

Interpopulation divergence in competitive interactions of the mosquito *Aedes albopictus*

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Abstract. Geographic variation in species interactions can have major effects on distributions. Effects of such variation can be particularly evident for invasive species, in which variation in competitive ability can influence invasive success and impacts. We tested the hypothesis that coexistence or exclusion of the resident mosquito *Aedes aegypti* results from variation among local populations of the invasive *Aedes albopictus* in competitive interactions with *A. aegypti*. We also examined the role of variation in fecundity–size relationships in these competitive interactions. We compared competitive abilities of nine North American populations of *A. albopictus*, three populations from each of three site types: extinction of *A. aegypti* following *A. albopictus* invasion, coexistence following *A. albopictus* invasion, and *A. albopictus* allopatric to *A. aegypti*. Competition among larvae from each *A. albopictus* population and a single *A. aegypti* population was tested in laboratory microcosms in a response surface design. We found interpopulation differences in competitive ability of *A. albopictus*, but no strong patterns among site types. Extinction sites had steeper average fecundity–size relationships than coexistence sites and allopatric sites, but this did not translate into superior population performance. Certain individual *A. albopictus* populations had exceptionally large competitive effects on *A. aegypti* or poor competitive responses to competition from *A. aegypti*, but competitive effect and response were not correlated. These results suggest that interpopulation variation in the competitive ability of *A. albopictus* may only partly explain the geographic pattern of coexistence with or extinction of *A. aegypti*. Environmental differences among regions may affect the competitive ability of *A. albopictus* and influence its invasion success and impact.

Key words: *Aedes aegypti*; *Aedes albopictus*; competitive asymmetry; competitive hierarchies; fecundity–size relationship; interpopulation divergence; invasive species; mosquitoes; reproductive tactics.

INTRODUCTION

Determining the strength, nature, and causes of intraspecific variation remains an important question for population and community ecology (Travis 1996, Keller and Taylor 2008). Geographic heterogeneity in both abiotic conditions and biotic interactions are likely to create a mosaic of local selection that, along with genetic variation derived from founder effects and gene flow, shape the spatial distribution of traits within a species (Keller and Taylor 2008). Geographic variation in species interactions can be a major cause of geographic patterns in the diversity of genotypes and phenotypes (Travis 1996, Gómez-Mestre and Tejedo 2002). Despite these important effects of geographic variation of species interactions, most empirical studies

of species interactions have been restricted to documenting the presence of species interactions as important factors for local populations (Travis 1996).

Geographic variation in competitive ability is particularly interesting in the context of biological invasions (Sakai et al. 2001, Keller and Taylor 2008). Differentiation of competitive ability is a prominent hypothesis for how invasive species vary between native and introduced ranges (the Evolution of Increased Competitive Ability hypothesis; Siemann and Rogers 2001). Less discussed is the hypothesis of local differentiation of competitive ability within the introduced range of a species, either in response to the different biotic environments encountered by a widespread invader (Sakai et al. 2001, Siemann and Rogers 2001) or because of the introduction of heterogeneous genotypes with different competitive abilities (Abbott et al. 2007, Keller and Taylor 2008). The outcome of local competition may play an important role in the invasion success of many species into occupied niches (e.g., Byers 2000, Yasuda et al. 2004, Duyck et al. 2006). Impacts of invasive species may vary across their introduced range from limited effects on natives to competitive displace-

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ment of natives (Juliano et al. 2004, Abbott et al. 2007). Investigations of the causes of such variation are of basic interest, as they provide an opportunity to understand how intraspecific variation in species interactions arises (Keller and Taylor 2008), and of potential practical importance, as understanding that variation may aid in forecasting where and when invasive species impacts will be most severe (Abbott et al. 2007). Ideal model systems for such investigations involve widespread, well-studied invaders that vary in their degree of contact with, and impact on, native species; from no contact, through competitive exclusion of natives, to coexistence with natives.

In the middle of the 1980s the Asian tiger mosquito, *Aedes albopictus*, invaded the continental United States from Japan. Since then, it has spread rapidly in the southeastern United States and become one of the most common human-biting mosquitoes in its new range (Lounibos 2002). The spread of *A. albopictus* has been associated with a decline, sometimes to local extinction, of a closely related species, *Aedes aegypti* (O'Meara et al. 1995). *Aedes aegypti* originated in tropical Africa and probably invaded the Americas in the 16th century (Lounibos 2002). Most field (Juliano 1998, Braks et al. 2004) and laboratory (e.g., Barrera 1996, Murrell and Juliano 2008) competition experiments have shown that *A. albopictus* are often superior in competition for resources with *A. aegypti* in water-filled containers. These experiments have typically only involved the effects of competition on the immature stages, ignoring effects that may be expressed in resulting adults (e.g., Costanzo et al. 2005, Leisnham et al. 2008). Despite an apparent competitive advantage for North American *A. albopictus*, *A. aegypti* remains dominant in some areas in the southern United States, particularly in urban and southern sites in the Florida peninsula (O'Meara et al. 1995).

