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THE DISTRIBUTION AND ABUNDANCE OF TREEHOLE MOSQUITOES IN
EASTERN NORTH AMERICA: PERSPECTIVES FROM NORTH FLORIDA

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ABSTRACT

Treehole mosquitoes in eastern North America partition their habitat by trophic specialization, drought resistance, predation avoidance, and level in the forest. At the southern portion of their ranges, drought and predation limit their distribution and abundance and, because of mortality from these factors, little, if any competition takes place within or between species. As one proceeds north, drought has a declining and freezing an increasing influence on mosquito populations. Within the range of *Toxorhynchites rutilus* and *Corethrella appendiculata*, predation by these species is the predominant regulator of prey populations. But, because these predators are among the most susceptible to drought and freezing, these factors indirectly reduce predation to affect both the absolute and the relative abundance of prey species. North of the range of *T. rutilus*, freezing is the major factor limiting the occurrence of species but intraspecific density-dependent factors and, perhaps, competitive displacement may take place. However, published evidence for density-dependent development in actual treeholes is lacking for eastern North America; evidence for competitive displacement is, at best, circumstantial. Nonetheless, available evidence indicates that the distribution and abundance of treehole mosquitoes in eastern North America are regulated primarily by the interactions between biotic and physical limiting factors.

INTRODUCTION

Ever since Malthus and Darwin, competition has been envisioned as a major factor organizing natural communities. Most theory over the last 20 years has emphasized competition as the major force affecting the number and coexistence of species in a community. Species may coexist only if they evolve sub-habitat specializations and so avoid competing for the limiting resources (e.g., Cody 1968; MacArthur & Levins 1967; Schoener 1974; Pianka 1969; Cody & Diamond 1975). One might well expect these considerations to be all the more acute in restricted habitats where the inhabitants are forced to deal with one another at close quarters and there is minimal outside interference. It is in this context that we set out to investigate competitive interactions among treehole mosquitoes where the very restricted nature of the habitat begged the question of coexistence.

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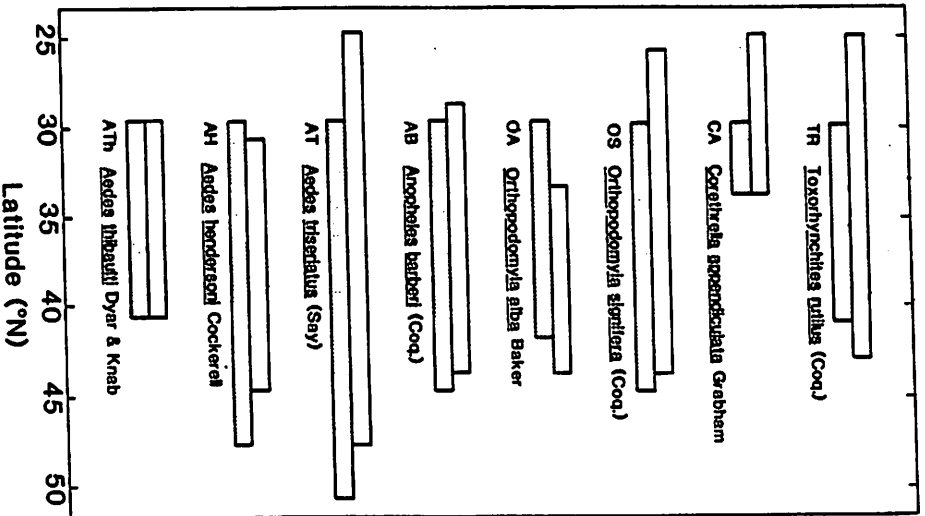


Fig. 1. Distribution of treehole mosquitoes in eastern North America based on Jenkins & Carpenter (1946), Davis & Ward (1961), and personal unpublished encounters. Open bars show the range of each species along the Atlantic coastal plain; shaded bars show the range of each species along the Mississippi River valley. Ranges along the latter transect end abruptly at about 30° N due to the Gulf of Mexico.

In eastern North America (east of the Mississippi River) there are seven culicid and one chaoborid species whose preferred habitat is the rot holes of deciduous trees (Fig. 1). Collectively, they range from subtropical south Florida (ca. 25° N) through the temperate zone to central Canada (ca. 50° N) but only one species, *Aedes triseriatus* (Say) extends over this entire range. Species richness is highest from northern Florida (30° N) to the mid-Atlantic states and lowest (40-42° N). Species richness is lower both north and south of this range.

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Nonetheless, 7-8 species are known to co-occur from 31-41° N. The basic questions we are addressing then, are (1) what factors limit the distribution and abundance of these species and (2) what factors permit the coexistence of 7-8 species in such a finite habitat? To answer these questions, we investigated the interactions among five coexisting species at a single locality in north Florida and then used these interactions to interpret conditions at other geographic localities.

HABITAT UTILIZATION IN NORTH FLORIDA

We chose as our study area the Tall Timbers Research Station (Leon Co.) where treeholes are colonized commonly by four species of mosquitoes, *Toxorhynchites rutilus septentrionalis*

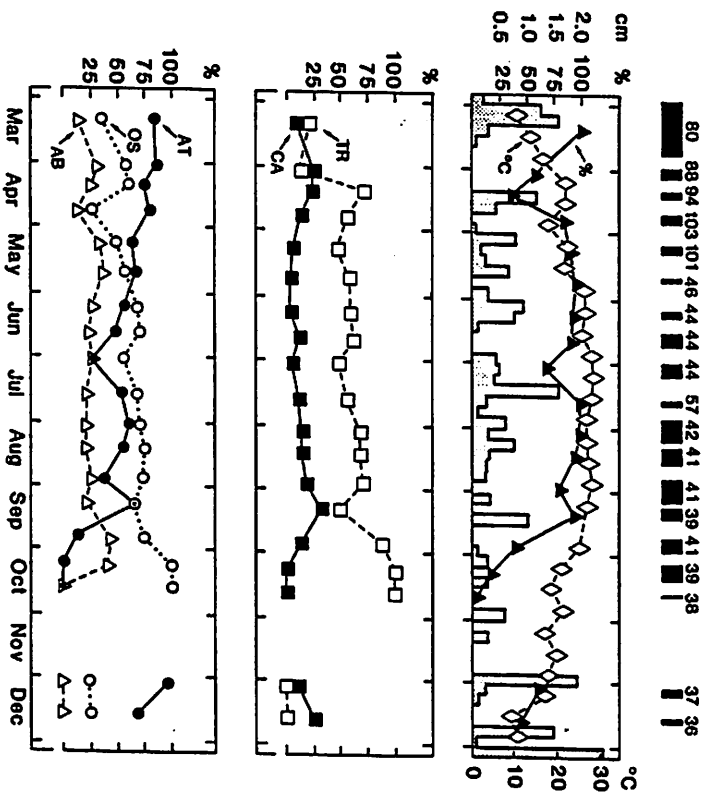


Fig. 2. Seasonal weather patterns and incidence of treehole mosquitoes at Tall Timbers, Florida, in 1978. Top line shows number of holes sampled per census and time period (bar width) during which that census took place. Top graph: histograms show rainfall per day averaged over five-day periods except for the 26th to last day of each month; open diamonds plot 10-day average air temperatures, which closely approximate treehole temperatures (Bradshaw & Holzapel 1977); closed triangles track percentage of holes examined that contained standing water. Bottom two graphs plot percentage of wet holes occupied by larvae and pupae of each species. Species abbreviations as in Fig. 1. (From Bradshaw & Holzapel 1984.)

