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A field test for competitive effects of *Aedes albopictus* on *A. aegypti* in South Florida: differences between sites of coexistence and exclusion?

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Abstract We tested whether interspecific competition from *Aedes albopictus* had measurable effects on *A. aegypti* at the typical numbers of larval mosquitoes found in cemetery vases in south Florida. We also tested whether the effect of interspecific competition from *A. albopictus* on *A. aegypti* differed between sites where *A. aegypti* either persists or went extinct following invasion by *A. albopictus*. Similar experiments manipulating numbers of *A. albopictus* in cemetery vases were conducted at three sites of *A. aegypti* persistence and three sites where *A. aegypti* was apparently extinct. The experiments were done using numbers of larvae that were determined by observed numbers of larvae for each site, and with resources (leaf detritus) that accumulated in experimental vases placed into each field site. In both the early rainy season (when number of mosquito larvae was low) and the late rainy season (when number of mosquito larvae was high), there was a significant effect of treatment on developmental progress of experimental *A. aegypti*. In the late rainy season, when numbers of larvae were high, there was also a significant effect of treatment on survivorship of *A. aegypti*. However, the competition treatment × site type (*A. aegypti* persists vs extinct) interaction was never significant, indicating that the competitive effect of *A. albopictus* on *A. aegypti* did not differ systematically between persistence versus extinction sites. Thus, although competition from *A. albopictus* is strong under field conditions at all sites, we find no evidence that variation in the impact of interspecific competition is associated with coexistence or exclusion. Interspecific competition among larvae is thus a viable explanation for exclusion or reduction of *A. aegypti* in south Florida, but variation in

the persistence of *A. aegypti* following invasion does not seem to be primarily a product of variation in the conditions in the aquatic environments of cemetery vases.

Keywords Interspecific competition · Mosquitoes · Biological invasion · Aquatic insects · Seasonal variation

Introduction

Biological invasions challenge our ability to understand the biotic and abiotic processes that govern distribution and abundance. Invading species interact with resident species and with local abiotic environments, and these interactions determine the eventual range and abundance of the invader, and in some cases, the fates of resident species and communities (Williamson 1996; Lounibos 2002). Though invasions allow direct observations of dynamics of species abundance and distribution, simple observation of patterns of colonization, displacement, or coexistence do not typically yield understanding of mechanisms. When invasion systems are amenable to experimentation, we can investigate how biotic and abiotic processes interact to determine species distribution and abundances. Investigations of invasion biology of lizards (Case et al. 1994; Petren and Case 1996, 1998; Hanley et al. 1998), frogs (Kupferberg 1997), ants (Human and Gordon 1996; Holway et al. 2002), and crayfish (Hill and Lodge 1999) have all served to illustrate the ecological processes that affect variation in the outcome of invasions.

The recent invasion of the Americas by the Asian Tiger Mosquito, *Aedes albopictus*, provides an ideal opportunity to investigate processes that operate during an invasion, and how those processes may vary in space. *A. albopictus* was first recorded in North America in the mid-1980s (Sprenger and Wuithiranyagool 1986; Hawley 1988). Since then it has spread throughout much of southeastern USA, where it is now one of the most common mosquitoes in many areas (Moore 1999). Its spread through Florida has been particularly well documented (O'Meara et al. 1995; Lounibos et al. 2002). *A. albopictus* larvae develop

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in water-filled discarded tires, cemetery vases, tree holes, and other containers (Hawley 1988). Adults are generalist blood feeders that lay desiccation-resistant eggs above the water line. These eggs hatch when flooded, and larvae feed on microorganisms and detritus. There has been considerable interest in the potential and observed impacts of *A. albopictus* on North American container-dwelling *Aedes* (e.g., Livdahl and Willey 1991; Edgerly et al. 1993; Juliano 1998; Daugherty et al. 2000; Teng and Apperson 2000). In Florida (Hornby et al. 1994; O'Meara et al. 1995), and southeastern USA in general (Hobbs et al. 1991; McHugh 1993; Mekuria and Hyatt 1995; Harrison et al. 1998), there has been a well documented decline in the abundance of *A. aegypti* (an introduced species that has been established in North America for centuries, Lounibos 2002), sometimes to local extinction, following invasion of *A. albopictus*. This decline is consistent with the hypothesis that interspecific competition, probably among larvae, is the mechanism by which *A. albopictus* displaces *A. aegypti*, which is a specialist developing in man-made containers (Christophers 1960; Frank 1981). Some alternative mechanisms of displacement can be ruled out based on natural history of these species (e.g., predation), whereas others are unlikely based on field studies (e.g., apparent competition; Garcia et al. 1994; Juliano 1998). Field (Juliano 1998) and laboratory (Barrera 1996; Daugherty et al. 2000) competition experiments using decaying plant material as a substrate for the bacterial food of larvae indicate that *A. albopictus* is superior to *A. aegypti* in resource competition, maintaining greater population growth at higher combined densities (Juliano 1998; Daugherty et al. 2000), and producing greater survivorship during periods of low food availability (Barrera 1996). Thus, it is possible that resource competition among larvae could contribute to the displacement of *A. aegypti* by *A. albopictus* in much of southeastern USA. These experiments, and indeed all other experiments on interspecific competition involving North American *A. albopictus* (e.g., Black et al. 1989; Ho et al. 1989; Livdahl and Willey 1991; Novak et al. 1993; Teng and Apperson 2000; Lounibos et al. 2002) were conducted under conditions in which interspecific competition among larvae would be obvious, and so were designed to answer the question: Which species has a competitive advantage, assuming that competition is occurring? Another important question remains: Is interspecific competition important under the typical conditions in which these species interact in the field? This question is one of the subjects of this paper.

