

# Prospects for an Invasion: Competition Between *Aedes albopictus* and Native *Aedes triseriatus*

TODD P. LIVDAHL AND MICHELLE S. WILLEY

Competition between larval populations of the native North American treehole mosquito *Aedes triseriatus* and *Aedes albopictus*, recently introduced from Asia to North America, was assessed by comparing per capita growth rate estimates for experimental cohorts of larvae developing under a variety of initial density combinations in fluid obtained from tires or from treeholes. Estimates of carrying capacities and competition coefficients indicate that competition between the two species will result in stable coexistence in treehole communities but local extinction of *A. triseriatus* in tire habitats.

**A**EDES ALBOPICTUS, A CONTAINER-breeding mosquito, has begun to colonize the North American continent during the last several years, after its introduction within imported used automobile tires. Successful colonization by this potential vector for disease transmission, most notably dengue fever (1), and which occupies much of Asia and the Pacific region, was first observed in Houston in 1985, where it had already achieved dominance in artificial containers (2). *Aedes albopictus* has since become widespread, occurring in much of the southeastern and into the midwestern United States (3). The introduction of *A. albopictus* has public health significance, and the ecological outcome of this introduction will enhance our understanding of community structure. Successful establishment of *A. albopictus* without the displacement of native filter-feeding and browsing species will imply that evolutionary niche diversification in response to prolonged competition between larval stages is not necessary for the coexistence of ecologically similar species.

*Aedes albopictus* has demonstrated an aptitude for rapid colonization of artificial aquatic larval habitats, such as discarded automobile tires (3). Egg diapause responses to photoperiod and freezing tolerance indicate that *A. albopictus* immigrated from temperate Japanese populations (4) preadapted for physical conditions in much of North America. Despite its colonizing ability and tolerance of physical conditions, the eventual success of *A. albopictus* may hinge on its ability to interact with native species within communities under invasion, particularly the mosquitoes that occupy treeholes and tires in eastern North America.

This experiment addresses the potential for competitive success of *A. albopictus* as a colonist of two habitats, tires and water-filled treeholes, both of which maintain well-developed native mosquito fauna. We exam-

ined competition between *A. albopictus* and *A. triseriatus*, a common filter-feeding and browsing inhabitant of treeholes and tires throughout the eastern United States (5), to determine whether *A. triseriatus* can prevent the establishment of this ecologically similar species. Previous comparisons of separate aspects of single and mixed species cohorts using artificial media in jars, tires, and cartons enable predictions that interactions of *A. albopictus* with resident species may result in a long-term establishment in tires (6).

Eggs obtained from laboratory colonies of *A. albopictus* and *A. triseriatus* (7) were hatched 24 hours before the experiment. Larvae of each species were disbursed, in all density combinations of 7, 14, 28, and 42 with single species controls for each density, into uncovered 120-ml plastic cups containing 0.5 g of dried leaf litter and 100 ml of treehole or tire fluid, depending on the habitat treatment (8). For treehole simulations, 25 ml of fluid was replaced weekly with fresh tree drainage water (stemflow), collected with a slit hose caulked about a maple tree. Both habitat simulations received weekly replacement of evaporated water with distilled water. Experimental populations were maintained in an insectary ( $22^\circ \pm 1^\circ\text{C}$ ,  $\approx 70\%$  relative humidity, and 16 hours light:8 hours dark photoperiod). Three replicates were raised for each two-species density combination and five replicates of all single-species density levels. Pupae were removed from experimental habitats and placed within vials of water topped with inverted vials. Adults were removed daily; female wings were measured at magnification  $\times 25$ .