least two sub-communities, one occupied by *A. triseriatus* and the other by the remaining four species. *Aedes triseriatus* is unique in this assemblage in possessing drought-resistant eggs. Females oviposit at the treehole - water interface so that as the treeholes dry out and water declines, the eggs accumulate on the side of the hole. Flooding of the hole during a rain then induces hatching. This scenario is supported by the data in Fig. 2. Although the incidence of *A. triseriatus* generally declined from March to October, deviations from this trend are associated with peaks in the rainfall. Thus, the incidence of *A. triseriatus* shows a rise following heavy rain in early July, early September, and especially, early December. But does *A. triseriatus* occupy a distinct subset of treeholes or do these responses to rainfall occur in all holes?

To answer the question of treehole specificity we examined a fixed set of 35 holes censused 17 times between March and October. For each hole, we calculated the probability of its containing standing water during the 17 censuses and measured the optical density of the water at 460 nm (OD₄₆₀) during the mid-July census. OD₄₆₀ correlates closely with conductivity ($r^2 = 0.70$) and tannin-lignin ($r^2 = 0.90$) in treehole water (Bradshaw & Holzapel, unpublished). OD₄₆₀ thus represents a general index of dissolved salts and humic acid. Figure 4 shows the 95% confidence ellipses about the average hole containing each species. *Aedes triseriatus* occurred in holes with the lightest colored water and the most likely to dry out while the remaining species all occurred in holes with more darkly stained water and less likely to dry out. Thus, *A. triseriatus* with its drought-resistant eggs occupies a distinct subset of more transient treeholes while *T. rutilus*, *O. signifera*, *A. barberi*, and *C. appendiculata* occupy more permanent holes. Further, treehole permanence is predictable not only from water volume (Bradshaw & Holzapel 1983) but color as well (Fig. 4).

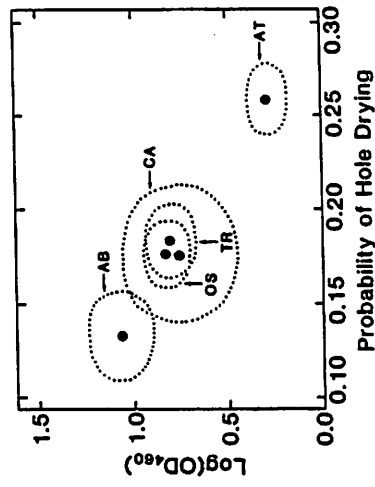


Fig. 4. 95% confidence ellipses for each species of treehole mosquito about the mean probability of a hole they occupy being dry during 17 censuses from February to October and the darkness (OD₄₆₀) of the water in that hole.

(Dyar & Knab), *Orthopodomyia signifera* (Coquillett), *A. triseriatus*, and *Anopheles barberi* Coquillett, and the chaoborid, *Corsethella appendiculata* Graham. Between February and December 1978, we made 19 censuses of mosquitoes from a total of over 100 treeholes (Fig. 2). During this interval there were two dry periods. The shorter drought occurred during the spring in late March and early April when 2/3 of the holes dried up; the longer drought started after the 14th census in mid-September. Subsequent rain did not sustain water in the treeholes, and by late October 100% of the holes had dried out. Standing water did not again appear in the holes until the end of November when heavy rains filled many of them. The incidence of mosquitoes in wet holes also varied with the season (Fig. 2). The frequencies of wet holes occupied during the year increased for *T. rutilus* and *O. signifera*, remained low but relatively steady for *A. barberi* and *C. appendiculata*, and declined for *A. triseriatus*. After the longer drought in the fall, *A. barberi* was absent, *T. rutilus* was present in only one hole, *C. appendiculata* persisted at about the same frequency as previously, and the relative frequencies of *O. signifera* and *A. triseriatus* were reversed. Qualitatively similar patterns emerged from an examination of total numbers or biomass of mosquitoes in a fixed subset of these holes (Bradshaw & Holzapel 1983). We then sought to determine what interactions among the mosquito species and their environment would generate these patterns and permit co-existence.

Initially, we performed 2 x 2 normal association analysis based on presence-absence of each species (Pielou 1977) and pairwise least-squares or rank correlation of numbers of biomass among the various species. All these analyses produced similar results (Fig. 3): a positive association among *T. rutilus*, *O. signifera*, *A. barberi*, and *C. appendiculata* and a negative association between *A. triseriatus* and *T. rutilus*, *O. signifera*, or *A. barberi*. Thus, the community appeared divisible into at

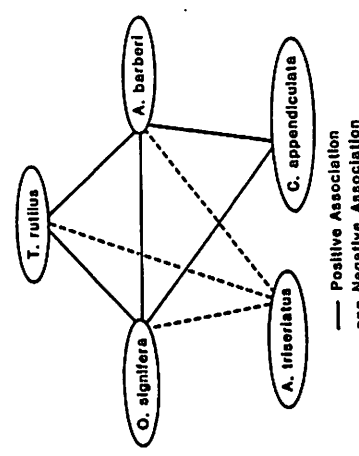


Fig. 3. General pattern revealed from 2 x 2 normal association analysis among the treehole mosquitoes at Tall Timbers. Significant associations (P<0.05) are indicated by lines connecting two species.

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The reason for the absence of species without drought-resistant stages from transient treeholes appears straightforward but reasons for the absence of *A. triseriatus* from more permanent holes are not immediately obvious. The more permanent holes are occupied by four species of which two, *T. rutilius* and *C. appendiculata*, are obligate carnivores. To investigate the effect of predation on emergence success of prey species, we set out 10 tires in a hardwood hammock at Tall Timbers (Bradshaw & Holzapfel 1983). From five of the tires we removed all eggs of *T. rutilius* at least every 72 hours and, at the same time, between mid-March and December the presence of *T. rutilius* resulted in an 89% reduction in prey emergence and a shift from an *A. triseriatus* to an *O. signifera*-dominated emerging population (Fig. 5). In fact, while 213 *A. triseriatus* emerged from the

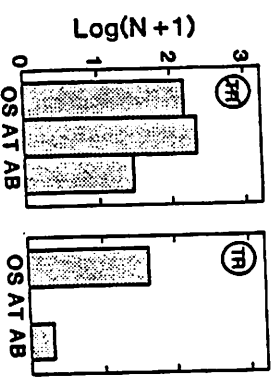


Fig. 5. Emergence success of prey species from five tires from which *T. rutilius* had been excluded (left) or from five tires into which *T. rutilius* had free access (right). N = total pupae emerging March-December 1978. Species abbreviations as in Fig. 1 (After Bradshaw & Holzapfel 1983).

five tires with no *T. rutilius*, none emerged from the tires in which *T. rutilius* had access. Substantiating these results in tires, we found that persistence and pupation of prey species in treeholes were also differentially affected by *T. rutilius* (Bradshaw & Holzapfel 1983). In the presence of *T. rutilius*, *A. triseriatus* were more likely to go extinct or fail to pupate than in holes without the predator; conversely, in the presence of *T. rutilius*, *O. signifera* and *A. barberi* were more likely to persist and pupate. Thus, although all species are affected by predation from *T. rutilius*, *A. triseriatus* suffer disproportionate mortality. It is this differential susceptibility to predation which may explain relative scarcity of *A. triseriatus* in otherwise suitable, more permanent holes.

