

Interspecific Differences in Feeding Behavior and Survival Under Food-Limited Conditions for Larval *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae)

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ABSTRACT *Aedes albopictus* has replaced *Aedes aegypti* in much of the latter species' historic range within the United States. The leading hypothesis for this displacement is exclusion via resource competition; however, the proximate mechanism producing a competitive advantage for *A. albopictus* over *A. aegypti* has not been identified. We performed laboratory experiments to test the hypotheses that these species differ in feeding behavior, and that these differences result in differences in survival when resources are scarce. Differences in feeding behavior were assessed in three environments with food (growing microorganisms) available: 1) in fluid only; 2) on leaf surfaces only; 3) or both in fluid and on leaf surfaces. We determined behavior of larvae in these environments, recording their positions (bottom, wall, leaf, top, or middle) and activities (browsing, filtering, resting, or thrashing) using instantaneous scan censuses. *A. albopictus* spent significantly more time at leaf surfaces, whereas *A. aegypti* spent more time engaging in nonfeeding activities. Both species showed a significant shift in foraging activity toward leaves when leaves were available. In a second experiment, we recorded survivorship for individuals raised in two treatment combinations: whole or half 17-mm disks of live oak leaves, with or without direct access to the leaf surface (controlled using nylon mesh, which allowed movement of microscopic organisms, but prevented mosquito larva movement between container sides). After 31 d, survivorship of *A. albopictus* was significantly greater than that of *A. aegypti* regardless of treatments. Moreover, *A. albopictus* showed significantly greater survivorship compared with *A. aegypti* when deprived of access to leaf surfaces and in whole leaf disk treatments, suggesting superior resource-harvesting ability for *A. albopictus*. Our experiments suggest that differences in foraging behavior contribute to the competitive advantage of *A. albopictus* over *A. aegypti* that has been observed in North America.

KEY WORDS resources, competition, invasive, mosquito, foraging

THE INVASIVE ASIAN TIGER mosquito, *Aedes albopictus* (Skuse), was introduced into North America in the mid-1980s, and that introduction has been followed by a significant range expansion into most of the southeastern and south central United States (Hawley et al. 1987, Moore 1999). *A. albopictus* is important for both its capacity as a vector of disease (Hawley 1988, Mitchell 1995, Turell et al. 2001) and its negative ecological effects on resident mosquito species (Juliano 1998, Lounibos et al. 2001, 2002). In southeastern North America, *A. albopictus* co-occurs in containers with the Yellow Fever mosquito, *Aedes aegypti* (L.). After the arrival of *A. albopictus*, there has been a precipitous decline of *A. aegypti* populations in many locations (Hobbs et al. 1991, O'Meara et al. 1995). Although early work suggested that *A. aegypti* was a superior resource competitor (e.g., Black et al. 1989, Ho et al. 1989), more recent work has shown that *A. albopictus* is superior to *A. aegypti* under laboratory

(Barrera 1996, Daugherty et al. 2000) and field conditions (Juliano 1998, Braks et al. 2004), especially when larvae are reared using leaves as the source of nutrients in the aquatic habitat.

Container-dwelling *Aedes*, including *A. albopictus* and *A. aegypti*, feed on heterotrophic microorganisms (i.e., bacteria, fungi, protozoans) that grow on container and detritus surfaces, or are suspended in fluid (Clements 1992, Merritt et al. 1992). Larvae use their mouth parts in two distinct ways to gather microorganisms: by browsing on hard surfaces and by filtering fluid (Merritt et al. 1992). Different environments may make one feeding mode more beneficial, although, to date, there has been little work on how larvae alter feeding patterns with changing resource environments. Nilsson (1986) found that larvae of *A. communis* changed their feeding mode in environments with and without leaf surfaces. For other mosquitoes, hunger alters the allocation of time to browsing versus filtering (Juliano et al. 1993). In addition to how larvae feed, the type and quantity of detritus can influence

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microorganism populations and communities (Walker et al. 1991, Cochran-Stafira and von Ende 1998, Kaufman et al. 2001), and therefore can influence mosquito performance (Fish and Carpenter 1982, Lounibos et al. 1993, Walker et al. 1997) and the outcome of competition (Barrera 1996, Daugherty et al. 2000). Barrera (1996) determined that *A. albopictus* was superior in competition with *A. aegypti* when leaves were the resource, but competitive asymmetry was reversed when the resource was animal protein (liver power). Daugherty et al. (2000) showed that the competitive disadvantage of *A. aegypti* could be reduced or eliminated by inputs of increasing amounts of invertebrate carcasses in addition to senescent leaves. Thus, the way in which larvae feed and the type of resource that supports microorganism growth may affect the performance and interactions between these *Aedes*.

