

## Interspecific Competition Between Two Invasive Species of Container Mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil

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**ABSTRACT** As a result of numerous successful invasions by both *Aedes albopictus* (Skuse) and *Aedes aegypti* (L.), the current worldwide distributions of these mosquito species overlap. Shared larval habitats and shifts in the distribution and abundance of resident *A. albopictus* or *A. aegypti* after the establishment of the other species suggest that competitive displacement occurs. Experiments on larval competition between North American populations of the two species showed that *A. albopictus* has the competitive advantage under local field conditions, which apparently accounts for displacement of *A. aegypti* from much of the United States after the invasion of *A. albopictus*. The role of competition, and potential shifts of competitive advantage in different parts of their worldwide ranges are unknown, but variation due to intraspecific or environmental differences is possible. In the current study, we measured the performance of larvae of Brazilian populations of *A. albopictus* and *A. aegypti* competing under field conditions in Rio de Janeiro, Brazil. Finite rates of increase for each species were estimated and the effects of species composition, larval density, and leaf litter resource levels were determined. *A. albopictus* maintained positive population growth at higher combined densities and lower per capita resource availability than did *A. aegypti*. *A. albopictus* showed higher survivorship than *A. aegypti* under all treatments and leaf litter resource levels. These results indicate that in Brazil, just as in North America, *A. albopictus* is a superior larval competitor to *A. aegypti* when exploiting leaf litter resources. Our results further suggest that this competitive advantage for *A. albopictus* is likely to be independent of mosquito population origin, local environmental conditions, and local differences in the types of leaves that form the resource base of the aquatic habitats of larvae.

**KEY WORDS** mosquito, finite rate of increase, invasion biology, resource competition

SPECIES COLONIZING NEW HABITATS provide opportunities for natural and manipulative experiments in population and community ecology, and recent colonizations allow for the study of species interactions as they shape newly modified communities (Krebs and Barker 1991). The yellowfever mosquito, *Aedes aegypti* (L.), originated from tropical Africa and invaded the Americas beginning in the 16th century. Toward the end of the 19th century, it became established in the native range of Asian tiger mosquito, *Aedes albopictus* (Skuse) (Tabachnick 1991). *A. albopictus* was restricted, until recently, to the eastern hemisphere: the Indian subcontinent, Southeast Asia, China, Japan, Indonesia, and the islands in the Indian Ocean. At the beginning of the 20th century, it invaded the Hawaiian Islands (Lounibos 2002). *A. albopictus* became estab-

lished and spread in the continental United States (Sprenger and Wuithiranyagool 1986, Hawley et al. 1987) and Brazil (R.L.d.O., unpublished data, Forattini 1986) in the mid-1980s. The aquatic larvae of these two closely related species (members of the subgenus *Stegomyia*) typically inhabit water-filled containers where they feed on microorganisms and other fine particulate food in the water column and on leaves and other organic detritus.

In its native range, the abundance of *A. albopictus* decreased in cities but not in rural areas upon the establishment of *A. aegypti* (Rudnick and Hammon 1960, Gilotra et al. 1967, Chan et al. 1971, Ho et al. 1973, Hawley 1988). In the continental United States, the abundance of *A. aegypti* decreased during the establishment of *A. albopictus* (O'Meara et al. 1995). O'Meara et al. (1995) noted that although displacement of *A. aegypti* was common, *A. aegypti* persisted in the most southern cities of Florida. Shared larval habitats and reports of shifts in distribution and abundance of resident *A. albopictus* or *A. aegypti* after the establishment of the other species suggest that com-

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petitive displacement may have occurred. In Florida, Juliano (1998) showed that in nature, *A. albopictus* had an advantage in larval competition over *A. aegypti* and that addition of resources (in the form of leaf litter) reduced the effects of competition. Observational evidence suggested that interspecific competition was probably common in typical habitats (Juliano 1998). He proposed that interspecific resource competition is the most obvious explanation of the observed decline of *A. aegypti* in the United States after the invasion of *A. albopictus*.