The above observations provide the bases for habitat segregation among the treehole mosquitoes in north Florida. *Aedes triseriatus* is susceptible to predation but finds a refugium in the more transient, drought-prone holes. Of the remaining four species, two are predators and two are primarily filter-feeders and browsers. Of the two predators, *T. rutilius* is the largest member of the community and preys primarily on older instars and pupae (Bradshaw & Holzapfel 1983) while *C. appendiculata* is the

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smallest species in the community and feeds mainly on younger prey instars (Lounibos 1983). Of the two prey in the more permanent holes, *A. barberi* is a highly specialized surface feeder while *O. signifera* feeds in the benthic and limnetic zones. Thus, the degree of habitat segregation when combined with the pervasiveness of *T. rutilius* (Fig. 2) explains the continued coexistence of these five species.

Coexistence based on habitat segregation does not necessarily mean that competition is not taking place. Competition "occurs whenever a valuable or necessary resource is sought together by a number of animals (of the same kind or of different kinds) when that resource is in short supply; or if the resource is not in short supply, competition occurs when animals seeking that resource nevertheless harm one another in the process" (Andrewartha & Birch 1954). In laboratory or quasi-natural cultures of mosquitoes, increased larval density and consequent resource depletion result in both longer larval development and reduced pupation success (Surtees 1959; Moore & Fisher 1969; Gilpin & McClelland 1979; Moeur & Istock 1980; Istock et al. 1975; Fish & Carpenter 1982; Carpenter 1982; Livdahl 1982; Frank & Curtis 1977a). Density-dependent development as a result of progressive resource depletion should, at a given time, be manifest as (1) younger populations, i.e., lower mean instar, and (2) lower pupal: total biomass ratios.

Biomass of treehole mosquitoes is readily estimated by assigning to each individual the mean weight of that instar (Fig. 6). The slopes relating biomass to stage of development do not

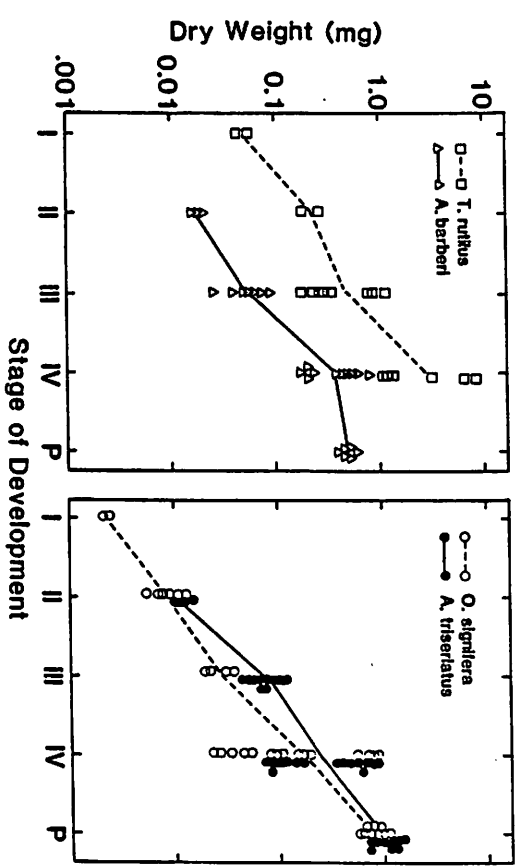


Fig. 6. Biomass of the various developmental stages of treehole culicids. Lines connect means. (After Bradshaw 1983b).

increased the duration of the third instar by 50% and assumed 50 and 25% mortality in the first and second instars, respectively (Fig. 7e). Thus, our index of pupation success still reflects retardation of development in the fourth instar despite slowing of earlier stages of development or mortality induced among younger instars by older instars under crowded conditions (Livdahl & Koenekoop, this volume).

Using pupae per milligram biomass as our criterion of pupation success, we regressed it on six predictor variables: intraspecific density (number of conspecifics per liter), interspecific density (number of heterospecific filter-feeders/browsers per liter), and predator density (number of *C. appendiculata* plus *T. rutilus* per liter) in the current and in the present census. At Tall Timbers, we found no evidence (Bradshaw & Holzapfel 1983) that intra- or interspecific density reduces pupation success of *A. triseriatus* or *A. barberi* at any time of year regardless of the presence or absence of *T. rutilus* and *C. appendiculata*. Interspecific density does have a negative effect on the development of *O. signifera* but only during the summer and only in the absence of any predators. At this time of year, treeholes lacking *T. rutilus* and, even in those holes without *T. rutilus*, intraspecific density had a positive and greater effect on pupation success than the negative effect of the putative competitors. In addition, while pupation among *A. barberi* and *A. triseriatus* declines during the summer, that of *O. signifera* is sustained. Thus, in north Florida, there is little evidence that competition is a selective force among co-existing treehole mosquitoes.

ROLE OF COMPETITION IN HABITAT SEGREGATION

Our observations above indicate that competition is currently not an important factor organizing the treehole mosquito community in north Florida. The question remains as to the evolutionary process leading to the described pattern of habitat utilization. Adherence to conventional dogma would suggest that these species, once similar, have diverged trophically and spatially and so are minimizing competition for limiting resources. The appeal of competitively driven, coevolved niche shifts is so pervasive that whenever one perceives populations or species that are not competing because of habitat specialization, one reflexively conjures up the spectre of competition to explain divergence in the past (Connell 1980). In fact, there may be no evidence for or against competition at this remote time.

What evolutionary alternatives to competition could one invoke to explain habitat segregation? We propose a model which we call the migration-adaptation syndrome (Fig. 8). Assume (1) that there is a habitat where there are two types of treeholes, TH-1 and TH-2, (2) that mosquito species A lives in this habitat and achieves greater fitness in TH-1 than in TH-2, and (3) that,

vary among culicid tribes and weight of a given stage may be estimated from a general mosquito equation adjusted for mean dry weight of fourth instars (Bradshaw 1983b):

$$LW_4 = -2.54 + 0.649I + LW_{IV}$$

where LW_4 is \log_{10} (Weight) of the 4th stage of development and LW_{IV} , the log weight of the fourth instar, is determined empirically for each species.

