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Drought and the organization of tree-hole mosquito communities

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Summary. In southeastern North America (North Florida, USA), the duration, frequency, and timing of drought differentially affect the survivorship of pre-adult tree-hole mosquitoes. Drought affects survivorship both by the direct action of dehydration on developing larvae and pupae and by the indirect modulation of predation. The drought-susceptible species, *Toxorhynchites rutilus, Orthopodomyia signifera,* and *Anopheles barberi* co-occur in more permanent holes that are larger, with larger, more vertical openings, lower down in larger trees, and contain darker water with higher conductivity, pH, and tannin-lignin content than the holes occupied by *Aedes triseriatus* that has drought-resistant eggs and rapid larval development. Ovipositing mosquitoes cue on physical and chemical attributes of tree holes independently of host tree species. These same attributes differ among drought-prone and drought-resistant holes but mosquitoes track these attributes more faithfully than the attributes predict tree-hole stability.

Key words: Competition – Predation – Disturbance – Stability

In aquatic habitats, drought, as well as other physical aspects of the environment, and predation may affect the potential for or the intensity of competition. In temperate ponds and lakes, the presence or effectiveness of predators is determined by the propensity of the pond or lake to freeze to the bottom in winter (Hall et al. 1970; Dodson 1970; Sprules 1972). In anuran populations, the degree of competition among juveniles depends upon density, upon the duration of the habitat, and upon the extent and timing of predation (Wilbur 1984). In wet African rock holes, the midge larvae that occupy a hole are determined by an interaction between rock-hole permanence and midge ability to invade unoccupied holes or holes with heterospecific residents, to resist such invasion, and to survive dehydration (McLachlan and Cantrell 1980). In subtropical Florida, water-filled tree holes (Lounibos 1983, 1985), predatory mosquito larvae greatly reduce the standing crop of prey mosquitoes except immediately following a drought when prey temporally escape the predators. Thus, in aquatic systems where variation in competition or the potential for competition occurs, this variation is associated with an interaction between biotic and abiotic limiting factors.

Tree-hole mosquitoes in north Florida partition their pre-adult habitat according to trophic affinity and spatial separation within and between holes (Bradshaw and Holzapfel 1983). *Toxorhynchites rutilus* (Coq.) and *Corethrella*

appendiculata Grabham are carnivores, *Aedes triseriatus* (Say) and *Orthopodomyia signifera* (Coq.) are filter feeders and browsers, and *Anopheles barberi* (Coq.) is a filter feeder and faculative carnivore. *T. rutilus* and *C. appendiculata* are the largest and smallest members of the community, respectively. *A. barberi* is a specialized surface feeder while *O. signifera* and *A. triseriatus* filter feed or browse in the limnetic or benthic portions of tree holes. *A. triseriatus* is predator-prone but has drought resistant eggs; *O. signifera* cannot tolerate drought but is predator resistant and predominates along with *A. barberi* and *T. rutilus* as a subcommunity distinct from *A. triseriatus.*

In this paper, we show that drought affects survivorship of mosquitoes and that the *T. rutilus–O. signifera–A. barberi* subcommunity segregates from the *A. triseriatus* subcommunity according to tree hole permanence. We then go on to ask whether mosquitoes might orient to specific tree species or to the physical and chemical attributes of the holes themselves.

Materials and methods

Study area and censusing

Details of the study area and sampling techniques are given in Bradshaw and Holzapfel (1983). Briefly, The Tall Timbers Research Station (30.6° N, 94.2° W, 30–60 m elevation) is situated on a 1200 hectare nature preserve along the northern edge of Lake Iamonia, Leon County, Florida. Between February and December, 1978, we made 19 censuses of tree holes at approximately 2-week intervals. Originally, we identified 78 holes but as we censused these, some dried up permanently and we located others. At the same time, it became clear that we could not census every hole regularly. Consequently, we censused all known holes during censuses 4–5 and then reduced our basic number to 44 of which 9 dried permanently sometime during the year, leaving us with 35 holes censused for 17 censuses. These holes were selected from the larger group to assure a wide range in host tree species and in hole size from large to small.

Physical and chemical properties

For each census, we checked the hole for the presence of standing water; if there was no standing water, we scored the hole as dry, even if the substrate was moist. If the hole contained standing water, we drained and measured the volume of water contained in the hole.