The interaction between *A. albopictus* and *A. aegypti* has been studied from multiple perspectives, including the influence of egg mortality (Juliano et al. 2002), hatching delays (Edgerly et al. 1993), larval survival (Lounibos et al. 2002), resource competition among larvae in controlled experiments (Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004), and the potential influence of apparent competition through shared enemies (Juliano 1998). Although *A. albopictus* is often shown to be the superior resource competitor, the proximate mechanism behind this advantage for *A. albopictus* larvae has not been documented. For example, Barrera (1996) suggests that larvae of *A. albopictus* resist starvation longer when grown on senescent leaf litter because of higher stored energy, but does not document the mechanism producing differences in energy storage. This lack of understanding about the mechanism for competitive superiority may hamper our ability to understand fully the dynamics of local extinction of *A. aegypti*, and to our overall understanding of competition as an ecological force structuring container communities.

We tested the hypotheses that *A. albopictus* and *A. aegypti* display differences in feeding behaviors in similar food environments, and that those differences in feeding behaviors are associated with differential development and survival under food-limited conditions. Because most data for environments dominated by leaf detritus indicate that *A. albopictus* is a superior resource competitor compared with *A. aegypti* (Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004), we predicted that *A. albopictus* would show patterns of feeding behavior that render it a better exploiter of leaf substrates compared with *A. aegypti*. We tested these hypotheses in two laboratory experiments. The first experiment quantified feeding behaviors in environments with different availabilities of leaves as a substrate for browsing. In the second experiment, we determined survival and development of individuals of both species in environments in which ability to exploit leaves should differentially affect growth and development.

Materials and Methods

Feeding Behavior. Larvae of both *A. albopictus* and *A. aegypti* were collected from southern Florida, raised to adults on bovine liver powder (ICN Biochemicals, Cleveland, OH), and then released into 0.6-m² flight cages. Adult females were blood fed on anesthetized laboratory mice or guinea pigs to obtain eggs used to produce larvae for this study. For hatching, eggs were placed in 20-ml glass tubes in a solution of 0.33 g of nutrient broth per 750 ml of deionized (DI) water. After 24 h, hatched larvae were rinsed to remove any nutrient solution and transferred to new individual 20-ml vials with 10 ml of DI water. Larvae were fed every other day standard volumes of a liver powder suspension (LPS) prepared with 0.30 g of liver powder per 1000 ml of DI water. LPS was held on a stirring plate during pipetting to ensure homogeneous delivery of food to larvae (Juliano and Gravel 2002). We added 0.50 ml of LPS on day 1, and 1.00 ml of LPS every other day thereafter, using a digital pipettor. Larvae were reared individually for 6 d, by which time they had reached the late third or early fourth instar. Twenty-four hours before behavioral measurements, all larvae were transferred into individual 50-ml beakers filled with 50 ml of DI water to standardize hunger.

Senescent live oak leaves (*Quercus virginiana*) were collected from Fort Myers City Cemetery, Florida, and stored at room temperature. Leaf strips (1 cm × 5 cm) were cut and placed individually into 50-ml beakers of DI water and maintained at 26°C in darkness, to prevent algal growth. Leaves were allowed to soak for 6 d, at which time they were used to construct three food environments: 1) microorganisms on leaf surfaces only; 2) microorganisms in fluid only; 3) microorganisms both in fluid and on leaf surfaces. Microorganisms on leaf only (hereafter "leaf only") were created by transferring the leaf to a new 50-ml beaker with fresh DI water. Microorganisms in fluid only (hereafter "fluid only") were created by transferring the 50 ml of the fluid in which the leaf strip had soaked into a new 50-ml beaker. This step eliminated any microorganisms that may have grown on the sides of the container during the 6-d preparation period. We also added a clean strip of plastic of the same size as the leaf strip to these containers. Microorganisms in fluid and on leaf surface (hereafter "mixed") were created by transferring 50 ml of the fluid in which the leaf strip had soaked and a leaf from a different container to a new 50-ml beaker. Within 5 min of creating the food environments, each replicate received an individually reared larva of one of the two species. This short interval before beginning measurements should minimize microorganism colonization on non-target locations (i.e., in the fluid in leaf only). We used 12 replicates of each species in each food environment for a total of 72 observations.

