

Intraguild Predation Among Larval Treehole Mosquitoes, *Aedes albopictus*, *Ae. aegypti*, and *Ae. triseriatus* (Diptera: Culicidae), in Laboratory Microcosms

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ABSTRACT We compared the tendency for 4th-instar larvae to prey on newly hatched larvae, and the vulnerability of those 1st instars to such predation for *Aedes triseriatus* (Say), *Ae. aegypti* (L.), and *Ae. albopictus* (Skuse), all container-breeding mosquitoes. The latter 2 species were introduced to North America and are now sympatric with *Ae. triseriatus*, a native species in eastern North America. The experiment also enabled the assessment of species-specific influences of food supplements and spatial heterogeneity on predatory behavior. *Ae. triseriatus* was substantially more predatory and less susceptible to attack than the other 2 species. These differences were amplified in food-deprived and spatially simple conditions, indicating that *Ae. triseriatus* predatory behavior may have important retarding effects on the colonization of occupied treehole habitats by *Ae. albopictus*. *Ae. aegypti* and *Ae. albopictus* were similar in imposing little (*Ae. aegypti*) or almost no (*Ae. albopictus*) predation on 1st instars and in being susceptible to predation by *Ae. triseriatus*. The general lack of species-specific differences between *Ae. aegypti* and *Ae. albopictus* indicates that interspecific predation is not a likely explanation for the rapid displacement of *Ae. aegypti* by *Ae. albopictus* in domestic containers in the southeastern United States.

KEY WORDS *Aedes albopictus*, *Aedes aegypti*, *Aedes triseriatus*, invasive exotic, cannibalism, mosquitoes

Aedes albopictus (SKUSE), a container-inhabiting mosquito recently introduced from Asia, has spread throughout southeastern and midwestern North America. Its range in the United States has expanded quickly from 1985 when it was first recorded (Sprenger and Wuithiranyagool 1986) to include 23 states, including New Jersey (Crans et al. 1996) and Chicago to the north, Texas to the west, and Florida to the south (O'Meara et al. 1992, 1995; Jamieson et al. 1994; Nasci 1995; Richardson et al. 1995). The ongoing colonization by this species has provided an excellent opportunity for ecologists to observe a mosquito invading habitats already occupied by ecologically similar species, particularly its congeners. *Aedes albopictus* has displaced a previously introduced, resident African mosquito, *Aedes aegypti* (L.), in some habitats in Florida (O'Meara et al. 1992) and apparently is in the process of displacing *Ae. aegypti* in South Carolina (Richardson et al. 1995) and Louisiana (Nasci 1995). In contrast, Lounibos et al. (1997) found that *Ae. albopictus* has not displaced the native treehole mosquito, *Aedes triseriatus* (Say), in natural treeholes in Florida.

Temperature extremes may limit the northern extent of the United States population of *Ae. albopictus* (Nawrocki and Hawley 1987, Hanson and Craig 1995),

which appears to have originated from a temperate zone population in Japan (Hawley et al. 1987). The biological factors that might promote or restrict range expansion have been less tractable. Numerous biological mechanisms promoting colonization by *Ae. albopictus* have been investigated, including mating interference (Black et al. 1989), competitive displacement by larvae (Barrera 1986, Black et al. 1989, Ho et al. 1989, Livdahl and Willey 1991, Novak et al. 1993, Juliano 1998), oviposition site preferences (Black et al. 1989, Titus 1996), parasitic protozoan parasitism (Fukuda et al. 1997, Juliano 1998), and egg hatch inhibition imposed by larvae (Edgerly et al. 1993).

To further our understanding of potentially significant behavioral interactions in *Aedes*, we investigated the role that intraguild predation might play in successful colonization by *Ae. albopictus*. Facultative predation may occur among *Aedes* larvae, and such predation might contribute to the displacement of *Ae. aegypti* from container habitats by *Ae. albopictus*. Differential predation also might contribute to a slow rate of colonization of natural treeholes by *Ae. albopictus* when they are occupied by *Ae. triseriatus*, despite prevalence of *Ae. albopictus* in nearby domestic habitats. Although their food is predominantly microorganisms and detritus (Merritt et al. 1992), both *Ae. aegypti* (MacGregor 1915) and *Ae. triseriatus* (Koenekoop and Livdahl 1986) are capable of cannibalism: 4th instars consume 1st-instar conspecifics in the laboratory. The ecological significance of canni-