Density-dependent development may be inferred from the relative incidence of larvae and pupae. The frequency of individuals in a given stage of development should be equivalent to the fraction of total development time from first instar to adult represented by that stage. As resources become limiting, development slows, primarily in the fourth instar. Since pupal duration is independent of previous development, the fourth instar will then constitute a disproportionate fraction of the population; pupation rate and fraction of the population represented by pupae will decline. Consequently, the number of pupae per milligram biomass will be inversely proportional to the prolongation of the fourth instar (Fig. 7). In *A. triseriatus*, a

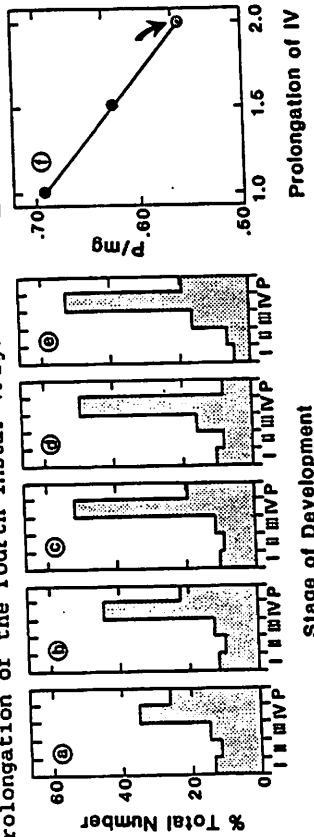


Fig. 7. Actual (a) and simulated (b-e) variation in relative abundances of larval and pupal stages of *A. triseriatus*. a, development at 21°C and long days of *A. triseriatus* from southern North Carolina with no density dependent constraints (Bradshaw & Holzapfel unpublished). b, same as a but assuming 50% prolongation of the fourth instar; c, same as a but with 100% prolongation of the fourth instar; d, same as c but with additional 50% prolongation of the third instar; e, same as d but with an additional 50% mortality in the first instar plus 25% mortality in the second instar; f, number of pupae per milligram of total population plotted as a function of prolongation of the fourth instar from a-c; the constraints added in d-e all fall within the open circle indicated by the arrow in f.

doubling of the duration of the fourth instar will increase the duration of pre-adult development by 35%. Livdahl (1982) found that going from an enriched to "normal" food level in quasi-natural microcosms of *A. triseriatus* increased total development time by about 45% so that the response in Fig. 7 is within the range of moderate density-dependent development. Pupae per milligram varied by less than 1% when, at doubling of the fourth instar, we added the following further constraints: (1) increased the duration of the third instar by 50% (Fig. 7d) or (2)

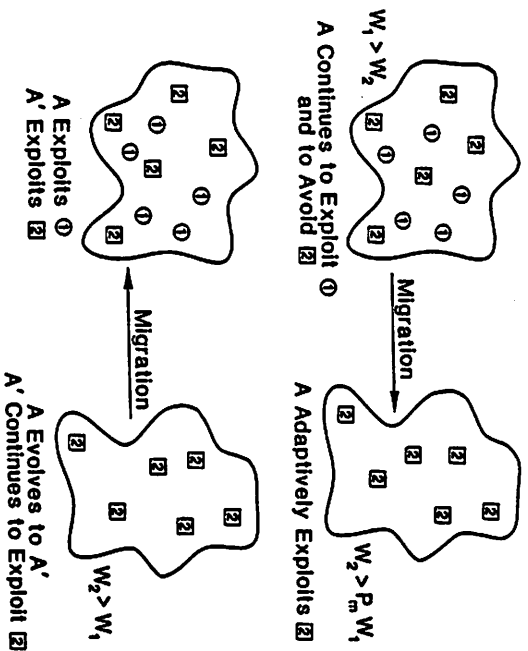


Fig. 8. Progress of the migration-adaptation syndrome in the ancestral (left) and new (right) habitats. M_1 = fitness in the 1st type of treehole; P_1 = probability of successfully migrating back to the ancestral habitat; 1 and 2, treehole types 1 and 2 respectively.

because of adverse climate, predation, or a combination of these factors, there is no intraspecific competition. Under circumstances, species A will continue to exploit TH-1 and avoid TH-2. Now, suppose some members of this population migrate passively to a new habitat where there are only TH-2 available. If the fitness of species A in TH-2 is greater than the product of its fitness in TH-1 and the probability of its migrating back to the ancestral habitat, species A will remain in the new habitat and adaptively exploit TH-2. After a number of generations, species A will evolve to species A' such that species A' has a greater fitness in TH-2 than in TH-1. Under these conditions, species A' will continue indefinitely to exploit TH-2 in the new habitat. If a member of species A' were to migrate back to the ancestral habitat, species A' would exploit TH-2 and avoid TH-1 which continues to be occupied by species A. When viewed in the present, species A and species A' would exhibit habitat segregation that might appear to have arisen as the result of competitively driven niche shifts. In fact, at no time during the migration-adaptation process did we have to invoke competition. Rather, evolutionary change and habitat specialization took place as the result of adaptive opportunism. Our migration-adaptation syndrome model resembles many of its essential features the concept of host-race formation by a number of insects (Bush 1969; Huettel & Bush 1972; Phillips

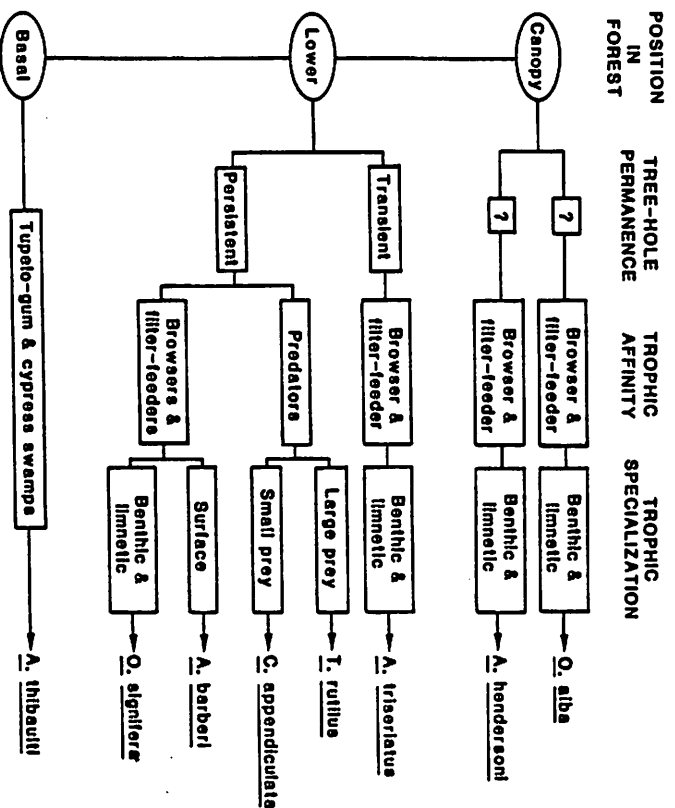


Fig. 9. Habitat segregation among treehole mosquitoes in eastern North America (see text for explanation).