Behavior Measurement and Analysis. We recorded behaviors of larvae in each treatment using a Panasonic Digital Video Camera onto a personal computer using Digital Video Creator (Dazzle Multimedia, Fre-

mont, CA) for 30 min. Each larva was given a 5-min acclimation period in the treatment before initiating the recording of behavior. Recordings were conducted in an isolated room with no observers present. A single 30-min video clip had images of only six treatment cups at a time because of resolution constraints. However, each video clip represented a single replicate of all treatment combinations (two species \times three food environments).

From each video clip, activity and position of each larva were recorded every minute for 30 min in instantaneous scan censuses (Martin and Bateson 1986, Juliano and Gravel 2002, Kesavaraju and Juliano 2004). Activities were classified into four categories: 1) browsing: larva moving along a surface (e.g., leaf) propelled by feeding movements of the mouth parts; 2) resting: larva completely still and not feeding; 3) filtering: larva drifting through the water column, propelled by feeding movements of mouth parts; and 4) thrashing: larva propelling itself through the water by energetic lateral flexion of the body (Juliano and Reminger 1992, Grill and Juliano 1996, Juliano and Gravel 2002, Kesavaraju and Juliano 2004). Positions were classified into five categories: 1) surface: larva's spiracular siphon in contact with the surface; 2) bottom: larva within 1 mm of the bottom of the container; 3) wall: larva within 1 mm of the sides of the container; 4) middle: larva not in contact with the surface, and >1 mm from the container's surfaces; and 5) leaf: larva in contact with the leaf strip or the plastic surrogate leaf strip. We predicted that feeding mode (Merritt et al. 1992) would vary with food environment, so that larvae would show high frequencies of filtering in the fluid only environment, browsing in the leaf only environment, and a combination of these activities in the mixed environment. We also predicted that positions would be associated with activities (e.g., at the leaf while browsing in leaf only environment; in the middle or at the surface while filtering in fluid only environment).

To meet assumptions of normality and homogeneous variances, we used an arcsine-square-root transformation on proportions of observations in each activity and position. To reduce the number of total variables and to obtain uncorrelated descriptors of behavior, we used principal component analysis on these transformed proportions (PROC FACTOR; SAS Institute 1990, Juliano and Gravel 2002). Principal components (PCs) with Eigen values >1.0 were retained for further analysis, whereas those with values <1.0 were ignored (Hatcher and Stepanski 1994). We tested main effects and interaction of species and food environments using multivariate analysis of variance (MANOVA-PROC GLM; SAS Institute 1990) with retained PCs as dependent variables. Significant MANOVA effects were interpreted using standardized canonical coefficients (Scheiner 2001), which quantify the magnitude of the contributions of the individual PCs in producing significant multivariate differences. When necessary, significant effects were further analyzed using multivariate pairwise contrasts

(Scheiner 2001) with Bonferroni adjustment to control for experimental-wise error rate.

Survival Experiment. Mosquito larvae were hatched as described for behavior measurements. After hatching, individual larvae were transferred to 50 ml of DI water in a 100-ml plastic beaker that was divided into two equal spaces by a vertical piece of 100- μ m mesh glued through the center of the beaker. Eight days before the introduction of a larva, we added a piece of live oak leaf in one of two sizes: a 17-mm disk (mean dry mass \pm SE = 0.0181 ± 0.0003 g; hereafter "whole"); or one-half of a 17-mm disk (mean dry mass \pm SE = 0.0081 ± 0.0001 g; hereafter "half"). In addition, two leaf access treatments were created by placing the leaf disk on the same side (hereafter "access"), or on the opposite side (hereafter "no access") of the mesh divider as the mosquito. The access and no access treatments paralleled the mixed (i.e., both fluid and leaf surface available for feeding) and fluid only (i.e., food available in fluid only) food environments from the behavioral experiment. Containers were maintained in a controlled environment room at 25°C on a 14:10 day:night cycle. We replicated each combination of leaf access, leaf size, and species 15 times for a total of 120 experimental units.