At least two hypotheses could account for the observation that *A. albopictus* is typically superior in competition to *A. aegypti* in experiments involving only the immature stages, yet *A. aegypti* coexists with *A. albopictus* at some sites. One hypothesis is that ecological context, including abiotic or biotic environments, differs among sites, with conditions at some sites favoring *A. aegypti* (Juliano et al. 2002, 2004, Costanzo et al. 2005). For example, Juliano et al. (2002) found that, in Florida, occupancy of containers was greater for *A. aegypti* but lower for *A. albopictus* at warm sites with little winter rainfall compared to relatively cool sites with greater winter rain. The second hypothesis, which we address in this paper, is that local populations of these *Aedes* differ in their competitive characteristics. This hypothesis has received little attention despite prior studies showing geographic variation in other life history traits of *A. albopictus*, such as incidence of diapausing eggs (Lounibos et al. 2003) and larval growth rate (Armbruster and Conn 2006).

At the same time that *A. albopictus* invaded the United States, *A. albopictus* originating in tropical Asia (Birungi and Munstermann 2002) invaded, established, and spread in Brazil (Lounibos 2002). Field competition experiments showed that *A. albopictus* from Brazil were also superior in competition for resources with *A. aegypti* (Braks et al. 2004), producing effects on *A. aegypti* that were strikingly similar to those observed for North American *A. albopictus* (Juliano 1998), and suggesting that competitive ability of *A. albopictus* from different continental regions (North America vs. Brazil) is broadly similar. However, both of these investigations focused only on differences in the responses of immatures to competitive interactions. Only Black et al. (1989) has evaluated interpopulation variation in the competitive ability of *A. albopictus*, finding differences in survival among populations. No experiments have compared the competitive abilities of different populations of *A. albopictus* from sites with different histories of interaction with *A. aegypti* (i.e., no contact with *A. aegypti*, *A. aegypti* extinct since *A. albopictus* arrival, *A. aegypti* coexists with *A. albopictus*). Thus, the role of geographic variation in the competitive ability of *A. albopictus* in determining coexistence with vs. exclusion of *A. aegypti* in the Americas remains unknown.

Experimental comparisons of competitive abilities are ideally based on competitive effects on and responses of per capita rate of change (r ; Goldberg and Fleetwood 1987). In competition experiments involving mosquitoes, population performance can be estimated by combining demographic data on survivorship, development time, and size (as a fecundity surrogate) into a composite index of population performance (Livdahl and Sugihara 1984, Juliano 1998). However, a problem with the composite index approach arises when investigators wish to compare different populations for competitive ability, but assume no interpopulation variation in the fecundity–size relationship of a species, which is used to estimate reproductive output in demographic models (Livdahl and Sugihara 1984). Such variation is well-known for insects (e.g., Hatle et al. 2002) including *A. albopictus* (Leisnham et al. 2008), and could be an important contributor to geographic variation in competitive ability.

In this paper, we test the hypothesis that variation in the outcome of *A. albopictus* invasion (i.e., coexistence vs. exclusion) results from variation among local populations of *A. albopictus* in competitive interactions with *A. aegypti*. We explicitly evaluate the role of adult reproductive tactics in these competitive outcomes. We compare the competitive abilities of nine North American populations of *A. albopictus* with known population histories of invasion and coexistence with *A. aegypti*. As in previous studies examining geographic variation in species interactions (e.g., Black et al. 1989), we compare populations under a single set of environmental conditions and thus reflect underlying genotypic variation.

To measure the absolute magnitude of heterospecific and conspecific competition, we employed a response surface design (Goldberg and Scheiner 2001), in which regression slopes of population performance vs. heterospecific and conspecific densities quantify per capita competitive effect and response to interspecific and intraspecific competition, respectively (Goldberg and Fleetwood 1987). We predict that *A. albopictus* from sites where *A. aegypti* have gone extinct since *A. albopictus* arrival (extinction) will have greater competitive effect, or better competitive response, than will *A. albopictus* from sites where *A. aegypti* coexist with *A. albopictus* (coexistence), or from sites where *A. aegypti* has never occurred (allopatry).