Although the effects of the invasion of *A. albopictus* on *A. aegypti* abundance in Brazil are unknown, larvae of both species co-occur in containers (Honório and Lourenço-de-Oliveira 2001, Galardo 2002, Braks et al. 2003), suggesting that interspecific larval competition could occur in Brazil. Diapause characteristics (Hawley et al. 1987) and mitochondrial DNA haplotypes (Birungi and Munstermann 2002) indicate that *A. albopictus* in the United States originated from temperate Japan and that the Brazilian *A. albopictus* has a tropical origin. Although *A. aegypti* populations have a common ancestry in Africa, Brazilian and North American populations of these species have evolved independently (Tabachnick 1991, Lourenço-de-Oliveira et al. 2003). Thus, the nearly simultaneous but independent introductions of *A. albopictus* in two disjunct localities, United States and Brazil, where *A. aegypti* already resided, present a unique opportunity to study larval competition between different populations of these species from different endemic regions under different conditions. Differences in both invader origin and local evolution since invasion may affect the outcome of competition in North and South America.

Other factors that may contribute to variation in the results of competition experiments, and which may contribute to real differences in the outcome of invasions, include local differences in abiotic and biotic factors (Dunson and Travis 1991). Experiments using leaves as a resource substrate have indicated that *A. albopictus* is the superior competitor (Barrera 1996, Juliano 1998, Daugherty et al. 2000), whereas experiments using alternative substrates have suggested other outcomes (MacDonald 1956, Moore and Fischer 1969, Sucharit et al. 1978, Black et al. 1989, Ho et al. 1989, Barrera 1996). Both theory and experimental results clearly indicate the potential for resource type to alter the outcome of competition (e.g., Tilman 1982, Gilpin et al. 1986), and sources of organic detritus in containers in Brazil differ from those in North America. Furthermore, abiotic factors such as temperature fluctuations and water chemistry are likely to differ, indicating that results from field experiments in North America may not predict the outcomes of competition in Brazil, or any other area where the two species come into contact.

Aside from differences between population origins and their local environments, the parameters used to quantify the effects of competition might account for some of the contradictory conclusions in competition experiments noted above. Competitive advantage is

attained by the species that maintains a stable or growing population, whereas its competitor's population declines (Pianka 1988). However, most previous studies have focused on individual fitness components such as survivorship or size at and time to adult emergence (Moore and Fischer 1969, Black et al. 1989, Ho et al. 1989, Barrera 1996), rather than composite measures of population growth. Any single fitness component is unlikely to provide an accurate evaluation of competitive ability (Grill and Juliano 1996). Composite indices of performance (Livdahl 1982, Juliano 1998) combine individual fitness parameters and avoid pitfalls of univariate measures.

In this article, we address how *A. albopictus* and *A. aegypti* interact in the larval stage, where resource competition is most likely. In an experiment designed to parallel Juliano's (1998) competition experiments in Florida, we measured the performance of larvae of Brazilian populations of these species competing for resources under field conditions in Rio de Janeiro. The similar experimental design and data analyses facilitated comparisons of results from the United States and Brazil. Comparisons were made between species for intra- and interspecific effects of larval density and resource level as well as between locales for effects of population and condition.

## Materials and Methods

**Experimental Design.** The experiment was conducted in the botanical garden of the Oswaldo Cruz Institute in Rio de Janeiro (22° 5' S; 43° 2' W), Brazil from February to April 2002 (average  $T_{\min}$  = 23.5°C, average  $T_{\max}$  = 31.3°C, average rainfall 2.7 cm d<sup>-1</sup>). *A. aegypti* was the most common culicid occupant of artificial containers on the Institute's property before the invasion of *A. albopictus* (R.L.d.O., unpublished data). Currently, *A. albopictus* and to a lesser extent *A. aegypti* occur in artificial containers in this locale. *Aedes* used in this experiment were the first generation progeny of individuals collected in Nova Iguaçu, a city within the greater metropolitan area of Rio de Janeiro.

Inter- and intraspecific larval competition was investigated by monitoring the development of larvae at different densities, species ratios, and food levels in water-filled plastic containers in the garden. Ten combinations of *A. aegypti*:*A. albopictus* (20:0, 40:0, 60:0, 0:20, 0:40, 0:60, 20:20, 30:30, 20:40, and 40:20) developed in 400-ml black plastic jars (9 cm in height, 11 cm base diameter) with two food levels. Food consisted of 0.25 or 0.50 g of fallen avocado leaves that had been collected, washed, sun-dried for at least 2 d, broken into pieces (4-cm<sup>2</sup> maximum), and weighed. Each of the combinations was replicated four times, resulting in 80 containers total. On 9 February, the containers were labeled with a unique number and assigned randomly to numbered sites in the shade of the garden where they were secured to wooden poles to prevent toppling. We used only shaded areas because in a preliminary trial, all larvae that were placed in full sun (31 of 80 containers) died, probably due to high water temperatures. Three days before the addition of lar-

vae, containers received the appropriate quantity of leaf litter, along with 200 ml of tap water and were covered with white plastic mesh (0.5 mm) secured with a rubber band to prevent oviposition by wild mosquitoes. In the laboratory, eggs of *A. aegypti* and *A. albopictus* were placed in water to hatch, and 24-h-old first instars of both species were counted into groups of 20, 30, 40, and 60 larvae. Within 1 h after counting, the larvae were put in appropriate containers.