Despite the apparent superiority of *A. albopictus* in competition, *A. aegypti* manages to persist in some locations in southeastern USA, coexisting with *A. albopictus* (O'Meara et al. 1995; Juliano et al. 2002). A second subject of this paper is the question: Is there a difference in the impact of competition from *A. albopictus* between sites where *A. aegypti* has gone extinct and sites where *A. aegypti* persists? This is one of the most fundamentally important questions that can be asked about interspecific competition in nature, because it directly addresses the

issue of how competition affects distribution and abundance of competitors and community composition (Goldberg and Scheiner 2001). Alteration of the outcome of competition due to differences in the environment in which competitors interact (Dunson and Travis 1991; Hemphill 1991; Warner et al. 1991, 1993; Barata et al. 1996; Travis 1996; Chesson 2000; Holway et al. 2002; Huckle et al. 2002) is one possible explanation for this variation, however only a few studies have investigated experimentally how the effects of competition vary between replicated sites of coexistence versus apparent competitive exclusion (e.g., Hairston 1980; Gurevitch 1986; McGraw and Chapin 1989; Losos and Spiller 1999). On the Florida peninsula, *A. aegypti* persists in southern, urban areas, despite invasion by *A. albopictus* (Hornby et al. 1994; O'Meara et al. 1995). This persistence of *A. aegypti* in particular geographic areas and habitats suggests that environmental factors, such as temperature, precipitation, macroscopic habitat structure, and water chemistry may affect the outcome of this competitive interaction (Juliano et al. 2002). The southern part of the Florida peninsula is characterized by a subtropical climate, with warm temperatures and low rainfall in the winter months. Farther north on the peninsula, there is greater winter rain, and in the Florida panhandle, there is a pronounced secondary peak in rainfall in the winter (Fernald and Patton 1985). There are several prominent examples of local persistence of poorer competitors when they can tolerate more extreme physical conditions than can superior competitors (e.g., Connell 1961; Hemphill 1991) or cases where different physical environments yield different competitive outcomes (e.g., Dunson and Travis 1991; Warner et al. 1993). There have been, however, no experiments testing whether geographic variation in the conditions in the aquatic environment, both physical and biotic, alters the impact of competition in this system.

This paper tests two hypotheses derived from these questions about this invasion. First, we test the hypothesis that the decline of *A. aegypti* following invasion by *A. albopictus* is a result of interspecific competition among larvae in the aquatic habitat. Second, we test the hypotheses that persistence of *A. aegypti* at some locations occurs because conditions in the aquatic habitats where larvae interact differ, and alter the outcome of competition. These hypotheses yield two predictions that we tested in field experiments in south Florida. We predict, first, that competition among larvae should be detectable (indeed, strong) at the numbers of mosquito larvae per container found in typical field sites. Second, if the conditions in aquatic habitats (e.g., type and amount of plant detritus that forms the base of the aquatic food chain) differ and alter the outcome of competition among larvae, then the outcomes of similar competition experiments, with homogeneous populations of experimental larvae, conducted at sites where *A. aegypti* persist or have gone extinct should differ. Thus, in the context of the experiment (see Materials and methods), we predict a significant effect of competition treatment, and a significant treatment by site

type interaction, with the effect of competition least at sites where *A. aegypti* now persists (see Hairston 1980; Gurevitch 1986).

Materials and methods

The experiment was done at six cemetery sites in South Florida (Fig. 1), chosen based on their accessibility and known history of invasion by *A. albopictus*. Ft. Denaud Cemetery, Joshua Creek Cemetery, and Oak Hill Cemetery are sites where *A. aegypti* no longer occurs, and which now harbor large populations of *A. albopictus*, which have been resident since at least 1993 (O'Meara et al. 1995; Juliano 1998). All three are rural cemeteries, with live oak (*Quercus virginiana*) the most common tree. Rose Hill Cemetery, Orange Hill Cemetery, and Ft. Myers Cemetery are sites where *A.*

albopictus and *A. aegypti* now coexist. All three are urban cemeteries that were invaded by *A. albopictus* in the early 1990s (O'Meara et al. 1995; Juliano 1998). Live Oaks and pine are the most common trees at Rose Hill Cemetery. Live Oaks are the most common tree at Ft. Myers Cemetery. Trees are relatively rare at Orange Hill, where junipers, arborvitae, and other shrubs are the most common woody plants.

We did the experiment in both the early rainy season (June 1999) and in the late rainy season (August–September 2000). Seasonal precipitation patterns and mean temperatures at all sites are similar (Fig. 1, bar graphs). Vases at all sites typically dry out for varying periods during the winter and spring, so we expected that ambient numbers of mosquito larvae per vase, hence experimental number per vase, would be higher in the late rainy season and low in the early rainy season (i.e., low following a prolonged dry period). Each year, we placed 40–50 standard green plastic cemetery vases (1.0 l) at each site. We placed vases near vegetation, which typically resulted in partial shade, because most occupied containers at