Data Collection and Analysis. For each larva, we recorded the day of death. After 31 d, we terminated the experiment and determined the number of individuals still alive. Longevity for the two species in the different treatments was analyzed by nonparametric survival analysis (PROC LIFETEST; SAS Institute 1990, Allison 1995). Individuals alive at the end of the experiment yielded censored observations, which are accounted for by PROC LIFETEST (see Allison 1995 for details). Because our focus was on species differences among treatments, we restricted our analyses to the full model containing all treatments (species, leaf access, and leaf size), and two reduced models containing species and either leaf access or leaf size. Pairwise differences for significant two-way interactions were evaluated by comparing species within a treatment, and by comparing levels of treatment for an individual species. To control for comparison-wise error rate, we used Bonferroni corrections.

Results

Feeding Behavior. Significant correlations were detected among many of the behaviors and positions (Table 1). Specifically, there were strong positive correlations among thrashing and time in the middle and at the bottom, between browsing and time at the leaf, between resting and time at the surface, and between filtering and time in the middle (Table 1). There also were strong negative correlations of time at the leaf with all other categories except for browsing (Table 1).

Principal component analysis reduced the four activities and five positions to four uncorrelated PCs, which summarized 89.8% of the variation in the data (Table 2). PC1 quantifies time resting versus browsing at the leaf. Large positive values on PC1 indicate

Table 1. Correlations of activities and positions for three food environments

	Thrashing	Browsing	Filtering	Surface	Bottom	Leaf	Wall	Middle
Resting	-1	-80	+11	+87	+9	-59	+8	+7
Thrashing		-46	+22	-3	+51	-40	+13	+58
Browsing			-45	-78	-30	+73	-11	-45
Filtering				+28	+20	-40	+16	+69
Surface					-11	-54	+9	+11
Bottom						-56	+18	+15
Leaf							-63	-44
Wall								+28

Boldfaced numbers represent significant ($P < 0.05$) correlations.

frequent resting, whereas large negative PC scores are associated with browsing on leaf surfaces (Table 2). PC2 summarizes three behaviors: thrashing, filtering, and time in the middle of the container (Table 2). PC3 quantifies the allocation of time between thrashing in the middle and being at the leaf (Table 2). Finally, PC4 summarizes being at the leaf (large negative values) versus at the wall (large positive values) (Table 2).

Main effects of species and food environment were significant, but the interaction was not (Table 3), indicating that the two species displayed similar behavioral responses to the food environments. The effect of food environment was highly associated with PC1 and PC4 (Table 3). Individuals in fluid only environments had high positive scores for both PCs that were associated with frequent resting at the surface and being at the wall (Fig. 1). In contrast, individuals in leaf only environments had high negative scores, indicating that those individuals tended to be browsing on leaf surfaces (Fig. 1). Individuals in mixed environments had PC scores that were intermediate to the other environments (Fig. 1), and thus showed combinations of behaviors.

Both PC3 and PC4 were strongly associated with the differences between species (Table 3). Scores for *A. albopictus* were negative for both PC3 and PC4, indicating that this species tended to be at leaf surfaces. In contrast, *A. aegypti* had large positive scores that were most closely associated with nonfeeding

activities (i.e., thrashing at bottom) and positions (i.e., wall) (Fig. 2).

Survival Experiment. No pupae were produced during this experiment, but all larvae reached the fourth instar. The full model (species, leaf access, and leaf size) was significant ($\chi^2 = 25.269$, $df = 3$, $P < 0.001$), indicating that survival times differed between species, leaf amounts, and access treatments. Regardless of treatments, survival time was greater for *A. albopictus* than for *A. aegypti* (Fig. 3) ($\chi^2 = 8.377$, $df = 1$, $P = 0.004$). In addition, survival times differed between whole versus half leaves ($\chi^2 = 8.937$, $df = 1$, $P = 0.030$; Fig. 4), and between access versus no access treatment levels ($\chi^2 = 17.777$, $df = 1$, $P < 0.001$; Fig. 5). We compared species survival times within different levels of the other factors (i.e., within leaf size or leaf access), and we compared survival times between treatment levels (e.g., whole versus half leaf) within each species. There were large significant interspecific differences in survival time for whole leaves ($\chi^2 = 6.991$, $df = 1$, $P = 0.008$) and for the no access treatment level ($\chi^2 = 5.990$, $df = 1$, $P = 0.014$), with *A. albopictus* surviving longer than did *A. aegypti* in both cases (Figs. 4 and 5). Survival time was statistically indistinguishable for the two species in the half leaf treatment level ($\chi^2 = 2.188$, $df = 1$, $P = 0.139$; Fig. 4) and the access treatment level ($\chi^2 = 3.459$, $df = 1$, $P = 0.063$; Fig. 5), although in both cases, survival time tended to be greater for *A. albopictus* than for