Each container was monitored daily for the presence of pupae, which were collected and housed in sealed vials (30 ml) with water in the laboratory until adult emergence. On the day of emergence, adults were killed with acetyl acetate, scored by container, species, sex, and day of emergence, and preserved. The experiment ended on 29 April (day 70) when the last larva pupated.

**Data Analyses.** Three population growth correlates were used to quantify the effects of intra- and inter-specific competition on mosquito population growth: larval survivorship, and size at adulthood and developmental time of females. To estimate adult body size, one wing was removed from each female and measured under a dissecting microscope with an ocular micrometer following methods of Packer and Corbet (1989). Median wing length and time to adulthood were calculated for each species and container because of non-normal distributions of these variables within cohorts. Developmental time was calculated as the number of days from hatching to adulthood. Survivorship was calculated for each container by dividing the total number of adults by the number of initial larvae. For the entire experiment, 8% of pupae were damaged during collection and died before emergence. These specimens were treated as emerging adults in our analysis, their sexes and species determined by pupal characteristics. Developmental time for these individuals was based on the day of the emergence of conspecifics collected as pupae on the same day. Ideally their size would be estimated by taking the mean wing length of conspecifics of the same sex emerging from the same container on the same day. However, in most cases such data were not available. Therefore, we estimated their size by taking the mean wing length of all emerging conspecifics of the same sex in the whole experiment. Twenty adults escaped during data collection, and their identities were determined from pupal skins, and their sizes were also estimated from the overall mean. Two replicates that yielded a survivorship for *A. albopictus* >100% were removed from analyses based upon the presumption that oviposition by wild *A. albopictus* had occurred in these containers. The population growth correlates were used in calculations of a composite index of mosquito population performance ( $\lambda'$ ) for each container (Juliano 1998). This composite index for performance is based on  $r'$  ( $\lambda' = \exp [r']$ ), which is an estimate of the realized per capita rate of population change (Livdahl and Sugihara 1984).

We calculated  $\lambda'$  for each replicate as follows:

$$\lambda' = \exp \left[ \frac{\ln \left[ (1/N_0) \sum_x A_x f(\omega_x) \right]}{D + \left[ \sum_x x A_x f(\omega_x) / \sum_x A_x f(\omega_x) \right]} \right] \quad [1]$$

where  $N_0$  is the initial number of females in a cohort (assumed to be 50% of the larvae added),  $A_x$  is the number of females eclosing on day  $x$ ,  $\omega_x$  is a measure of mean female size on day  $x$ ,  $f(\omega_x)$  is a function relating fecundity to female size, and  $D$  is the time required (in days) for a newly eclosed female to mate, obtain a blood meal, and oviposit.  $D$  is assumed to be 12 and 14 d for *A. aegypti* and *A. albopictus*, respectively (Grill and Juliano 1996). The size-fecundity relationships used in the calculation of  $\lambda'$  were as follows:

*A. aegypti* (Briegel 1990):

$$f(\omega_x) = 2.50 \omega_x - 8.616 \quad [2]$$

$$r^2 = 0.875, N = 206, P < 0.001$$

where  $\omega_x$  is the cube of wing length in millimeters on day  $x$ .

*A. albopictus* (Lounibos et al. 2002):

$$f(\omega_x) = 78.02 \omega_x - 121.240 \quad [3]$$

$$r^2 = 0.713, N = 91, P < 0.001$$

where  $\omega_x$  is wing length in millimeters on day  $x$ .

Equations 2 and 3 are assumed to yield approximate individual reproductive capacities. Juliano (1998) showed that conclusions for analyses of  $\lambda'$  for North American populations of these species were not sensitive to the fecundity-size relationship used.