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ballistic behavior is not known, and for *Ae. triseriatus*, at least, was of limited significance compared with egg hatch dynamics and density-dependent competition in influencing mosquito productivity in artificial microcosms in Massachusetts (Edgerly and Livdahl 1992). Because *Ae. albopictus* is similar ecologically and morphologically to *Ae. aegypti* and *Ae. triseriatus*, we suspected that *Ae. albopictus* would have similar larval foraging strategies, including cannibalism by 4th instars. We designed an experiment to determine if *Ae. albopictus* is predaceous and to test for differential effects of larval predation in the 3 species.

Materials and Methods

We tested the responses of *Ae. aegypti*, *Ae. albopictus*, and *Ae. triseriatus* in 48 different combinations: 4 levels of a predation treatment (including controls), 3 different species of prey (1st instar), 2 physical environments, and 2 food levels. *Predators* were defined as 4th instars that have the potential to consume newly hatched *Aedes* larvae, designated as prey herein. All replicates were placed in 100-ml clear plastic cups stocked with 50 ml of autoclaved treehole water previously filtered to remove sediment. Each cup received 25 larvae hatched within 2 h of the experiment, and either 0 or 6 fourth instars of one of the 3 *Aedes* species. The possible combinations yielded controls (no predators) and 9 inter- and intraspecies experimental treatments. The experimental density was comparable to that used by Koenekoop and Livdahl (1986) who observed cannibalism among *Ae. triseriatus*, but the habitats were >3 times as large in the present experiment.

Food. The intensity of intraguild predation may depend on availability of alternative food sources (Fox 1975, Polis 1981). In container-inhabiting mosquitoes, variation in nutrients can be extreme with domestic containers being relatively oligotrophic compared with treeholes filled with leaf litter and periodically inoculated with bacteria carried in by stemflow (references in Merritt et al. 1992). Koenekoop and Livdahl (1986) found that the intensity of cannibalism by 4th-instar *Ae. triseriatus* was greater when food was limited. Therefore, we expected intraguild predation to be more intense in food-poor than in food-rich conditions. To create such a disparity, we supplemented half the habitats with food (20 mg brewer's yeast).

Environment Complexity. Theoretically, predation rates should be higher if prey lack refugia (e.g., Vepsäläinen and Nummelin 1986). The *Aedes* species in the current study breed in containers that vary from cemetery vases to discarded tires to natural treeholes. We suspected that the availability of refugia increases as the complexity of the substrate increases. To emulate this feature of the predator-prey system, we added refugia to half of the replicates and left the remainder as the smooth surfaces of the plastic cups. To provide a heterogeneous substrate, we lined the bottoms of the cups with disks of fiberglass (Scotch brand scouring pads, 3M, St. Paul, MN). The mesh-

Table 1. ANOVA testing for responses of mortality rate (fraction of prey absent at the end of the experiment) to the main effects of the experiment

Source	df	MS	F	P
Main effects				
Predator (P)	3	0.98	46.83	<0.001
Prey (H)	2	0.06	3.08	<0.05
Food (F)	1	0.32	15.40	<0.001
Environment (E)	1	0.03	1.51	NS
Interactions				
P×H	6	0.01	0.56	NS
P×F	3	0.28	13.52	<0.001
P×E	3	0.17	7.98	<0.001
H×F	2	0.02	0.72	NS
H×E	2	0.01	0.61	NS
F×E	1	0.03	1.26	NS
P×H×F	6	0.02	1.07	NS
P×H×E	6	0.02	0.73	NS
H×F×E	2	0.01	0.33	NS
P×F×E	3	0.17	8.24	<0.001
P×H×F×E	6	0.01	0.39	NS
Error	192	0.02		

Predator, 4th instars of 3 different species, plus a control that had no 4th instars; prey, represented by 3 different species; food, supplement added or not added; environment, simple or complex; NS, $P > 0.05$.

work of the pad excludes larger larvae but is large enough to allow small larvae to forage within.

Overall Design. We replicated each combination of treatment level (predators, prey, food, and environment) 5 times, for a total of 240 cups. After 24 h we removed the predator larvae and then the prey from each habitat. We determined the proportion of 1st-instar larvae lost in 24 h in response to the 4 experimental factors. An angular transformation was used to enhance normality and reduce the dependence of cell variances on cell means. The effects of experimental treatments and interactions among them were tested by analysis of variance (ANOVA); specific comparisons among groups were performed with orthogonal contrasts (SAS Institute 1997).