Table 2. Principal component analysis for the feeding behavior experiment

Variable	PC1	PC2	PC3	PC4
Eigen value	3.950	1.950	1.164	1.038
Proportion of variance	0.438	0.216	0.129	0.115
Cumulative proportion of variance	0.438	0.654	0.783	0.898
Resting	+97	-5	+3	+7
Thrashing	+1	+40	+80	-5
Browsing	-85	-36	-35	-1
Filtering	+18	+86	+3	+9
Surface	+95	+12	-16	+6
Bottom	+5	-3	+89	+19
Leaf	-58	-24	-46	-61
Wall	+2	+13	+6	+97
Middle	+5	+91	+23	+14
Interpretation	Resting, Surface vs. Browsing, Leaf	Thrashing, Filtering, Bottom	Thrashing, Bottom vs. Browsing, Leaf	Leaf vs. Wall

Principal components (PCs) with Eigen values > 1.0. Large (≥ 40) loading values are listed in boldface.

Table 3. Results of two-way (species, food environment) MANOVA on behavior patterns

Source	df	Error df	Pillai's trace	P value	Standardized canonical coefficients			
					PC1	PC2	PC3	PC4
Environment (E)	8	128	0.8123	<0.0001	1.055	0.474	0.471	1.385
Species (S)	4	63	0.1983	0.0068	0.164	0.145	1.020	0.853
S × E	3	128	0.1348	0.3297	1.081	0.705	0.425	1.173

The magnitude of the standardized canonical coefficients (SCC) indicates the degree of contribution by each factor to the significant MANOVA effect. SCC deemed large are indicated in boldface.

A. aegypti (Figs. 4 and 5). For within-species comparisons, survival times differed between access and no access treatments for *A. aegypti* ($\chi^2 = 3.850$, $df = 1$, $P = 0.050$) and *A. albopictus* ($\chi^2 = 3.851$, $df = 1$, $P = 0.050$) (Fig. 5). Differences between leaf sizes were not significant for either species (*A. aegypti*, $\chi^2 = 0.165$, $df = 1$, $P = 0.685$; *A. albopictus*, $\chi^2 = 0.001$, $df = 1$, $P = 0.972$; Fig. 4).

Discussion

Larvae of another container mosquito, *Ochlerotatus triseriatus* (formerly in the genus *Aedes*; Reinert 2000), require initial oak leaf masses of 50 mg for full development (Kaufman et al. 2001), but fail to develop on 25 mg (Carpenter 1982). Our leaf disks had a mean mass of 1.80 mg, suggesting that food limitation was probably a major cause of the failure of larvae in this experiment to reach adulthood. As such, larvae were probably maximally exploiting the food available, and thus we believe the effectiveness with which larvae

exploited food resources was a major contributor to interspecific differences in survival. All else being equal, had all larvae died at a similar time, we could infer that observed differences in feeding behavior were irrelevant to survival.

Larvae in this experiment displayed consistent feeding behaviors that appeared to be correlated with the food environments. Individuals allocated more time to browsing on the leaf in containers with natural leaves, and spent considerably less time engaging in these behaviors when only an artificial leaf (which added no food resources) was present. This finding is consistent with the work of Nilsson (1986), who found that larvae of *A. communis* switched from filtering to browsing when presented with leaf surfaces instead of tap water. Mosquito larvae feeding behavior is most likely regulated by phagostimulants (e.g., nucleic acids, nucleotides) present in all organisms, and these may stimulate greater foraging effort in areas in which more food resources are available (Merritt et al. 1992, Walker and Merritt 1991). Thus, our data suggest that