For analyses of  $\lambda'$  for *A. albopictus*, we used a least squares two-way analysis of variance (ANOVA) (PROC GLM, SAS Institute 1989) with litter (0.25 and 0.50 g) and treatment (seven different density-species combinations) as factors. For analyses of  $\lambda'$  for *A. aegypti*, no transformation yielded data that met the assumptions of normality and homogeneous variance. Therefore, randomization ANOVA (Manly 1991a,b) was used for the analyses of  $\lambda'$  for *A. aegypti*. Because conclusions of least squares ANOVA and randomization ANOVA were similar, we tested for pairwise differences for all significant litter, treatment, or litter-treatment effects by using the parametric Tukey's test (experimentwise  $\alpha = 0.05$ ). For both species, we determined 95% confidence intervals for means. In the randomization ANOVA these intervals were determined with the percentile bootstrap method (Dixon 1993). We examined these intervals for inclusion of  $\lambda' = 0$  (cohort dies out in one generation) and  $\lambda' = 1.0$  (cohort is stable, with no net growth or decline).

To determine which correlates of population growth were most affected by competition, we analyzed survivorship, and median size of adults and developmental time by two-way ANOVA, with litter, treatment, and interaction as effects. Survivorship was arcsine square root transformed to meet assumptions of homogeneous variance and normality. For median

Table 1. ANOVA results for survivorship and estimated finite rate of increase ( $\lambda'$ ) for *A. albopictus* and *A. aegypti* cohorts (randomization ANOVA for  $\lambda'$  for *A. aegypti*, least squares ANOVA for remaining variables)

Source	Finite rate of increase						Survivorship					
	<i>A. albopictus</i>			<i>A. aegypti</i>			<i>A. albopictus</i>			<i>A. aegypti</i>		
	df	F	P	df	F	P	df	F	P	df	F	P
Litter	1	19.07	0.0001	1	4.96	0.0395	1	28.66	0.0001	1	16.02	0.0003
Treatment	6	32.20	0.0001	6	4.73	0.0019	6	7.42	0.0001	6	46.53	0.0001
Litter $\times$ Treatment	6	1.72	0.1403	6	1.30	0.2785	6	0.67	0.6772	6	1.93	0.0992
Error	40			42			40			41		

For randomization ANOVA,  $F$  is the standard  $F$  statistic calculated from the real data. The associated  $P$  value indicates the proportion of randomized data sets that yielded  $F$  values as great or greater than the real data. See Manly (1991a,b) for details. Effects significant at  $P \leq 0.05$  are in bold.

wing length, untransformed data came closest to meeting assumptions of normality and homogeneous variance. Because litter-treatment interactions were often nonsignificant, most treatment effects were further analyzed using pairwise comparisons among treatments of least square means (PROC GLM, SAS Institute 1989) across litter level with a sequential Bonferroni method (experimentwise  $\alpha = 0.05$ ).

### Results

**Estimated Finite Rate of Increase ( $\lambda'$ ).** For *A. albopictus*, all mean  $\lambda'$  values were  $>1$ , and 95% confidence intervals do not include 1, implying that *A. albopictus* cohorts would be increasing under all conditions used in this experiment. For *A. aegypti*, using 0.25 g of litter, means for  $\lambda'$  of all but the lowest density treatment (20AEG) were  $<1$ , and the bootstrap 95% confidence intervals of all but the lowest density treatment (20AEG) and 30AEG + 30ALB, did not include 1. With 0.50 g of litter, means of all but two high-density treatments (60AEG and 20AEG+40ALB) were larger than one, and only the bootstrap 95% confidence interval of 20AEG + 40ALB did not include 1. These results imply that *A. aegypti* cohorts would often be decreasing under these experimental conditions, especially when the litter availability is low, but also when litter availability is high and *A. albopictus* are abundant.

For both *A. albopictus* and *A. aegypti* the pattern of results from ANOVA (randomization ANOVA for *A. aegypti*) was the same; both litter and treatment significantly affected  $\lambda'$ , but litter-treatment interaction was not significant (Table 1). For both species,  $\lambda'$  was significantly greater with 0.50 g of litter than with 0.25 g of litter (data not shown). For *A. albopictus*, pairwise comparison among treatments (pooling across litter levels) indicated that  $\lambda'$  was significantly greater for the treatment with 20 initial *A. albopictus* (20ALB) than other density treatments (Fig. 1). Pairwise comparisons (Fig. 1) indicate that for *A. aegypti*,  $\lambda'$  was significantly less for 20AEG + 40ALB (treatments with 20 *A. aegypti* and 40 *A. albopictus* initially) than for any of the other density treatments, which did not differ significantly (Fig. 1).