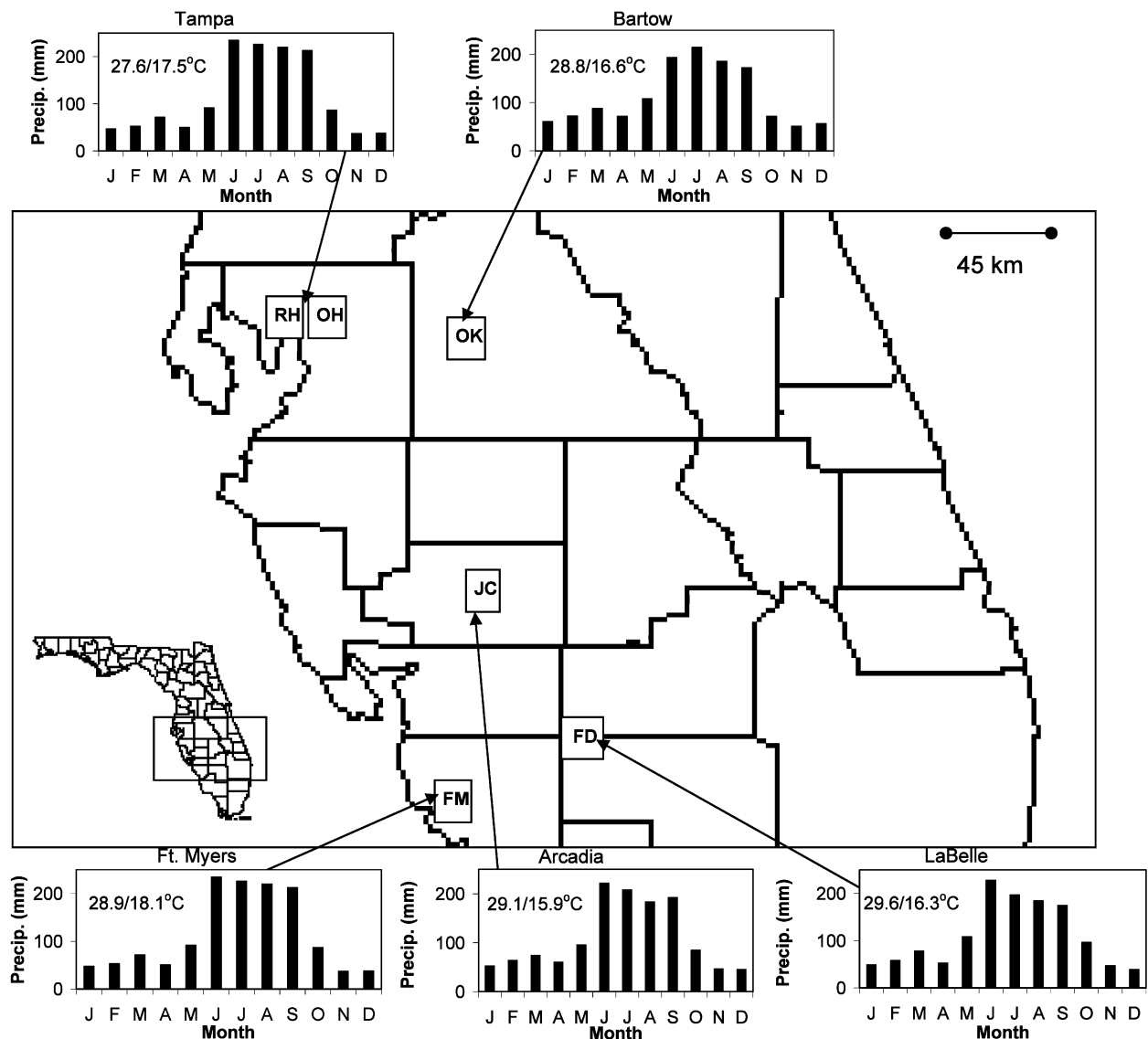


Fig. 1 Locations of cemeteries in Florida, USA, where competition experiments were conducted, and mean monthly precipitation and mean annual high / low temperatures for the nearest weather station (http://www.dnr.state.sc.us/climate/sercc/climateinfo/historical/historical_fl.html). Means based on the period from 1971 to 2000. Abbreviations for sites where *A. aegypti* persists: RH Rose Hill

Cemetery, Tampa; OH Orange Hill Cemetery, Tampa; FM Ft. Myers City Cemetery, Ft. Myers. Abbreviations for sites where *A. aegypti* went extinct following invasion by *A. albopictus*: OK Oak Hill Cemetery, Polk Co., JC Joshua Creek Cemetery, DeSoto Co., FD, Ft. Denaud Cemetery, Hendry Co

cemeteries seem to be partially shaded, and, more practically, because vases placed further from vegetation are often damaged by lawn-care equipment. In 2000 we placed a completely new set of vases near the locations used in 1999, except in cases where vases had been damaged. We left the vases undisturbed for a minimum of one month, during which time water, plant detritus, mosquitoes, and other macroinvertebrates accumulated in vases. After this 1 month period, we collected the vases, removed and counted all *Aedes* larvae and pupae, including *A. albopictus*, *A. aegypti*, and *Ochlerotatus* (formerly *Aedes*) *triseriatus*, in order to estimate the number of immatures per vase. In both years we preserved and later identified the removed immatures to obtain a quantitative assessment of the relative abundances of the species at these sites. We also removed any other macroinvertebrates that had colonized the vases. While the vases were empty, we removed any *Aedes* eggs adhering to the walls of the vases by scrubbing the sides and bottom of the vases with a nylon pot scrubber, rinsing, and repeating the scrubbing process (1999), or by filling each vase with a 50% solution of chlorine bleach, letting the vase stand for 1 min, then removing the bleach and rinsing the vase twice with water (2000). Preliminary trials in the laboratory showed that 50% chlorine bleach killed all eggs in 1 min (unpublished data). We then returned water and detritus to each vase, covered the vase with 0.5 mm nylon mesh secured with a rubber band (to deter oviposition), and left the vase in place overnight prior to adding experimental larvae.

Experimental larvae were first-generation progeny of individuals collected in the field at multiple sites in Hillsborough and Manatee counties, where two of the experimental cemeteries are located (Fig. 1), and raised to adulthood in the laboratory. By using larvae from the same laboratory colony for experiments at all six cemeteries, we ensured that any differences in the outcome of the experiments between cemetery types are due to differences in the environments in which the larvae interact. Colony adults took blood meals from chickens (University of Florida animal care protocol VB-17) and laid eggs on paper towels that were stored under humid conditions until needed. To begin the experiment, we hatched eggs synchronously using 1% nutrient broth solution in 25 ml vials. We allotted larvae into batches of the desired size (determined for each cemetery in each year), placed them in 2 ml shell vials sealed with corks, and then transported them to the cemetery site where the larvae were added to vases in the appropriate numbers. Thus, at the start of each experiment, larvae were approximately 24 h old and vases had been without larvae for approximately 24 h. Upon

addition of larvae, we replaced the nylon mesh and secured it with duct tape. We then left the vases in place in the cemetery until the experiment was finished.