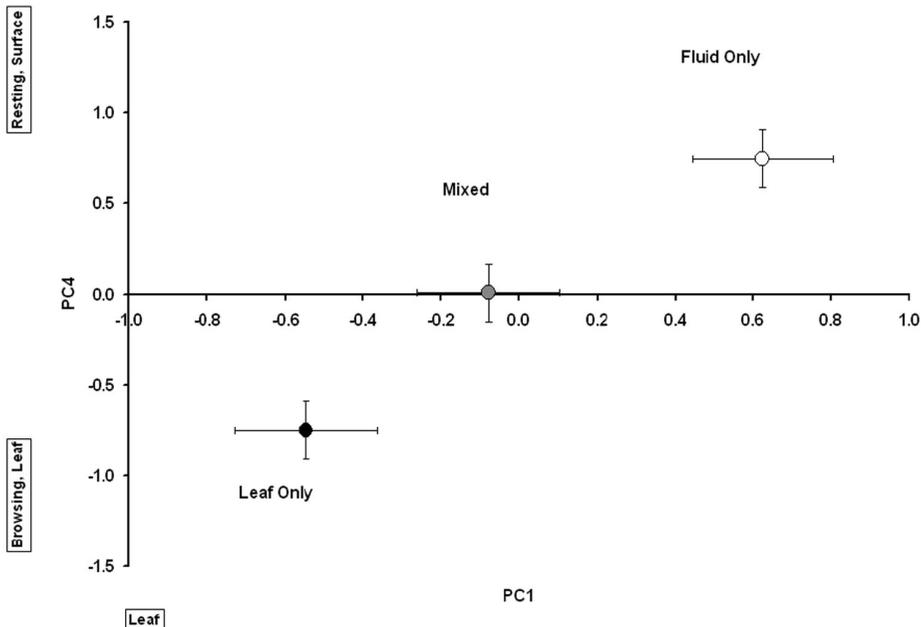


Fig. 1. Bivariate means (\pm SE) for PC1 and PC4, which made the greatest contributions to multivariate differences among three food environments (Table 3). Activities and positions most closely associated with large positive or large negative PC scores are indicated parallel to each axis. All multivariate differences among all pairs of food environments were significant (Bonferroni adjustment, experiment-wise $\alpha = 0.05$).

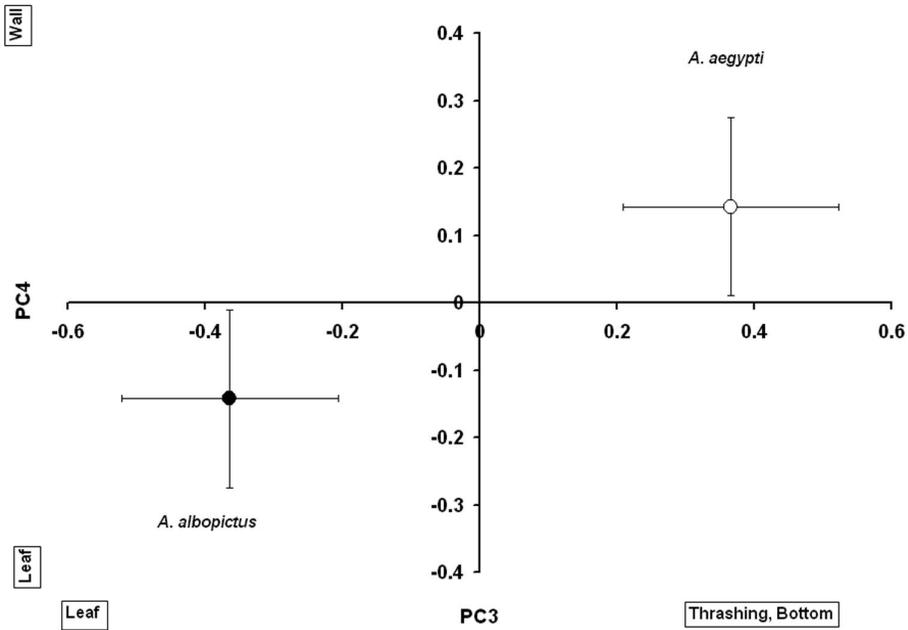


Fig. 2. Bivariate means (\pm SE) for PC3 and PC4, which made the greatest contributions to multivariate differences between species. Activities and positions most closely associated with large positive or large negative PC scores are indicated parallel to each axis.

larvae detect the presence of microorganisms and alter their feeding accordingly.

