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Spatial and temporal patterns of coexistence between competing *Aedes* mosquitoes in urban Florida

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Abstract Understanding mechanisms fostering coexistence between invasive and resident species is important in predicting ecological, economic, or health impacts of invasive species. The mosquito *Aedes aegypti* coexists at some urban sites in southeastern United States with invasive *Aedes albopictus*, which is often superior in interspecific competition. We tested predictions for three hypotheses of species coexistence: seasonal condition-specific competition, aggregation among individual water-filled containers, and colonization–competition tradeoff across spatially partitioned habitat patches (cemeteries) that have high densities of containers. We measured spatial and temporal patterns of abundance for both species among water-filled resident cemetery vases and experimentally positioned standard cemetery vases and ovitraps in metropolitan Tampa, Florida. Consistent with the seasonal condition-specific competition hypothesis, abundances of both species in resident and standard cemetery vases were higher early in the wet season (June) versus late in the wet season (September), but the proportional increase of *A. albopictus* was greater than that of *A. aegypti*, presumably due to higher dry-season egg mortality and strong wet-season competitive superiority of larval *A. albopictus*. Spatial partitioning was not evident among cemeteries, a result inconsistent with the colonization-competition tradeoff hypothesis, but both species were highly independently aggregated among standard cemetery vases and ovitraps, which is consistent with the aggregation hypothesis. Densities of *A. aegypti* but not *A. albopictus* differed among land use categories, with *A. aegypti* more abundant in ovitraps in residential areas compared to industrial and commercial areas. Spatial partitioning among land use types probably results from effects of land use on conditions in both terrestrial and aquatic-container environments. These results suggest that both temporal and spatial variation may contribute to local coexistence between these *Aedes* in urban areas.

Keywords Aggregation · Coexistence · Condition-specific competition · Spatial partitioning

Introduction

Ecological theory and empirical work indicate that competition should result in competitive exclusion when resources are limited. However, competitive exclusion may be avoided via a number of mechanisms, including differential resource use (e.g., Tilman 1982), temporally varying condition-specific competition (e.g., Chesson 2000a), and colonization-competition tradeoff across a patchy environment (e.g., Calcagno et al. 2006). Understanding mechanisms of coexistence is particularly interesting in the context of biological invasions. Competitively superior invasive species may impact resident species without causing extinction of residents over their entire introduced range (e.g., Juliano and Lounibos 2005). Testing hypotheses for mechanisms contributing to local or spatially patterned coexistence of invasive and resident species is important for predicting future ecological,

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economic, or health impacts of invasive species, and tests our understanding of the general mechanisms by which competing species coexist.

The Asian Tiger mosquito, *Aedes albopictus*, is native to Asia and has invaded North and South America, Europe, and Africa in the past two decades (see Juliano and Lounibos 2005, and references therein). This species is well studied (Lounibos 2002) and provides us with an opportunity to determine whether patterns of coexistence with natives in its new range are consistent with any of these coexistence mechanisms. *Aedes albopictus*, along with many of its competitors, are vectors of arboviruses, including dengue, La Crosse encephalitis, and West Nile virus (Gerhardt et al. 2001; Ibañez-Bernãl et al. 1997; Turell et al. 2005), and understanding mechanisms of coexistence of these vectors is of some human health importance.

Most laboratory (e.g., Barrera 1996; Daugherty et al. 2000) and field (Juliano 1998) studies show convincingly that larval *A. albopictus* are superior competitors for resources compared to *A. aegypti*, the resident species it encounters most frequently in the Americas. This competitive superiority is the likely mechanism for displacement of *A. aegypti* in some locations in the field (Juliano 1998; Juliano et al. 2004). However, despite this frequently observed competitive advantage for *A. albopictus*, *A. aegypti* manages to coexist with invading *A. albopictus* at some sites in the southeastern United States (Juliano et al. 2004; O'Meara et al. 1995).

A number of hypotheses could explain the persistence of *A. aegypti* after the invasion of *A. albopictus* at some sites. Here we focus on three alternative (but not mutually exclusive) hypotheses that seem likely to be testable using field data. One hypothesis is condition-specific competition, wherein the outcome of competition is altered or reversed under different biotic conditions. When there is temporal or spatial variation in abiotic environments, and when species respond differently to those environments, the competitive outcome can be altered and coexistence can result (Chesson 2000a). A second hypothesis is a colonization-competition tradeoff, wherein species coexist in patchy environments when the superior ability to disperse among patches prevents local and regional exclusion of competitively inferior species (Amarasekare and Nesbit 2001; Calcagno et al. 2006). A third hypothesis is aggregation, in which species coexist because of spatial separation. Such spatial separation due to independent aggregation is most likely to arise due to attraction of competitors to different environmental conditions that have some spatial independence (Ives 1988; Chesson 2000b; Hartley and Shorrocks 2002). Some of the conditions necessary for the coexistence mechanisms postulated by these hypotheses are present in this system.

