Interspecific Larval Competition Between *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae) in Northern Virginia

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Abstract

Aedes albopictus (Skuse) and *Aedes japonicus* (Theobald) are two of the most recent and widespread invasive mosquito species to have become established in the United States. The two species co-occur in water-filled artificial containers, where crowding and limiting resources are likely to promote inter- or intraspecific larval competition. The performance of northern Virginia populations of *Ae. japonicus* and *Ae. albopictus* competing as larvae under field conditions was evaluated. Per capita rates of population increase for each species were estimated, and the effects of species composition and larval density were determined. In water-containing cups provided with oak leaves, *Ae. albopictus* larvae exhibited a competitive advantage over *Ae. japonicus* as a consequence of higher survivorship, shorter developmental time, and a significantly higher estimated population growth rate under conditions of interspecific competition. Intraspecific competition constrained population performance of *Ae. albopictus* significantly more than competition with *Ae. japonicus*. In the context of the Lotka-Volterra model of competition, these findings suggest competitive exclusion of *Ae. japonicus* in those habitats where this species co-occurs with *Ae. albopictus*.

Keywords

invasive; mosquito; containers; competition

Aedes albopictus (Skuse) and *Aedes japonicus* (Theobald) are two of the most prominent exotic mosquito species to become recently established in the United States. *Ae. albopictus* was introduced into the United States from Japan in tire shipments (Hawley et al. 1987, Reiter and Sprenger 1987), which led to its establishment in Texas in 1985 (Sprenger and Wuithiranyagool 1986). State and local mosquito surveillance records indicate that it has since spread rapidly, becoming established across much of the eastern United States from southern Florida to New Jersey, Illinois, Indiana, Ohio, and Missouri (Moore 1999). The westward spread of this invader has been much slower; presumably because of the drier summers and cool, wet winters on the West Coast (Washburn and Hartmann 1992). *Ae. albopictus* has been intercepted and eradicated in California (Linthicum et al. 2003) and Washington (Craven et al. 1988). The invasion success and rapid spread of *Ae. albopictus* in the United States has been attributed to its generalized habitat and food requirements, ability to live in human-dominated habitats (Hawley 1988), desiccation-resistant eggs (Focks et al. 1994, Juliano et al. 2002), and larval competitive superiority to resident species (Livdahl and Willey 1991, Juliano 1998).

The introduction of *Ae. japonicus* into the United States was initially reported by Peyton et al. (1999) from light trap collections from New York and New Jersey in August and September

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1998. However, an archival search by Andreadis et al. (2001) showed that this species was actually first detected 1 mo earlier in Connecticut. *Ae. japonicus* has since been detected along the East Coast, with reports as far south as Alabama (Mullen 2005), north to Maine (Foss and Dearborn 2001), and west to Missouri (Gallitano et al. 2006), from what seem to be multiple introductions from Japan (Fonseca et al. 2001). *Ae. japonicus* seems to have become established on the West Coast in Washington (Roppo et al. 2004) and has recently been detected in Mississippi, Nevada (Moore 2005), and Hawaii (Larish and Savage 2005). The used tire trade is the suspected mode of introduction of *Ae. japonicus* into the United States as it was for *Ae. albopictus* (Peyton et al. 1999, Lounibos 2002).

The current U.S. distributions of these two species overlap considerably, although *Ae. japonicus* seems to be more cold tolerant (Tanaka et al. 1979) than *Ae. albopictus*, as evidenced by the establishment of the former species in eastern Canada (Thielman and Hunter 2006). It has been predicted that the American range of *Ae. albopictus* may eventually expand northward as far as the −5°C isotherm, as it does in Asia; however, at such latitudes, populations would likely not overwinter (Nawrocki and Hawley 1987). Furthermore, both species are container-inhabiting mosquitoes commonly found in water-filled artificial container habitats such as automobile tires, bird baths, and flower pot saucers; however, rock pools seem to be the favored habitat of *Ae. japonicus* in its native range (Tanaka et al. 1979). The aquatic larvae of both species feed on microorganisms and particulate matter in the water column as well as on leaves and other organic detritus (Merritt et al. 1992).

Severe crowding and limiting resources are frequent in these habitats; thus, it is likely that larval competition, inter- or intraspecific, may have important effects on the growth, survivorship, and reproductive success of these species (Juliano and Lounibos 2005). Therefore, larval conditions may have a significant impact on overall population growth. Those species that can maintain positive population growth under interspecific conditions of greater density or lower resource availability than a competitor are considered to have a competitive advantage. Such a competitive advantage is even greater if one species can maintain positive population growth under conditions that result in negative population growth for a competitor.

The role of interspecific competition in structuring communities of container-dwelling mosquitoes has been well documented, perhaps best so for *Ae. albopictus* and *Ae. aegypti* in the southeastern United States (Barrera 1996, Juliano 1998, Juliano et al. 2004), where interspecific larval competition was the probable cause of the decline in range and abundance of the latter species throughout most of this area (O'Meara et al. 1995, Juliano et al. 2004, Juliano and Lounibos 2005). *Ae. albopictus* has also been shown experimentally to be a superior larval competitor to the U.S. resident mosquito species *Aedes triseriatus* (Say) (Livdahl and Willey 1991), *Aedes sierrensis* (Ludlow) (Washburn and Hartmann 1992), and *Culex pipiens* L. (Costanzo et al. 2005). Although the invasion of an introduced species may negatively impact resident species as a result of interspecific larval competition, the effects of other interactions such as predation, habitat alteration, or apparent competition mediated by shared enemies should also be considered when assessing invasion outcomes (Juliano and Lounibos 2005).

Understanding the invasion dynamics of *Ae. albopictus* and *Ae. japonicus* is important not only because of the ecological consequences resulting from their interactions with native container-inhabiting mosquitoes, but also because these species may transmit arboviruses that cause human and animal disease. In its native range, *Ae. albopictus* is a known vector of dengue virus, which has been isolated from wild-caught individuals of this species in its invasive range in the Americas (Ibañez-Bernal et al. 1997, Méndez et al. 2006). This species was also implicated as the vector in the 2001 outbreak of dengue in Hawaii (Effler et al. 2005). Invasive *Ae. albopictus* have also been recovered infected with eastern equine encephalitis (Mitchell et

al. 1992) and LaCrosse encephalitis viruses (Gerhardt et al. 2001) in the United States and chikungunya virus in Italy (Enserink 2007).

Although *Ae. japonicus* is not considered an important disease vector in its native range in Asia, it is capable of transmitting Japanese encephalitis virus (Takashima and Rosen 1989) and has also been indicated as a competent experimental vector of eastern equine (Sardelis et al. 2002a), LaCrosse (Sardelis et al. 2002b), and St. Louis encephalitis viruses (Sardelis et al. 2003). Both *Ae. albopictus* and *Ae. japonicus* have been shown to be competent vectors of West Nile virus in the laboratory (Turell et al. 2001), and wild-caught adults of both species have been recovered infected with this virus (Holick et al. 2002, Scott 2003, Godsey et al. 2005).