MATERIALS AND METHODS

Collection and maintenance of mosquitoes

Aedes albopictus larvae were collected from nine geographic populations in the eastern United States (Appendix A), representing three populations from each of three site types: extinction of *A. aegypti* following *A. albopictus* invasion; coexistence of the two species; and *A. albopictus* allopatric to *A. aegypti*. At extinction sites (Bartow, Florida; Fort Denaud, Florida; and Gainesville, Florida) *A. albopictus* became established in the early 1990s, and its arrival was associated with a decline and extinction of local *A. aegypti* in 1990 in Gainesville, 1992 in Bartow, and 1993 in Fort Denaud, as recorded by regular site surveys (Juliano et al. 2004; G. F. O'Meara, unpublished data). At coexistence sites (Daytona, Florida; Fort Myers, Florida; and Tampa, Florida) *A. albopictus* has been established since the early 1990s, yet *A. aegypti* remains present. Among the allopatric sites, *A. albopictus* has been established in East St. Louis, Illinois, since the middle of the 1980s (Hawley 1988), in Bloomington, Indiana, since the early 1990s, and in Washington, D.C., since the late 1990s. Allopatric populations are at latitudes beyond the permanent geographic range of *A. aegypti* (Darsie and Ward 2005), and therefore likely to have had no contact with *A. aegypti* since their arrival. All *A. albopictus* populations originated from artificial containers, in urban or suburban areas, where encounters with other *Aedes* species (e.g., the native tree hole mosquito, *Aedes triseriatus*) were relatively rare. Collections sometimes yielded *Culex* spp., but these were present at coexistence, exclusion, and allopatric sites. *Aedes aegypti* for this experiment were collected as larvae from a single population in Miami, Florida, where *A. albopictus* is locally absent (S. A. Juliano, unpublished data).

Field-collected larvae of *A. albopictus* and *A. aegypti* were reared to adulthood at 26°C at L:D 16:8 h photoperiod and then released into 0.6-m³ cages. Adults were kept at 26°C and 75% relative humidity at L:D 17:7 h photoperiod with a graduated dawn–dusk period. Adults had continuous access to 20% sugar solution. Females regularly fed on anesthetized guinea pigs and

laid eggs on paper towels in water-filled cups. Individuals from these eggs were used in the experiment.

Experiment 1: competition

The experiment had a replicated, blocked design with within-block replication of each site type. Egg availability prevented us from replicating each population in every block. For each block, eggs of both species were hatched synchronously in a solution of 0.44 g nutrient broth per 1 L deionized (DI) water. Within 24 h, larvae were rinsed and transferred into the experiment. The experiment consisted of the following initial combinations of larvae (*A. albopictus*: *A. aegypti*): 10:0, 20:0, 40:0, 10:10, 20:20, 10:30, 30:10, 0:10, 0:20, and 0:40 to create a response surface design (Goldberg and Scheiner 2001). Each combination was replicated three times for each of the nine *A. albopictus* populations, yielding 189 experimental units with *A. albopictus*, 189 experimental units with *A. aegypti*, and 270 total experimental units (400-mL cups containing 350 mL DI water and provisioned with 0.70 g of dried senescent live oak, *Quercus virginiana*, leaves). Cups were set up four days prior to the addition of larvae to allow microbial communities to establish. On days 14, 28, 42, and 56 after the start of each replicate, 0.70 g of additional dried live oak was added to each cup to avoid complete resource depletion and to mimic the natural condition of continuing resource inputs to containers. One cup containing high density *A. albopictus* (40:0) was lost.

The experiment was housed in an environmental chamber at 28°C with a L:D 14:10 h photoperiod to approximate summer climate and photoperiod conditions at all sites. Treatments were randomly assigned cups, and cup position was shuffled daily. Each day we collected pupae into individual vials and held them until adult emergence. Adults were killed by drying (24 h, 50°C), females were weighed, and their wing lengths were measured. Dry mass and wing length of adult females were highly correlated (*A. albopictus*, $r^2 = 0.760$, $n = 1127$, $P < 0.0001$; *A. aegypti*, $r^2 = 0.744$, $n = 766$, $P < 0.0001$), and wing length was used as a measure of female size to estimate fecundity of *A. albopictus* and *A. aegypti* (see *Experiment 2: Fecundity–size relationship* below).

For each cup, proportion survivorship to adulthood (both sexes), mean female dry mass, and mean female wing length were recorded. Daily eclosion of females and their wing lengths were used to calculate λ' , a composite index of population finite rate of increase based on r' , which estimates the realized per capita rate of population change ($dN/N dt = r$, the exponential growth rate) for each replicate cohort (Livdahl and Sugihara 1984; details in Appendix B).

Experiment 2: fecundity–size relationship

We used a regression equation relating female wing length to fecundity for *A. aegypti*: $f(w_x) = 0.5 [-8.616 + 2.50(w_x^2)]$ ($r^2 = 0.875$, $n = 206$, $P < 0.001$; Briegel 1990),

where w_x is female wing length. To test differences in the relationship between fecundity and body size in *A. albopictus*, *A. albopictus* larvae from each colony were reared to adulthood in the laboratory. As adults eclosed they were placed in 20-L nylon screen cages and within 5–10 days were fed to repletion from an anaesthetized mouse, then isolated in 600-mL containers with a 40-mL cup of water lined with paper towel for oviposition. Eggs were counted and the mean dry mass determined for 10 randomly chosen eggs from each female. Eggs were weighed in groups of 5–10, to 0.1 μg . After oviposition, all females were killed, dissected, and numbers of mature eggs (stages 4 and 5; Detinova 1962) in their ovaries counted. Fecundity was calculated by adding laid and unladen mature eggs. Wings of all females were removed and measured. A total of 318 females (24–43 for each population) entered the experiment. Killing and dissecting females after the first gonotrophic cycle is consistent with most prior studies that have examined the fecundity of *A. albopictus* (e.g., Armbruster and Hutchinson 2002). Data on the parity of wild *A. albopictus* females suggest that the average female matures but one batch of eggs (Hawley 1988).