**Survivorship.** For both *A. albopictus* and *A. aegypti*, survivorship was significantly affected by litter and treatment but not by litter-treatment interactions

(Table 1). For both species, survivorship tended to be lower with 0.25 g than 0.50 g of litter (Fig. 2). For *A. albopictus*, survivorship decreased with increasing total density (summing initial density of both species) with the exception of 40AEG + 20 ALB, which yielded a high survivorship indistinguishable with the lowest density treatment (20ALB). For *A. aegypti*, the low-density treatment (20AEG) yielded significantly greater survivorship than all other treatment densities, which were indistinguishable (Fig. 2). For this species, the high-density treatment (20AEG + 40ALB) yielded the lowest survivorship, indistinguishable from the two other high-density treatments (40AEG + 20ALB and 30AEG + 30ALB).

**Size of Female Adults.** For female *A. albopictus*, treatment significantly affected the median wing length (Table 2) and the pairwise comparison of treatments across litter levels showed that median wing length of the lowest density treatment was significantly  $>20AEG + 40ALB$  and  $40AEG + 20ALB$  (Fig. 3). There were no significant differences among mean median wing lengths for female *A. aegypti* (Fig. 3).

**Developmental Time.** For both species, treatment significantly affected the median time to emergence of adults. In addition, the development time for female *A. albopictus* was significantly affected by litter (Table 2; Fig. 4). The median time to adulthood for females of both species showed a similar trend: median times for high-density treatments were greater than those of the lowest density treatment.

### Discussion

**Resource Competition among Larvae: Florida versus Brazil.** In this field experiment, *A. albopictus* was clearly the superior competitor, maintaining positive population growth at higher combined densities and lower per capita resource availability than *A. aegypti*. These results are strikingly similar to those reported for a similar resource competition experiment between the same species, done in tires in Florida (Juliano 1998). Although it may seem obvious that similar field competition experiments between the same species should yield similar results, there were a number of major differences between the current experiment and that done by Juliano (1998) that could have produced differences. One important difference was that different populations of the two mosquito

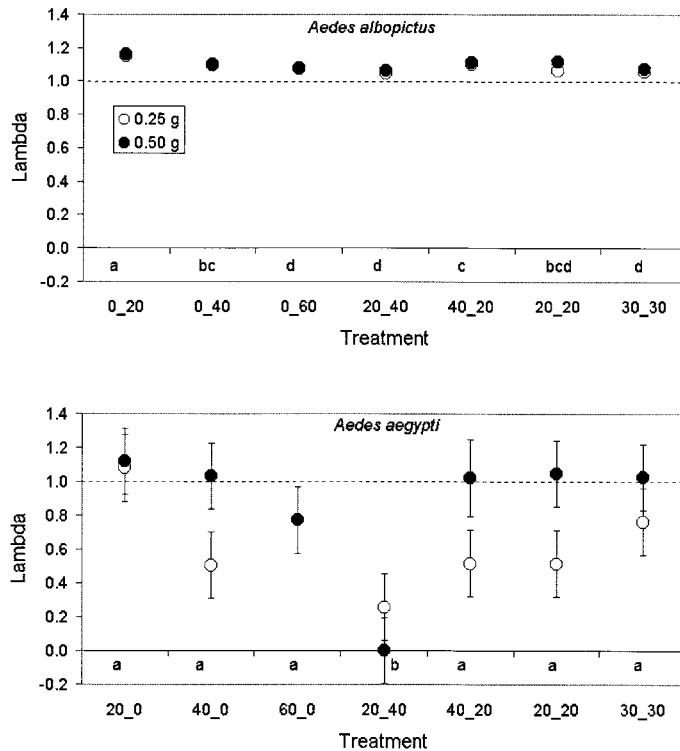


Fig. 1. Least squares means ( $\pm$ SE) of estimated finite rate of increase ( $\lambda'$ ) for each litter-treatment combination. The different treatments are indicated with a two number code, in which the first number indicates the initial density of *A. aegypti* and the second number indicates the initial density of *A. albopictus*. For all but two litter-treatment combinations for both *A. aegypti* and *A. albopictus*,  $N = 4$ . For litter-treatment combinations 0.5 g: 40\_20 and 0.5 g: 0\_20,  $N = 3$ . For *A. albopictus*, SE bars are obscured by the points. Treatment means across litter levels sharing the same letter are not significantly different at Bonferroni experimentwise  $\alpha = 0.05$ .