For each hole, we recorded the species of the host tree and measured (1) the height of the hole at its lower lip,

Offprint requests to: W.E. Bradshaw

508

(2) the circumference of the tree at the lower lip of the hole, (3) the angle of the orifice of the hole with respect to horizontal, and (4) the longest and shortest dimension of the orifice. We determined the following properties of the water in the hole: conductivity, pH, optical density at 460 nm, and tannin-lignin content. The latter determinations used water collected from all holes on July 13, 1978, after an especially heavy rain (6 cm in one day) on July 12, which filled most holes to capacity. We measured conductivity with a Yellow Springs conductivity meter, pH with a Corning pH meter, and optical density on a Markson portable field colorimeter. We chose to measure optical density at 460 nm since this wavelength produced maximum light adsorption of a tree-hole water sample that was characteristically stained a dark tea color. For tannin-lignin determinations, we used a scaled-down version of the Hach tannin-lignin test as described in the model TA-3 test kit. To 2 ml of sample, we added one drop of Hach Tanniver III # 2560 tannin-lignin reagent and 3 drops of sodium carbonate solution (Hach Tannin II # 675), shook the sample with parafilm over the mouth of the tube, and allowed 25 min at room temperature (ca. 21–23° C) for color development. For colorimetric determination, we blanked the colorimeter against 2 ml of sample without reagents and read optical density at 610 nm, the wavelength which resulted in high readings of an experimental sample but low readings of the reagents added to distilled water. For both tannin-lignin determinations at OD_{610} and readings of untreated tree-hole water at OD_{460}, we observed departures from linearity above readings of 0.9 OD. Consequently, when OD readings for full strength tree-hole water exceeded 1.0, we made serial dilutions until the OD readings fell below 1.0, assumed linearity with dilution, and calculated full strength equivalent by multiplying the OD readings times the dilution factor.

Oviposition behavior

To determine whether the water in the tree-holes by itself could be an important oviposition stimulant, we removed water from 5 holes in May, 1978, which contained no *A. triseriatus* (*Orthopodomyia* holes) and from 5 holes which contained no *O. signifera* or *A. barberi* (*Aedes* holes). We filtered the water through Mellita coffee filters and pipetted 300 ml from each source hole into a glass wide-mouth 1 quart (0.95 L) jar which had been painted flat black on the outside. To each jar we added a straight piece of oak branch, 2.0–1.5 cm in diameter and protruding about 5 cm from the top of the jar. We hung the jars in wire baskets 1.2–1.4 m off the ground in an oak-hickory woods containing both *Orthopodomyia* and *Aedes* holes on May 30, 1978, and censused the mosquitoes therein on July 6, 1978. To determine whether tree-hole water might contain a dilutable factor, we made serial dilutions of filtered water from an *Orthopodomyia* hole (TH163) with uncholorinated well water. Jars then contained full strenght TH163 water and dilutions of 1/2, 1/4, 1/8, and 1/16 TH163 water. We interspersed *Orthopodomyia*, *Aedes*, and serial dilution jars and spread them out over about a 1 ha area.

Statistical analyses

Analyses of variance were carried out after Bartlett's test for homogeneity of variance and appropriate transformations according to methods outlined in Sokal and Rohlf

(1969). Canonical correlations, axis rotation, and the generation of factor scores were performed by the SPSS package on the University of Oregon IBM 4361 computer.

Results

Drought and mosquito survivorship

To address the question of whether tree-hole desiccation, independently of other factors, affects mosquito survivorship, we examined pupation success in a fixed set of 30 holes both during and after a spring drought. The spring drought occurred during the second and third censuses and impacted the overwintering generations; the first summer generation predominated by the fifth census and enjoyed continuously wet holes (Bradshaw and Holzapfel 1983, 1984). This drought enabled us to compare relative pupation success through a drought and, in the same holes, through a period of continuous standing water. We calculated pupation success through the drought as:

$$\frac{\text{cumulative number of pupae during censuses 2–5}}{\text{maximum number of larvae during censuses 1 or 2}}$$

and through the period of continuous wetness as:

$$\frac{\text{cumulative number of pupae during censuses 5–8}}{\text{maximum number of larvae during censuses 4, 5, or 6}}$$

Table 1 shows that during the drought, pupation success was significantly higher in continuously wet than in dry holes for *Aedes triseriatus* and *Anopheles barberi* but not *Orthopodomyia signifera*. Among *Toxorhynchites rutilus* there were insufficient numbers for a meaningful calculation of χ^2. During the subsequent period of continuous wetness, pupation success for any species did not vary significantly between holes that had previously dried up and those which had previously remained wet.

Tree-hole desiccation and species occurrence

To investigate habitat segregation in relation to tree-hole desiccation, we followed the frequencies of holes containing *T. rutilus, O. signifera, A. barberi*, and *A. triseriatus* through the first 5 censuses. These censuses represent both a larger number of holes than we subsequently sampled and also encompass the dry period from mid-March through early April (censuses 2–3). The first census sampled the overwintering generation and the fifth census sampled the first summer generations (Bradshaw and Holzapfel 1983, 1984). Thus, we were able to compare both past and future inhabitants of holes that dried up with those that remained wet during the drought.