Regardless of the food environment, *A. albopictus* spent significantly more time associated with leaf surfaces than did *A. aegypti*. This is consistent with our prediction that behavior of these species would differ, and would contribute to the competitive advantage of

A. albopictus in environments in which leaves are the predominant resource (Barrera 1996, Juliano 1998, Daugherty et al. 2000). Access to resources on leaf surfaces is an important determinant of mosquito growth and development (Léonard and Juliano 1995, Kaufman et al. 2001). Specifically, Léonard and Juliano (1995) demonstrated that *O. triseriatus* larvae had in-

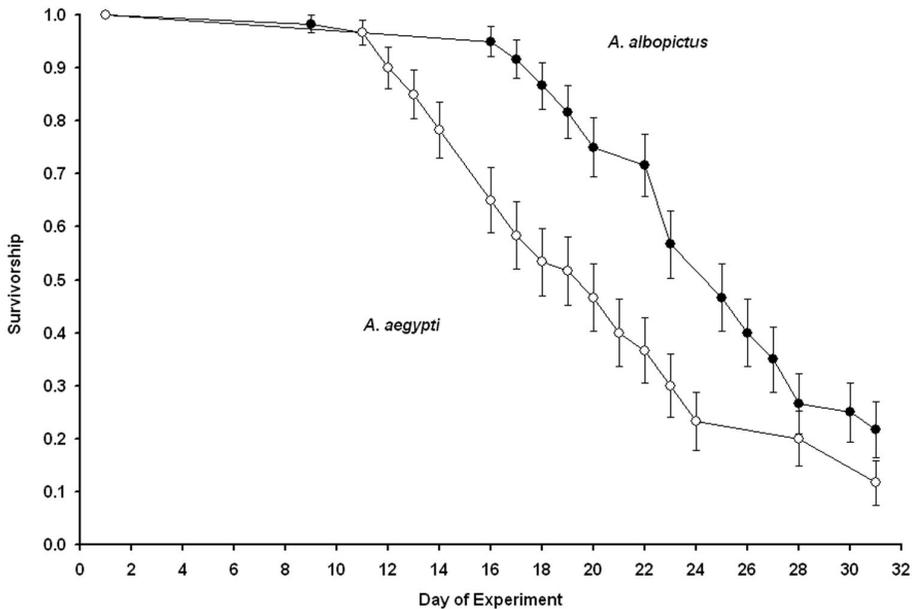


Fig. 3. Survivorship curves for *A. albopictus* and *A. aegypti* larvae (proportions alive \pm 95% confidence interval).

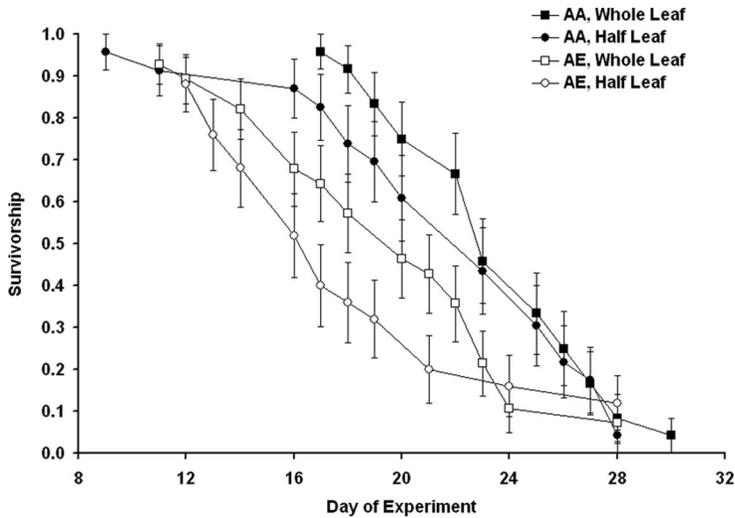


Fig. 4. Survivorship curves for *A. albopictus* (AA) and *A. aegypti* (AE) larvae in leaf size treatments (proportions \pm 95% confidence interval). Whole leaf is a single 17-mm live oak leaf disk; half leaf is one-half of a 17-mm live oak leaf disk. No mortality occurred before d 8. Within each treatment combination, early points indicating 100% survivorship are not shown.