Per capita growth rates were estimated for all larval cohorts from the composite index (9)

$$r' = \frac{\ln \left[ \frac{1}{N_0} \sum_x A_x f(w_x) \right]}{D + \left[ \frac{\sum_x A_x f(w_x)}{\sum_x A_x f(w_x)} \right]} \quad (1)$$

in which  $N_0$  represents the initial number of females,  $A_x$  the number of females emerging on day  $x$ , and  $w_x$  the mean winglength of females emerging on day  $x$ ;  $f(w_x)$  predicts numbers of female offspring based on female body size; and  $D$  is an estimate of the delay between female emergence and first oviposition. Separate studies of individual females, offered blood daily after emergence, provide estimates of  $D = 11.9$  days for *A. triseriatus* and  $D = 14.2$  days for *A. albopictus*. Linear functions describe size-dependent fecundity:  $f(w_x) = 23.2w_x - 51$  for *A. triseriatus* ( $r^2 = 0.38$ ) and  $f(w_x) = 17.2w_x - 14$  ( $r^2 = 0.03$ ) for *A. albopictus* (10).

Regression of  $r'$  on the initial densities of *A. triseriatus* and *A. albopictus* can be expressed in the form

$$r'_i = \frac{dN_i}{N_i dt} = r_{m_i} + b_i N_i + b_j N_j \quad (2)$$

When  $(r_{m_i} + b_i N_i + b_j N_j)$  is set equal to zero and  $N_j$  is plotted as a function of  $N_i$ , the result is a line that defines the combinations of initial densities that result in no population growth for species  $i$ , the zero growth isocline (Fig. 1). Density combinations falling below an isocline permit continued growth of the species associated with that isocline; density combinations above an isocline will result in the species' decline.

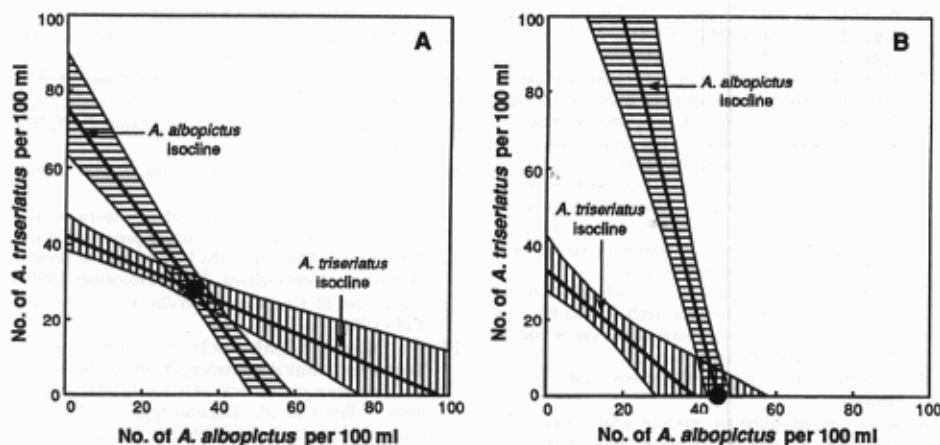
In treehole fluid (Fig. 1A), the isoclines intersect at positive densities for both species; long-term interaction between these species should therefore result in their continued coexistence in treeholes. In tire fluid (Fig. 1B), the isoclines do not intersect at a positive density for *A. triseriatus*; long-term association between these species should result in the competitive exclusion from tires of *A. triseriatus* by *A. albopictus*.

The Lotka-Volterra model of two-species competition provides a useful starting point for the analysis of this interaction, in which the per capita rate of change for species  $i$  is a direct analog of Eq. 2

$$\frac{dN_i}{N_i dt} = r_{m_i} - \frac{r_{m_i}}{K_i} N_i - \frac{r_{m_i} \alpha_{ij}}{K_i} N_j \quad (3)$$

Within this framework, the stability of the interactions depends on a combination of the competition coefficients ( $\alpha_{ij}$ ), which convert the per capita influence of species  $j$  on the growth rate of species  $i$  into the equivalent number of species  $i$  and carrying capacities ( $K_i$ ). These quantities are calculated indirectly from the intercept and regression coefficients of Eq. 2.