Although considerable data exist regarding the interspecific interactions and competitive outcomes involving *Ae. albopictus* and other container-inhabiting mosquito species, there are no comparable reports on its interactions with *Ae. japonicus*. Because *Ae. albopictus* and *Ae. japonicus* co-occur frequently in containers where their ranges overlap, an investigation of larval competitive interactions between these two species was proposed. An experiment designed similar to those of Juliano (1998) and Braks et al. (2004), with the exception that only a single resource level was implemented, was conducted to test for competitive advantage between Virginia populations of these species in competition under field conditions in Fairfax, VA. Comparisons were made between species for intra- and interspecific effects of larval density on survivorship, development time, body size, and population growth.

Materials and Methods

The experiment was conducted in forest surrounding a streambed located directly behind the Fairfax County Department of Health in Fairfax, VA (latitude 38°50′ N, longitude 77°19′W) from August to October 2006. Routine surveillance data collected by the Department of Health indicated that both *Ae. albopictus* and *Ae. japonicus* were commonly detected on this property as both larvae in artificial containers and as adults in CO_2-baited CDC light traps and gravid traps. The *Ae. albopictus* and *Ae. japonicus* used in this experiment were the progeny of females caught in Reiter-Cummings modified gravid traps (Bioquip, Rancho Dominquez, CA) in Fairfax, VA.

Inter- and intraspecific larval competition was studied by monitoring the survivorship and development of larvae in 400-ml black polypropylene cups (10.5 cm in height, 6.5 cm base diameter). Field surveys of habitats in the area (unpublished data) showed that these species co-occurred in approximately one fifth of containers sampled, the majority of which contained <1 liter of water and were shaded. Mean number of *Ae. albopictus* per container was 42.4 ± 12.8 (SE), with a range of 1–250, whereas an average of 17.3 ± 4.1 *Ae. japonicus* was collected per container, with a range of 1–77.Based on these data, three density-composition combinations for each species (*Ae. albopictus:Ae. japonicus*: 10:0, 50:0, 0:10, 0:50, and 25:25) were used in a randomized block design. One replicate of each density-composition combination was placed at each of five experimental sites, spaced ≈30 m apart, for a total of five replicates per treatment and 25 cups. Although both species have been found locally in containers with varying sun exposure (i.e., none, partial, and full exposure), all five sites used were heavily shaded.

On 10 August, each cup was randomly labeled with a unique number and letter corresponding to one of the five treatments and sites, where they were secured to plastic stakes to prevent toppling. A larval resource base was provided by fallen pin oak leaves (*Quercus palustris*) that had been collected, washed with distilled water, and dried at room temperature for 1 wk before quartering, weighing, and sorting. To allow for the leaves to soak and be colonized by

microorganisms, 4 d before the start of the experiment, 1 g was added to each of the 25 cups containing 200 ml of distilled water. Each container was covered with fiberglass screen (0.5-mm mesh) and secured with a rubber band to prevent entry of other macrofauna and detritus. In the laboratory, eggs of *Ae. albopictus* and *Ae. japonicus* were synchronously hatched (Novak and Shroyer 1978), and 24 h later, first-instar larvae were counted into aliquots of 10, 25, and 50. Within 1 h after counting, the larvae were distributed into appropriate cups.

Each container was monitored daily for the presence of pupae, which were collected and housed singly in sealed 50-ml vials containing water from their respective field cup. Each vial was labeled with the appropriate site and treatment identifier before being secured with a rubber band to a plastic stake at the field site. On emergence, adults were killed by freezing before scoring by container, species, sex, and day of emergence. The experiment ended on 11 October when the final adult emerged. Ambient temperature was monitored hourly for the duration of the experiment with three Onset HOBO data loggers located in the middle and at either end of the experimental area. The average ambient temperature during the experiment was $18.77 \pm 0.06°C$, with a range of $7.76–29.73°C$ ($n = 4,197$ hours). For 2 d (31 August and 1 September), the area was subjected to intense wind and rain because of a hurricane off the Atlantic Coast. To prevent damage to experiments and loss of data, the cups at each site were successfully covered and secured with a tarpaulin during this time

Population Growth Correlates

To quantify the effects of inter- and intraspecific competition on *Ae. albopictus* and *Ae. japonicus*, the mean survivorship, median development time of males and females, and median body size at adulthood of females per replicate were analyzed by one-factor, randomized complete block analysis of variance (ANOVA; SAS Institute 1989, PROC GLM), with treatment as effect and sites as blocks. Median development times and body size were used to meet assumptions of homogeneous variance and normality. Significant treatment effects were further analyzed using pairwise comparisons among treatment means with a sequential Bonferroni adjustment for the number of tests done (experimentwise $\alpha = 0.05$). Survivorship was calculated as the proportion of adults that emerged from the initial cohort of first instar larvae. Development time was calculated as the number of days from hatching to adult emergence. Adult body size was estimated from the length of one wing, which was removed from each female and measured under a dissecting microscope with an ocular micrometer (Packer and Corbet 1989).

Composite Index of Population Performance

Survivorship, female development time, and wing length were used to estimate the per capita rate of population change using a composite index of population performance for each species per replicate, r' (Livdahl and Sugihara 1984):

$$r' = \frac{\ln\left(\frac{1}{N_0}\sum_x A_x\, f(w_x)\right)}{D + \left(\dfrac{\sum_x xA_x f(w_x)}{\sum_x xA_x\, f(w_x)}\right)}$$

where N_0 is the initial number of females (assumed to be 50% of the cohort), A_X is the number of females eclosing on day x, w_X is the mean wing length of females eclosing on day x, and $f(w_X)$ is a function relating egg production to wing length. D is the time from adult eclosion to reproduction, taken as 14 d for *Ae. albopictus* (Livdahl and Willey 1991) and 12 d for *Ae.*

japonicus (unpublished data). A regression relating female wing length to fecundity for *Ae. albopictus* was obtained from Lounibos et al. (2002):

$$f(w_x) = 78.02 w_x - 121.240 \; (r^2 = 0.713; \; N = 91; P < 0.001)$$

where w_x is the wing length in millimeters on day x. Because no suitable equation could be derived from the literature, a regression for *Ae. japonicus* was determined experimentally. The mean estimated per capita rates of change (r') for *Ae. albopictus* and *Ae. japonicus* were analyzed by one-factor, randomized complete block ANOVA (SAS Institute 1989, PROC GLM), with treatment as effect and sites as blocks. Significant treatment effects were further analyzed using pairwise comparisons among treatment means with a sequential Bonferroni adjustment for the number of tests done (experimentwise $\alpha = 0.05$).

Estimation of *Ae. japonicus* Fecundity from Wing Length

A regression for *Ae. japonicus* was determined experimentally under controlled conditions of 26°C and 12 h:12 h light:dark in an insectary at the Florida Medical Entomology Laboratory in Vero Beach, FL. *Ae. japonicus* eggs used for this experiment were obtained from a colony maintained at the Headlee Research Laboratory Mosquito Research and Control Unit at Rutgers University in New Brunswick, NJ. This colony originated from larval collections from a horse farm in New Egypt, Ocean County, NJ, in 2001.

Eggs were hatched simultaneously using a medium of Brewer's yeast and lactalbumen, and 24 h later, larvae were transferred into enamel pans containing ≈1 liter of distilled water at a density of 100 per pan, where they were reared under conditions of varying food availability. Food consisted of pin oak leaves (*Q. palustris*) from Fairfax, VA, that were collected and dried at room temperature before quartering, weighing, and sorting into 0.5-, 1.5-, and 3-g allotments. These varying food levels were used to generate adult females with a large range of body size. Four days before the start of the experiment, three allotments of each leaf size were added to the enamel pans. This period allowed for the leaves to soak and be colonized by microorganisms.