Figure 1 A shows that in the first census most holes contained *A. triseriatus* while less than half of them contained *T. rutilus, O. signifera*, and *A. barberi*. By the time of the second census about half of these holes had dried out. If overwintering species were distributed at random among holes with respect to their probability of drying out, the frequency of the species in wet holes during the second census should remain the same as during the first census. Figure 1 B shows that among holes which remained wet during the second census, there were higher than expected frequencies of *T. rutilus, O. signifera*, and *A. barberi*. Likewise, examination during the first census of the species composition of holes which were fated to dry out by the second

Table 1 A, B. Pupation success during the spring and early summer as affected by drought in 30 tree holes at Tall Timbers

A Spring	T. rutilus		O. signifera		A. triseriatus		A. barberi	
Condition[a]	wet	dry	wet	dry	wet	dry	wet	dry
Number of holes	8	1	12	5	11	18	8	2
larvae (pupae)	56 (41)	4 (0)	2291 (606)	104 (20)	829 (187)	1473 (128)	216 (50)	48 (3)
pupation success	73.2	0.0	26.5	19.2	22.6	8.7	23.1	6.3
χ^2	iss[b]		1.99^{ns}		74.60^{**}		5.73^{*}	

B Summer	T. rutilus		O. signifera		A. triseriatus		A. barberi	
Condition	wet	dry	wet	dry	wet	dry	wet	dry
Number of holes	11	12	12	10	9	18	11	5
larvae (pupae)	103 (43)	24 (12)	3364 (292)	279 (18)	185 (8)	1712 (91)	265 (16)	93 (3)
pupation success	41.7	50.0	8.7	6.5	4.3	5.3	5.8	3.2
χ^2	0.31^{ns}		1.63^{ns}		0.33^{ns}		0.90^{ns}	

[a] wet, wet during all censuses 1–5; dry, dry during census 2 and/or 3
[b] iss, insufficient sample size for χ^2; significance designated by: ^{ns} not significant; * $P<0.05$; ** $P<0.01$
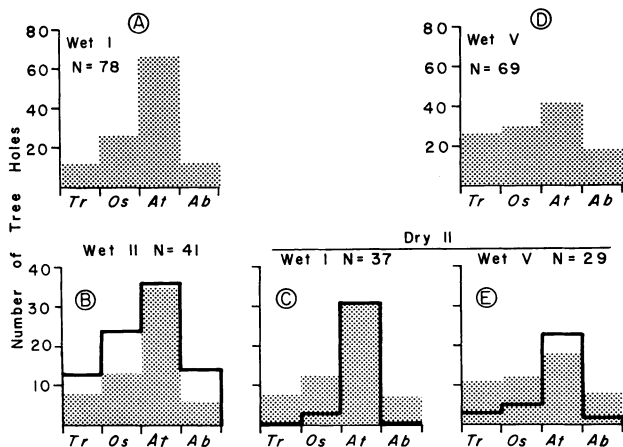
Fig. 1 A–E. Persistence and re-colonization of tree holes through and after a drought. **A** Number of holes containing each species during the first census; this distribution provides the expected frequencies of holes in the second census. **B** Observed (outline) and expected (screen) number of holes with each species in the 41 holes that remained wet during the second census. **C** Observed (outline) and expected (screen) number of holes with each species during the first census in those 37 holes fated to dry up by the second census. **D** Number of holes containing each species during the fifth census (after the drought); this distribution provides the expected frequencies of holes for **E**. **E** Observed (outline) and expected (screen) number of holes with each species in the fifth census that had dried out during the second census

census reveals under-representation of these same species (Fig. 1 C).

The above observations support the contention that desiccation is an important determinant of tree-hole mosquito species distribution. These observations, because they dealt with long-standing, overwintering populations, do not provide the means to distinguish between differential oviposition and differential survival as causative agents. Thus, we may have found *T. rutilus, O. signifera,* and *A. barberi* to be less prevalent in drought-prone holes either because these holes had dried up in the past, thereby eliminating these

species, or because females did not oviposit in holes likely to dry up. Although there is some overlap with pupae of the overwintering generation, the fifth census sampled primarily the first summer generation and represented the results of ovipositions during and after the March–April drought (Bradshaw and Holzapfel 1984). Figure 1 D shows the number of holes containing *T. rutilus, O. signifera, A. barberi,* and *A. triseriatus* during the fifth census. If oviposition were at random without regard to past desiccation, these frequencies should be the same in holes which had dried during the second census as in holes which remained wet. Figure 2 E shows, contrary to this expectation, that *T. rutilus, O. signifera,* and *A. barberi* were under-represented in the 5th census in holes which had dried up during the second census and *A. triseriatus* were over-represented in these same holes.