Results

All factors (predator species, prey species, food, environment) affected the number of prey disappearing, either as main effects or as factors involved in significant interactions (Table 1). Prey species was a factor with a significant main effect, but was not involved in any higher order interactions. Predators consumed 1st-instar *Ae. albopictus* more frequently than *Ae. triseriatus* (Fig. 1; orthogonal contrast, $F = 5.27$; $df = 1, 192$; $P < 0.05$). The vulnerability of *Ae. aegypti* was intermediate, and did not differ significantly from either of the other species (*Ae. aegypti* versus *Ae. albopictus*: $F = 0.31$; $df = 1, 192$; $P > 0.5$; *Ae. aegypti* versus *Ae. triseriatus*: $F = 3.03$; $df = 1, 192$; $P > 0.08$). Prey disappearance rates differed significantly between the control and predator-containing cups (Fig. 1; orthogonal contrast for predator-exposed versus control prey: $F = 42.2$; $df = 1, 192$; $P < 0.001$), and no differences were significant in contrasts of the disappearance rates of 1st instars of each of the 3

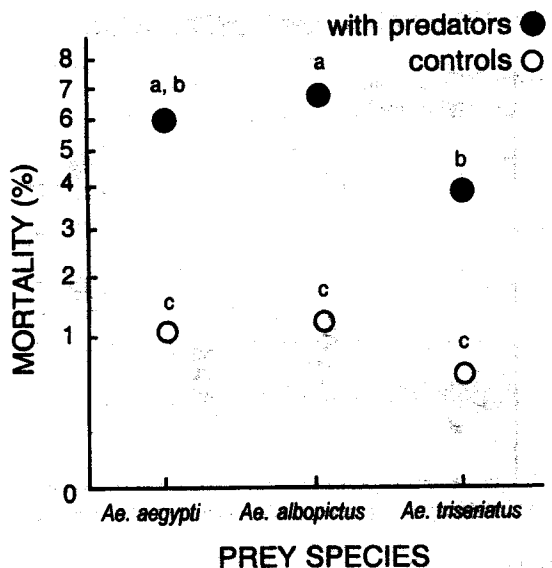


Fig. 1. Vulnerability of the prey species to predation by 4th-instar mosquito larvae, relative to control habitats that lacked 4th instars. Points represent mean percentages of prey absent at the end of the experiment, pooled across all other treatments (habitat complexity, food, and predator species). Means with common letters were not found to differ ($P > 0.05$) in pairwise orthogonal contrasts testing for differences among prey species. Data were analyzed after the angular transformation $y' = \arcsin \sqrt{y}$ had been applied. The vertical axis converts the transformed values back to the more familiar percentage units.

species in control cups ($F = 0.3$; $df = 2, 192$; $P = 0.720$). We infer that the significant main effect of prey species resulted from differential vulnerability to predation, with *Ae. albopictus* the most vulnerable, and *Ae. triseriatus* the least.

In addition to the significantly lower disappearance rates of 1st instars in control cups, the main effect caused by the predator treatment also results from differences in predation rate by different species (Fig. 2). *Ae. triseriatus* and *Ae. aegypti* caused disappearance rates that significantly exceeded the controls (*Ae. aegypti*, $F = 8.9$; $df = 1, 192$; $P = 0.003$; *Ae. triseriatus*, $F = 121.0$; $df = 1, 192$; $P < 0.001$). Disappearance rates of prey in the presence of *Ae. albopictus* did not significantly exceed the controls, although this contrast was nearly significant ($F = 3.8$; $df = 1, 192$; $P = 0.053$). Tests for differences among species indicated that *Ae. triseriatus* consumed more prey than either of the other species (*Ae. triseriatus* versus *Ae. aegypti*, $F = 64.3$; $df = 1, 192$; $P < 0.001$; *Ae. triseriatus* versus *Ae. albopictus*, $F = 82.0$; $df = 1, 192$; $P < 0.001$) and that *Ae. aegypti* and *Ae. albopictus* were not significantly different in their prey consumption ($F = 1.1$; $df = 1, 192$; $P = 0.300$).