& Barnes 1975; Wood 1980) and reflects some of the trade-offs between ability to exploit the current habitat and to colonize new ones (Edmunds & Alstad 1978). Habitat segregation of treehole mosquitoes in north Florida can now be viewed in light of both competitive and non-competitive models. Among five species, two are obligate carnivores preying differentially on larger and smaller prey (Fig. 9). However, the other species in the genera *Toxorhynchites* and *Corethrella* are also obligate carnivores and tend to be the largest and smallest members of their respective communities. Thus, *T. kullijug* and *C. appendiculata* have evolved their carnivorous habits so as to avoid competition with *O. signifer*, *A. triseriatus*, and *A. barberi*; nor did they evolve size-specific predation in order to avoid competing with one another. Rather, each possessed its distinguishing characters at the time of their first encounter and entrance into the community. Similar arguments can be made for *A. barberi* which belongs to a genus of highly specialized surface feeders and for *A. triseriatus* which belongs to a genus characterized by their drought-resistant eggs. *Anopheles barberi* and *A. triseriatus* did not evolve these attributes to avoid competing

to replace itself there (Frank et al. 1984). In Malaya, species of *Armigeres* in the subgenus *Leicesteria* partition bamboo internodes by height above the ground, age of the internode, and type of hole permitting access (Macdonald 1960). On the Kenya coast (Lounibos 1981), species of *Aedes* which overlap in space in treeholes exhibit divergent hatching patterns which decrease the overlap in their development time. This degree of habitat segregation does not occur among the eastern North American treehole mosquito fauna. Thus, neither the exploitation nor the refinement of exploitation of available container-habitats yet approaches that found in the more persistent tropics.

In sum, these observations suggest that the lower faunal diversity in north Florida as compared with culicids and chaoborids in the tropics has resulted from fewer potential colonists due to time, geography, and availability of alternate container habitats, not from massive competitive exclusion by the currently established species.

DISTRIBUTION AND ABUNDANCE IN EASTERN NORTH AMERICA

Two latitudinal trends occur in species abundance in eastern North America. To the south of Tall Timbers, species number declines; to the north, it increases and then, eventually, declines to zero (Fig. 1). These changes in species number are accompanied by changes in relative abundance of the persistent species. Figure 10 shows the relative numerical abundance of mosquitoes in natural treeholes and in automobile tires from peninsular Florida north to Michigan and Massachusetts. The tires censused during 1974 constitute a uniform group that we put in oak-hickory wood lots during January 1974, after the autumnal leaf fall. We set each tire at the base of an oak or hickory tree and put two handfuls of sterilized treehole detritus originating from a single treehole in Pennsylvania into each tire. We thus established a set of larval traps in similar macrohabitats with relatively uniform microhabitats so that geography provided the major differences between localities. Several patterns were observed.

(1) Relative species abundance in sentinel tires closely approximates that in actual treeholes. Thus, our tire censuses in Michigan during 1974 revealed a similar pattern to that observed by Mitchell & Rockett (1981) in nearby northern Ohio during 1976-1977. In northern Florida, tire populations during September 1977 closely approximated those found in treeholes at the same locality among 35 holes sampled 17 times from February to October 1978.

(2) In treeholes south of Tall Timbers in peninsular Florida, *A. barberi* is absent, the abundance of *C. appendiculata* relative to *T. rutilus* increases, and the abundance of *Q. signifera* relative to *A. triseriatus* declines.

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with each other or with *Q. signifera*; rather, each was already a surface feeder or had drought resistant eggs at the time of their first encounter and entrance into the community. Thus, the major determinants of habitat segregation among treehole mosquitoes in north Florida are genus-, not species-level adaptations. Consequently, they do not result from co-evolved niche shifts among the immediate ancestors of the present species but from adaptations evolved during the divergence of genera, subfamilies (Anophelinae, Toxorhynchitinae, and Culicinae), or families (Culicidae and Chaoboridae). It is even more contorted to attempt fitting a competition-based model to these more remote events than to recent ones.

In addition to co-evolved niche shifts, competition in the past may have prevented new species from invading treeholes or forced the extinction of previously established species. However, consideration of (1) the number of potentially colonizing species, (2) the variety of available container habitats, and (3) evolutionary time suggest that competitive exclusion has not been an important limiting factor within the range of *T. rutilus*.

First, Florida is largely isolated from species-rich source areas. Eastern North America is cut off from the great variety of Central and South American container-breeding Culicidae and Chaoboridae by the Caribbean to the south and the Great Plains and Sonoran desert to the west. Second, the variety of container habitats in Florida is small when compared with tropical areas where treehole communities have far richer faunas (Lu et al. 1980; Macdonald & Traub 1960; Lounibos 1981). In these areas there is available a rich diversity of pitcher plants, fruit husks, snail shells, bamboo nodes, and plant axils (Lounibos 1978, 1979b, 1980; Beaver 1983; Frank 1983; Machado-Allison et al., this volume). In Florida, in addition to treeholes, there are only three species of native bromeliads and one species of pitcher plant capable of supporting year-round populations of mosquitoes. Thus, the diversity of alternate container habitats which might act as adaptive stepping stones is much lower in Florida than in the tropics.

Third, evolutionary time may be an important consideration affecting the number of treehole mosquito species in eastern North America. On the Kenya coast, Lounibos (1981) observed macro-habitat segregation according to peridomestic, cultivated, ecotonal, woodland, and riparian habitats. Bradshaw & Holzapfel (1983) detected no macro-habitat partitioning among treehole mosquitoes in north Florida and studies by Means et al. (1977) and Beier et al. (1983) suggest the specific adaptation to human-generated containers is only just beginning to take place in eastern North America. In the tropics, both *Corathrella* and *Toxorhynchites* occupy bromeliads and pitcher plants (Beaver 1983; Frank 1983; Frank & Curtis 1981). In eastern North America, neither has yet invaded pitcher plants despite the presence of abundant prey, especially in Florida (Bradshaw 1983a); only *Toxorhynchites* has been found in bromeliads but may not be able