species were used in the two experiments. Both *Aedes* species used in our experiment were first generation progeny ( $F_1$ ) of individuals caught in Rio de Janeiro state, Brazil, whereas Juliano (1998) used  $F_1$  progeny of mosquitoes from south Florida. Although differences in vector competence (Severson et al. 2001) and susceptibility to insecticides (Hemingway and Ranson 2000) between mosquito populations have frequently been reported, interpopulation differences in life history characteristics that may be relevant to competition or predation or that may influence invasion ability are not often described. Mogi et al. (1996) showed intra- and interspecific variation in resistance to desiccation of adult *Aedes* mosquitoes. Livdahl (1984) found differences in the composite index of performance between geographic strains of *Ochlerotatus triseriatus* (Say) within the United States that are under different predation pressure from *Toxorhynchites rutilus* (Coquillett). He suggested that growth rate and competitive ability might be reduced as a result of the evolution of effective predator avoidance mechanisms. Brazilian *A. albopictus* seem to be of tropical origin (Hawley 1988, Birungi and Munstermann 2002), and it seems likely that the ancestors of Brazilian *A. albopictus* encountered the cosmopolitan *A. aegypti* over decades, if not centuries, and may have

adapted to competition with the latter. In contrast, North American *A. albopictus* likely originated from temperate Japan and probably have had no recent encounters with *A. aegypti*.

Several features of our experiment differed from Juliano's (1998), including container type and volume (400-ml plastic containers versus mesh cages in tires), resource quality and quantity (0.25–0.5 g of avocado leaves versus 0–1 g of oak leaves and tire water), and abiotic conditions (different ambient temperature and rainfall). Livdahl and Willey (1991) showed that container medium affects the outcome of competition between *A. albopictus* and *O. triseriatus*. Juliano et al. (2002) found differences between the frequencies of *A. albopictus* and *A. aegypti* in tires and cemetery vases, but they were unable to identify the underlying cause. Our results suggest that the use of plastic containers instead of tires, both commonly used artificial larval habitats, did not affect the outcome of the competition experiment.

Effects of resource type on production and competition among *Aedes* are well documented (Barrera 1996, Daugherty et al. 2000). Resource type affects other invertebrate dynamics in treehole systems (Fish and Carpenter 1982, Walker and Merritt 1988, Yanoviak 1999). Differences between the decompo-

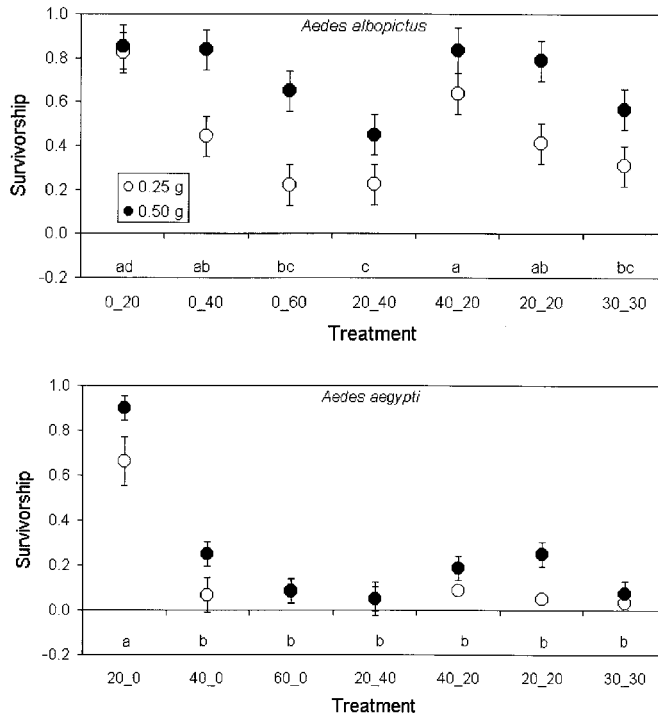


Fig. 2. Least squares means ( $\pm$ SE) of survivorship with for each treatment–food combination. Treatment codes and number of replications as in Fig. 1. Treatment–food combinations of survivorship sharing the same letter are not significantly different at Bonferroni experimentwise  $\alpha = 0.05$ .

sition rate and nutritional value of resources are indicated as important factors for mosquito productivity (Dieng et al. 2002). Barrera (1996) showed that using leaves as a substrate, instead of protein-rich resources (e.g., liver powder) shifted the competitive advantage from *A. aegypti* to *A. albopictus*. The addition of flowers and invertebrate carcasses has been shown to increase mosquito production more than the addition of leaves, and can reduce, but not reverse, competitive advantages (Lounibos et al. 1993, Daugherty et al. 2000). Our results in the competition experiment using avocado leaves were similar with those using tire water and oak leaves (Juliano 1998). These results suggest that *A. albopictus* is likely to be the superior competitor when exploiting microorganisms growing on senescent leaves; however, more investigations of the resources found in the field are needed.