Interactions among predator species and food availability, and predator species and environmental complexity differentially affected the predation rate (Table 1). Food alone, and in interaction with predator

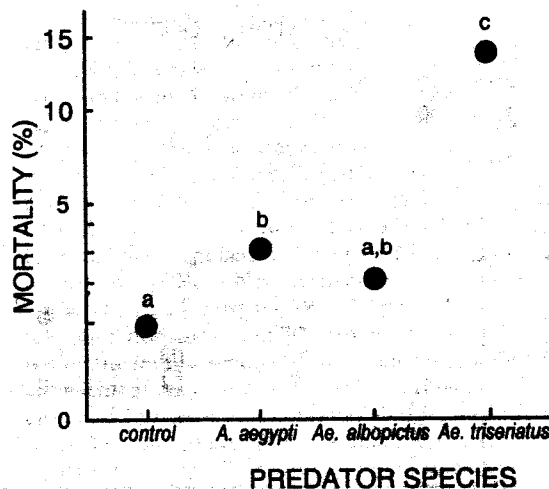


Fig. 2. Relative predatory tendencies of the 3 species. Points represent percentages of prey that were absent at the end of the experiment for each predator species, pooled across all other treatments (habitat complexity, food, and prey species). The control group received no 4th-instar larvae, and provides an indication of the background loss rate for newly hatched larvae under these conditions. Means with common letters were not found to differ ($P > 0.05$) in orthogonal contrasts constructed for all pairs of means. Data were analyzed after the angular transformation $y' = \arcsin \sqrt{y}$ had been applied. The vertical axis converts the transformed values back to the more familiar percentage units.

species, affected the number of prey eaten: *Ae. triseriatus*, but not *Ae. aegypti* or *Ae. albopictus*, consumed fewer prey in food-rich treatments than in food-poor treatments (Fig. 3). The predator \times food interaction resulted from the species-specific nature of this effect. Although environment alone did not affect the number of prey eaten, a significant interaction occurred between predator species and environment treatments: *Ae. triseriatus* consumed fewer prey in complex than in simple environments, whereas *Aedes aegypti* consumed more prey in complex compared with simple environments (Fig. 3). The predator \times environment interaction resulted from the species-specific nature of this influence.

A significant 3-way interaction (predator \times food \times environment) occurred (Table 1). In the simple environment, regardless of food treatment, and in the complex environment without a food supplement, *Ae. triseriatus* consumed more prey than either *Ae. aegypti* or *Ae. albopictus* (Fig. 4).

We inspected the 2- and 3-way interactions further by excluding each predator species in turn and repeating the analysis on the remaining subsets of data. Our rationale was that a switch from a significant to a nonsignificant interaction would indicate that the excluded data contributed to the significant interaction obtained in the full analysis. Both 2-way interactions (predator \times food and predator \times environment) and the 3-way interaction (predator \times food \times environment) became nonsignificant when we excluded *Ae. triseriatus* from the analysis ($P > 0.3, 0.2$, and 0.6 ,