On pupation, mosquitoes were transferred to plastic cups containing distilled water and placed in 0.028-m^3 (30.5 by 30.5 by 30.5 cm) rearing cages. Each cage was checked daily for adult emergence, after which any remaining pupae were removed to maintain separate adult cohorts by date of emergence. Cotton soaked in a 20% sucrose solution was provided as a source of carbohydrates for adults at all times. Beginning 2 d after emergence, adult females of each cohort were offered a blood-meal from a restrained chicken placed within the cage daily for 1 h. It should be noted that chickens were also used by Lounibos et al. (2002) to determine the fecundity of *Ae. albopictus* from wing length. On visual inspection immediately after the bloodfeeding opportunity, those females that appeared to have fed to repletion were removed from the cage using a mouth aspirator and placed singly in 12-dram plastic vials containing a 2.5 by 7.6-cm strip of wet seed germination paper (Anchor Paper, St. Paul, MN) to serve as an oviposition substrate (Steinly et al. 1991). Those females that did not feed to repletion on the first bloodfeeding opportunity were excluded from the study. Laid eggs were counted, and females were subsequently frozen and killed.

One wing was removed from each female and measured under a dissecting microscope with an ocular micrometer (Packer and Corbet 1989) to provide an estimate of body size for each female. The terminal abdominal segment of each female was subsequently removed, and the ovaries were teased out with the aid of a dissecting microscope to count any retained (fully formed and chitinous) eggs. This experiment was limited to the first gonotrophic cycle for each

species because the majority of female mosquitoes will most likely complete only one cycle (Packer and Corbet 1989).

Results

Survivorship to Adulthood

Mean survivorship to adulthood of *Ae. albopictus* was affected by treatment ($F_{2,8} = 7.16$, $P = 0.017$) but that of *Ae. japonicus* was not ($F_{2,8} = 2.89$, $P = 0.113$). Mean survivorship of *Ae. albopictus* was significantly higher in the 10:0 treatment than the 50:0 or 25:25 treatments, which were not different from one another (Fig. 1). Within density treatments, mean survivorship of *Ae. albopictus* was consistently higher than that of *Ae. japonicus* (Fig. 1). Mean survivorship to adulthood for neither *Ae. albopictus* ($F_{4,8} = 0.89$, $P = 0.514$) nor *Ae. japonicus* ($F_{4,8} = 0.30$, $P = 0.871$) was affected by site.

Developmental Time

The average median time from hatch to adulthood was significantly affected by density treatment for female ($F_{2,8} = 22.90$, $P<0.001$) but not male ($F_{2,8} = 2.92$, $P = 0.112$) *Ae. albopictus*. Comparisons of means for *Ae. albopictus* showed that development time was significantly shorter for females in the 10:0 and 25:25 density-composition treatments than in the 50:0 treatment (Fig. 2 and Fig 3). The mean median development time of both male ($F_{2,8} = 9.46$, $P = 0.008$) and female ($F_{2,8} = 6.02$, $P = 0.025$) *Ae. japonicus* was significantly affected by treatments; however, the pattern of significant differences in pairwise comparisons differed between the sexes in this species (Fig. 2 and Fig 3). Within any individual density-composition treatment, mean median development times of both male and female *Ae. albopictus* were consistently lower than those of *Ae. japonicus* (Fig. 2 and Fig 3). Development time of males and females, respectively, was unaffected by site for *Ae. albopictus* ($F_{4,8} = 0.87$, $P = 0.521$ and $F_{4,8} = 1.35$, $P = 0.332$) or *Ae. japonicus* ($F_{4,8} = 0.92$, $P = 0.496$ and $F_{4,8} = 0.58$, $P = 0.687$).

Female Wing Length

Mean median wing lengths of *Ae. japonicus* females were significantly affected by density treatments ($F_{2,8} = 23.12$, $P<0.001$), but those of *Ae. albopictus* were not ($F_{2,8} = 4.03$, $P = 0.062$). For *Ae. japonicus*, the low density mean median wing length was significantly greater than those from either high density treatment (Fig. 4). The average median wing length of *Ae. albopictus* was not affected by site ($F_{4,8} = 0.50$, $P = 0.5737$); however, that of *Ae. japonicus* was affected ($F_{4,8} = 5.24$, $P = 0.023$).

Estimation of *Ae. japonicus* Fecundity from Wing Length

A total of 79 *Ae. japonicus* females oviposited one or more eggs, and total egg production per female ranged from 18 to 122 eggs. The mean total eggs produced per female was 64.5 ± 23.0 (SD). The average wing length of females was 3.4 ± 0.2 mm, with a range of 2.6–3.9 mm. A single combined linear regression (SAS Institute 1989) was obtained for all three larval diet regimens, and the relationship of fecundity to wing length was determined for *Ae. japonicus* (Fig. 5). There was a positive regression of total number of eggs produced per female on wing length, yielding the following regression equation for *Ae. japonicus*:

$$f(w_x) = 53.078 w_x - 113.91 \quad (r^2 = 0.319; N = 79; P < 0.001)$$

where w_x is the wing length in millimeters on day x.

Composite Index of Population Performance (r′)

The mean estimated per capita rate of increase was significantly affected by density treatments for both *Ae. albopictus* ($F_{2,8} = 21.31$, $P < 0.001$) and *Ae. japonicus* ($F_{2,8} = 12.56$, $P = 0.003$; Fig. 6). Comparisons of means showed that r′ of both *Ae. albopictus* and *Ae. japonicus* was significantly higher for the low-density treatment than either of the high-density treatments, which in turn did not differ (Fig. 6). Within any individual density-composition treatment, mean r′ of *Ae. albopictus* was consistently higher than that of *Ae. japonicus*. Mean per capita rate of population increase for neither *Ae. albopictus* ($F_{4,8} = 0.73$, $P = 0.597$) nor *Ae. japonicus* ($F_{4,8} = 0.46$, $P = 0.762$) was affected by site.

Discussion

Invasion success and spread of non-native species can be enhanced by superiority in interspecific competition, particularly when similar species and limited resources are encountered (Williamson 1996). Inter-specific larval resource competition plays an important role in structuring the mosquito communities of artificial container habitats that are subject to invasion (Juliano and Lounibos 2005). In the context of this experiment, although both species were able to maintain positive population growth under interspecific conditions, it seems that *Ae. albopictus* may have a competitive advantage over *Ae. japonicus*. This is supported by the consistently higher survivorship, shorter development time, and higher per capita rate of population increase of *Ae. albopictus* compared with *Ae. japonicus* across density treatments.