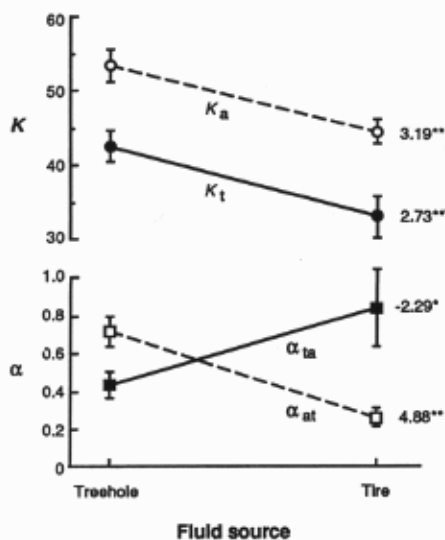
The difference in the predicted outcome for the two fluids is clarified by comparing



**Fig. 1.** Density combinations that permit equilibrium for *Aedes triseriatus* and *A. albopictus*. Hatched regions overlay combinations for each species for which the 95% confidence interval of the predicted per capita rate includes zero in (A) treehole and (B) tire-simulated habitats. The equilibrium combination of densities is circled for each fluid treatment. Differences between the intercepts of the two isoclines are statistically significant on both axes in treehole fluid and on the vertical axis in tire fluid ( $P < 0.01$  in each case); the difference between intercepts on the horizontal axis in tire fluid is not significant. Standard errors for these  $t$  tests were obtained with the jackknife technique (11).

$K_i$  and  $\alpha_{ij}$  in each fluid for each species (Fig. 2). The difference does not result from altered  $K_i$ 's alone, which are significantly lower in tire fluid for both species, reduced by nearly the same amount for each. The weekly addition of nutrients and removal of metabolic wastes by replacing 25 ml with stemflow in treehole fluid may account for much of this difference in  $K_i$ .

The differential competitive outcome in the two fluid types results primarily from



**Fig. 2.** Comparisons of parameters of competition in treehole and tire fluid.  $K_t$  and  $K_a$  depict carrying capacities for *A. triseriatus* and *A. albopictus*. Competition coefficients translate the competitive effect of an *A. albopictus* individual on *A. triseriatus* into the equivalent number of *A. triseriatus* individuals ( $\alpha_{ta}$ ), and the reverse translation ( $\alpha_{at}$ ). Standard errors for each estimate, obtained with the jackknife technique (11), are shown as vertical bars. The  $t$  statistics for differences of parameters estimated for treehole and tire fluid treatments are shown (\* $P < 0.05$ , \*\* $P < 0.01$ ).

significant and opposite differences in  $\alpha_{ij}$ 's for the two species. If these coefficients reflect overlap of resource use, the differences suggest that resources exist within tires that can be used much more effectively by *A. albopictus* than *A. triseriatus*, and that treehole fluid contains resources that each species exploits differentially. Detailed studies of the larval diets of these two species in the two habitat types should be informative.

This analysis could be enhanced by the incorporation of a wider variety of initial densities of the two species, which would permit tests for nonlinear concave responses to density, known to occur in *A. triseriatus* growing in an artificial medium (11), as well as nonadditive interactions between the competitors. However, the narrow isocline regions defined by the linear model for *A. triseriatus* in treehole fluid suggest that nonlinear isoclines resulting from such nonlinear models should not vary substantially from this linear case, leaving intact the prediction of coexistence. More likely, our prediction of competitive exclusion of *A. triseriatus* in tire fluid may require modification to include the possibility of its coexistence

with *A. albopictus* at very low densities.