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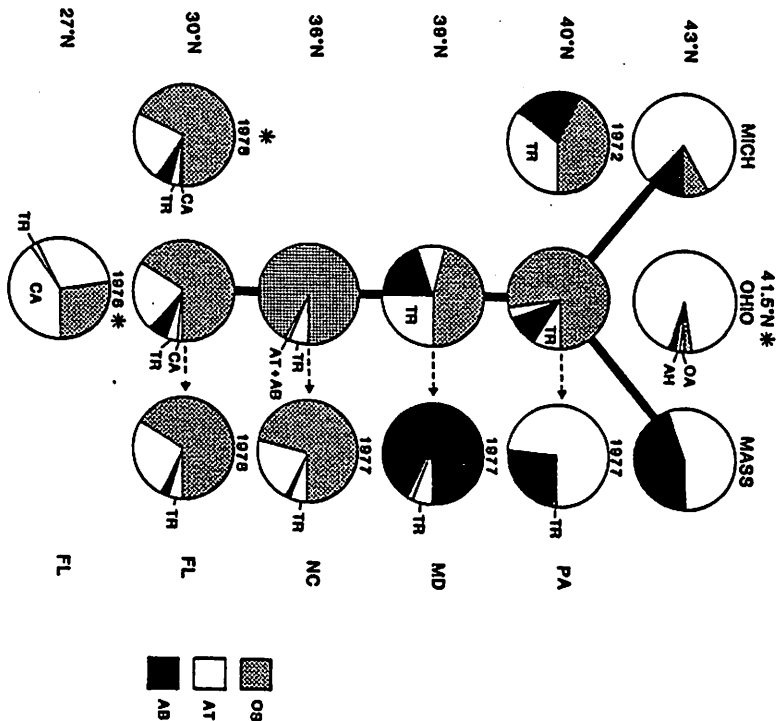


Fig. 10. Relative abundance of treehole mosquitoes in automobile tires seeded with treehole detritus and in real treeholes (species abbreviations as in Fig. 11). Percentage of the total population represented by each species is proportional to the area taken up in each diagram. Latitudes are shown on the left and states on the right or on top. The six sets of data connected by the heavy solid line show tires set out and seeded in January 1974, and then censused during August (39°N) or September (all others) 1974. Four of these sets, as indicated by the dashed lines, were sampled again during September of 1977 or 1978. Real treehole data from Ohio represent 34 holes sampled from 98 holes (Mitchell & Rockett 1981), from 30°N in Florida represent 17 holes sampled in 17 times each from February to October (Bradshaw & Holzapel 1983), and from 27°N in Florida represent 29 holes sampled once (Lounibos 1983).

(3) In tires to the north of Tall Timbers during 1974, the pattern observed at Tall Timbers persisted over a 10° shift in latitude into Pennsylvania but changed dramatically between Pennsylvania and either Michigan or Massachusetts over a 2.5° shift in latitude. This change was characterized by the complete absence of *T. fulvius* and a reversal in the relative abundance of *A. triseriatus* and *O. signifera* at the more northern latitudes. This latter reversal is against the seasonal gradient since at northern latitudes *A. triseriatus* enter diapause as embryos

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(Holzapfel & Bradshaw 1981; Sims 1982; Shroyer & Craig 1983) while *O. signifera* diapause as larvae (Baker 1935; Bradshaw 1973); during September *O. signifera* should then be increasingly more abundant than *A. triseriatus* as one proceeds north.

(4) Relative abundance of species was most consistent between 1974 and 1977 at lower latitudes and most divergent at higher latitudes. The greatest changes occurred in Pennsylvania and Maryland where *O. signifera* was absent and *T. fulvius* less abundant but *A. barberi* and *A. triseriatus* more abundant in 1977 than 1974. Thus, between 1974 and 1977, tires in Pennsylvania, Maryland, and, to a lesser extent, North Carolina, exhibited species abundances more characteristic of tires in Michigan and Massachusetts during 1974.

The differences between peninsular and northern Florida may be due to the increase in the frequency of prolonged drought at the former locality. As one proceeds from continental North America down the Floridian peninsula, the probability of a long dry period increases (Bradshaw & Holzapel 1984). We have already noted (Bradshaw & Holzapel 1983, 1984) that, after a long drought at Tall Timbers, *A. barberi* is absent, *T. fulvius*, *O. signifera*, and *C. appendiculata* decline in abundance but persist, and the relative abundance of *A. triseriatus* rises dramatically. A similar pattern is observed in peninsular Florida (Lounibos 1983). Prolonged rains in southern Florida are accompanied not only by an increase in treeholes containing *T. fulvius* and *O. signifera* but also a decline in *A. triseriatus* that is associated directly to predator abundance, especially that of *C. appendiculata* (Lounibos 1983). Thus, the distribution and abundance of treehole mosquitoes south of Tall Timbers appears to be limited by weather either directly or by its effect on predator populations.

The distribution and abundance of treehole mosquitoes remains relatively constant from 30° to 40° N latitude (Figs. 2, 10). Between 40° and 42° N, the first species to drop out of the community is *T. fulvius*. At Tall Timbers, the presence of *T. fulvius* was associated with a rise in the local extinction and a decline in the pupation success of *A. triseriatus*; the opposite effects occurred among *O. signifera* and *A. barberi* (Bradshaw & Holzapel 1983). Chambers (this volume) has shown that pupation success of *A. triseriatus* relative to *O. signifera* is similarly reversed by *T. fulvius* in laboratory microcosms. At Tall Timbers, *T. fulvius* is a limiting predator and in its continued presence, prey species do not compete (Bradshaw & Holzapel 1983). When *T. fulvius* is absent, *O. signifera* in New Mexico (Bradshaw, unpublished) and *A. triseriatus* in Indiana (Fish, unpublished) reach self-limiting densities. Based on these observations, it is tempting to conclude that in the absence of *T. fulvius*, prey populations are limited by resources and their relative abundance reflects competitive ability. If so, the patterns observed in Michigan, Ohio, and Massachusetts suggest that *A. triseriatus* dominates *O. signifera* but that *A. barberi* is able to persist at higher frequencies, perhaps because it is able

DeFoliart 1977; Sinsko & Grimstad 1977; Mitchell & Rockett 1981) in more deeply stained water (Mitchell & Rockett 1981; Truman & Craig 1968), is associated more with *O. alba* than with *O. signifera* (Grimstad 1977), and is distinct from *A. triseriatus* in a variety of other biological traits. Again, it is tempting to invoke competitive displacement from each special sub-habitat. Discussion above indicates that resource-limiting conditions prevail outside of the range of *T. kuttilus* and *C. appendiculata* but what happens within the range of these species? *Aedes hendersoni* is uncommon or absent in Florida where *T. kuttilus* and *C. appendiculata* both occur, and data from automobile tires (Fig. 11) show that in Pennsylvania, oviposition of *T. kuttilus* declines exponentially with height in the forest. If *A. hendersoni* were a better competitor but excluded from lower holes because of predation, then one would expect to find *A. hendersoni* in basal holes where *T. kuttilus* is absent. Similarly, if *A. triseriatus* were the better competitor, one would expect it to prevail at all levels in the forest. Thus, there is no consistent pattern to support competitive displacement from their respective sub-habitats.