creased population growth rates and higher survivorship when given access to leaves for browsing as compared with no access. Leaves provide direct resource to fungi and bacteria, and fungi grow at faster rates on leaves (Newell et al. 1995, Weyers and Suberkropp 1996). Furthermore, hungry larvae of *O. triseriatus* increase time spent browsing relative to filtering, suggesting that browsing of surfaces has the potential to yield greater benefits than filtering (Juliano et al. 1993). Thus, resources on surfaces appear to provide a more profitable food source to mosquito larvae, and individuals that are

better able to exploit them are likely to be favored in low resource environments.

Barrera (1996) found that *A. albopictus* larvae survived significantly longer than did *A. aegypti* after feeding for 3.5 d on live oak leaves. He suggested that *A. albopictus* was able to acquire more energy within the feeding period. Our data are consistent with the hypothesis that interspecific differences in feeding behavior are a mechanism by which this difference in resource acquisition arises. There are, however, other explanations for the differences between species per-

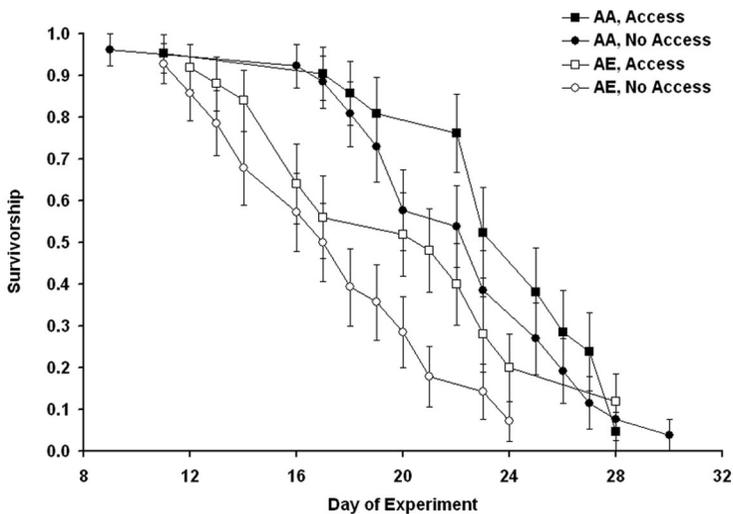


Fig. 5. Survivorship curves for *A. albopictus* (AA) and *A. aegypti* (AE) larvae in leaf access treatments (proportions \pm 95% confidence interval). Access indicates the leaf was on the same side of a mesh divider as the mosquito. No access indicates that the leaf was on the opposite side of a mesh divider as the mosquito. No mortality occurred before d 8. Within each treatment combination, early points indicating 100% survivorship are not shown.

formance in the different environments. Excreted ammonia can negatively affect mosquito larvae (Carpenter 1982, David et al. 2000), and it is possible that the two species differ in amount of ammonia produced or in their tolerance to ammonia. Tannins leached from leaves can affect the growth of *A. albopictus*, although this species appears to do better in higher tannin levels than a tree-hole specialist (Sota 1993). We measured tannin levels after 8 d in a set of nonexperimental containers ($n = 10$ each leaf size) identical with those used in the survival experiment, but without larvae, and we found no significant difference between whole (3.76 ± 0.71 mg/L tannic acid) and half (5.02 ± 0.97 mg/L tannic acid) leaf treatments ($F_{1,18} = 1.09$, $P = 0.310$). These tannin concentrations are far lower than levels known to affect *Aedes* larvae (≥ 100 mg/L; Sota 1993). The fact that tannin levels were similar, but *A. albopictus* fared better in whole leaf treatments, suggests that tannin concentrations were not an important contributor to differences in survival time.

Ours is the first study to implicate differences in feeding behavior as a source of the competitive advantage of *A. albopictus* over *A. aegypti* that has been evident in experiments with these species from North and South America (Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004). Investigations into how feeding behavior may influence competitive interactions between these species are needed to determine the importance of these behavioral mechanisms in the displacement of *A. aegypti* by *A. albopictus* in North America, and how other factors may modify the roles of behavior and competition across the wide geographic ranges of these species.

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