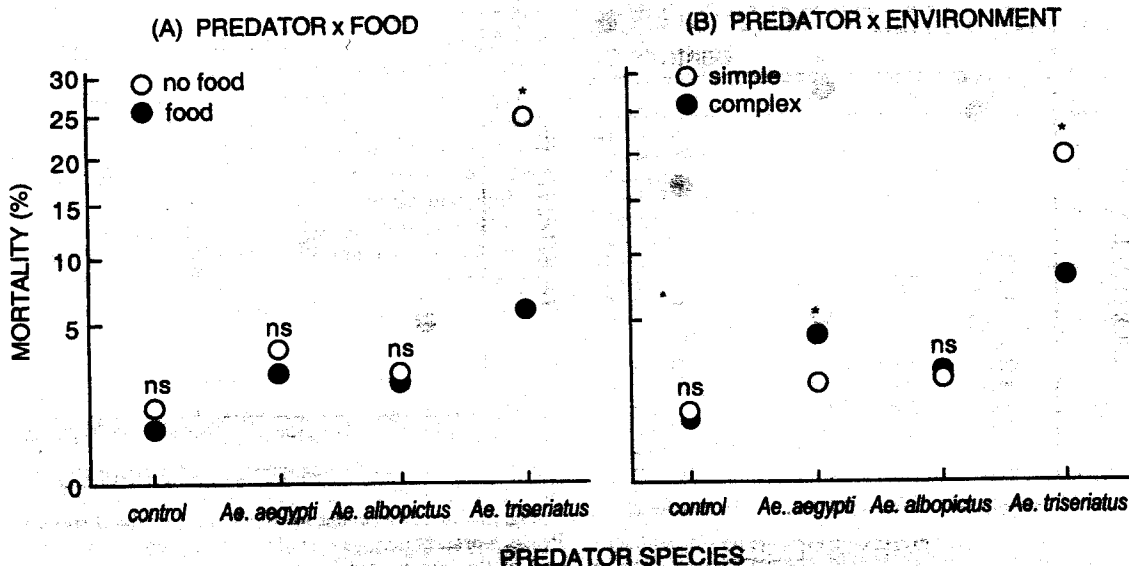


Fig. 3. Species-specific modification of predation by (A) food conditions and (B) environmental complexity. Mean values are shown for the percentage of prey that were absent at the end of the experiment, pooling (A) across Prey Species and Environmental Complexity treatment levels and (B) across Prey Species and Food treatment levels. Pairs of points for each predator species were compared using orthogonal contrasts, and the results of those tests are summarized by ns ($P > 0.05$) or * ($P < 0.02$ for all significant differences found). Data were analyzed after the angular transformation $y' = \arcsin \sqrt{y}$ had been applied. The vertical axis converts the transformed values back to the more familiar percentage units.

respectively); that neither the presence nor absence of *Ae. aegypti* or *Ae. albopictus* contributed to the interactions is supported by the persistent significance of those terms, with or without either species ($P < 0.001$ in all cases when either *Ae. aegypti* or *Ae. albopictus* predator data were removed).

Discussion

Collectively, higher mortality occurred in vials containing 4th instars than in controls. Because more 1st-instar larvae remained in control vials at the end of the trial, we suggest that the disappearance of 1st instars in experimental vials depended on the presence of 4th instars and not on our ability to locate small larvae or on 1st-instar mortality because of factors other than predation.

Mortality of 1st instars occurred at the highest rate in the presence of 4th-instar *Ae. triseriatus*. Furthermore, the death rate increased when these larvae were placed in simple habitats with less food. The possibility remains that 1st instars died because of competitive interactions, and subsequently were consumed by scavenging 4th instars. However, because we have observed 4th-instar *Ae. triseriatus* eating 1st instars in the laboratory, we know that predation does occur and was very likely the cause of mortality in the current study.

Prey species were affected differentially by encounters with 4th instars. *Ae. triseriatus* larvae were susceptible to predation but at a significantly lower rate than were the other 2 species. Some of this difference may be attributed to the larger size of *Ae. triseriatus*

(Willey 1995) making them less likely to be eaten by filter-feeding 4th instars or stronger in their escape response.

One significant effect in this experiment was not anticipated; as such, we have no firm explanation for it. *Ae. aegypti* 4th instars preyed more effectively on 1st instars in complex environments than in simple ones in the absence of food, but this difference did not occur in food-supplemented habitats. This finding runs counter to our intent of providing refugia for the prey, and indicates that *Ae. aegypti* foraging behavior is modified by food shortage, as might the location preferences of the prey. We anticipate that more detailed behavioral studies may find that the predators and prey are brought together more often by these 2 behavioral changes under low food conditions. Why this response should occur with *Ae. aegypti* predators, but not the other species, remains obscure.

Predation by mosquitoes such as *Toxorhynchites* affects the relative abundance of prey in treehole communities in the southeastern United States (Bradshaw and Holzapfel 1983, Lounibos 1983). Whether differential intraguild predation among *Aedes* also influences population dynamics of congeners remains to be determined. Our results indicate that intraguild predation between *Ae. aegypti* and *Ae. albopictus* should have little effect on community structure in their shared domestic habitats, such as cemetery containers or discarded tires. Although they are both capable of predation as 4th instars, their interactions are symmetrical, and the mortality of 1st instars is relatively low. However, in laboratory containers, these species experienced increased mortality in their interactions