The goal of the experiments was to manipulate number of *A. albopictus* larvae per vase and to determine the effects of these manipulations on survivorship, growth, and development of *A. aegypti*. The three treatments at each cemetery spanned the mean number of hatchling larvae per vase at each site. For each cemetery, we determined the mean number of *Aedes* larvae and pupae present in occupied vases, and determined the “baseline number per vase” for each cemetery based on this mean. This observed mean is necessarily an underestimate of the number of larvae at hatching, as most of the immatures present in vases were 3rd or 4th instar larvae or pupae, and it is likely that they represented only the survivors of larger hatching cohorts of larvae. Because it was the number of hatching larvae that our manipulations were designed to simulate, we chose to use baseline numbers 10–20 larvae greater than the observed mean number per vase. Mortality of larvae is often density dependent and can be high (Service 1985), hence our baseline number probably represents a conservative estimate of the density at hatching. Based on the observed numbers (Table 1) we determined baseline numbers for each site using the following categories: observed mean =11–20/vase—baseline number =30 1st instar larvae; observed mean =21–30/vase—baseline number =40 1st instar larvae; and observed mean =31–40/vase—baseline number =50 1st instar larvae.

Number of larvae per vase in preliminary samples (square-root transformed to meet assumptions of normality and homogeneity of variances) was analyzed by ANOVA (SAS 1990, PROC GLM), with site type (*A. aegypti* persists vs extinct), year (1999, 2000), and interaction as fixed effects, and cemetery (type) and cemetery \times year (type) as random effects. We were primarily interested in the fixed effects, which, if significant, would indicate differences in number of larvae per vase between persistence versus extinction sites, or between early versus late rainy season. The design was unbalanced due to unequal replication at cemeteries, hence denominator mean squares for *F*-tests were linear combinations of mean squares calculated using Satterthwaite’s formulas (Montgomery 1976; SAS 1990). Resulting non-integer degrees of freedom are reported to the nearest 0.1 degree of freedom.

There were three treatments in these experiments. For all vases we added newly hatched (approximately 24 h old) larvae of *A. aegypti* at 1/2 the baseline number. Treatments were defined by the number

Table 1 Observed number/vase of mosquito immatures at each site prior to the experiment. Mean number/vase and SD are determined for occupied vases only, counting only larvae and pupae of *Aedes albopictus*, *A. aegypti*, and *Ochlerotatus* (formerly *Aedes*) *triseriatus*.

Cemetery	Number of water filled vases	<i>A. albopictus</i> only	<i>A. aegypti</i> only	<i>A. albopictus</i> + <i>A. aegypti</i>	Neither	Proportion <i>A. aegypti</i> (N)	Observed number per vase			Baseline number
							Mean	SD	Maximum	
Early rainy season (June 1999)										
Ft. Myers	39	12	0	3	16	0.215 (269)	18.4	17.4	51	30
Rose Hill	38	10	1	8	6	0.165 (532)	29.2	27.3	120	40
Orange Hill	41	No data on composition; six vases with larvae			35	No data	17.2	16.7	47	30
Ft. Denaud	42	18	0	0	5	0 (273)	11.7	13.5	118	30
Joshua Cr.	39	15	0	0	4	0 (301)	16.8	15.6	56	30
Oak Hill	41	18	0	0	2	0 (420)	28.1	23.7	110	40
Late rainy season (August–September 2000)										
Ft. Myers	35	7	2	24	1	0.295 (739)	27.3	21.6	83	40
Rose Hill	30	6	0	22	2	0.310 (681)	32.1	34.6	137	50
Orange Hill	31	10	1	20	0	0.213 (747)	27.3	30.3	84	40
Ft. Denaud	41	41	0	0	0	0 (960)	35.4	24.0	86	50
Joshua Cr.	39	39	0	0	0	0 (757)	35.7	23.8	107	50
Oak Hill	35	35	0	0	0	0 (1063)	37.5	30.3	103	50

in 1999, some preserved samples of field-collected larvae were lost; hence species composition was determined for only a subset of water filled vases with larvae

of newly hatched *A. albopictus* that we added. The REDUCED treatment received no *A. albopictus* (i.e., it had only *A. aegypti* at 1/2 the baseline number). The CONTROL treatment received *A. albopictus* at 1/2 the baseline number, so that total number of *Aedes* was the baseline number. The INCREASED treatment received *A. albopictus* at the full baseline number, so that total *Aedes* number was equal to 1.5× the baseline number.

The experiments were ended after 10 and 7 days in 1999 and 2000, respectively. The duration was reduced in 2000 to minimize the potential for adult eclosion during the experiment, because adults often die in the confines of the vases and become difficult to identify and impossible to weigh accurately. For each vase, we placed dry ice on top of the screen so that sublimating CO₂ anaesthetized any adults in the container. We placed adults individually into labeled vials for later identification. We then removed all surviving larvae and pupae, placing them in labeled vials for later identification. Upon return to the laboratory, we killed and dried adults at 50°C, and identified species and sexes. For undamaged adults we determined dry mass to the nearest 0.1 µg using a microbalance. We identified, counted, and determined the stages of larvae and pupae.

Because *A. aegypti* is the focal species and *A. albopictus* is the associate species (Goldberg and Scheiner 2001), statistical analysis focused only on the response of *A. aegypti*, across the range of cemeteries, to the manipulation of *A. albopictus* abundance. *Aedes albopictus* is thus present only as a treatment. Because of the difference in the duration of the experiments, we analyzed the early (1999) and late (2000) rainy season experiments separately. In order to assess both survival of larvae, and their progress toward completion of development, we analyzed: proportion of *A. aegypti* surviving to the end of the experiment (arcsine transformed, to meet assumptions of normality and homogeneity of variances); mean developmental stage (instar = 1, 2, 3, 4, pupa = 5, adult = 6) (transformed by squaring), and mean masses of undamaged adult males and females (in 1999 only; log transformed) by nested ANOVA and pairwise contrasts. In these ANOVAs, Treatment (REDUCED, CONTROL, INCREASED), site Type (*aegypti* extinct, *aegypti* persists), and interaction were fixed effects, and Cemetery(Type) and Treatment × Cemetery(Type) were random effects because we wish to draw inferences about the larger population of cemetery sites where either *A. aegypti* has gone extinct or now coexists with *A. albopictus*. The design was unbalanced due to unequal replication of treatments at cemeteries, hence denominator mean squares for *F*-tests were linear combinations of mean squares calculated using Satterthwaite's formulas (Montgomery 1976; SAS 1990), resulting in non-integer degrees of freedom, which are reported to the nearest 0.1 degree of freedom (see Tables 2, 3). Pairwise comparisons of least squares means were done using the Tukey-Kramer method (SAS 1990, PROC GLM).