Condition-specific competition between these *Aedes* mosquitoes has been observed in the laboratory (Costanzo et al. 2005). Experimental manipulation of container drying regime in laboratory colonies shows that, in dry conditions, *A. albopictus* suffers a greater interspecific density effect than does *A. aegypti*, whereas under wetter conditions, *A. aegypti* suffers a greater interspecific density effect than does *A. albopictus* (Costanzo et al. 2005). Under dry conditions, *Aedes albopictus* eggs suffer greater mortality than do *A. aegypti* eggs (Costanzo et al. 2005). This paradoxical effect of differential mortality of eggs likely arises because mortality affects R^*, the level of resources (in this case, for larvae) necessary to produce zero net population growth (Tilman 1982). For resource competition, advantage is determined by R^* (Tilman 1982). Abiotic conditions that differentially affect mortality, even in non-competing life-stages like eggs, can alter the outcome of interspecific competition by differentially changing species' R^*s (Chase and Leibold 2002; Costanzo et al. 2005). The southern part of the Florida peninsula experiences a distinct cycle of rainy and dry seasons (Juliano et al. 2004), and field data show that *A. albopictus* and *A. aegypti* coexist most commonly in warmer, seasonally dry sites in South Florida (Juliano et al. 2002). For coexistence to occur under this circumstance, environments must fluctuate between conditions favoring the different species, and there must be resistant life stages (e.g., dormant eggs) that persist through times when a species is at a disadvantage (Chesson 2000a). Together, these field and laboratory results suggest that condition-specific competition due to temporally varying drying regime, along with storage of resistant eggs is a potential mechanism for coexistence in southern Florida.

Some of the conditions required for a colonization-competition tradeoff are met by the environment in which *A. albopictus* and *A. aegypti* interact. These species are more likely to coexist in urban areas of Florida (O'Meara et al. 1995; Rey et al. 2006), and in urban areas high densities of water-filled containers appear to be patchy and associated with certain local land uses, such as cemeteries containing flower vases (O'Meara et al. 1995) that may act as discrete patches of habitat. A poorer competitor in a metapopulation may escape local and regional exclusion if it has a superior ability to colonize newly vacant, sparsely populated, or even well-occupied individual containers or patches (Amarasekare and Nesbit 2001; Calcagno et al. 2006).

A similar mechanism for coexistence on patchy resources is invoked in the aggregation hypothesis (Chesson 2000b; Hartley and Shorrocks 2002), which predicts coexistence if the competing stage of the competitively superior species is aggregated over divided, ephemeral resources, independently of the competitively inferior species. Aggregation is most likely to be effective in this way when species are attracted to different, spatially independent environmental cues, which is a form of spatial

resource partitioning (Chesson 2000b), though some (Hartley and Shorrocks 2002) have argued that if random aggregation is sufficiently strong, competitors could be more influenced by intraspecific competition than interspecific competition, resulting in coexistence (see Chesson 2000b; Hartley and Shorrocks 2002, for caveats about the conditions necessary to produce coexistence via this mechanism).

In this paper, we test whether temporal and spatial distributions of immature *A. albopictus* and *A. aegypti* in metropolitan Tampa, Florida, are consistent or inconsistent with these three hypotheses for coexistence of *A. aegypti* with invading *A. albopictus*. Metropolitan Tampa is ideal for such tests because it has numerous sites with water-filled containers (cemeteries) within a few kilometers of one another, and because these species have coexisted at some sites in metropolitan Tampa for over 15 years (G.F. O'Meara, unpublished data), suggesting stability. Because our investigation is observational, it is but the first step in evaluating these hypotheses; however, our hypotheses lead to testable predictions about the distribution and abundance of these *Aedes* in Tampa for each coexistence hypothesis:

1. Condition-specific competition predicts strong seasonal patterns of coexistence with both species predicted to be more abundant late in the wet season (May–October—see http://www.dnr.state.sc.us/climate/sercc/climateinfo/historical/historical_fl.html), after a lengthy period of wet conditions, but with the proportional increase of *A. albopictus* from early to late wet season expected to be greater than that of *A. aegypti* due to high dry-season (November–April) egg mortality and strong wet-season competitive superiority of *A. albopictus*.

2. Spatial partitioning and a colonization-competition trade-off across cemeteries predicts highest abundances of *A. albopictus* and *A. aegypti* in cemeteries compared to non-cemetery urban sites.

3. The aggregation hypothesis of coexistence among individual containers predicts that *A. albopictus* and *A. aegypti* distributions will be aggregated among containers and independently associated with one another.

Materials and methods

Three discrete areas in metropolitan Tampa (Tampa, St. Petersburg, and Bradenton), all separated by Tampa Bay, were selected for study. These areas have a number of cemeteries within an 8 km radius (Tampa, $n = 10$; St. Petersburg, $n = 5$; and Bradenton, $n = 4$). Other sites with high densities of container habitats, such as tire yards, were present in each area but preliminary observations

suggested that few had long-standing piles of tires outside that would fill with water and provide larval mosquito habitat. Thus, we decided not to survey tire yards in this study. Habitat between cemeteries (hereafter 'urban matrix') is characterized by a high density of human-created structures, but also includes diverse vegetation, and residential, commercial, and industrial land use.