Physical and chemical attributes of habitat segregation

To consider the physical and chemical bases for habitat segregation of species, we examined 4 chemical (water conductivity, pH, tannin-lignin content, and optical density) and 5 physical (height of hole, circumference of tree at level of hole, dimension [L × W] of opening, angle of the opening with horizontal, and water volume) properties of 100 holes. We measured the chemical properties once, on 13 July, 1978, and the physical properties on the date we censused the hole. We sampled holes during early March to census the overwintering generation, during early May to census the first summer generation, and during mid July to census a mid-summer generation. One census and the physical chemical properties of each hole were used only once; holes were assigned to March, May, or July censuses so that each census was represented by 32–35 holes and did not differ in mean or standard deviation of tree-hole volume. Data from these 100 holes were then subjected to canonical correlation after $\log_{10}$ (number of mosquitoes + 1)/$\log_{10}$ (tree-hole volume) transformation to achieve homogeneous variance with 5 mosquito species and 9 physical-chemical properties as the two vector variables.

510
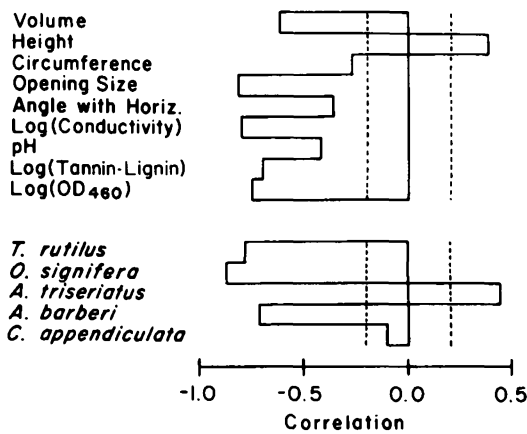
Fig. 2. Canonical correlation between species densities (log-[number + 1] per log[liter]) and physical attributes of 100 tree holes. This histogram plots correlation between the first canonical variate and each of the original variables. The vertical dashed lines indicate the correlations required for the 95% level of confidence

Canonical correlation produced only one significant canonical variate ($R_c^2 = 0.58$; Wilks' $\lambda = 0.270$; $\chi^2 = 117.1$; $P < 0.001$). The first canonical variate correlated significantly (Fig. 2) with all physical and chemical properties and four of the mosquito (*T. rutilus, O. signifera, A. triseriatus,* and *A. barberi*) densities. All correlations with the first canonical variable were negative except for those with height above the ground and with *A. triseriatus* which were both positive.

Altogether, we examined the physical and chemical properties of 100 individual tree holes that occurred in 14 tree species (Fig. 3). Of these 14 species, three (*Quercus alba, Magnolia grandiflora,* and *Ilex opaca*) were represented by a single tree. The remaining 11 species were represented by two or more individual trees. Among these 11 species, 1-way ANOVA revealed no significant effect of tree species on mean canonical variate score for mosquito densities ($F_{10, 86} = 1.25$; $P > 0.05$) with tree species accounting for 13% of the total sum of squares. Tree species did have a significant effect on mean canonical variate score for physical and chemical properties ($F_{10, 86} = 2.81$; $P < 0.01$) with tree species accounting for 25% of the total variance. Duncan's multiple range test indicated a significant difference ($0.01 < P < 0.05$) of mean canonical variate scores for physical and chemical properties only between *Nyssa sylvatica* ($n = 11$) and *Prunus serotina* ($n = 2$) or *Carya tomentosa* ($n = 2$).

Ignoring tree species and partitioning canonical variate scores for all available holes (Fig. 4) according to whether holes (1) dried out during the second census, (2) remained wet in the second but dried by the third, or (3) remained continuously wet revealed a significant effect of drought both on mosquito densities ($F_{2, 63} = 8.17$; $P < 0.001$) and on physical and chemical properties ($F_{2, 63} = 11.39$; $P < 0.001$). In the case of both mosquito densities (Fig. 4A) and physical and chemical properties (Fig. 4B), mean canonical variate scores were highest in the most drought-prone holes and declined with increasing tree-hole permanence.