Data analyses

Competition.—For each species, linear models with effects of densities of *A. albopictus* and *A. aegypti* (continuous variables), population (class variable), and block (class variable) were tested with λ' and its main demographic components (survivorship and mean female mass) as dependent variables. Collectively we refer to these dependent variables as “population performance.” An effect of competition was detected as a significant slope for the performance of a species vs. heterospecific or conspecific density. If population affects the outcome of competition, we expect an interaction between density and population on λ' , survivorship, and mean female mass. *Aedes albopictus* populations with stronger effects on *A. aegypti* will yield steeper slopes of *A. aegypti* population performance vs. *A. albopictus* density. Populations of *A. albopictus* with better competitive responses to *A. aegypti* will yield shallower slopes of *A. albopictus* population performance vs. *A. aegypti* density. Interactions between heterospecific and conspecific densities were tested but not significant, and thus they were removed from models. Association of competitive effect and response among populations was tested by estimating Spearman rank correlation between slopes, with a strong negative correlation expected if strong competitive effect and response are associated across populations.

Populations selected for this study were not a random sample of all possible populations of each site type. Therefore, in all analyses, population was treated as a fixed effect and statistical inferences extend only to the populations selected. This approach follows that of previous studies on geographic variation of life history traits (e.g., Reznick et al. 2001, Leisnham et al. 2008).

For all analyses, we tested for significant differences among populations using pairwise contrasts (Scheiner 2001), with sequential Bonferroni correction for all possible comparisons (33) within each analysis. We tested for effects based on site type using the a priori contrast comparing mean values of λ' , survivorship, and mean female mass among extinction vs. coexistence vs. allopatric sites.

We arcsine square-root transformed proportion surviving, and log-transformed both $\lambda' + 1$ and mass to meet assumptions of normality and homogeneity of variances. All analyses were done using SAS (SAS Institute 2003) with experiment-wise $\alpha = 0.05$.

Fecundity–size relationship.—MANCOVA was used to test for differences between populations (predictor variable) in the relationships of wing length (predictor variable) with fecundity and egg size (dependent variables), using *F* statistics derived from Pillai's Trace (SAS Institute 2003). We interpret contributions of dependent variables to significant MANCOVA effects using standardized canonical coefficients (SCCs; Scheiner 2001). Population was a class variable and wing length a continuous variable. Interaction of wing length with population was also included. Thirty-seven females either did not lay eggs before dying or their eggs were damaged, and thus their eggs were not weighed and they were excluded from the MANCOVA. Although we tested population differences in the relationship of wing length with fecundity and egg size using data from all populations, we conducted separate univariate linear regressions of fecundity on wing length for each population to estimate $f(w_x)$ for calculating λ' for each population.

RESULTS

Experiment 1: competition

Estimated finite rate of increase λ' .—The origin of *A. albopictus* influences its competitive effect on *A. aegypti* ($F_{8,159} = 2.42$, $P = 0.0170$) and response to competition from *A. aegypti* ($F_{8,158} = 3.28$, $P = 0.0017$; Fig. 1, Appendix C). Bartow had the strongest negative effect of *A. albopictus* density on *A. aegypti* λ' (i.e., steepest negative slope; Fig. 1, Appendix C), and there was a difference between Bartow and Bloomington ($P < 0.0001$). Fort Denaud had the strongest negative effect of *A. aegypti* density on *A. albopictus* λ' (Fig. 1, Appendix C), and was different from all other populations ($P < 0.0002$). *Aedes albopictus* (conspecific) density negatively affected *A. albopictus* λ' ($F_{1,158} = 4.10$, $P = 0.0447$) similarly for all populations ($F_{8,158} = 0.04$, $P = 1.0000$). Competitive effect and response slopes were uncorrelated ($r_s = 0.0167$, $P = 0.948$), indicating inconsistent ranking of populations of *A. albopictus* in competitive effect and response (Appendix C). Separate linear regressions of fecundity on wing length for use in estimating λ' for each population yielded r^2 values from 0.336 to 0.763.