Sufficient time may not have elapsed since the introduction of *A. albopictus* to enable the test of these predictions in field populations, but coexistence between *A. albopictus* and *A. triseriatus* within treehole communities is suggested by the appearance of *A. triseriatus* and *A. albopictus* as the first and second most abundant filter-feeding species in glass jars attached to trees in a Louisiana forest (14), making up 81% and 17% of the filtering and browsing larvae collected. The co-occurrence of these two species has also been noted in other studies of treehole communities (15). Field studies of *A. albopictus* with *A. aegypti* in artificial habitats, tires in Texas (2) and cemetery vases in Florida (15), suggest success by *A. albopictus* as a competitor in such containers, with a concomitant reduction of *A. aegypti* populations. *Aedes triseriatus* is only abundant in tire habitats located within shaded areas, and few detailed census data are available for such habitats in areas that have been reached by dispersing *A. albopictus*. However, the potential for *A. albopictus* to dominate artificial habitats has been clear since its discovery in Texas, where *A. albopictus*' abundance was three times that of *A. aegypti* and 20 times that of *A. triseriatus* (2).

Although *A. triseriatus* may be the most likely potential treehole competitor, other treehole species might interact with *A. albopictus*. Differences among filter-feeding species in vulnerability to the predatory mosquito larva *Toxorhynchites rutilus* in the Southeast could influence the outcome of the *A. albopictus* invasion. Additional species of potential importance to the establishment of *A. albopictus* in treehole communities include *Anopheles barberi*, a potential filter-feeding competitor that becomes a facultative predator on small larvae during its fourth instar (16), and three additional filter-feeding and browsing species: *Aedes hendersoni*, *Orthopodomyia signifera*, and *O. alba*. However, all four of these potential competitors have marked preferences for restricted types of treeholes (5), and are therefore unlikely to present consistent ob-

**Table 1.** Responses of per capita growth rate estimates for each species to the initial density of *Aedes triseriatus* and *A. albopictus* larval cohorts in two types of fluid. Regression analyses are based on Eq. 2. Standard errors for each regression term and the coefficient of determination ( $r^2$ ) are shown. All regression coefficients are statistically significant ( $P < 10^{-4}$ ). Units are as follows:  $r_m$ , days $^{-1}$ ;  $b_1$  and  $b_2$ , days $^{-1} \times (\text{individuals}/100 \text{ ml})^{-1}$ . The numbers of  $r^2$  values obtained for each regression ( $n$ ) differ because some cohorts produced no survivors, especially *A. triseriatus* growing at high densities in tire fluid (10).

Fluid	Species	n	$r_m$	$b_1$	$b_2$	$r^2$
Treehole	<i>triseriatus</i>	65	0.0514 $\pm$ 0.0029	-0.0012 $\pm$ 0.0001	-0.0005 $\pm$ 0.0001	0.74
	<i>albopictus</i>	64	0.0798 $\pm$ 0.0036	-0.0015 $\pm$ 0.0001	-0.0011 $\pm$ 0.0001	0.80
Tire	<i>triseriatus</i>	35	0.0591 $\pm$ 0.0070	-0.0018 $\pm$ 0.0003	-0.0015 $\pm$ 0.0003	0.66
	<i>albopictus</i>	65	0.0904 $\pm$ 0.0036	-0.0020 $\pm$ 0.0001	-0.0005 $\pm$ 0.0001	0.82

stacles to the establishment of *A. albopictus*; a large fraction of treeholes contain only *A. triseriatus* as potential competitors (5). Our results indicate that competition with the predominant species in treehole communities, *A. triseriatus*, will be insufficient to prevent the establishment of *A. albopictus*.

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7. *Aedes albopictus* and one *A. triseriatus* population were established by mosquitoes collected in New Orleans, LA. Additional *A. triseriatus* populations were established by females from central Massachusetts. A three-way analysis of variance of the interactions of Louisiana and Massachusetts *A. triseriatus* with *A. albopictus* reveal no statistically significant differences between *A. triseriatus* strains (T. Livdahl, unpublished data), and the results presented here combine the results of both strains.
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17. We thank J. Edgerly-Rooks, S. Gaimari, and J. Turner for technical assistance, O. Sholes, R. Bertin, and two anonymous reviewers for helpful suggestions, J. Freier for *A. albopictus* eggs, and NIH for financial support (R15AI27940 to T.P.L.).

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