Ignoring tree species, an examination of the canonical variate scores (Fig. 4C) for the same 30 holes used to generate the data in Table 1 shows that holes which were prone to dry out had a higher, positive mean canonical variate
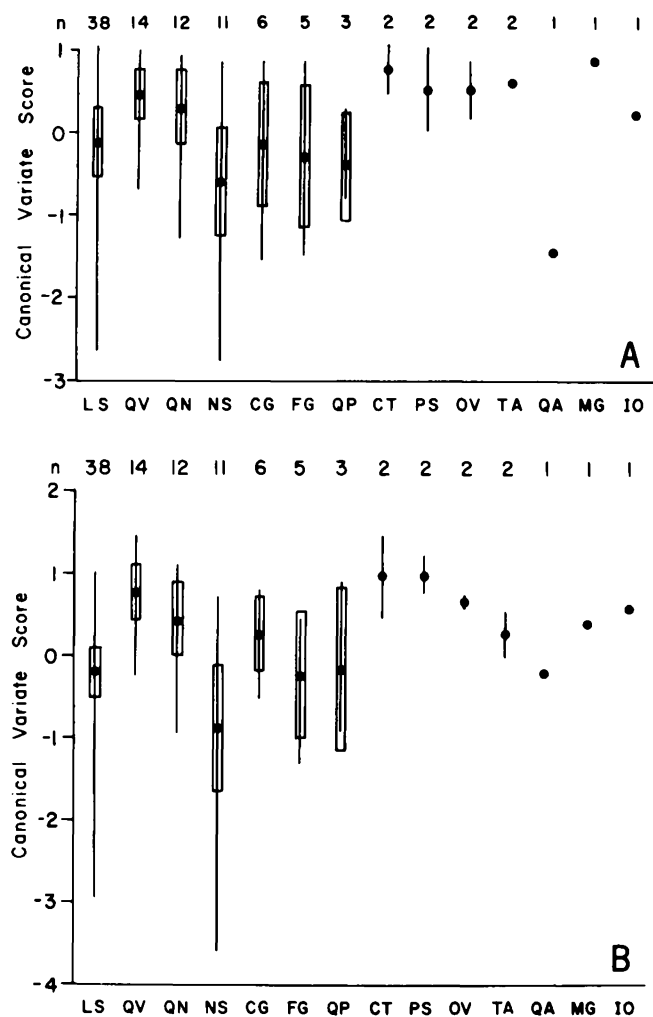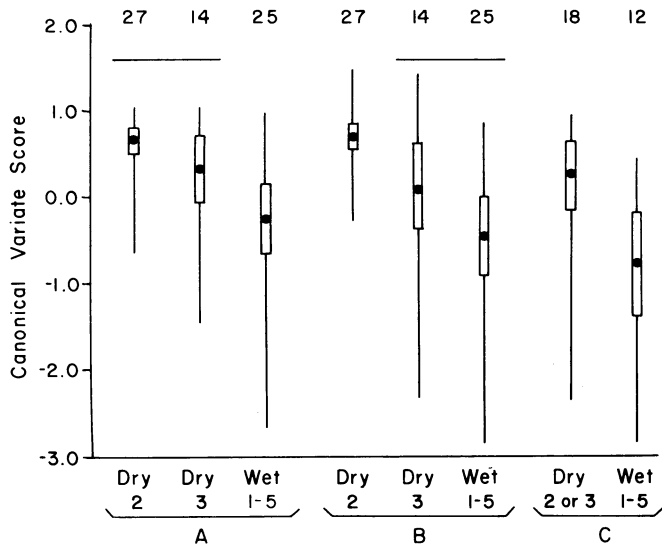

Fig. 3 A, B. Canonical variate scores for A mosquito densities and B physical and chemical properties of tree holes partitioned according to species of the host tree. Means ± 1.96 SE and ranges are shown by dots, vertical bars, and vertical lines, respectively. The numbers above each plot show number of holes occurring in each tree species. Tree species are abbreviated by genus and species as follows: CG, *Carya glabra* (Mill.) Sweet; CT, *Carya tomentosa* Nutt.; FG, *Fagus grandifolia* Ehrh.; IO, *Ilex opaca* Ait.; LS, *Liquidambar styraciflua* L.; MG, *Magnolia grandiflora* L.; NS, *Nyssa sylvatica* Marsh.; OV, *Ostrya virginiana* (Mill.) K. Koch; PS, *Prunus serotina* Ehrh.; QA, *Quercus alba* L.; QN, *Quercus nigra* L.; QP, *Quercus phellos* L.; QV, *Quercus virginiana* Mill.; TA, *Tilia americana* L.

score while drought-resistant holes had a lower, negative mean canonical variate score.

Oviposition behavior

Oviposition into water-filled jars reflected the species composition of the source hole (Figs. 5, 6). Figure 5 shows the frequencies of mosquito species found in jars and tree holes. From these data we made two types of comparisons: First, the distribution of each species between jars whose water came from *Orthopodomyia* holes and *Aedes* holes, and second, the distribution of each species between jars and their respective source tree holes at the time of jar census.