Survivorship.—Heterospecific (*A. aegypti*) density negatively affected *A. albopictus* survivorship (Fig. 2), with a steeper slope for Fort Denaud compared to Fort

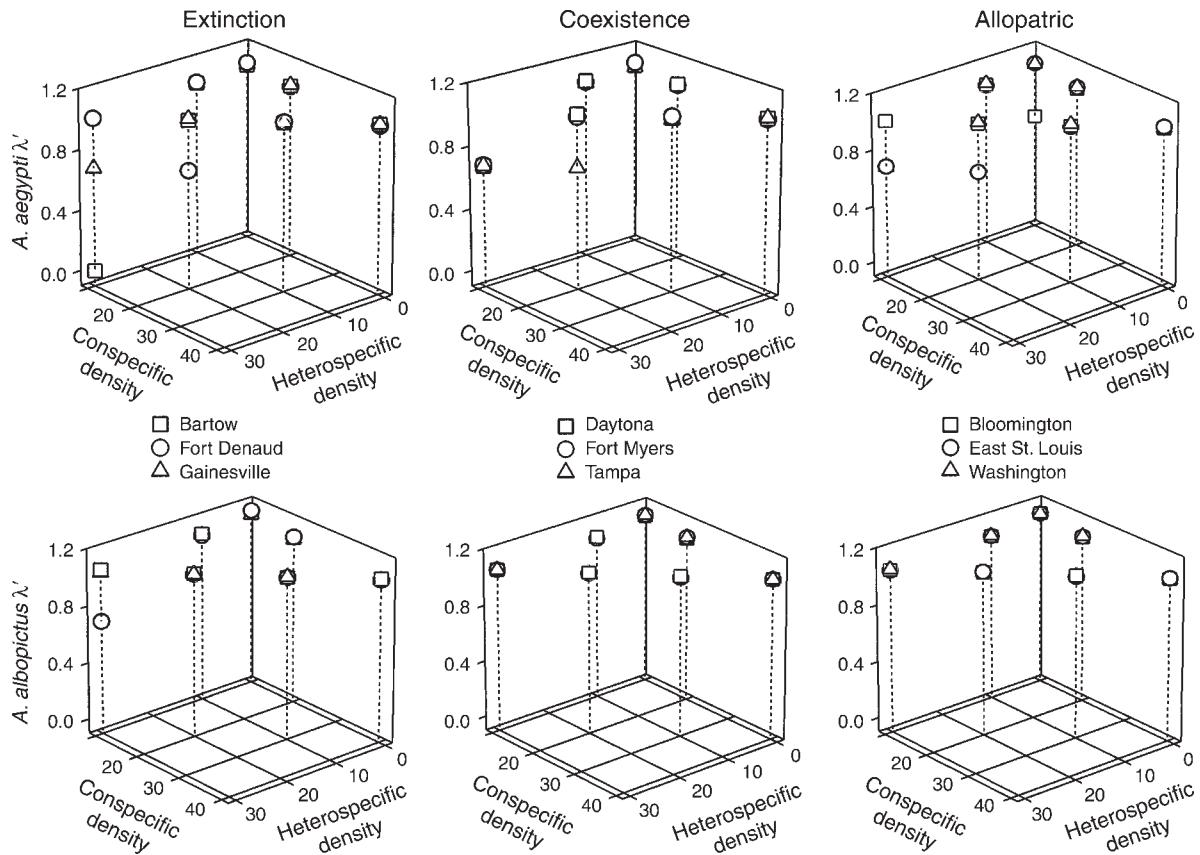


FIG. 1. Observed heterospecific and conspecific effects of larval densities on back-transformed λ' of *Aedes aegypti* and *A. albopictus*. Panels are grouped by species (rows) and place of origin of *A. albopictus* populations where *A. aegypti* has gone extinct, coexists, or has never been (allopatric; columns). Predicted slopes are presented in Appendix C: Fig. C1.

Myers and for extinction sites compared to coexistence sites ($F_{8,158} = 2.23$, $P = 0.0280$; Appendix C). Conspecific density negatively affected *A. albopictus* survivorship ($F_{1,158} = 149.65$, $P < 0.0001$) similarly for all populations ($F_{8,158} = 1.25$, $P < 0.2746$). Heterospecific ($F_{1,159} = 324.95$, $P < 0.0001$) and conspecific ($F_{1,159} = 195.36$, $P < 0.0001$) densities negatively affected *A. aegypti* survivorship similarly for all populations ($F_{1,159} = 1.20$, $P = 0.3025$ and $F_{1,159} = 0.81$, $P = 0.5918$; Appendix C).

Adult female size.—Heterospecific and conspecific densities negatively affected *A. albopictus* mass ($F_{1,157} = 32.28$, $P < 0.0001$ and $F_{1,157} = 4.72$, $P = 0.0314$) and *A. aegypti* mass ($F_{1,146} = 18.95$, $P < 0.0001$ and $F_{1,157} = 14.50$, $P = 0.0002$; Appendix C). Density effects on body size were consistent among populations (Appendix C).