In each year there were cases of incomplete removal of existing eggs, probably because both species sometimes lay eggs on the

water's surface (Christophers 1960; personal observation) which would have been returned to the cleaned vase with the water. As a convention we chose to omit from analysis any vase in which: (a) apparent proportion survivorship of *A. aegypti* >1.0; (b) >5 unidentified individuals (exclusively damaged adults in 1999) were present; (c) *A. albopictus* recovered at the end of the experiment were in excess of the stocked number by >5 individuals. The vast majority of omitted observations resulted from excess *A. albopictus*. We also omitted vases contaminated by any predatory species (*Corethrella appendiculata*, *Toxorhynchites rutilus*, *Chaoborus* spp.), which resulted in omission of 0 and 3 vases in 1999 and 2000, respectively. The end result was 174 and 147 usable observations in 1999 and 2000, respectively.

Results

Preliminary samples

As anticipated, mean numbers of larvae per vase were significantly ($F_{1, 4.8}=10.65$, $P=0.0235$; nested ANOVA) higher (by 10–200%) in the late rainy season in 2000 than they were in the early rainy season in 1999 (Table 1). Mean numbers of larvae per vase also appeared to be less variable among cemeteries in the late season sample of 2000 (Table 1). Site type (*aegypti* persistence vs *aegypti* extinct), cemetery (type), and all interactions were not significant ($P>0.05$; not shown). At the three persistence sites (Rose Hill, Orange Hill, Ft. Myers), co-occurrence within vases was common, with the majority of vases from 2000 containing both species (Table 1). In both years, proportions of larvae that were *A. aegypti* were similar, ranging from 0.16 to 0.31 (Table 1). Maximum numbers of larvae per vase were very high in both years, typically >2× the baseline density for each cemetery (Table 1)

Survivorship and development

In both the early and late rainy season, for both variables, there was no significant Site Type × Treatment interaction (Table 2), indicating that the effects of *A. albopictus* manipulations on *A. aegypti* performance did not depend

Table 2. Nested ANOVA on survivorship and mean instar at the end of the experiment for both years. Effects significant at $\alpha=0.05$ are indicated in bold type. Because the design includes random effects [Cemetery (Type) and Treatment × Cemetery (Type)] and is unbalanced, *F* tests were done using Satterthwaite's formula (Montgomery 1976), which uses weighted sums of two mean squares to from the denominator for *F*-tests. This results in

noninteger degrees of freedom for the denominator, which are reported to the nearest 0.1 unit. In all cases Satterthwaite's denominator gave greatest weight to the mean squares that would have been appropriate for a balanced design [Cemetery (Type) for the Site Type effect and Treatment × Cemetery (Type) for Treatment, Treatment × Type, and Cemetery (Type) effects] and mean square for error

Source	Early rainy season (June 1999)						Late rainy season (August–September 2000)					
	Survivorship			Mean Instar			Survivorship			Mean Instar		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Treatment	2.62	2, 8.5	0.1298	15.74	2, 8.5	0.0014	8.71	2, 8.4	0.0089	21.27	2, 8.5	0.0005
Site Type	6.43	1, 4.0	0.0640	0.85	1, 4.0	0.4080	3.46	1, 4.2	0.1327	3.31	1, 4.0	0.1423
Treatment × Type	0.32	2, 8.5	0.7321	1.14	2, 8.5	0.3631	0.06	2, 8.4	0.9429	1.39	2, 8.5	0.3006
Cemetery (Type)	8.29	4, 8.2	0.0057	6.63	4, 8.2	0.0113	0.67	4, 8.1	0.6294	6.33	4, 8.2	0.0129
Treatment × Cemetery (Type)	0.73	8, 156	0.6665	0.84	8, 156	0.5708	1.30	8, 129	0.2493	1.10	8, 129	0.3693

Table 3 Nested ANOVA on masses of male and female *A. aegypti* at the end of the experiment in the early rainy season of 1999. Effects significant at $\alpha=0.05$ are indicated in bold type. See Table 2 for explanation of statistical procedures for unbalanced mixed

	Males			Females		
Source	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Treatment	5.07	2, 8.4	0.0359	2.89	2, 10.9	0.0984
Site type	1.42	1, 4.0	0.2991	6.30	1, 4.5	0.0590
Treatment \times Type	0.04	2, 8.4	0.9637	2.09	2, 10.9	0.1707
Cemetery (Type)	2.95	4, 8.3	0.0875	2.79	4, 8.6	0.0955
Treatment \times Cemetery (Type)	2.35	8, 75	0.0275	1.65	8, 57	0.1307

on whether the cemetery was an *aegypti* persistence site or an *aegypti* extinction site. This same conclusion was also reached if the cemeteries were treated as fixed effects in a simple two-way ANOVA (not shown). Thus, for these variables we have no evidence that the fundamental nature of interspecific competition in the aquatic environment differs between these site types. In both early and mid-rainy season, there was a significant effect of Treatment on mean instar, and in the late season (2000) there was also a significant effect of treatment on survivorship (Table 2). Thus, there is strong evidence for an impact of competition from *A. albopictus* on *A. aegypti*, in both the early and late rainy season. Treatment means for mean instar (Fig. 2A) show that in the early rainy season when numbers were low (1999), mean developmental stage was significantly less for the INCREASED treatment than for the CONTROL or REDUCED treatments, which in turn did not differ. In the late rainy season, when numbers were greater (2000), the pattern of pairwise differences was altered, so that mean developmental stage was significantly greater for the REDUCED treatment than for the CONTROL and INCREASED treatments, which in turn did not differ (Fig. 2A). For survivorship, the pattern of differences among treatments for the late rainy season (2000) was similar to that for mean instar (Fig. 2B), with REDUCED yielding significantly greater survivorship than did CONTROL and INCREASED, which did not differ. For the early rainy season (1999) there were no obvious trends in survivorship (Fig. 2B).