T. rutilus exhibited no significantly different frequencies either between *Orthopodomyia* jars and *Aedes* jars or be-
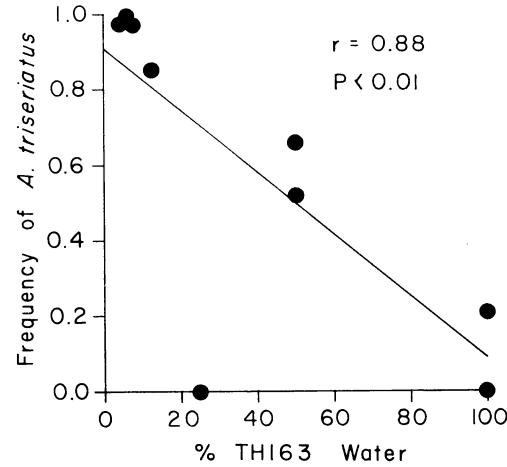
Fig. 4 A–C. Canonical variate scores for **A** mosquito densities and **B** physical and chemical properties of tree holes that dried out before the second census (Dry 2), remained wet during the second but dried during the third census (Dry 3), or remained wet for the first 5 censuses (Wet 1–5) and **C** physical and chemical properties of the 30 tree holes used to estimate pupation success in Table 1. Means ±1.96 SE and ranges as in Fig. 3. The numbers above each plot indicate sample size; the horizontal line above each plot extends over means that are not significantly different ($P>0.05$)
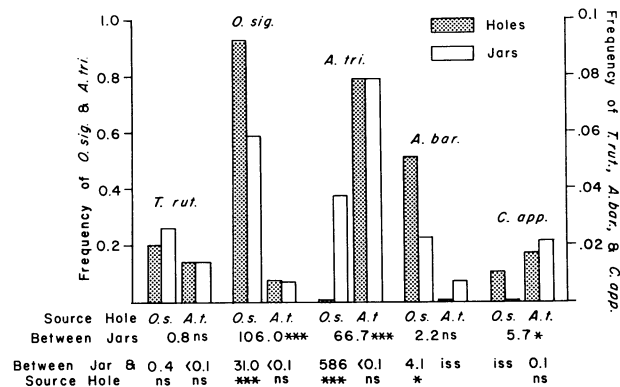
Fig. 5. Comparisons of mosquito frequencies (larvae and pupae) between source holes and jars at the end of the jar experiment. The numerical values at the bottom of the figure list χ_2 values; ns, not significant; *, $P<0.05$; ***, $P<0.001$; iss, insufficient sample size for χ^2

Fig. 6. Species composition of jars containing serial dilutions of water from an *Orthopodomyia* hole (TH163). Frequency of *Aedes triseriatus* is calculated as number of *Aedes triseriatus* in the jar divided by number of (*Aedes triseriatus* + *Orthopodomyia signifera* + *Anopheles barberi*) in the jar

tween *Orthopodomyia* or *Aedes* jars and their respective source holes. *O. signifera* and *A. triseriatus* were, by marked contrast, found in a significantly higher frequency in jars whose water originated from *Orthopodomyia* and *Aedes* holes, respectively. Progressive dilution of TH163 water in jars resulted in a species composition that shifted from predominantly *Orthopodomyia-Anopheles* to *Aedes* (Fig. 6). These results show that tree-hole water by itself can be an important determinant in the distribution of these two species.

In comparing jars with their respective source holes, we observed no significant differences between *Aedes* jars and *Aedes* source holes; but, the frequency of *O. signifera* was lower and that of *A. triseriatus* higher in *Orthopodo-*

myia jars than in *Orthopodomyia* source holes. Among *A. barberi* we found no significant differences in frequency between *Orthopodomyia* and *Aedes* jars but did find them at a significantly lower frequency than expected in *Orthopodomyia* jars than in *Orthopodomyia* holes. *C. appendiculata* appeared at a higher frequency than expected in *Aedes* than in *Orthopodomyia* jars.

Discussion

The results in Table 1 show that there were significant differences in pupation success of mosquitoes between drought-prone and drought-resistant holes. The relative abundance of tree-hole mosquitoes at Tall Timbers segregated according to tree-hole susceptibility to drought. *T. rutilus, O. signifera,* and *A. barberi* were less likely to be present in holes fated to dry up or that had been dry in the recent past (Fig. 1 B, C, E). Presence of *A. triseriatus* was not associated with future expectation of drought (Fig. 1 C), but was more likely to occur in holes which had been dry previously (Fig. 1 E). *A. triseriatus* possesses drought-resistant eggs and, upon refilling of a previously dry hole, may immediately hatch. *T. rutilus, O. signifera* and *A. barberi* do not possess drought-resistant eggs and depend upon continuous moisture for survivorship. The occurrence of the latter 3 species in the more permanent holes (Fig. 1) is then consistent with these requirements.