In the early rainy season (June) in 2006, we placed five standard green cemetery vases within each cemetery and three other randomly chosen parts of the urban matrix, to obtain estimates of oviposition activity at each site. Each cemetery and urban site was divided into five equally sized blocks, and one vase was placed in the shade as close to a randomly selected point within each block as possible. Most occupied vases at cemeteries are partially shaded (O'Meara et al. 1995). Vases were provisioned with 0.70 g oak (*Quercus virginiana*) leaves and filled 400 ml deionized water, providing roughly natural amounts of leaves, which form the resource base in resident vases. A Masonite paddle was clipped to the inside of each vase as an oviposition substrate. Holes were drilled in vases just above the waterline to prevent vase flooding.

After sufficient time for mosquitoes to oviposit (10 days), we collected the vases and removed and counted all larvae and pupae. Paddles from all vases were stored under humid conditions for 10 days, and then eggs were synchronously hatched in a solution of 0.44 g nutrient broth/l deionized water. Numbers of field-collected larvae and pupae and laboratory-hatched larvae were summed by species to quantify the relative abundances of each species at these sites.

In addition to vase ovitrapping, which measures pre-interaction habitat choice, we also sampled the presence/absence of larvae and pupae in resident vases at each cemetery in Tampa to examine the distribution of *Aedes* among containers after community interactions. Three sample points within each block at a cemetery were randomly chosen and the closest shaded wet vase to each point sampled (3 vases × 5 blocks = 15 total vases). No samples were taken from bronze vases or vases lined with copper because of their toxicity to *Aedes*, or from vases with cut flower arrangements, as the arrangements usually decay rapidly, fouling the water, and rarely do such vases support *Aedes* larvae (O'Meara et al. 1995). Mosquitoes were collected from vases by either extracting the water with a kitchen baster, or, when possible, by dumping the contents (Juliano et al. 2002; O'Meara et al. 1995). The contents of vases were sieved and examined for the occupancy of *A. albopictus* and *A. aegypti*.

During the late rainy season (September) in 2006, we repeated our sampling of standard green vases and resident vases in cemeteries and standard vases in non-cemetery urban sites in Tampa only. Because June data indicated

substantial oviposition of *Aedes* in urban sites (see Results), we undertook a new sampling approach to relate urban land use to *Aedes* oviposition. A 6 × 10 km area encompassing the ten cemeteries in Tampa was divided into 60 1 km^2 grid cells. Three oviposition traps were placed in shade near the center of each cell. Ovitraps were placed at ground level and within 20 m of one another (180 total traps). Sample sites were categorized as residential, commercial, or industrial according to the Florida Land Use Cover Classification System (FLUCCS, Geographic Mapping Section 1999) of the South West Florida Water Management District (http://www.swfwmd.state.fl.us/data/gis/layer_library/category/physical_dense).

Ovitraps consisted of black plastic cups (400 ml), with holes drilled 4 cm from the base to prevent flooding and hatching of *Aedes* eggs. Ovitraps were lined with seed germination paper (Nasco Science, Fort Atkinson, WI), filled with 225 ml deionized water, and baited with an additional 25 ml grass/oak leaves (72 g senescent live oak leaves and 36 g Zoisa grass in 5.4 l deionized water for 3 days). Ovitraps at alternating sampling sites were set out over 3 days, with 20, 18, and 22 sites being provisioned with traps on each successive day. The relatively small size and inconspicuous color of these ovitraps was expected to minimize chances of them being disturbed in areas of relatively high human activity, and has been used in previous oviposition surveys in urban landscapes (Rey et al. 2006). After 10 days, ovitraps were collected and all larvae identified. Germination paper from each ovitrap was stored in humid conditions for 10 days, then immersed in nutrient broth solution to hatch *Aedes* eggs. Numbers of field-collected larvae and pupae and laboratory-hatched larvae were summed by species. All larvae and pupae from standard green vases, resident vases, and black ovitraps were reared to 4th instar to facilitate identification and stored in 70% ethanol for later examination in the laboratory.

Aggregation at the level of the competing stages (measured as eggs and early instar larvae) could result from two processes: aggregation of female oviposition visits and deposition of eggs aggregated in clutches (Hartley and Shorrocks 2002). Considerable debate has occurred on which of these two processes is most important in facilitating coexistence (see Heard and Remer 1997; Hartley and Shorrocks 2002 for a discussion). Recent models indicate that a model incorporating both processes allows coexistence, and that a model in which ovipositing females are randomly distributed and clutches are the only source of aggregation can produce coexistence if interspecific competition is partially reduced by some form of within-patch resource partitioning (Hartley and Shorrocks 2002). We, like most prior studies on Diptera in patchy and ephemeral systems (see Chesson 2000b, Hartley and Shorrocks 2002),

test only whether competing stages are aggregated, and do not attempt to separate aggregation of ovipositing females from aggregation due to multi-egg clutches.