Experiment 2: fecundity–size relationship

Wing length positively affected fecundity of *A. albopictus* in all populations, and showed steeper slopes in extinction sites than coexistence and allopatric sites (Table 1, Fig. 3). Wing length had a small positive effect on egg size of *A. albopictus* from extinction sites, but not in coexistence and allopatric populations (Fig. 3). Differences between extinction sites and coexistence

sites and between extinction sites and allopatric sites were approximately equally attributable to differences in both fecundity and egg size (see SCCs in Table 1). All multivariate pairwise contrasts between individual populations for the wing \times population interaction were not significant after Bonferroni correction.

DISCUSSION

There are inherent interpopulation differences in competitive effect and response of *A. albopictus*. We predicted that *A. albopictus* from sites where *A. aegypti* has gone extinct (extinction) would have stronger competitive effects on or better competitive responses to *A. aegypti*, compared to *A. albopictus* from sites where *A. aegypti* persists (coexistence), or is absent (allopatric). However, our data yielded no strong patterns among extinction, coexistence, or allopatric sites. Instead, certain populations stood out as having large competitive effects (Bartow) or poor competitive responses (Fort Denaud). As both of these populations are from extinction sites, interpopulation variability in competitive ability is unlikely to explain variation in invasion success or impact of *A. albopictus* among these sites.

Most *A. albopictus* populations, except Fort Denaud, yielded greater λ' than *A. aegypti* at high combined

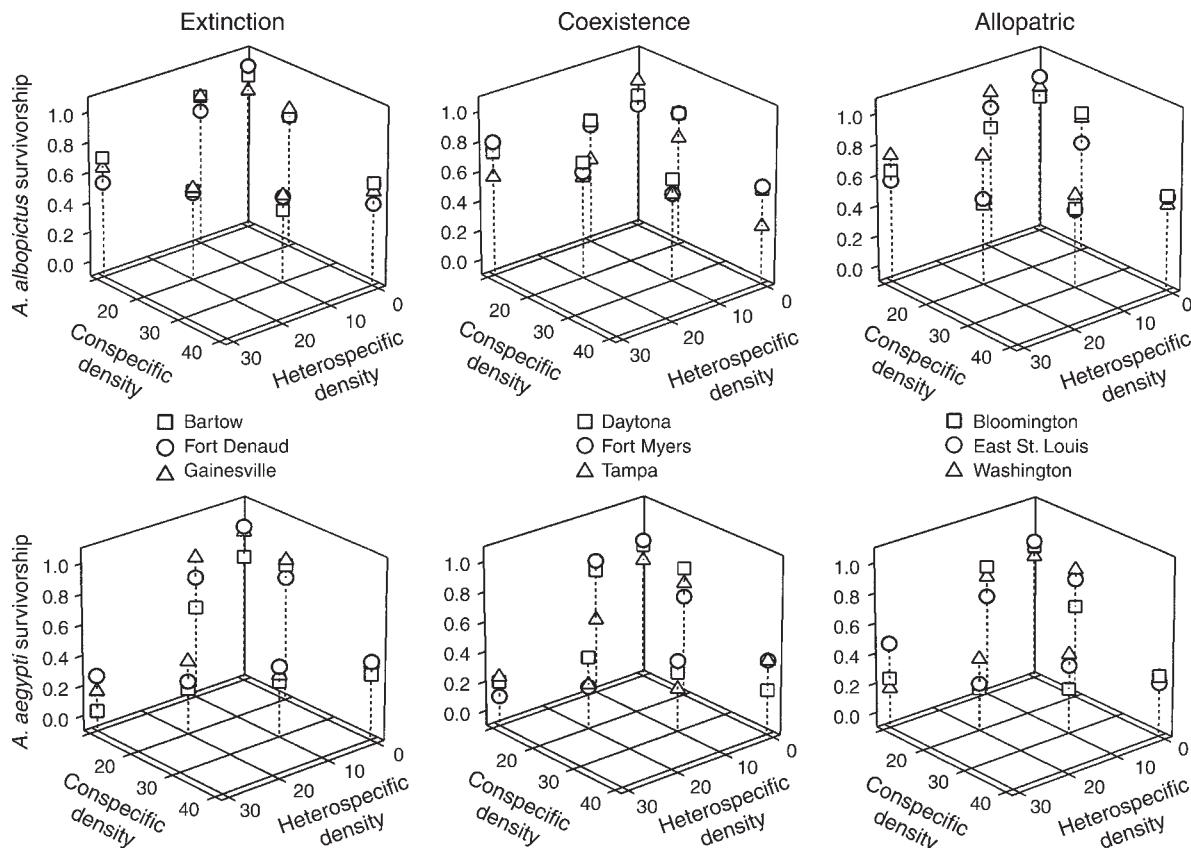


FIG. 2. Observed heterospecific and conspecific effects of larval densities on back-transformed survival of *A. aegypti* and *A. albopictus*. Panels are grouped by species (rows) and place of origin of *A. albopictus* populations where *A. aegypti* has gone extinct, coexists, or has never been (allopatric; columns). Predicted slopes are presented in Appendix C: Fig C3.