The average ambient temperature during the summer of the Juliano’s experiment (reported in Lounibos

et al. 2002) was 24.8°C, which is lower than the temperature in Rio de Janeiro during our experiment (27.4°C). Russell (1986) demonstrated that a change in temperature could reverse the outcome of interspecific competition between *A. aegypti* and *A. notoscriptus*. In tires maintained at 24 and 30°C in the laboratory, Lounibos et al. (2002) found higher finite rates of increase for both *A. albopictus* and *A. aegypti* populations at the higher temperature, but no obvious difference in competitive abilities due to temperature. When comparing our results with Juliano (1998), we deduce that temperature did not affect the outcome of competition. Differences in rainfall between the two locales might also have had an effect on the amount of flushing of the containers.

The parameters used to assess competitive advantage are a possible source of variation in results of competition experiments. To avoid this problem, we performed similar analyses to those used by Juliano

Table 2. Least squares ANOVA results for median wing length and time to adulthood for female *A. albopictus* and *A. aegypti*

Source	Wing length						Developmental time					
	<i>A. albopictus</i>			<i>A. aegypti</i>			<i>A. albopictus</i>			<i>A. aegypti</i>		
	df	F	P	df	F	P	df	F	P	df	F	P
Litter	1	0.53	0.3392	1	0.59	0.4491	1	16.33	<b>0.0002</b>	1	0.82	0.3723
Treatment	6	2.96	<b>0.0179</b>	6	1.31	0.2954	6	2.88	<b>0.0200</b>	6	3.74	<b>0.0082</b>
Litter $\times$ Treatment	6	0.89	0.5042	5	3.36	0.0736	6	1.25	0.2999	6	0.36	0.8996
Error	38			34			40			26		

Effects significant at  $P = 0.05$  are in bold.

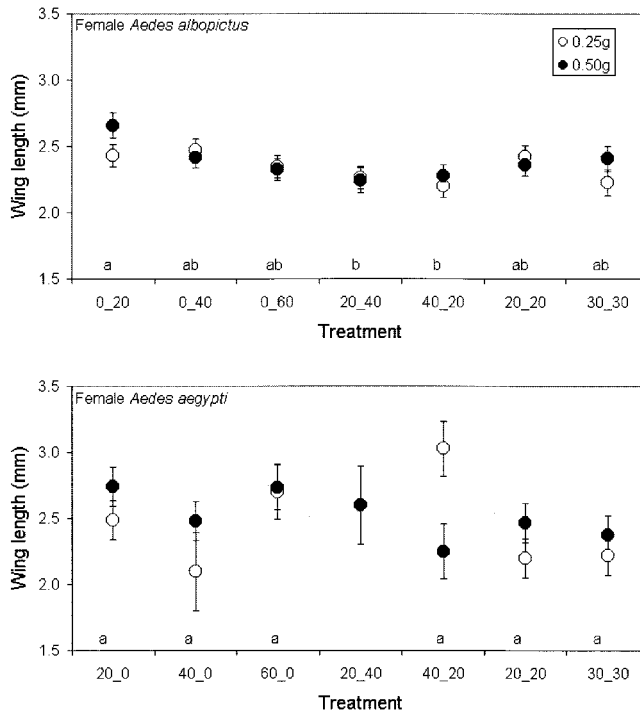


Fig. 3. Least squares means ( $\pm$ SE) of median wing lengths for each litter-treatment combination. Treatment codes and number of replications as in Fig. 1. Treatment means across litter levels sharing the same letter are not significantly different at Bonferroni experimentwise  $\alpha = 0.05$ . No females were collected from treatment 20AEG + 40ALB with 0.25 g of leaf litter.

(1998). In both cases, the conclusion that *A. albopictus* is the superior competitor depended primarily on the index  $\lambda'$  which, in turn, was dependent upon the estimation of female fecundity, time to adulthood, and survivorship. The most important factor determining  $\lambda'$  in the two experiments was survivorship to adulthood. Survivorship in our experiment showed remarkable similarity to that reported by Juliano (1998). *A. albopictus* survived better than *A. aegypti* under all treatments and litter levels. In our experiment, survivorship was significantly affected by litter and treatment but not by litter-treatment interactions (Table 1). For both species, survivorship tended to be much lower with less litter (Fig. 1). Juliano (1998) also reported no significant interactions, supporting the general conclusion that the litter effect was not dependent on the mosquito combination-density treatment.