Statistical analyses

Numbers of resident cemetery vases occupied vs unoccupied in early and late season were analyzed using paired *t*-tests. Abundances of each species in standard green vases and ovitraps were analyzed using four nested ANOVAs. In the first ANOVA on vase data from Tampa, Season (June, September), Site Type (cemetery, urban site) and Interaction were fixed effects, and Site nested within Site Type and Season × Site nested within Site Type were random effects because we want to draw inferences about the population of sites (cemetery or urban) where *Aedes* might oviposit. In the second and third ANOVAs on St Petersburg and Bradenton vase data, respectively, Site Type (cemetery, urban site) was a fixed factor and Site nested within Site Type was a random factor. In the fourth ANOVA on Tampa ovitrap data, Land Use (residential, commercial, and industrial) and Date were fixed factors and Site nested within Land Use was a random factor. A preliminary analysis revealed that Date was not significant, and it was removed from the model. Significant differences between individual Land Uses were tested a posteriori by Tukey's test. All ANOVAs were unbalanced because of trap loss, hence denominator mean squares were calculated using Satterthwaite's formulas (SAS Institute 2003), resulting in non-integer degrees of freedom. For all analyses of abundances, proportions were arcsine-square-root transformed and abundance data were square-root transformed to meet assumptions of normality and homogeneity of variances.

Associations between *A. albopictus* and *A. aegypti* among resident cemetery vases and green vases were tested using Mantel-Haenszel tests on multiple 2 × 2 tables (Sokal and Rohlf 1995). Mantel-Haenszel tests control for site effects even when individual sites contain few observations as long as the overall sample size is adequate. Fisher's Exact tests were used to test species associations among black ovitraps. Low sample sizes of each species prevented controlling for site when testing for the aggregation of each species, thus departures of randomness were investigated by pooling data from all sites and using χ^2 goodness-of-fit tests for Poisson distribution. The ratio of variance to mean ($s^2/\overline{Y}$) was used to indicate the nature of any departure from Poisson expectation. ANOVAs on data from standard green vases tested for significant differences between sites using pairwise contrasts, with sequential Bonferroni correction for all possible comparisons (19) within each analysis. The results of these ANOVAs identified sites with significantly greater abundances, which

were then removed from χ^2 goodness-of-fit tests to control for site density differences. These modified tests gave similar conclusions and are not reported. Frequency classes were grouped until all frequencies were greater than 2. Other grouping criteria (>5 and >0.05) were also tested, but yielded similar conclusions and are not reported.

Results

Aedes albopictus and *A. aegypti* were the most frequent species sampled in resident cemetery vases, being collected from 31.9% (84/263) and 24.3% (64/263) vases, respectively (Table 1). The third most common taxon was *Culex* spp., collected from only 15 vases (5.7%). *Aedes albopictus* and *A. aegypti* also were the most common species collected in our experimentally placed standard vases (pooled data across sites, *A. albopictus*: 65.5%, 1650/2518; *A. aegypti*: 18.1%, 455/2518) and ovitraps (*A. albopictus*: 66.7%, 3131/4695; *A. aegypti*: 32.2%, 1513/4695). All other mosquito species (*Aedes triseriatus*, *Toxorhynchites rutilus*, *Anopheles* sp., *Uranotaenia* sp.) collected from resident vases, standard vases, and ovitraps constituted less than 1% of the total number of individuals.

Seasonal patterns relating to condition-specific competition

As predicted, the proportions of occupied resident vases in Tampa cemeteries were significantly greater in the late rainy season compared to the early rainy season for both *A. aegypti* ($t = -2.76$, $P < 0.022$) and *A. albopictus* ($t = -5.73$, $P < 0.0001$) (Table 1). In the early rainy season, more vases were occupied by *A. aegypti* than *A. albopictus*, but in the late season *A. albopictus* was more frequent (Table 1). When pooling data across all cemeteries, the proportion increase in vase occupancy from early to late season was clearly greater for *A. albopictus* (485%, 0.553/0.114) than *A. aegypti* (290%, 0.374/0.129).

Compared with resident vases, proportions of standard green vases in Tampa that were occupied by *A. albopictus* and *A. aegypti* showed similar seasonal trends, although proportions for some individual cemeteries (e.g., June at Orange Hill) differed considerably (Table 1). When pooling data from resident and standard vases, *A. albopictus* was collected from two cemeteries and *A. aegypti* from one cemetery during September at which they were not collected during June (Table 1). Neither species was sampled at a cemetery in June and then not found in either resident or standard vases in September.