densities. This result is consistent with previous field (Juliano 1998, Braks et al. 2004) and laboratory (Barrera 1996, Murrell and Juliano 2008) experiments using natural leaf detritus as the nutrient base, and with competitive superiority of *A. albopictus* over *A. aegypti* under these conditions. Competition affected female size in the same way for all *A. albopictus* populations, and all *A. albopictus* populations had the same effect on *A. aegypti* size. This suggests that differential effects of *A.*

albopictus population on λ' are mostly the result of effects on survivorship. Nevertheless, we observed slightly different conclusions for λ' and survivorship of both species, reaffirming the importance of estimating population rate of increase in competition studies (Livdahl and Sugihara 1984).

Although extinction sites had steeper average fecundity–size relationships than did coexistence sites and allopatric sites, this did not translate into generally

TABLE 1. Least-squares MANCOVA on fecundity and mean egg size of *Aedes albopictus* in response to the independent variables of population and wing length.

Source of variation	MANCOVA			Standardized canonical coefficients (SCCs)	
	Pillai's Trace (<i>F</i>)	df	<i>P</i>	Fecundity	Egg size
Population	1.76	16, 526	0.0341	1.08	0.73
Wing length	163.34	2, 262	<0.0001	1.47	0.13
Population × wing length	1.89	16, 526	0.0194	1.17	0.67
Extinction vs. allopatric	4.44	2, 262	0.0127	0.71	0.92
Extinction vs. coexistence	4.50	2, 262	0.0120	0.81	0.88
Allopatric vs. coexistence	0.03	2, 262	0.9703	1.20	−0.53

Notes: For brevity, multivariate pairwise contrasts among site types for the slopes are only shown for the population × wing length interaction (sequential Bonferroni correction, three comparisons). See *Experiment 2: fecundity–size relationship* for the results of pairwise contrasts between populations. Significant ($P \leq 0.05$) effects and pairwise comparisons are indicated in bold. Only first canonical variates are shown; all second canonical variates are nonsignificant.

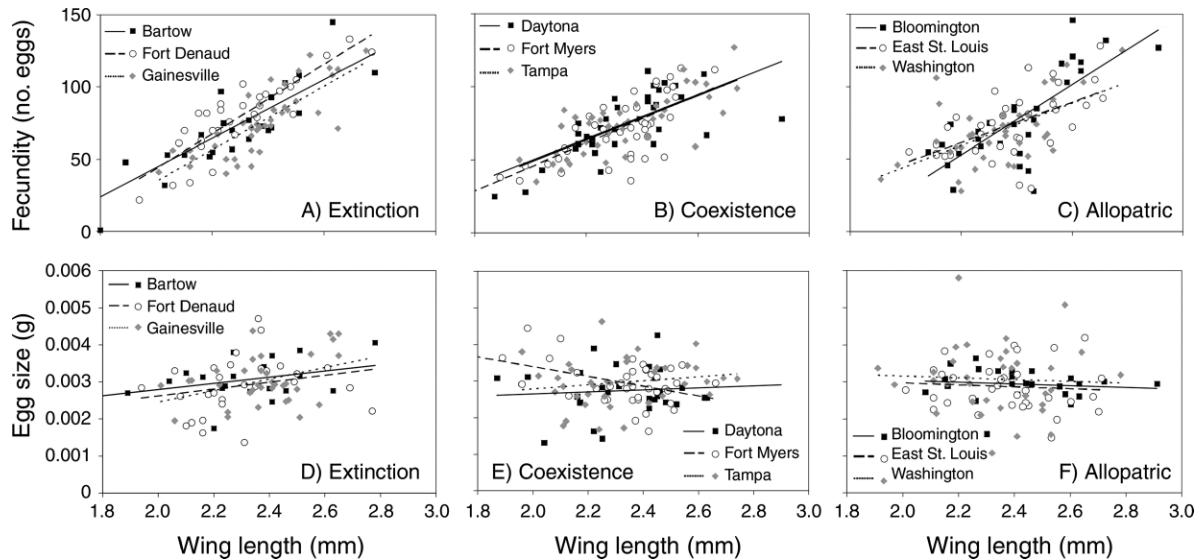


FIG. 3. Relationships of wing length with fecundity (A–C) and egg size (D–F) in *A. albopictus* from populations originating from sites where *A. aegypti* has gone extinct, coexists, or has never been (allopatric).

superior population performance. To test whether interpopulation differences in fecundity–size relationships, $f(w_x)$, were important determinants of overall competitive interactions, we also calculated λ' using one $f(w_x)$ from a regression pooling data from all populations. Although λ' values changed, statistical conclusions about competitive advantage and interpopulation differences in competitive effects and responses were unchanged. Thus, as observed by Juliano (1998), patterns in competitive interactions for these populations are not strongly related to fecundity–size relationships.