The effect of Site Type was not significant for either survivorship or developmental stage in either early or late rainy season (Table 2, Fig. 3), though there was a marginally significant trend toward better survivorship of *A. aegypti* at persistence sites in the early rainy season (1999) (Fig. 3B). Cemeteries varied significantly within types for both variables in the early rainy season (1999) and the late rainy season (2000) (Table 2). Thus, there is considerable variation among cemeteries in the performance of *A. aegypti* in this experiment, however, that variation is not consistently associated with whether *A. aegypti* persists or went extinct at that cemetery. The interaction of Treatment with Cemetery (Type) was never significant (Table 2) indicating once again that effects of the treatments were similar at all sites.

model. Across all six cemeteries there were 93 vases that yielded males and 75 vases that yielded females that were suitable for mass determinations. Across all vases, there were 260 males and 209 females

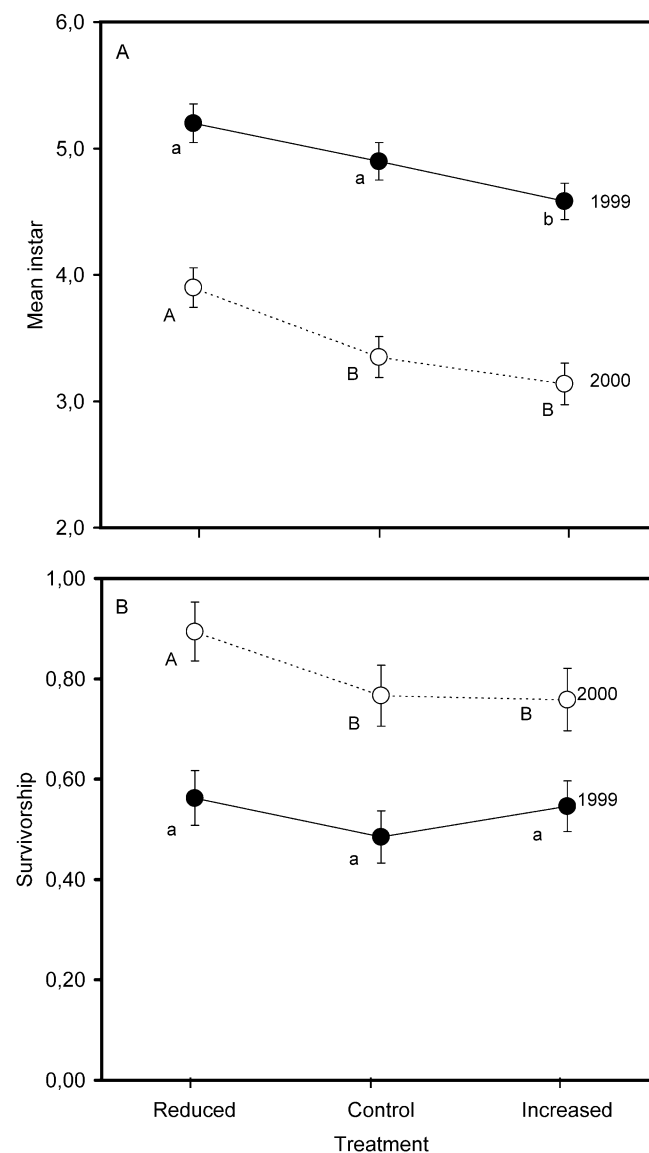


Fig. 2 Least Squares Means (± 2 SE) for competition treatments for **A** mean instar of surviving *A. aegypti* and **B** survivorship of *A. aegypti* in early rainy season (1999) and late rainy season (2000). Means within a year associated with the same letter are not significantly different (Tukey-Kramer test, experimentwise $\alpha=0.05$)

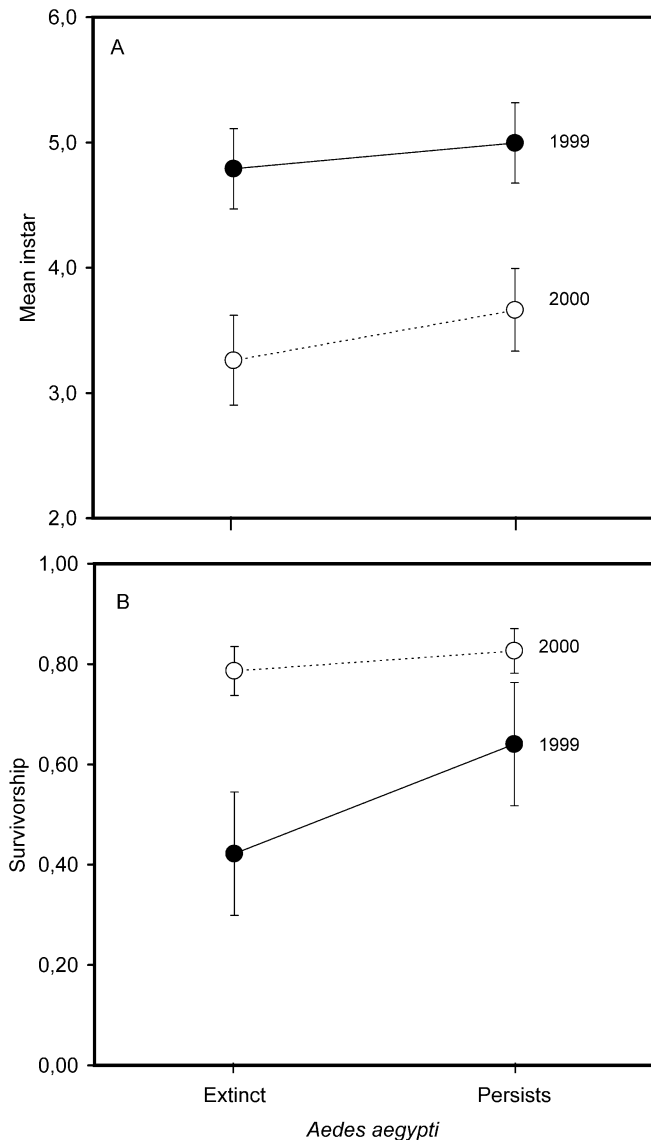
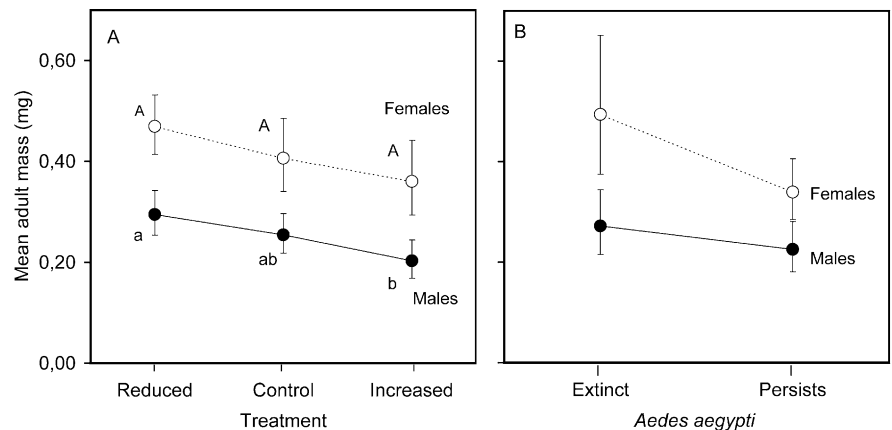