Despite the numerous possible factors that could have contributed to differences, the conclusion that *A. albopictus* is superior in larval competition is consistent between our field experiment and those of Juliano (1998). Despite competitive superiority of *A. albopictus*, these two *Aedes* species coexist in much of Brazil (Galardo 2002), and in some parts of south Florida (Hawley 1988, O'Meara et al. 1995). The mechanisms of their coexistence must be investigated to understand and to predict the outcomes of invasions by *A. albopictus* and *A. aegypti*.

**Coexistence with a Superior Competitor.** Life history trade-offs play a major role in species coexistence.

Advantages that one species may have over others may be offset by compensating disadvantages (Tilman 1990, Vincent et al. 1996). Juliano et al. (2002) proposed that local coexistence of the two species is possible because warm, seasonally dry climates favor *A. aegypti* and alleviate effects of larval competition from *A. albopictus* via differential mortality of *A. albopictus* eggs. That research was partially based on data from peninsular Florida but may be applicable to other tropical and subtropical regions. In regions of sympatry, *A. aegypti* and *A. albopictus* coexist in some habitats but not in others (Juliano et al. 2002). *A. aegypti* is often considered to more urban, whereas *A. albopictus* is more rural, but these species frequently co-occur in suburban areas (Hawley 1988, Braks et al. 2003).

Juliano et al. (2002) and Lounibos et al. (2002) suggested that abiotic factors may also contribute to the described habitat segregation, because urban areas may be warmer than surrounding areas (McIntyre 2000). High temperatures are not likely to be the only community-structuring factor, because habitat segregation of *A. albopictus* and *A. aegypti* is found all over the world, covering a wide temperature range. Urbanization is generally associated with temporal or spatial changes in the type and amount of vegetation, human population density, number of buildings, and pollution (McIntyre 2000). For mosquitoes, this translates into a change in the abundance and type of resting and oviposition sites and sugar sources, abundance of human or other hosts for blood feed-

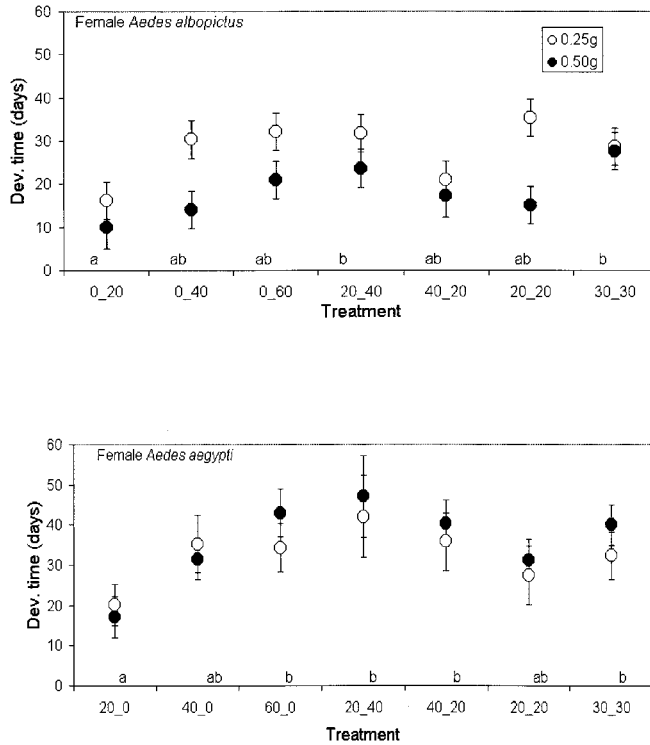


Fig. 4. Least squares means ( $\pm$ SE) of median time to adulthood for each treatment–litter combination. Treatment codes and number of replications as in Fig. 1. Treatment means across litter levels sharing the same letter are not significantly different at Bonferroni experimentwise  $\alpha = 0.05$ .

ing, type of larval resources, amount of shadow, relative humidity, and temperature. In contrast to *A. albopictus*, *A. aegypti* has been suggested to be more adapted to urban life through a high desiccation resistance of adults (Mogi et al. 1996) and eggs (Sota and Mogi 1992, Juliano et al. 2002), dependence on humans as their blood source, independence of female reproductive success from sugar sources, and other adaptations to life indoors (Harrington et al. 2001). *A. albopictus* is considered a more opportunistic feeder (Hawley 1988) that prefers to rest outdoors in vegetation. More detailed description and quantification of habitats will be needed to determine the mechanisms accounting for local distributions of these two species.

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