Consistent with prior work on *A. albopictus* reproduction (e.g., Leisnham et al. 2008), fecundity and egg size were positively correlated, yielding no evidence of a trade-off between fecundity and investment per offspring across populations. Although interpopulation differences in reproduction were primarily attributable to fecundity, differences in egg size were not trivial. *Aedes albopictus* from extinction sites had a strong relationship between wing length and egg size compared to coexistence sites (Fig. 1). Egg size does not enter into calculations of λ' but it may be related to fitness of *A. albopictus*. In *A. aegypti* and other insects, females hatching from large eggs grow faster, attain greater adult size, and lay more and larger eggs than females hatching from small eggs (Steinwascher 1984, Azevedo et al. 1997, Fox and Czesak 2000). Interspecific comparisons among *Aedes* mosquitoes also show egg survival time is correlated with egg volume at both high and low humidity (Sota and Mogi 1992). Thus, larger eggs may yield superior fitness in *A. albopictus*, and this advantage for large females may contribute to greater population-level competitive ability of *A. albopictus* at certain sites, and contribute to displacement of *A. aegypti*.

Our experiment is one of the first to show interpopulation divergence in competitive effect and response for an insect. Competitive effect is usually associated with ability to harvest and deplete scarce resources (Tilman 1982). Harvesting efficiency can contribute to competitive response as well, but response is also affected by physiological efficiency and flexibility, such as reduced metabolic demands when resources are scarce, or plasticity of size and time to maturity that may enable a species to maintain positive dN/dt despite competition. Such phenotypic plasticity will not necessarily alter competitive effect (Tilman 1982). In our experiment, there were significant interactions involving population only for interspecific competition, and the magnitudes of competitive effect and response were uncorrelated among *A. albopictus* populations. Competitive effect and response are at least partially independent for plants and invertebrates (e.g., Goldberg and Fleetwood 1987, Joshi and Thompson 1995, Byers 2000). Thus, independent evolution of enhanced effect or response among populations of a wide ranging species, such as *A. albopictus*, seems possible.

Competition between *A. albopictus* and *A. aegypti* is widely assumed to occur via resource depletion, and manipulating resources levels can alter the impact of competition (Juliano 1998, Braks et al. 2004). However, both species may be affected by interference competition produced by water-borne substances (Moore and Fisher 1969, Dye 1984, Broadie and Bradshaw 1991). Competition between invertebrates can involve multiple mechanisms (Byers 2000). Intrapopulation differences in the mechanisms of competition between *A. albopictus* and *A. aegypti* merits further investigation as it may explain geographic variation in heterospecific, but not conspecific, effects between these species in this study.

Our sites were grouped according to the presence/absence of *A. aegypti* recorded during annual and multi-annual surveys. But site types also differ in environmental conditions. Coexistence sites are warmer, more urban, and seasonally drier compared to extinction sites (O'Meara et al. 1995, Juliano et al. 2002). Allopatric sites differ considerably in climate compared to coexistence and extinction sites because of latitude (Leisnham et al. 2008). Despite these differences between site types, we observe relatively little consistent difference in competitive ability of *A. albopictus* populations under the single set of environmental conditions in this study.

Our results suggest that coexistence of *A. aegypti* with *A. albopictus* may be mainly determined by the phenotypic responses of both species to environmental conditions, which differ among sites, with conditions at some sites favoring *A. aegypti* (Juliano et al. 2002, 2004, Costanzo et al. 2005). *Aedes albopictus* eggs are more sensitive to desiccation than *A. aegypti* eggs (Juliano et al. 2002, Costanzo et al. 2005), and local coexistence of these species may be possible because warm, dry climates favor *A. aegypti* and alleviate effects of competition from *A. albopictus* via differential mortality of *A. albopictus* eggs (Juliano et al. 2002).

We must also look to other ecological or genetic factors, especially those particular to specific populations, to understand the divergent evolution in competitive ability of *A. albopictus*. These may include intrapopulation variation of selection on *A. albopictus* due to local differences in the larval and terrestrial environment, intrapopulation variation of selection on *A. albopictus* due to temporal changes in the presence/absence of *A. aegypti*, and non-adaptive variation due to founder effects, genetic drift, and inbreeding. Additionally, geographic differentiation in the competitive ability of *A. aegypti* may also affect the spread of *A. albopictus* in North America.

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APPENDIX A

Geographic origin of populations of *A. albopictus* collected (*Ecological Archives* E090-170-A1).

APPENDIX B

Equation for calculating λ' , a composite index of population performance based on r' , which estimates the realized per capita rate of population change for each replicate cohort (*Ecological Archives* E090-170-A2).

APPENDIX C

Statistical tables and additional figures (*Ecological Archives* E090-170-A3).