The Lotka-Volterra model of two-species competition (Lotka 1925, Volterra 1926, 1931) provides a useful frame of reference for interpreting these findings. This model accounts for the effect that the presence of one species will have on the population of another species, relative to the competitive effect that two members of the same species would have on each other. In this respect, the Lotka-Volterra competition equations may be used to predict the potential outcome when two species are in competition for the same resources. Consider that *Ae. albopictus* and *Ae. japonicus*, occurring at densities N_a and N_j, respectively, have the carrying capacities K_a and K_j, at which each reaches an equilibrium population size ($dN/dt = 0$), and instantaneous rates of increase, r_a and r_j, in the absence of one another. The simultaneous growth of the two competing species occurring together can be described by the following pair of differential logistic equations:

$$\frac{dN_a}{dt} = r_a N_a \left(\frac{K_a - N_a - \beta N_j}{K_a} \right)$$
$$\frac{dN_j}{dt} = r_j N_j \left(\frac{K_j - N_j - \alpha N_a}{K_j} \right)$$

where α and β are competition coefficients; α is the effect of *Ae. albopictus* on *Ae. japonicus* and β is the effect of *Ae. japonicus* and *Ae. albopictus*. The outcome of competition depends on the relative values of K_a, K_j, α, and β

Stable coexistence can occur only when both $K_j/\alpha > K_a$ and $K_a/\beta > K_j$; that is, each population must inhibit its own growth more than that of the other species. This is most likely to occur when the carrying capacities of the two species are equivalent and the competition coefficients are less than one. The equal inter- and intraspecific effects on *Ae. japonicus* imply that $\alpha \approx 1$, whereas the lesser interspecific effect on *Ae. albopictus*, compared with intraspecific effect, suggests that $\beta < 1$. Similar results have been reported from experiments with *Ae. albopictus* in competition with *Ae. sierrensis* (Washburn and Hartmann 1992) and *Ae. triseriatus* (Teng and Apperson 2000).

Although no estimates of carrying capacities were obtained for either species in this experiment, because r′ for *Ae. japonicus* at high density was closer to zero, indicating little or no growth, the dN_j/dt is presumably closer to zero at high density and *Ae. japonicus* is closer to K_j than *Ae. albopictus* is to K_a. Therefore, it is likely that $K_j < K_a$. When isoclines of both species are superimposed on one another, the N_a isocline lies above the N_j isocline, and the elimination of *Ae. japonicus* by competitive exclusion is predicted (Fig. 7), because the only point of stable equilibrium under this scenario occurs when $N_a = K_a$ and $N_j = 0$.

Although the shorter development times of *Ae. albopictus* may simply reflect intrinsic metabolic differences between the species, when coupled with the higher mean per capita rate of increase, it may suggest that *Ae. albopictus* is able to forage and acquire re-sources more efficiently or uses different feeding behaviors that are more effective in this type of larval habitat. A recent comparison of foraging behaviors found *Ae. japonicus* to be the more active of the two species in various media that included leaves and tire water (O'Donnell and Armbruster 2007), which suggests that activity per se does not necessarily mirror competitive ability. Ho et al. (1973) suggested that perhaps the higher content of proteinases in the gut of *Ae. albopictus* facilitates a more efficient feeding style, which ultimately allows this species to develop faster than other container-inhabiting mosquitoes.

These results imply that *Ae. albopictus* has a slight competitive advantage over *Ae. japonicus*; however, these two species may coexist in areas where they overlap despite this observation. Although this experiment was conducted in the field under manipulated but ecologically realistic conditions, it is important to consider that variations in resource level, type, or frequency (Braks et al. 2004), temperature (Lounibos et al. 2002), sun exposure, container type (Livdahl and Willey 1991), larval density, and season (Teng and Apperson 2000) may influence larval competition differently among mosquito species. Furthermore, these findings should be viewed in context with field observations of co-occurrences, as well as seasonal distributions, habitat preferences, and overwintering behaviors, because these factors may ultimately influence niche segregation and the community structure of the artificial containers in which these species coexist. Similarly, although interspecific larval competition is likely an important factor influencing the survivorship, growth, reproductive success, and population performance of mosquitoes in container environments with limited resources, other factors such as predation (Griswold and Lounibos 2005), 2006, intraguild predation (Edgerly et al. 1999), apparent competition mediated by shared enemies (Juliano 1998), habitat alteration (Bertness 1984), and differences in foraging behavior (Yee et al. 2004, O'Donnell and Armbruster 2007) may also be important and warrant further research with respect to interactions between these two species. Finally, it should be noted that noncompetitive characteristics such as adult survival and mating and bloodfeeding success might ultimately influence the relative success of larger mosquito populations.

In addition to these ecological consequences, these findings may potentially have epidemiological implications, particularly with respect to LaCrosse encephalitis virus, in which both *Ae. albopictus* and *Ae. japonicus* are competent vectors. Their continued coexistence in containers in LaCrosse endemic regions may be important in epizootic, or potentially even epidemic, transmission of the disease, although this will require further study. Because larval competition has been linked to greater infection and dissemination rates of dengue and Sindbis viruses for *Ae. albopictus* (Alto et al. 2005, 2008), similar effects are possible with respect to arboviruses circulating in areas in which this species is sympatric with *Ae. japonicus*.

References Cited

Alto BW, Lounibos LP, Higgs S, Juliano SA. Larval competition differentially affects arbovirus infections in *Aedes* mosquitoes. Ecology 2005;86:3279–3288. [PubMed: 19096729]

Alto BW, Lounibos LP, Mores CN, Reiskind MH. Larval competition alters susceptibility of adult *Aedes* mosquitoes to dengue infection. Proc. Biol. Sci 2008;275:463–471. [PubMed: 18077250]

Andreadis TG, Anderson JF, Munstermann LE, Wolfe RJ, Florin DA. Discovery, distribution, and abundance of the newly introduced mosquito *Ochlerotatus japonicus* (Diptera: Culicidae) in Connecticut, USA. J. Med. Entomol 2001;38:774–779. [PubMed: 11761373]

Barrera R. Competition and resistance to starvation in larvae of container-inhabiting *Aedes* mosquitoes. Ecol. Entomol 1996;21:117–127.

Bertness MD. Habitat and community modification by an introduced herbivorous snail. Ecology 1984;65:370–381.

Braks MAH, Honório NA, Lounibos LP, Lourenço-de-Oliveira R, Juliano SA. Interspecific competition between two invasive species of container mosquitoes in Brazil. Ann. Entomol. Soc. Am 2004;97:130–139.

Costanzo KS, Mormann K, Juliano SA. Asymmetrical competition and patterns of abundance of *Aedes albopictus* and *Culex pipiens* (Diptera: Culicidae). J. Med. Entomol 2005;42:559–572. [PubMed: 16119544]

Craven RB, Eliason DA, Francy DB, Reiter P, Campos EG, Jakob WL, Smith GC, Bozzik CJ, Moore GG, Maupin GO, Monath TP. Importation of *Aedes albopictus* and other exotic mosquito species into the United States in used tires from Asia. J. Am. Mosq. Control Assoc 1988;4:138–142. [PubMed: 2903907]

Edgerly JS, Willey MS, Livdahl T. Intraguild predation among treehole mosquitoes *Aedes albopictus, Ae. aegypti*, and *Ae. triseriatus* (Diptera: Culicidae), in laboratory microcosms. J. Med. Entomol 1999;36:394–399. [PubMed: 10337114]

Effler PW, Pang L, Kitsutani P, Vorndam V, Nakata M, Ayers T, Elm J, Tom T, Reiter P, Rigau-Perez JG, Hayes JM, Mills K, Napier M, Clark GG, Gubler DJ. for the Hawaii Dengue Outbreak Investigation Team. Dengue Fever, Hawaii, 2001–2002. Emerg. Infect. Dis 2005;11:742–749. [PubMed: 15890132]