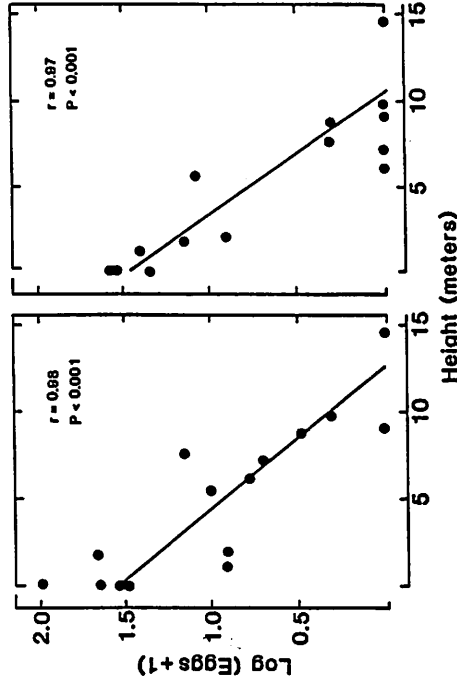


Fig. 11. Number of *T. kuttilus* eggs in automobile tires seeded with treehole detritus and hung at various heights in an oak-hickory woodland in Pennsylvania (40° N) during the summer of 1972 when *T. kuttilus* was prevalent at this locality. The graphs plot results of two censuses on 26 August (left) and 3 September (right).

We know little about selective factors which favor oviposition by females of *A. hendersoni* in higher and of *A. triseriatus* in lower holes. Treeholes in the canopy are likely to be in smaller, thinner branches and more separated from the boundary layer on the forest floor than are basal treeholes. In the winter, these higher holes would hold less heat, be more subject to convective heat loss through the surrounding wood, and be more subject to convective heat loss through greater exposure to cold winter winds. Consequently, they would be colder and

to exploit an exclusive surface-particle resource.

Change in community structure may come about very rapidly. The winters of the decade prior to 1976 were milder than normal, but January of 1977 averaged over 6° C colder than normal (Holzapfel & Bradshaw 1981). Whereas we had been able to collect overwintering larvae from tires and treeholes from 1972 to 1975, these collections were not possible in 1977 when tires were frozen solid as far south as southern North Carolina (34° N), those in South Carolina (33° N) were frozen but for a small amount of water, and those at Tall Timbers had 1-2 cm of ice in them. From melted ice, we recovered only dead *T. kuttilus*, *O. signifera*, and *A. barberi* in Pennsylvania and Maryland and reduced densities of live larvae in North Carolina (36° N). The following September, the abundance of treehole mosquitoes from North Carolina to Pennsylvania had shifted to patterns similar to those previously observed at respectively more northern latitudes. These observations suggest that freezing cold has a more dramatic effect on *O. signifera* and *T. kuttilus* than on *A. triseriatus* or *A. barberi*. Thus, within the range of persistent *T. kuttilus*, prey species are limited primarily by drought and predation; north of this zone, prey populations are affected differentially by freezing and, perhaps competition.

Besides those species we regularly found in treeholes and tires, three others are generally considered to be treehole mosquitoes in eastern North America: *Aedes thibaulti* Dyar & Knab, *Aedes hendersoni* Cockerell and *Orthopodomyia alba* Baker. *Aedes thibaulti* is described by Jenkins & Carpenter (1946) as being a highly specialized species which is restricted to the tupelo gum - cypress swamps. Ovipositing females seem to prefer the peculiar basal and root cavities formed by *Nyssa aquatica* Marsh., *Nyssa biflora* Marsh., and *Taxodium distichum* Rich. *Aedes thibaulti* were particularly abundant in holes which were subject to flooding or stood in semi-permanent pools. Shields and Lackey (1938) report that *A. thibaulti* in Alabama co-occurred with *Culex restuans* Theobald, *Culex territans* Walker, *Culiseta melanura* Coquillett and *A. triseriatus*. Further north, *A. thibaulti* has been found in association with *Aedes canadensis* (Theobald) and *C. melanura* in wet hollows beneath uprooted trees (McNelly 1984). We have found *C. restuans* and *C. melanura* occasionally in basal treeholes (Bradshaw & Holzapfel 1983); in tires, they are more abundant in those set on the ground as opposed to higher in the tree and in those containing no treehole detritus. *Aedes triseriatus* similarly occurs in less highly stained treeholes (Fig. 4) so its co-occurrence with *A. thibaulti* and the absence of other treehole species is not surprising. Taken together, these observations suggest that *A. thibaulti* occupies a sub-habitat which is very distinct from the other treehole mosquitoes and is halfway between a basal treehole and a floodwater pool. Nothing is known about factors limiting *A. thibaulti* within this sub-habitat.

Aedes hendersoni, when compared with *A. triseriatus* & oviposits and is found at higher levels in the forest (Scholl &

cool faster, increasing the probability of freezing temperatures and decreasing the opportunity for supercooling. The greater abundance of *A. hendersoni* in the canopy would thus indicate that they are more cold tolerant than *A. triseriatus*. This concept is supported by their relative abundances over their ranges. *Aedes triseriatus* persists in the absence of *A. hendersoni* on the Florida peninsula but the abundance of *A. triseriatus* relative to *A. hendersoni* declines at northern latitudes. Wood et al. (1979) report that in Ottawa (45-46 N latitude) *A. hendersoni* is "usually associated with but always outnumbered by its sister species *A. triseriatus*." Third, Galloway & Brust (1982) found that in the Manitoba, Winnipeg area (50° N latitude) *A. triseriatus* outnumbered *A. hendersoni*, but by only 3:2 in treeholes 0.75 m or less above the ground. Clearly, there is considerable opportunity for study on the comparative physiology, ecology, and behavior of these two species.

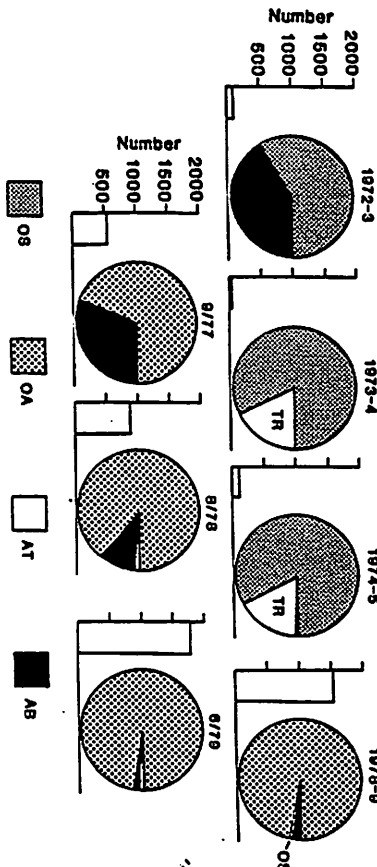


Fig. 12. Relative abundance of treehole mosquitoes in a single five liter treehole in Pennsylvania (40° N) from 1973 to 1979. The bar graph at the left plots the total number of larvae and pupae in the hole and the diagram shows the relative frequency of each species. Top row, winter censuses in late December or in January; bottom row, summer censuses. Species abbreviations as in Fig. 1.