Fig. 3 Least Squares Means (± 2 SE) for each site type for **A** mean instar of surviving *A. aegypti* and **B** survivorship of *A. aegypti* in early rainy season (1999) and late rainy season (2000). Differences between types were not significant (Table 2)

Fig. 4 Least Squares Means (± 2 SE) for mean masses of adult male and female *A. aegypti* **A** within each treatment and **B** within each site type in early rainy season (1999). Means within a sex associated with the same letter are not significantly different (Tukey-Kramer test, experimentwise $\alpha=0.05$)



Mass of adults

The shorter duration of the experiment in the late rainy season (2000) succeeded in minimizing number of adults produced, hence we only analyzed masses of adults in the early rainy season experiment (1999). There was no significant Site Type \times Treatment interaction on either male or female adult mass (Table 3), indicating that the effects of manipulations of *A. albopictus* number on *A. aegypti* adult size did not depend on whether the cemetery was an *aegypti* extinction or persistence site. The same conclusion was obtained when the cemeteries were treated as fixed effects in a two-way ANOVA (not shown). Thus, for adult size we have no evidence that the nature of interspecific competition in the aquatic environment differs between these cemetery types. The effect of treatment was significant for mass of adult males, but not for mass of adult females (Table 3), though there was a marginally significant trend in masses of adult females that was virtually identical to that for males (Fig. 4A). Males were significantly smaller in the INCREASED treatment than in the REDUCED treatment, and the CONTROL treatment was statistically indistinguishable from the other two treatments (Fig. 4A).

The effect of Site Type was not significant for either sex (Table 3), though there was a marginally significant trend toward larger females at *aegypti* extinction sites (Fig. 4B). There was no significant variation due to cemetery (type) in the masses of either males or females (Table 3), though in both cases effects approached significance. There was a significant interaction of Treatment with Cemetery (Type) for males (Table 3) indicating that effects of the treatments on adult mass varied among cemeteries, but as with all other variables, there was no consistent difference between *aegypti* persistence and extinction sites.

Discussion

We addressed two questions in this paper: (1) Is interspecific competition important under typical field conditions? (2) Is there a difference in the impact of competition from *A. albopictus* between *A. aegypti* extinction and persis-

tence sites? We have obtained unambiguous answers for both questions.

The effect of interspecific competition from *A. albopictus* is evident in experiments in both early and late rainy season, though it is more obvious, and affects more performance variables (survivorship, mean instar) in the late rainy season (2000) experiment, when numbers of *Aedes* per vase are typically higher. Numbers of larvae per vase in this experiment were determined by the observed numbers of immatures in the field containers prior to the experiment; hence we have shown that interspecific competition has an impact under typical field conditions. Further, there are several lines of evidence that suggest that increasing number per vase in the field increases the intensity of the impact of competition, as predicted. First, we note that numbers of larvae/vase in the late rainy season (2000) were significantly greater (by up to 2×) than in the early rainy season (1999), and that effects of competition on survivorship of *A. aegypti* were only evident at the greater numbers of 2000. The effect on survivorship is particularly important as survivorship is the life history variable most closely associated with fitness (Juliano 1998) and most directly related to potential for local extinction of a species. Second, the pattern of differences among treatment means for mean instar in the two seasons also suggests greater competitive effect at higher density. In the early rainy season (1999), only the INCREASED treatment yielded significant negative effects on mean instar, however in the late rainy season (2000) both CONTROL and INCREASED yielded significant negative effects, relative to REDUCED, on mean instar. Thus, the apparent impact of competition appears to vary seasonally, and is associated with number of immatures/vase. In addition to these effects, mean mass of males differed between REDUCED and INCREASED. A similar, nonsignificant trend was present in females, and the apparent difference in effects of competition on the two sexes may simply be a result of greater variability of female mean masses (see Fig. 4), resulting in lower statistical power to detect effects on female mass. Previous field surveys have supported the premise that competition is an important process in nature for these species (e.g., Juliano 1998); however, the present results provide the most convincing demonstration that interspecific competition has important effects on these mosquitoes in South Florida. This is consistent with the hypothesis that competition from *A. albopictus* has contributed to the declines in *A. aegypti* in southern North America.