Enserink M. Tropical disease follows mosquitoes to Europe. Science 2007;317:1485. [PubMed: 17872417]

Focks DA, Linda SB, Craig GB, Hawley WA, Pumpuni CB. *Aedes albopictus* (Diptera: Culi-cidae)—a statistical model of the role of temperature, photoperiod, and geography in the induction of egg diapause. J. Med. Entomol 1994;31:278–286. [PubMed: 8189418]

Fonseca DMS, Campbell WJ, Crans M, Mogi I, Miyagi T, Toma M, Bullians TG, Andreadis RL, Berry B, Pagac MR, Sardelis, Wilkerson RC. *Aedes (Finlaya) japonicus* (Diptera: Culicidae), a newly recognized mosquito in the United States: analyses of genetic variation in the United States and putative source populations. J. Med. Entomol 2001;38:135–146. [PubMed: 11296814]

Foss, KA.; Dearborn, RG. Preliminary faunistic survey of mosquito species (Diptera: Culicidae) with a focus on population densities and potential breeding sites in greater Portland, Maine. Augusta, ME: Maine Department of Conservation, Maine Forest Service, Forest Health and Monitoring Division; 2001.

Gallitano S, Blaustein L, Vonesh J. First occurrence of *Ochlerotatus japonicus* in Missouri. J. Vector Ecol 2006;30:347–348. [PubMed: 16599178]

Gerhardt RR, Gottfried KL, Apperson CS, Davis BS, Erwin PC, Smith AB, Panella NA, Powell EE, Nasci RS. First isolation of LaCrosse virus from naturally infected *Aedes albopictus*. Emerg. Infect. Dis 2001;7:807–811. [PubMed: 11747692]

Godsey MS, Blackmore MS, Panella NA, Burkhalter K, Gottfried K, Halsey LA, Rutledge R, Langevin SA, Gates R, Lamonte KM, Lambert AM, Lanciotti RS, Blackmore CGM, Loyless T, Stark L, Oliveri R, Conti L, Komar N. West Nile virus epizootiology in the southeastern United States, 2001. Vector-Borne Zoonot. Dis 2005;5:82–89.

Griswold MW, Lounibos LP. Does differential predation permit invasive and native mosquito larvae to coexist in Florida? Ecol. Entomol 2005;30:122–127.

Griswold MW, Lounibos LP. Predator identity and additive effects in a treehole community. Ecology 2006;87:987–995. [PubMed: 16676542]

Hawley WA. The biology of *Aedes albopictus*. J. Am. Mosq. Control Assoc 1988;4:1–40. [PubMed: 3193094]

Hawley WA, Pumpuni CB, Brady RH, Craig GB. *Aedes albopictus* in North America: probable introduction in used tires from Northern Asia. Science 1987;236:1114–1116. [PubMed: 3576225]

Ho, BC.; Chan, KL.; Chan, YC. The biology and bionomics of *Aedes albopictus* (Skuse). In: Chan, YC.; Chan, KL.; Ho, BC., editors. Vector Control in Southeast Asia. Singapore: Southeast Asian Ministers for Education Organization Workshop; 1973. p. 125-143.

Holick J, Kyle A, Ferraro W, Delaney RR, Iwaseczko M. Discovery of *Aedes albopictus* infected with West Nile virus in southeastern Pennsylvania. J. Am. Mosq. Control Assoc 2002;18:131. [PubMed: 12083357]

Ibañez-Bernal S, Briseño B, Mutebi J-P, Argot E, Rodriguez G, Martinez-Camposc C, Paz R, de la Fuente-San Roman P, Tapia-Conyer R, Flisser A. First record in America of *Aedes albopictus* naturally infected with dengue virus during the 1995 outbreak at Reynosa, Mexico. Med. Vet. Entomol 1997;11:305–309. [PubMed: 9430106]

Juliano SA. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? Ecology 1998;79:255–268.

Juliano SA, Lounibos LP. Ecology of invasive mosquitoes: effects on resident species and on human health. Ecol. Lett 2005;8:558–574. [PubMed: 17637849]

Juliano SA, O'Meara GF, Morrill JR, Cutwa MM. Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes. Oecologia (Berl.) 2002;130:458–469.

Juliano SA, Lounibos LP, O'Meara GF. A field test for competitive effects of *Aedes albopictus* on *Aedes aegypti* in south Florida: differences between sites of coexistence and exclusion? Oecologia (Berl.) 2004;139:583–593. [PubMed: 15024640]

Larish LB, Savage HM. Introduction and establishment of *Aedes (Finlaya) japonicus japonicus* (Theobald) on the island of Hawaii: Implications for arbovirus transmission. J. Am. Mosq. Control Assoc 2005;21:318–321. [PubMed: 16252525]

Linthicum KJ, Kramer VL, Madon MB, Fujioka K. the Surveillance-Control Team. Introduction and potential establishment of *Aedes albopictus* in California in 2001. J. Am. Mosq. Control Assoc 2003;19:301–308. [PubMed: 14710730]

Livdahl TP, Sugihara G. Non-linear interactions of populations and the importance of estimating per capita rates of change. J. Anim. Ecol 1984;53:573–580.

Livdahl TP, Willey MS. Prospects for an invasion: competition between *Aedes albopictus* and native *Aedes triseriatus*. Science 1991;253:189–191. [PubMed: 1853204]

Lotka, AJ. Elements of physical biology. Baltimore, MD: Williams and Wilkins; 1925.

Lounibos LP. Invasions by insect vectors of human disease. Annu. Rev. Entomol 2002;47:233–266. [PubMed: 11729075]

Lounibos LP, Suárez S, Menédez Z, Nishimura N, Escher RL, O'Connell SM, Rey JR. Does temperature affect the outcome of larval competition between *Aedes aegypti* and *Aedes albopictus*? J. Vector Ecol 2002;27:86–95. [PubMed: 12125878]

Méndez F, Barreto M, Arias JF, Renfigo G, Muñoz J, Burbano ME, Parra B. Humanand mosquito infections by dengue viruses during and after epidemics in a dengue-endemic region of Colombia. Am. J. Trop. Med. Hyg 2006;74:678–683. [PubMed: 16607005]

Merritt RW, Dadd RH, Walker ED. Feeding behavior, natural food, and nutritional relationships of larval mosquitoes. Annu. Rev. Entomol 1992;37:349–376. [PubMed: 1347208]

Mitchell CJ, Niebylski ML, Karabatsos N, Martin D, Mutebi J-P, Craig GB, Mahler MJ. Isolation of eastern equine encephalitis from *Aedes albopictus* in Florida. Science 1992;257:526–527. [PubMed: 1321985]

Moore CG. *Aedes albopictus* in the United States: current status and prospects for further spread. J. Am. Mosq. Control Assoc 1999;15:221–227. [PubMed: 10412117]

Moore, CG. Arthropod-borne and Infectious Diseases Laboratory and Department of Environmental and Radiological Health Sciences. Fort Collins, CO: Colorado State University; 2005. Exotic and invasive vectors of public health importance in the United States.

Mullen GR. First report of *Ochlerotatus japonicus* in Alabama. Ala. Vector Manage. Soc. Newsl 2005;15:2.

