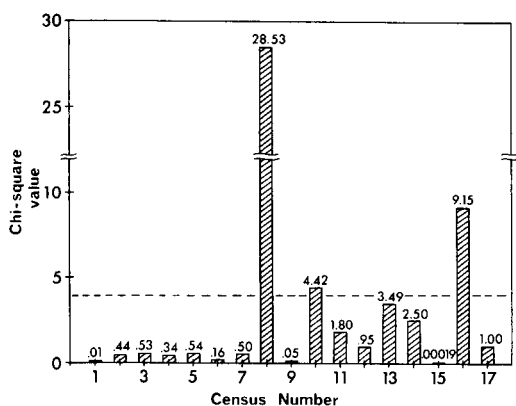


Fig. 1. Effect of the presence of *Toxorhynchites rutilus septentrionalis* on *Aedes triseriatus*.¹

¹ The vertical axis plots χ^2 with 1 degree of freedom for the association between presence of *Toxorhynchites rutilus septentrionalis* and persistence/existence of *Aedes triseriatus*. The dashed line shows the cutoff value for $P = 0.05$.

bopictus, is apparent in this study because there was no discernible vertical stratification between these two species (Table 1). In our study, however, the low overlap values tend to suggest a high amount of resource partitioning (tables 2 and 3) and that competition between these two species is nonexistent. Competition as the apparent causal agent of community structure has been challenged in general (Menge and Sutherland 1976, Connell 1980), and in tree hole mosquitoes specifically (Bradshaw and Holzapfel 1983).

Our results can be explained by predator-mediated coexistence (Caswell 1978, Connell 1980, Bradshaw and Holzapfel 1983). Studies on predators influencing the diversity and structure of communities are common (Caswell 1978). The overall chi-square analysis in our study helps support this possibility, because *Toxorhynchites* does effect *Ae. triseriatus* abundance at least partially through the year. Conversely, the chi-square analysis of tree holes, without *Toxorhynchites*, indicated a nonsignificant effect of *Ae. triseriatus* impinging on *Ae. albopictus* persistence. When *Ae. albopictus* invaded ovijars, previously occupied by *Ae. triseriatus*, a significant decrease in persistence or extinction was not observed.

While we have no direct evidence to explain differential predator susceptibility, we propose that *Ae. albopictus* escaped *Toxorhynchites* predation because of their lower overall abundance (Table 1). *Toxorhynchites* may feed on prey species that are the most abundant, i.e., they are opportunists. Bradshaw and Holzapfel (1983) stated that *Toxorhynchites* may alter their feeding behavior to the more abundant prey. Thus, this feeding on *Ae. triseriatus* would result in the lowering of mosquito populations below the carrying capacity, allowing for *Ae. albopictus* to enter readily. *Aedes albopictus* has been introduced in a number of habitats via the introduction of used tires (Moore 1985) with variable effects on the new habitat or community structure once they leave the tires. In nutrient poor habitats such as tires, competi-

tion may indeed take place and maybe a major factor in species interactions especially between *Ae. aegypti* and *Ae. albopictus*.

Additionally, the behavior of *Ae. triseriatus* and *Ae. albopictus* larvae appear to be different. We commonly observed *Ae. albopictus* foraging in the leaf litter and debris in the bottom of our jars. *Aedes triseriatus* was observed browsing on the surface and edges. This feeding behavior by *Ae. triseriatus* may result in more encounters with *Toxorhynchites*, thus resulting in differential predator susceptibility.

Predation by *Toxorhynchites* on *Ae. triseriatus* may not be the only way *Ae. albopictus* can inhabit the same jars/holes. *Aedes triseriatus* has been demonstrated to be cannibalistic (Koenekoop and Livdahl 1986). This may further reduce the population below the carrying capacity of an individual jar (tree hole).

Thus, the above analysis can partially explain the observed community structure. How many niches, without the effect of predation are vacant in the first place? This aspect was not observed. Diversification and species packing may take place before any direct competition occurs. Janzen (1985), who addressed the complex interactions enacted by an introduced species in Costa Rica, stated that the introduced species need not evolve in a habitat in order to participate in its interactions. *Aedes albopictus* is genetically pliable (Rai 1986) and can therefore enter new areas without adapting to them. *Aedes albopictus* has established itself and interacts in the tree hole community. Its ability to fit into this system is enhanced in part by predator-mediated coexistence (i.e., holding native species populations below their carrying capacity or creating vacant niches), thus allowing new species to readily enter rather than by competitive displacement. Additionally, the possible occurrence of many unoccupied tree holes prior to *Ae. albopictus* introduction may have aided its establishment.

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