The density of each species was correlated both with other species and with a particular suite of physical and chemical properties of tree holes. Canonical correlation of mosquito densities with tree-hole properties reaffirmed the previously noted segregation (Bradshaw and Holzapfel 1983) of *A. triseriatus* from the *T. rutilus–O. signifera–A. barberi* subcommunity. This segregation was correlated with physical and chemical properties of the holes such that co-occurrence of *T. rutilus. O. signifera,* and *A. barberi* was associated with holes that were larger, with larger more vertical openings, lower down in larger trees, and contained darker water with higher conductivity, pH, and tannin-lignin content than holes occupied by *A. triseriatus*. Mean

canonical variate scores for physical and chemical properties varied significantly between drought-prone and drought-resistant holes (Fig. 4). Comparison of these mean scores with correlations between the first canonical variate and the original physical and chemical properties (Fig. 2) showed that drought-resistant holes are distinguished from drought-prone holes by the same respective suite of properties that distinguish T. rutilus–O. signifera–A. barberi holes from A. triseriatus holes.

The correlations between tree-hole properties, mosquito subcommunities, and drought resistance discussed above suggest that drought is the ultimate determinant of habitat segregation. The selective oviposition of mosquitoes into their respective tree hole types (Fig. 1C, E) during a period of continuously wet holes suggests further that it is not drought, per se, that stimulates oviposition. Rather, some combination of physical and chemical cues associated with drought is providing the proximal cue for selective oviposition.

While mosquito sub-communities did not vary among tree species, physical and chemical properties appeared to do so (Fig. 3). Nyssa sylvatica would then appear to have physical and chemical properties more attractive to the Toxorhynchites–Orthopodomyia–Anopheles subcommunity then Prunus serotina and Carya tomentosa that would seem more attractive to the Aedes subcommunity. We believe this conclusion to be misleading due to the availability of the latter two species. Age of tree stands can be an important factor affecting the types of holes and mosquitoes found in that stand (Bradshaw and Holzapfel 1986). We found only younger stands of Prunus serotina and Carya tomentosa at Tall Timbers so that the age-availability of these species biassed our samples towards smaller trees able to contain only the smaller, more transient rot holes. We found Carya glabra, a congener of C. tomentosa, extending over a wider range of tree sizes and, not surprisingly, containing wider ranges of mosquito sub-communities and of physical and chemical properties (Fig. 3). Among trees represented at Tall Timbers by a wide range of ages and sizes, we observed smaller, more transient holes than we would expect only in Quercus virginiana. Even in this species, however, we found a single tree (TH193) that harbored holes containing contrasting mosquito sub-communities (canonical variate scores of -0.07 and $+0.10$) as well as physical and chemical properties (canonical variate scores of -0.10 and $+0.97$) respectively. From these considerations, we conclude that mosquito oviposition is stimulated by the physical and chemical properties of the holes themselves independently of the species of tree in which that hole resides.

Tree-hole mosquito occurrence (Fig. 2; Lunt and Peters 1976; Petersen and Chapman 1969; Mitchell and Rockett 1981) and oviposition behavior of A. triseriatus (Wilton 1968; Zaim and Newsom 1979; Bentley et al. 1979, 1981; Slaff et al. 1975) are associated with physical and chemical properties of holes. In addition, ovipositing A. triseriatus may be stimulated by prior occupancy of conspecifics (Bentley et al. 1976; McDaniel et al. 1976, 1979) and T. rutilus by prior occupancy of potential prey (Trimble 1979). In combination the above factors may interact additively or synergistically with one another to stimulate oviposition (McDaniel et al. 1976; Slaff et al. 1975; Wilton 1968) so that oviposition site selection and oviposition stimulation in nature probably result from complex integration of available cues. Regardless of the specific cues used or the manner

in which these cues are integrated by ovipositing females, the important point is that the behavior of ovipositing females is the initial determinant of community composition and that this behavior is in turn affected by physical and chemical attributes of tree holes. During the spring and early summer, tree holes fated to dry out or remain wet varied with respect to their physical and chemical properties (Fig. 4) but differential survivorship occurred only in the spring when holes actually dried out (Table 1). Thus, these attributes are not the major causes of mortality but are likely used as oviposition cues which predict the future survivorship of offspring in these holes.