ANOVAs on Tampa data showed significantly higher densities of both species in standard vases in the late rainy season compared to early in the rainy season (Table 2, Fig. 1). There was no significant interaction between season and site type, indicating that the season effect was consistent between cemeteries and urban sites.

Spatial patterns among habitat patches

ANOVAs on Tampa data showed no difference in abundances for both species between cemeteries vs urban sites (Table 2, Fig. 1). Non significant differences between cemeteries and urban sites in the abundances of both species were also seen in June in both St. Petersburg and Bradenton (Table 2).

Consistent with results from standard green vases, most individual ovitraps from Tampa in the late rainy season were colonized by *Aedes* (73.5%, 97/132). When data were grouped by sample site, only 12.5% (7/56) of sites had no *Aedes*. *Aedes albopictus* was collected in relatively similar numbers in different types of land use, whereas *A. aegypti* was collected predominantly from residential sites and never collected from commercial sites (Fig. 2). Abundance of *A. aegypti* but not *A. albopictus* differed significantly among land use types (Table 2). Multiple pairwise comparisons showed that *A. aegypti* oviposition was greater in residential sites compared with commercial and industrial sites ($P = 0.0234$), but not different between commercial and industrial sites ($P = 0.2344–0.5678$) (Fig. 2).

Spatial patterns among individual containers

Aedes albopictus and *A. aegypti* were significantly negatively associated in resident cemetery vases in both June and September, but not green cemetery vases or black ovitraps (Table 3). Both species were highly significantly aggregated among green vases and black ovitraps (Table 4).

Discussion

Although *A. albopictus* is usually superior in competition to *A. aegypti*, these species coexist at some sites in the southeastern United States, including metropolitan Tampa. The results of this field study in metropolitan Tampa show clear patterns in temporal and spatial abundances of *A. aegypti* and *A. albopictus* that are consistent with seasonal condition-specific competition and local aggregation as potential mechanisms of coexistence.

The proportion of resident cemetery vases that were occupied by *Aedes* and numbers of larvae in standard green vases were significantly greater late in the rainy season compared to early in the rainy season for both species. This result is consistent with numerous studies showing that the seasonal patterns of abundance of both *A. albopictus*

Table 1 Numbers of resident vases and experimentally positioned standard vases (in parentheses), and proportions of vases, occupied by immatures of *Aedes albopictus* and *Aedes aegypti* at each cemetery in Tampa
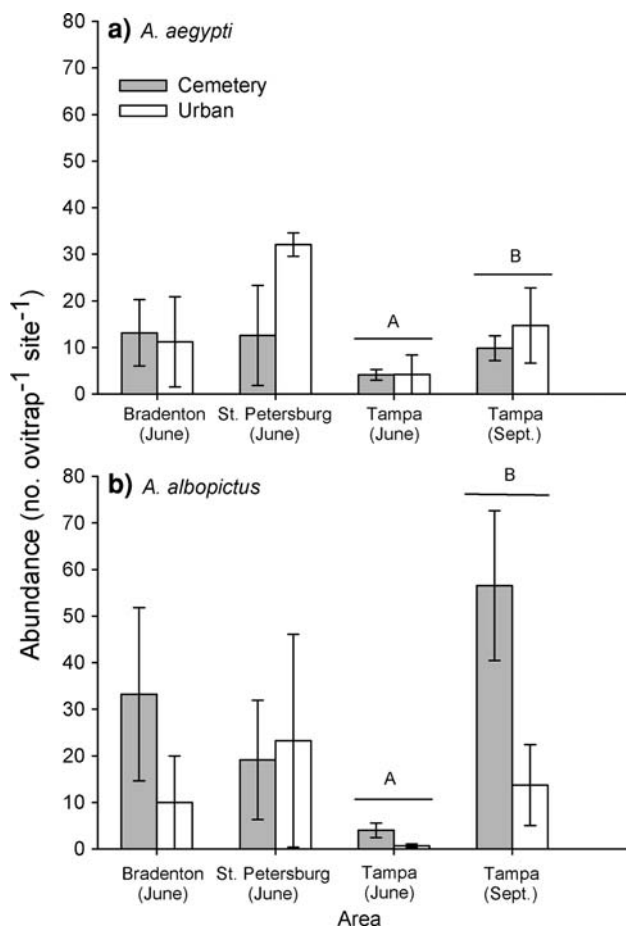
	Number of vases sampled	*A. albopictus* only	*A. aegypti* only	*A. albopictus* and *A. aegypti*	Neither	Proportion *A. albopictus*	Proportion *A. aegypti*
Early rainy season (June)							
American Legion	9 (5)	0 (0)	2 (1)	0 (0)	7 (4)	0 (0)	0.222 (0.200)
Centro Asturiano	15 (5)	1 (1)	0 (0)	0 (0)	14 (4)	0.067 (0.200)	0 (0)
Marti Cemetery	15 (5)	0 (0)	3 (1)	1 (0)	11 (4)	0.067 (0)	0.267 (0.200)
Myrtle Hill	15 (5)	1 (2)	1 (0)	1 (0)	12 (3)	0.133 (0.400)	0.167 (0)
N25	15 (4)	1 (2)	0 (0)	1 (0)	13 (2)	0.133 (0.500)	0.067 (0)
Oaklawn	11 (4)	0 (0)	2 (1)	0 (0)	9 (3)	0 (0)	0.222 (0.250)
Orange Hill	15 (4)	1 (1)	0 (1)	0 (1)	14 (1)	0.067 (0.500)	0 (0.500)
Rose Hill	15 (4)	4 (0)	1 (0)	1 (0)	9 (4)	0.333 (0)	0.111 (0)
Shady Grove	15 (5)	0 (0)	0 (0)	1 (1)	14 (4)	0.067 (0)	0.067 (0.200)
Woodlawn	15 (5)	1 (0)	2 (3)	2 (1)	10 (1)	0.200 (0.200)	0.133 (0.600)
Early total	140 (46)	9 (6)	11 (7)	7 (3)	113 (30)	0.114 (0.196)	0.129 (0.217)
Late rainy season (Sept)							
American Legion	9 (4)	0 (1)	5 (1)	2 (0)	2 (2)	0.222 (0.250)	0.778 (0.250)
Centro Asturiano	13 (4)	5 (3)	0 (0)	2 (1)	6 (0)	0.538 (1.000)	0.154 (0.250)
Marti Cemetery	15 (5)	0 (0)	3 (1)	1 (0)	11 (4)	0.067 (0)	0.067 (0.200)
Myrtle Hill	13 (5)	6 (3)	0 (0)	5 (2)	2 (0)	0.846 (1.000)	0.385 (0.400)
N25	15 (5)	5 (3)	0 (0)	0 (2)	10 (0)	0.333 (1.000)	0 (0.400)
Oaklawn	10 (5)	1 (3)	1 (0)	7 (2)	1 (0)	0.800 (1.000)	0.800 (0.400)
Orange Hill	11 (4)	4 (1)	0 (0)	1 (2)	6 (1)	0.455 (0.750)	0.091 (0.500)
Rose Hill	12 (5)	5 (1)	1 (0)	6 (3)	0 (1)	0.917 (0.800)	0.583 (0.600)
Shady Grove	12 (5)	6 (2)	0 (0)	2 (2)	4 (1)	0.667 (0.800)	0.167 (0.400)
Woodlawn	13 (5)	1 (0)	1 (0)	9 (3)	2 (2)	0.769 (0.600)	0.769 (0600)
Late total	123 (47)	33 (17)	11 (2)	35 (17)	44 (11)	0.553 (0.723)	0.374 (0.404)