The separation of *O. albipennis* from *O. signifer* remains much more enigmatic. Various authors have noticed a sudden, abundant appearance of *O. albipennis* where it was previously rare or absent. Sudia & Gogel (1953) report that surveys of treeholes around Atlanta, Georgia from 1946 to 1953 yielded but one *O. albipennis*. Yet, in March 1953 they found over 1,000 *O. albipennis* in a 5.6-liter treehole. From a single 5-liter treehole in Pennsylvania (Fig. 12) we obtained modest numbers of mosquitoes, generally less than 150 in all species, for three years. Yet, in 1978, this hole contained more *O. albipennis* than all species combined in any hole we had sampled in north Florida, including ones of over 20 liters. Wilkins & Breland (1951) made the following conclusions about the distribution and abundance of *O. albipennis*: "All work to date indicates that although the species may be regularly common within a limited area, it is very sparsely distributed over its range. Even in areas that have been searched intensively over a period of several years, larvae have been recovered from only a

small percentage of the treeholes investigated." Where do the *O. albipennis* come from? We suspect that they have been there all the time but higher in the canopy. Grinstead (1977) observed that whereas *O. signifer* in Michigan tended to be associated with *A. triseriatus*, *O. albipennis* (unpublished) found *O. albipennis* to be highly abundant in canopy holes in Indiana wood lots. We propose that *O. signifer* and *O. albipennis* may be vertically partitioning the forest habitat similarly to *A. triseriatus* and *A. hendersoni*, respectively, and that the selective force mediating this partitioning is winter temperature. We draw our conclusions from the following reasoning. First, *O. albipennis* may be more tolerant of subzero (°C) temperatures than *O. signifer* (Baker 1936). Second, the unexpected rise in both absolute and relative abundance of *O. albipennis* as compared to *O. signifer* (Fig. 12) occurred following a series of unusually cold winters (Holzpfel & Bradshaw 1981) and the disappearance or decline in the summers of 1976 and 1977 of previously abundant *O. signifer* from sentinel automobile tires in a woodlot less than 1 km distant from the treehole (Fig. 10). Third, as discussed above, holes in the upper canopy are likely to cool faster and freeze harder than lower holes. It is again tempting to conclude that *O. signifer* competitively excludes *O. albipennis* from lower treeholes and it is for unusually cold weather that opened up this sub-habitat for invasion. However, there is no direct evidence to support this conclusion. Further, morphological characters support an allopatric divergence of these two species (Zavortink 1968). Thus, even if there is current competitive displacement, habitat segregation may not have arisen through co-evolved niche shifts but as the result of independent, sub-habitat exploitation. As with the *A. hendersoni* - *A. triseriatus* complex, there is opportunity here for an interesting study of comparative physiology, ecology, and behavior.

Unfortunately, we know a great deal less about interactions between *O. albipennis* and *A. hendersoni*. They appear to coexist abundantly in Indiana in the forest canopy in the absence of predation by *T. fulvipes* (Copeland, unpublished). Even within the range of *T. fulvipes*, predation may be less important in regulating prey numbers since oviposition by *T. fulvipes* females declines exponentially with height in the forest (Fig. 11). Thus, there is no information in the literature concerning their densities or levels of intra- and interspecific encounter in nature. If *A. hendersoni* is "the species nobody knows," (Craig, unpublished), then the canopy populations comprise the community nobody knows.

CONCLUSIONS

Factors limiting the distribution and abundance of treehole mosquitoes in eastern North America vary with geography. Within the range of regular occurrence of *T. fulvipes*, there is no evidence that competition, past or present, has been important in

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limiting treehole mosquitoes; rather, predation and drought are the major limiting factors. North of the range of *T. kuitilus*, freezing and, perhaps, competition are the significant limiting factors.

Drought has an adverse effect in proportion to its duration on all the treehole mosquitoes except members of the genus *Aedes*. *Anopheles barberi* is the most susceptible to drought. It is the slowest to recover after a short drought, is absent after a long drought (Bradshaw & Holzapfel 1983), and has not been encountered during seven years of sampling on peninsular Florida (Lounibos 1983, this volume) where longer droughts are more frequent than further north (Bradshaw & Holzapfel 1984). By the same criteria, drought susceptibility decreases from *A. barberi* to *A. triseriatus* in the following order:

AB >> TR > CA > OS = OA >> AT = AH

Along the northern border of their ranges, freezing eventually limits each species. However, based on their relative geographic ranges and response to the cold winters of 1976-77 (Figs. 1, 10, 12) we conclude that freezing susceptibility decreases from *C. appendiculata* to *A. triseriatus*:

CA >> OS > TR > OA = AB >> AT = AH

Among the prey species, Lounibos' (1983) work with *Corethrella* and Bradshaw & Holzapfel's (1983) work with *Toxorhynchites* suggest that predator susceptibility declines from *A. triseriatus* to *O. signifera*:

AT = AH >> AB > OS = OA

We have no means to evaluate the relative susceptibility of *A. hendersoni* or *O. alba* to predation other than concluding that predator susceptibility, like other aspects of habitat segregation, is likely to be a generic rather than specific character.

Interspecific competition is the most difficult of the interactions to infer. It does not appear to be an important interaction where drought and predation are the major limiting factors (Bradshaw & Holzapfel 1983). Quantitative studies to detect competition between species have not been made further north where *T. kuitilus* is less abundant or absent and where rainfall is more regular. If competition is an important limiting factor in the north, we expect that it will be most intense between the congeneric species *O. signifera* - *O. alba* and *A. triseriatus* - *A. hendersoni*. The invasion of treeholes where *O. signifera* was previously present (Fig. 12) indicates that *O. signifera* may be excluding *O. alba* from lower holes. No data are available to surmise competitive interactions between *A. triseriatus* and *A. hendersoni*. Finally, the persistence but reduced incidence of *O. signifera* north of the range of *T. kuitilus* when combined with Chambers' (this volume) laboratory

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studies suggest that *A. triseriatus* may competitively displace *O. signifera* when resources are limited.

Among treehole mosquitoes in eastern North America, the distribution and abundance of species are then limited locally and geographically by drought, freezing, predation, and, perhaps, competition (Fig. 13). While these factors have a geographic trend from drought in the south, predation at intermediate latitudes, to freezing and competition in the north, at least two of them are interacting at each locality. Thus, physical limitations imposed by drought or freezing may affect populations either directly or indirectly by reducing the abundance of predators or competitors. Treehole mosquitoes in eastern North America illustrate the futility of forcing limiting factors into a single dimension, be it competition, predation, or a climatically variable environment.

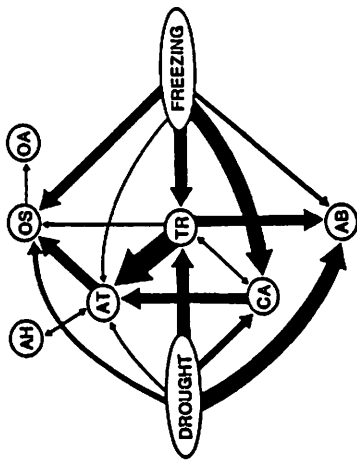


Fig. 13. Factors limiting the distribution and abundance of treehole mosquitoes excluding *A. thibaulti*. The width of each arrow indicates the relative importance of a given limiting factor. Species abbreviations as in Fig. 1.

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