Both components of the interaction between ovipositing females and the physical-chemical properties of holes are far from perfect. The range and standard error of canonical variate scores associated with the drought categories in Fig. 4 show the variation in tree-hole attributes within each category. Even though mosquitoes are not likely to integrate cues in the same manner as canonical correlation analyses, it is clear from this variation that cues may often be ambiguous. Of the mosquitoes, O. signifera most assiduously avoided ovipositing in jars with water from the "wrong" tree holes (Fig. 5) and was least affected by the spring drought in actual holes (Table 1A). A. triseriatus was more catholic in its choice of jars (Fig. 5) and holes (Fig. 1). A. barberi did not distinguish between Aedes and Orthopodomyia jars (Fig. 5) and occurred at a lower frequency in Orthopodomyia jars than holes (Fig. 5). It would thus appear that chemical properties of the water are less important and physical properties of the holes themselves more important cues to ovipositing A. barberi than O. signifera or A. triseriatus. Whether due to reliance on poorer cues or lower adherence to hese cues, sufficient A. barberi occurred in the "wrong" holes so that they, unlike O. signifera, suffered significant mortality from the spring drought (Table 1A). Tree-hole mosquitoes thus appear to vary with respect to the cues they use, their fidelity to those cues, and the hydrological consequences therefrom.

In automobile tires in the field (Bradshaw and Holzapfel 1983) and in laboratory microcosms (Chambers 1985), Aedes triseriatus achieves higher emergence success than Orthopodomyia signifera in the absence of predation. When Toxorhynchites rutilus was allowed access to tires or placed in lab microcosms, total mosquito emergence declined but O. signifera achieved greater relative emergence success than did A. triseriatus. Chambers (1985) also found that older O. signifera could effectively compete against younger A. triseriatus. Thus, in more permanent holes, predation from T. rutilus and a continuous population of older, predator-resistant, slower-developing O. signifera should combine to greatly reduce or eliminate fitness of A. triseriatus in these holes.

Frequent rains can maintain continuous water in otherwise drought-prone holes and T. rutilus are, next to A. triseriatus, the most rapid colonizers of previously dry holes (Bradshaw and Holzapfel 1983). During the frequent summer rains, T. rutilus occupied an increasing fraction of all holes (Bradshaw and Holzapfel 1984) so that drought-prone holes no longer served as refugia for A. triseriatus. The net result is that with frequent rains, the incidence of A. triseriatus declined and that of O. signifera + A. barberi increased during the year (Bradshaw and Holzapfel 1983, 1984). This process continued until there was a drought which dried out all the holes in October. Upon the return

of rains in December, the incidence of *A. triseriatus* rose to its highest level of the year. In south Florida, where droughts are more prevalent (Bradshaw and Holzapfel 1984), *A. barberi* is absent and the prevalence of *O. signifera* and *T. rutilus* greatly reduced relative to north Florida (Lounibos 1983). Also in southern Florida, Lounibos (1985) found that intraspecific competition among *A. triseriatus* is alleviated either by sustained rains allowing penetrance of predators into even the most drought-prone holes or by prolonged droughts allowing for nutrient accumulations.

Thus, the duration, frequency, and timing of drought differentially affect the survivorship of pre-adult mosquitoes either by the direct action of dehydration on developing larvae and pupae or by the indirect modulation of predation.

Intraspecific competition has been demonstrated clearly in tree-hole mosquitoes by Hawley (1985a, b) who showed that in nature, adult longevity and fecundity of *Aedes sierrensis* Ludlow are direct consequences of limiting larval density. Intraspecific competition among *A. triseriatus* has been observed (1) in tree holes in south Florida during periods of intermittant rains when tree holes dry often enough to inhibit the dispersal of *T. rutilus* but not long enough for substantial resources to accumulate (Lounibos 1985), (2) in artificial laboratory microcosms (Carpenter 1982, 1983; Fish and Carpenter 1982; Chambers 1985), and (3) in populations on natural substrates transferred to 300 ml Nalgene bottles in the field (Livdahl 1982). Of these studies, only Lounibos' and Hawley's directly examined the effects of density in actual tree holes; all have found what one would expect: In the natural or artificial absence of predators tree hole mosquitoes reach or can be concentrated into self-limiting densities. None of these studies was designed to show or support the idea that density-dependent factors are operating under the conditions of drought and predation that prevail at Tall Timbers.

Schoener (1983) and Connell (1983) both point out that investigators may choose to examine competitive interactions where they perceive competition to be important; hence estimates of the importance of competition, based on the incidence of published examples, may be biased. We suspect that investigators of aquatic populations and communities might similarly be predisposed to select study sites which are most likely to persist for the duration of their study. If so, there is a potentially compound bias in freshwater systems towards documenting the importance of biotic over abiotic limiting factors (especially drought) or their interaction as well as towards the liklihood that competition or predation will be prominent among the biotic interactions.

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