A total of 17, 3, and 1 standard green vases from Tampa (both seasons), St. Petersburg, and Bradenton, respectively, were either lost or damaged. Lack of wet vases sometimes yielded samples of fewer than 15 resident vases in a cemetery

Table 2 Nested ANOVAs on abundance of *A. aegypti* and *A. albopictus* in standard green vases from Tampa, St. Petersburg, and Bradenton and black ovitraps from Tampa
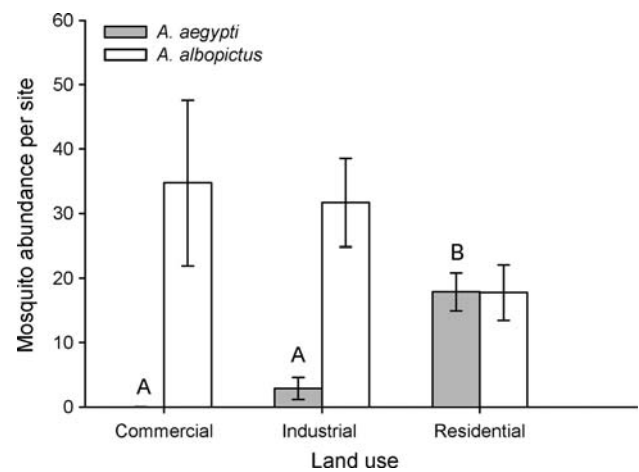
	A. aegypti			*A. albopictus*		
	df	F	P	df	F	P
Standard green vases						
Tampa						
Season	1, 12.8	17.94	0.0010*	1, 11.7	13.65	0.0032*
Site type	1, 12.5	1.01	0.3344	1, 11.6	1.95	0.1886
Season × site type	1, 13.1	0.97	0.3432	1, 11.8	1.23	0.2891
Site (site type)	11, 11	1.38	0.3019	11, 11	1.33	0.3238
Season*site (site type)	1, 13.1	0.92	0.3432	1, 11.8	1.23	0.2891
St. Petersburg						
Site type	1, 5.9	0.15	0.7147	1, 5.9	0.51	0.5012
Site (site type)	6, 29	4.47	0.0025*	6, 26	4.31	0.0032*
Bradenton						
Site type	1, 5.0	0.92	0.3806	1, 5.0	0.17	0.7003
Site (site type)	5, 27	2.54	0.0521*	5, 27	3.29	0.0190*
Black ovitraps in Tampa						
Land use	2, 69.3	12.64	<0.0001*	2, 64.4	1.96	0.1495
Site (land use)	54, 75	1.51	0.0499*	54, 75	2.22	0.0007*