Nawrocki SJ, Hawley WA. Estimation of the Northern limits of the distribution of *Aedes albopictus* in North America. J. Am. Mosq. Control Assoc 1987;3:314–317. [PubMed: 3504917]

Novak RJ, Shroyer DA. Eggs of *Aedes triseriatus* and *A. hendersoni*: a method to stimulate optimal hatch. Mosq. News 1978;38:515–521.

O'Donnell DL, Armbruster P. Comparison of foraging behavior of *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae). J. Med. Entomol 2007;44:984–989. [PubMed: 18047196]

O'Meara GF, Evans LF, Gettman AD, Cuda JP. Spread of *Aedes albopictus* and decline of *Ae. aegypti* (Diptera: Culicidae) in Florida. J. Med. Entomol 1995;32:554–562. [PubMed: 7650719]

Packer MJ, Corbet PS. Size variation and reproductive success of female *Aedes punctor* (Diptera: Culicidae). Ecol. Entomol 1989;14:297–309.

Peyton EL, Campbell SR, Candeletti TM, Romanowski M, Crans WJ. *Aedes (Finlaya) japonicus japonicus* (Theobald), a new introduction into the United States. J. Am. Mosq. Control Assoc 1999;15:238–241. [PubMed: 10412119]

Reiter P, Sprenger D. The used tire trade: a mechanism for the worldwide dispersal of container breeding mosquitoes. J. Am. Mosq. Control Assoc 1987;3:494–501. [PubMed: 2904963]

Roppo MR, Lilya JL, Maloney FA, Sames WJ. First occurrence of *Ochlerotatus japonicus* in the state of Washington. J. Am. Mosq. Control Assoc 2004;20:83–84. [PubMed: 15088708]

Sardelis MR, Dohm JD, Pagac B, Andre RG, Turell MJ. Experimental transmission of eastern equine encephalitis virus by *Ochlerotatus j. japonicus* (Diptera: Culicidae). J. Med. Entomol 2002a;39:480–484. [PubMed: 12061444]

Sardelis MR, Turell MJ, Andre RG. Laboratory transmission of LaCrosse virus by *Ochlerotatus j. japonicus* (Diptera: Culicidae). J. Med. Entomol 2002b;39:635–639. [PubMed: 12144295]

Sardelis MR, Turell MJ, Andre RG. Experimental transmission of St. Louis encephalitis virus by *Ochlerotatus j. japonicus*. J. Am. Mosq. Control Assoc 2003;19:159–162. [PubMed: 12825669]

SAS Institute. SAS/STAT user's guide. Version 6. 4th ed. Volume 2. Cary, NC: SAS Institute; 1989.

Scott, JJ. PhD dissertation. New Brunswick, NJ: Rutgers, The State University of New Jersey; 2003. The ecology of the exotic mosquito *Ochlerotatus (Finlaya) japonicus japonicus* (Theobald 1901) (Diptera: Culicidae) and an examination of its role in the West Nile virus cycle in New Jersey.

Sprenger D, Wuithiranyagool T. The discovery and distribution of *Aedes albopictus* in Harris County, Texas, USA. J. Am. Mosq. Control Assoc 1986;2:217–219. [PubMed: 3507493]

Steinly BA, Novak RJ, Webb DW. A new method for monitoring mosquito oviposition in artificial and natural containers. J. Am. Mosq. Control Assoc 1991;7:649–650. [PubMed: 1787411]

Takashima I, Rosen L. Horizontal and vertical transmission of Japanese encephalitis virus by *Aedes japonicus* (Diptera: Culicidae). J. Med. Entomol 1989;26:454–458. [PubMed: 2552120]

Tanaka K, Mizusawa K, Saugstad ES. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Contrib. Am. Entomol. Inst 1979;16(ii–vii):1–987.

Teng HJ, Apperson CS. Development and survival of immature *Aedes albopictus* and *Aedes triseriatus* (Diptera: Culicidae) in the laboratory: effects of density, food, and competition on response to temperatures. J. Med. Entomol 2000;37:40–52. [PubMed: 15218906]

Thielman A, Hunter FF. Establishment of *Ochlerotatus japonicus* (Diptera: Culicidae) in Ontario, Canada. J. Med. Entomol 2006;43:138–142. [PubMed: 16619591]

Turell MJ, O'Guinn ML, Dohm DJ, Jones JW. Vector competence of North American mosquitoes (Diptera: Culicidae) for West Nile virus. J. Med. Entomol 2001;38:130–134. [PubMed: 11296813]

Volterra V. Fluctuations in the abundance of a species considered mathematically. Nature (Lond.) 1926;118:558–560.

Volterra, V. Animal ecology. New York: Chapman; 1931.

Washburn JO, Hartmann EU. Could *Aedes albopictus* (Diptera: Culicidae) become established in California tree holes? J. Med. Entomol 1992;29:995–1005. [PubMed: 1460642]

Williamson, M. Biological invasions. New York: Chapman & Hall; 1996.