Our results are equally clear concerning the hypothesis that the competitive effect of *A. albopictus* on *A. aegypti* is different at sites of persistence versus extinction of *A. aegypti*. This hypothesis makes a clear prediction: there should be a significant treatment × type interaction, with the impact of competition from *A. albopictus* less at sites where the two species now coexist. For all variables, in both parts of the rainy season, the treatment × type interaction was not significant, hence we find no evidence supporting this hypothesis. Thus it appears that when these two species compete in South Florida cemetery vases, the

fundamental effects of competition are the same. This suggests that there is no systematic difference in the conditions of the larval habitat that determines whether coexistence or exclusion is the outcome of competition. As suggested by Juliano et al. (2002) and Fontinille and Rodhain (1989), the pattern of local abundance and co-occurrence of these species may be determined by environmental differences that impinge on the adult and egg stages (e.g., desiccation), rather than by variation in the outcome of competition among aquatic larvae. This apparent lack of variation in the impact of competition contrasts with the conclusions reached by Juliano (1998), that there was evidence that competition had a greater impact at sites where *A. aegypti* had been driven extinct compared to those where coexistence occurred. Juliano (1998) based this conclusion on variation in masses of field collected *A. albopictus* pupae, which were significantly heavier at sites where *A. aegypti* persists than at sites where *A. aegypti* has gone extinct. That observational study, necessarily, could not compare the impact of *A. albopictus* on *A. aegypti* at both types of sites, because of the absence of *A. aegypti* at extinction sites. Further, Juliano's (1998) result is a product of nonexperimental surveys, and is thus affected by many uncontrolled variables. The present experimental results show the impact of controlled *A. albopictus* numbers is similar at both persistence and extinction sites, and is therefore more conclusive. There was some suggestion of differences in *A. aegypti* performance with site type. Survivorship of *A. aegypti* was greater at persistence sites in 1999 (but not in 2000), but female mean mass was less at persistence sites in 1999. Though nonsignificant, these results suggest *A. aegypti* life histories may differ in complex ways between persistence and exclusion sites. These nonsignificant effects do not indicate differential impacts of competition at the two types of sites. Nevertheless, if there are correlated differences in survivorship and growth rates between site types, even if these effects only occur in some years, the likelihood of persistence by *A. aegypti* could be affected. Our experiments provide, at best, limited support for this proposed difference, and further investigation is needed.

The similarity of competitive impacts across these sites is also consistent with other observations on this species pair across a wider geographic area (Juliano 1998; Braks et al. 2004). Braks et al. (2004) showed in a field experiment in Brazil that the effects and results of interspecific competition between strains of these species from Rio de Janeiro, Brazil, were virtually identical to the effects observed by Juliano (1998) in a field experiment in Vero Beach, Fla., using South Florida strains of both species. The similarity of the results of competition experiments by Juliano (1998) and Braks et al. (2004) is striking because the Brazilian and North American populations of introduced *A. albopictus* originated from different parts of Asia (Birungi and Munstermann 2002). In those two studies, and in the present experiments, the substrates present in field containers were predominantly deciduous tree leaves, and Barrera (1996) showed that deciduous leaves as a

microbial substrate provide an environment that is more favorable to *A. albopictus* in competition with *A. aegypti*. Barrera (1996) also suggested that other substrates may favor *A. aegypti*, and Daugherty et al. (2000) provided some evidence for this in a laboratory experiment. Thus, although we have found no evidence for local variation in the outcome of competition, there is a need to survey natural containers for the presence and relative abundances of different detrital substrates (e.g., tree leaves, coniferous needles, grass, animal carcasses), and to determine whether variation in the relative abundances of these substrates may be contributing to extinction versus persistence of *A. aegypti*. Lounibos et al. (2002) showed in the laboratory that temperature in the 24–30°C range had no detectable effect on the outcome of competition between these species. The temperatures used by Lounibos et al. (2002) probably encompass the range of temperatures in the present field experiments, and in those done by Juliano (1998) and Braks et al. (2004).

The present experiment, and indeed all other field experiments on competition in these species (Braks et al. 2004; Juliano 1998), has excluded effects of other aquatic invertebrates that may modify the competitive interaction of *A. aegypti* and *A. albopictus*. Lounibos et al. (2001) showed that the presence of predatory larvae of *T. rutilus* is likely to affect competition between *A. albopictus* and *O. triseriatus*, and this may contribute to the relatively limited effects of invading *A. albopictus* on the distribution and abundance of *O. triseriatus* in Florida, particularly in tree holes (Lounibos et al. 2001). Predators like *T. rutilus* and *C. appendiculata* seem to be relatively rare in cemetery vases, tires, and more urban containers in south Florida (Frank 1981; O'Meara et al. 1995; personal observation), but there has been relatively little systematic investigation of the question of the potential effects of predators in modifying interspecific competition in these habitats. Although there has been considerable interest in the impact of parasitic protozoa in the genus *Ascogregarina* on the competitive interaction of *A. albopictus* and *A. aegypti* (e.g., Blackmore et al. 1995) both observational (Garcia et al. 1994) and experimental (Juliano 1998) evidence suggests that *Ascogregarina* play, at best, a secondary role in determining the outcome of this invasion.

Past field and laboratory experiments (Barrera 1996; Juliano 1998; Daugherty et al. 2000) have shown that when larvae of *A. albopictus* and *A. aegypti* compete, it is *A. albopictus* that has the competitive advantage, indicating that competition could be the mechanism producing decline and extinction of *A. aegypti* populations in southern USA (Hornby et al. 1994; O'Meara et al. 1995; Hobbs et al. 1991; McHugh 1993; Mekuria and Hyatt 1995; Harrison et al. 1998). The present field experiments, conducted at sites of interaction, show clearly that competition is strong under field conditions, further strengthening the case for interspecific competition as the mechanism causing declines of *A. aegypti*. Our present results did not indicate a difference in the intensity of competition between sites of persistence versus extinction,

leaving unanswered the question of what enables these species to coexist at some sites and not at others. An answer to this question must explain both why coexistence occurs most commonly in warmer, seasonally dry sites (Juliano et al. 2002), and in urban areas (O'Meara et al. 1995; D. Wesson, personal communication). Differential effects of climate on survivorship of eggs (e.g., Juliano et al. 2002; Sota and Mogi 1992a, 1992b), and adults (Mogi et al. 1996) of these two species are well documented and probably account, in part, for coexistence in warmer, seasonally dry sites. Though various explanations have been proposed for the persistence of *A. aegypti* in urban environments (Juliano 1998), there have been no convincing experimental tests of hypotheses for variation along the urban-rural gradient. Availability of preferred human hosts (Harrington et al. 2001; Braks et al. 2003), and metapopulation dynamics in an urban landscape (Hanski 1999) are among the explanations of persistence of urban *A. aegypti* that merit investigation.

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