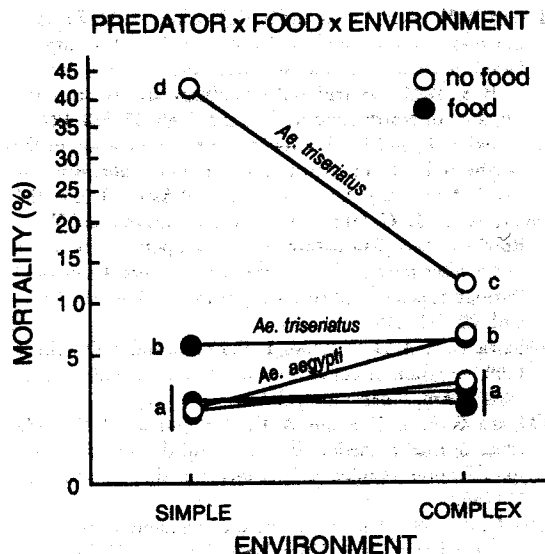


Fig. 4. A higher-order interaction among the predator species, food, and environment treatments. Mean values are shown, after pooling across prey species. Orthogonal contrasts were performed for all pairs of means within the simple and complex environmental groups. Additional contrasts testing simple versus complex were performed for all predator species. Sets of means that were not found to differ ($P > 0.05$, orthogonal contrasts) are identified by common letters. Predator species involved in producing treatment-specific differences are identified; no significant differences were found among the means forming the lower 3 lines, so no attempt is made to distinguish them here. Data were analyzed after the angular transformation $y' = \arcsin \sqrt{y}$ had been applied. The vertical axis converts the transformed values back to the more familiar percentage units.

with *Ae. triseriatus*. The outcome of this latter interaction may explain, in part, the limited invasion of *Ae. albopictus* and *Ae. aegypti* into natural treeholes in North America, the typical habitat for *Ae. triseriatus*. However, higher basic hatch rates of *Ae. albopictus* and *Ae. aegypti* (Edgerly et al. 1993) compared with *Ae. triseriatus*, as well as faster larval development, may reduce the severity of interactions among cohorts for these species. If so, the potential for predation may be limited because, at least for *Ae. triseriatus*, larvae are only susceptible to cannibalism during their 1st d after hatch (Koenekoop and Livdahl 1986).

Predicting the outcome of the *Ae. albopictus* invasion is made risky by the variety of interactions that are possible, and more so by the conflicting directions that various mechanisms can have. For example, a prediction based on inter- and intraspecific predation would favor *Ae. triseriatus*, whereas the results of differential egg hatch inhibition would promote a takeover of treeholes by *Ae. albopictus* at the expense of *Ae. triseriatus* (Edgerly et al. 1993). This latter outcome has not occurred; presently, the 2 species seem to coexist in treeholes that have been surveyed, with no sign that *Ae. triseriatus* is being displaced (Lounibos et al. 1997).

The long-term information needed to gauge the success of *Ae. albopictus* in treehole habitats is extremely limited. We note that the occupation of treehole habitats by *Ae. albopictus* has not occurred at high rates throughout its range. For example, in Northern Virginia, *Ae. albopictus* was found to be the only *Aedes* mosquito in an urbanized shaded tire pile, whereas *Ae. triseriatus* was the only species found in a mature beech forest only 1 km away (T.L., unpublished data). Collections of eggs laid in ovitraps in 29 mature forests in 1997 and 1998 in New Jersey, Delaware, Pennsylvania, Maryland, Virginia, West Virginia, North Carolina, and northern South Carolina and Georgia, all within the reported range of *Ae. albopictus*, yielded *Ae. albopictus* at only 2 sites (in North Carolina and Georgia), and 1 of those was contaminated by water-filled domestic containers (T.L., unpublished data). Although *Ae. albopictus* has been found in all of those states, there is little evidence to support its prevalence in natural treehole communities, except in the warmer parts of its North American range.

In conclusion, our experimental results add to our knowledge of possible interactions among 3 congeners that are experiencing range expansion (*Ae. albopictus*) or local extinction (*Ae. aegypti*). How well these laboratory results can be generalized to field populations remains to be determined. A field test of competing hypotheses would be a logical next step in the search for mechanistic explanations for the pattern of invasion by *Ae. albopictus* and of local extinctions or persistence by resident mosquitoes. Such a cross-species test might manipulate factors to assess the differential impacts of intercohort interactions such as larva-induced egg hatch inhibition, larval interactions between and within instars, and oviposition choices by females in response to habitat characteristics including larval composition.

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