Yee DA, Kesavaraju B, Juliano SA. Interspecific differences in feeding behavior and survival under food-limited conditions for larval *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). Ann. Entomol. Soc. Am 2004;97:720–728.
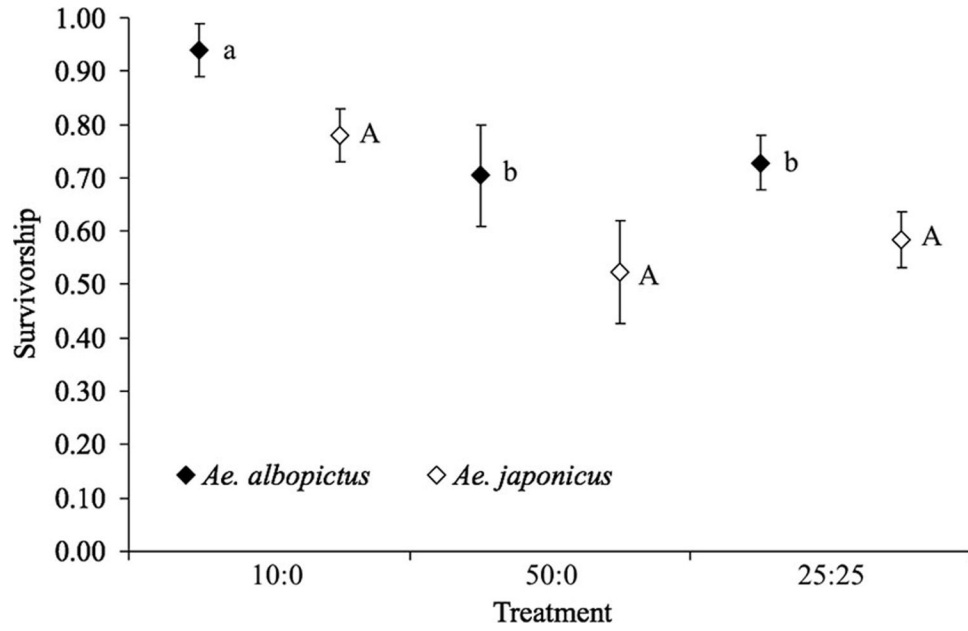
Fig. 1.
Mean survivorship (proportion of the original number of larvae surviving to adulthood) of *Ae. albopictus* and *Ae. japonicus* (±SE). Lowercase and uppercase letters indicate significant differences among competition treatments resulting from pairwise comparisons ($P < 0.05$) for *Ae. albopictus* and *Ae. japonicus*, respectively. ANOVA did not indicate a significant difference in survivorship among treatments for *Ae. japonicus*.
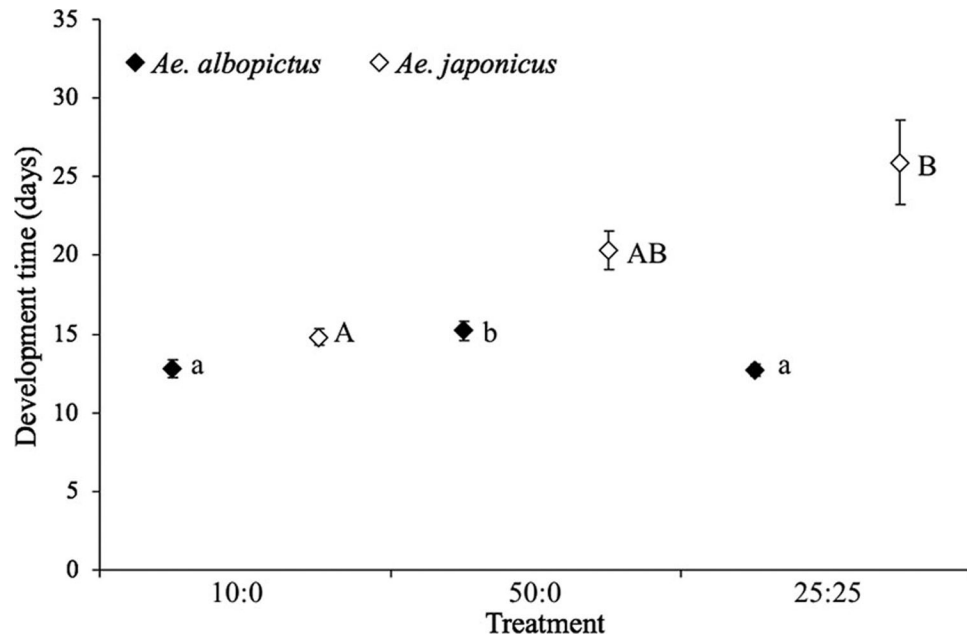
Fig. 2.
Means of median time to adulthood for male *Ae. albopictus* and *Ae. japonicus* (±SE).
Lowercase and uppercase letters indicate significant differences among competition treatments
resulting from pairwise comparisons ($P < 0.05$) for *Ae. albopictus* and *Ae. japonicus*,
respectively.
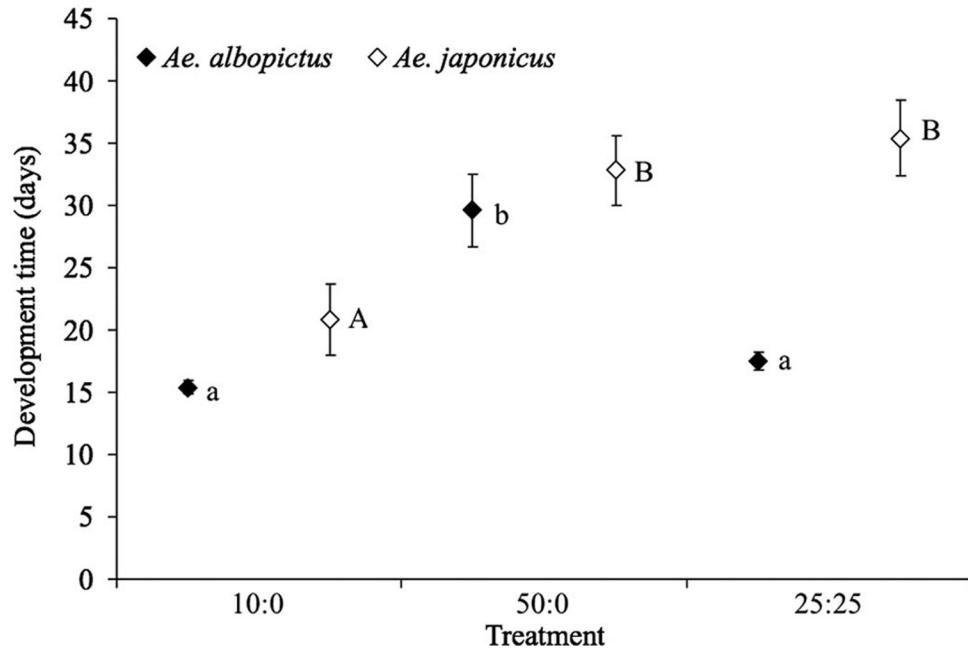
Fig. 3.
Means of median time to adulthood for female *Ae. albopictus* and *Ae. japonicus* (±SE).
Lowercase and uppercase letters indicate significant differences among competition treatments
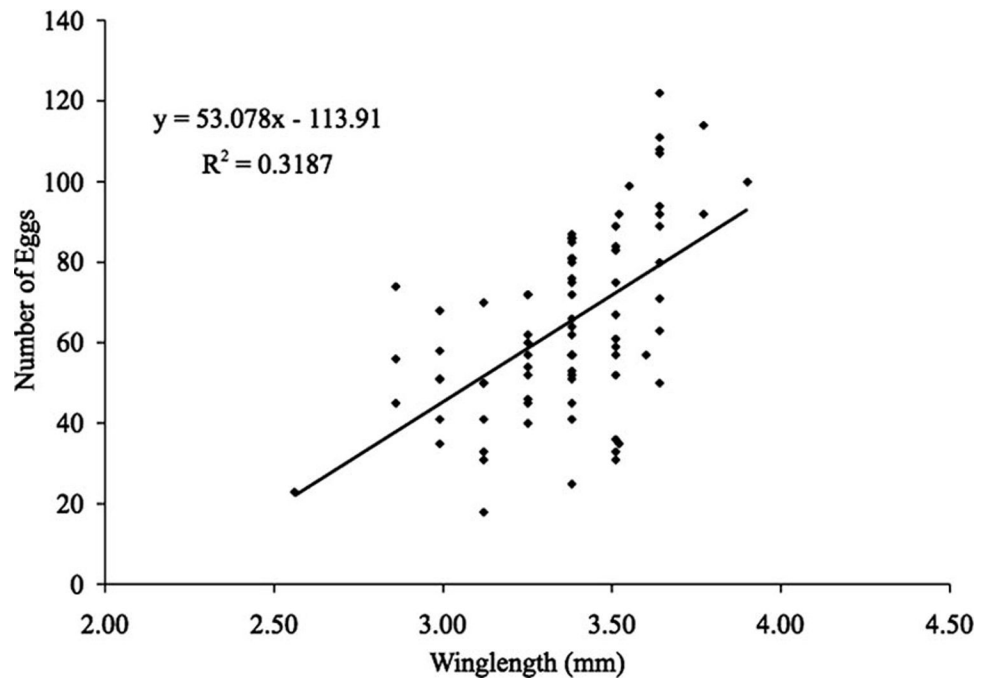resulting from pairwise comparisons ($P < 0.05$) for *Ae. albopictus* and *Ae. japonicus*,
respectively.
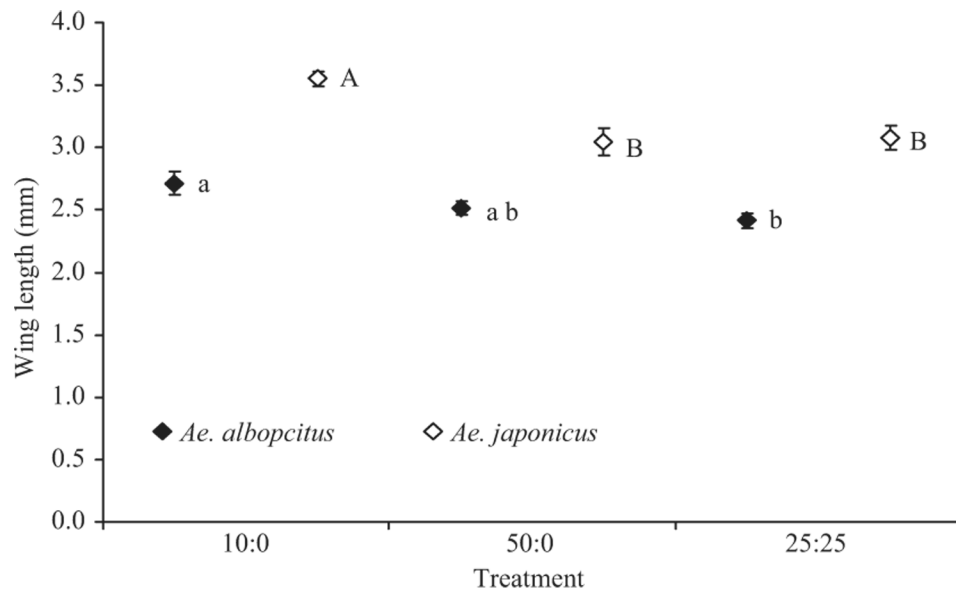
Fig. 4.
Means of median wing lengths of *Ae. albopictus* and *Ae. japonicus* adult females (±SE). Lowercase and uppercase letters indicate significant differences among competition treatments resulting from pairwise comparisons (*P*< 0.05) for *Ae. albopictus* and *Ae. japonicus*, respectively.
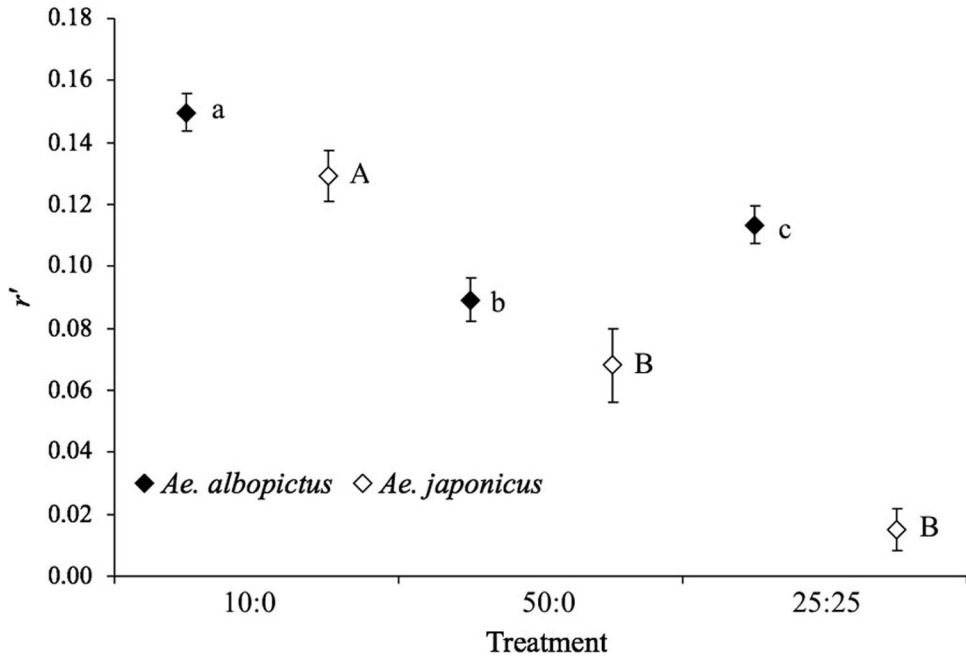
Fig. 5.
Relationship between wing length (mm) and total eggs produced for *Ae. japonicus*.