A total of 48 black ovitraps were lost (26.7%) during the Tampa-wide study in September, including all three traps at four grid cells, giving a total of 56 replicated sample areas

* Significant effect

Fig. 1 Abundance (mean ± SE) of **a** native *Aedes aegypti* and **b** invasive *Aedes albopictus* collected in standard green vases in cemeteries (*grey bars*) or urban areas (*white bars*) from metropolitan Tampa, Florida in 2006: Bradenton and St. Petersburg in June and Tampa in June and September. Significant (*P* < 0.05) differences between June and September was found for both species in Tampa, denoted by different letters above bars

Fig. 2 Abundance (mean ± SE) of *A. aegypti* and *A. albopictus* collected in ovitraps from commercial, industrial or residential land use sites in Tampa. Significant (*P* < 0.05) differences between types of land use was found only for *A. aegypti,* determined a posteriori by Tukey's test and denoted by different letters above bars

Table 3 Association of *A. albopictus* and *A. aegypti* using Mantel-Haentzel tests for resident cemetery vases and standard green cemetery vases, and Fishers Exact tests for black ovitraps

Data set	χ^2	*P*
Resident vases in Tampa		
June	12.30	0.0005*
September	8.55	0.0001*
Standard green vases		
Tampa, June	0.188	0.665
Tampa, Sept	3.140	0.076
St. Petersburg	0.042	0.838
Bradenton	1.561	0.212
Black ovitraps in Tampa		
Commercial	–	–
Industrial	–	0.202
Residential	–	0.109

For Mantel-Haentzel tests *df* = 1. There were insufficient data for a test of ovitraps in commercial sites

* Significant effect

and *A. aegypti* are linked with local rainfall (e.g., Barrera et al. 2006; Serpa et al. 2006). Consistent with the condition-specific competition hypothesis, the increase in proportion occupancy and larval abundance per vase between early vs late rainy season was clearly greater for *A. albopictus* than for *A. aegypti*. Based on laboratory evidence (Costanzo et al. 2005), this result suggests low numbers of *A. albopictus* in the early rainy season are a result of higher egg mortality in the dry season leading up to that sample, and the more limited increase of *A. aegypti* during the wet season is consistent with strong negative effects of interspecific competition on *A. aegypti* during the wet season. Our results, combined with the findings of Costanzo et al. (2005) provide evidence that condition-specific competition is a mechanism that may contribute to persistence of *A. aegypti* in south Florida. These results are consistent with theoretical work (e.g., Chesson and Huntly 1997) indicating that simple population reductions caused

by environmental harshness are insufficient for species coexistence, but rather that differential response of competitors to environmental variation is required.

Aedes aegypti and *Aedes albopictus* were independently aggregated among experimental containers, a result consistent with the spatial independence mechanism of the aggregation hypothesis. Such aggregation is likely to result in high intraspecific competition among hatching larvae, and spatially low interspecific competition if the aggregation is greater within each species than across species (Ives 1988; Chesson 2000b; Hartley and Shorrocks 2002). Consistent with low aggregation between species, *Aedes*

Table 4 Aggregation of *A. albopictus* and *A. aegypti* among resident cemetery vases, standard green vases, and black ovitraps using the criteria of s^2/Y and goodness-of-fit for the Poisson distribution

Data set	A. albopictus				A. aegypti			
	s^2/m	χ^2	df	P	s^2/m	χ^2	df	P
Standard green vases								
Tampa, June	22.81	646.74	6	<0.0001*	24.32	432.13	4	<0.0001*
Tampa, Sept	65.37	340.84	7	<0.0001*	20.94	306.81	10	<0.0001*
St. Petersburg	102.25	40.22	4	<0.0001*	39.84	42.33	1	<0.0001*
Bradenton	70.18	95.36	4	<0.0001*	41.12	157.59	6	<0.0001*
Black ovitraps								
Commercial	129.62	70.07	7	<0.0001*	–	–	–	–
Industrial	36.28	13.40	2	<0.0001*	–	–	–	–
Residential	43.03	577.24	7	<0.0001*	30.81	763.39	14	<0.0001*

There were insufficient data for a test of *A. aegypti* among ovitraps in commercial and industrial sites

* All effects were significant

aegypti and *A. albopictus* were negatively associated in resident cemetery vases, but showed no significant negative association in experimental containers. These results suggest that although these *Aedes* species may oviposit independently of one another, the conditions present in resident vases (including competitive interactions) affect *Aedes* larvae over time so that developing larvae become negatively associated. Even within one cemetery, resident vases vary considerably in their biotic and abiotic conditions (O'Meara et al. 1995), and such environmental variation among vases may favor either *A. aegypti* or *A. albopictus*. It is also likely that these *Aedes* species choose to oviposit in containers with particular conditions, and that observed aggregation of each species is partly caused by attraction environmental cues that have some independence (Chesson 2000b). Aggregation caused both by random processes and cuing on the environment may reduce the competitive impact of *A. albopictus* on *A. aegypti* and facilitate the coexistences of these species. Although we did not measure larval abundances in resident vases, it is likely that *A. albopictus* larvae were aggregated, at least upon hatching and before larval interactions occur, in resident vases as *A. albopictus* eggs were in experimental vases and ovitraps.