Fig. 6.
Mean estimates (±SE) of population performance (r′, the per capita rate of population increase for the cohort) for female *Ae. albopictus* and *Ae. japonicus* adults. Lowercase and uppercase letters indicate significant differences among competition treatments resulting from pairwise comparisons ($P < 0.05$) for *Ae. albopictus* and *Ae. japonicus*, respectively.
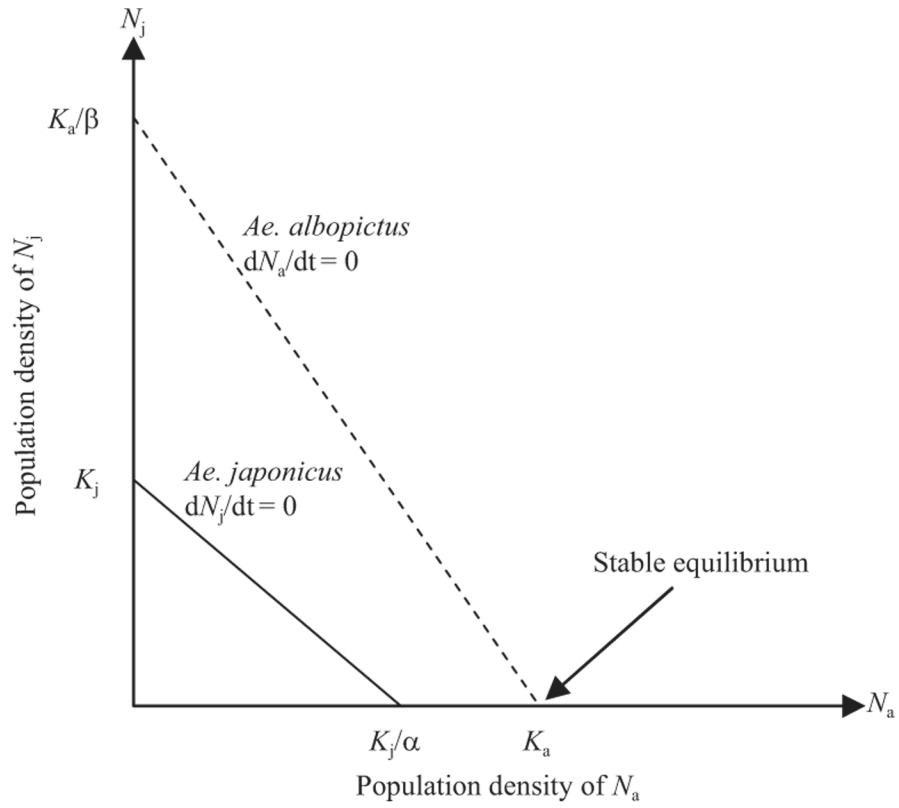
Fig. 7.
Isoclines of *Ae. albopictus* and *Ae. japonicus*, based on a Lotka-Volterra model (see text), with stable equilibrium occurring at $N_a = K_a$ and $N_j = 0$, suggesting competitive exclusion of the latter species.