We found no difference in abundances of *A. aegypti* and *A. albopictus* between cemeteries and randomly selected areas in the intervening urban matrix, a result inconsistent with the colonization-competition tradeoff and suggesting that these species do not form metapopulations within habitat patches in urban areas, but rather form a more contiguous population with varying abundances across a mosaic of urban habitats of varying suitability.

Standard ovitrapping across Tampa in the late rainy season indicated spatial partitioning between *Aedes* species by land use. *Aedes aegypti* was more abundant in residential areas, compared to sites in industrial and commercial areas. *Aedes albopictus* had the lowest mean abundance at residential sites compared to industrial and commercial sites, although this trend was not significant.

Higher abundances of *A. aegypti* in ovitraps placed in residential areas may arise if *A. aegypti* avoids oviposition in commercial and industrial areas dominated by *A. albopictus* already inhabiting containers. Some mosquitoes alter their oviposition behavior in response to conspecifics or to controphic non-mosquito larvae (e.g., Mokany and Shine 2003) and conspecific eggs (Chadee et al. 2002) already present in the habitat. However, we are unaware of any evidence for oviposition deterrence by other competing mosquito species, and this is an area for future research. Another explanation for higher *A. aegypti* oviposition in residential areas is that females may choose to oviposit where conditions in the aquatic habitat are more suited to the physiological tolerances of *A. aegypti* larvae, implying that the environmental conditions of domestic containers are closer to optimal than those in industrial and commercial areas. Our ovitraps likely gave an accurate representation of species distributions in resident containers among the different land uses.

A third and probably most plausible explanation for species-specific differences in oviposition ecology may be the attraction of female *A. aegypti* to higher densities of humans, the preferred bloodmeal hosts of this highly anthrophilic species (Harrington et al. 2001). *Aedes albopictus* takes its bloodmeals from a broader range of hosts (Gomes et al. 2003) and is likely to derive a greater proportion of its energy requirements from vegetation-based sugar (Braks et al. 2006). Total vegetation and host number may not be concentrated in any particular land use, thus explaining their generalist oviposition patterns.

Local habitat segregation in oviposition between *A. albopictus* and *A. aegypti* has been well documented along rural to urban gradients (Braks et al. 2003; Rey et al. 2006). Braks et al. (2003) showed that in zones of sympatry, *A. albopictus* is more common in rural areas, *A. aegypti* predominates in urban areas and the two species overlap in suburban areas (Braks et al. 2003). Relative to other land uses, urban areas sampled by Braks et al. (2003) were characterized by high human densities that likely

provided numerous human bloodmeals and immature habitats; two shared factors in residential areas in our study. Rey et al. (2006) related *Aedes* abundance to a range of habitat variables in three counties in South Florida and found that *A. aegypti* was only positively correlated with the urban-related variable, buildings, and negatively related to variables related to more rural or open settings (bare ground, canopy vegetation, mixed vegetation, and unpaved road). In contrast, *A. albopictus* abundance was significantly negatively related to urbanization-related variables (building, paved road, and open building) but positively related to rural variables, such as ground vegetation, unpaved road, and bare ground. Carbajo et al. (2006) analyzed the spatial pattern of *A. aegypti* oviposition in Buenos Aries and its relationship with demographic and environmental variables, showing *A. aegypti* oviposition was higher in areas that had higher densities of houses and were closer to industrial sites, and lower in areas with higher human populations or higher densities of flats. To our knowledge, our study is the first to compare the spatial patterns of competing mosquitoes at the within-city scale and relate them across different land uses in an entirely urban environment.

Although *A. albopictus* and *A. aegypti* densities do not appear specifically associated with cemeteries, the patchiness of urban landscapes still may contribute to the coexistence of these competitors. Such a scenario would likely foster the coexistence of the inferior competitor *A. aegypti* with *A. albopictus* given that *A. aegypti* starts the rainy season with the numerical advantage. *Aedes aegypti* may be able to escape competitive exclusion at the city scale despite extinctions in localized areas as long as it persists until the end of the rainy season when it regains competitive advantage. These findings suggest that the roles of specific habitat variables, including vegetative, topographic, and demographic factors, in driving *Aedes* oviposition (and species coexistence) in purely urban environments merits further investigation, and will be needed to assess accurately local disease risk in densely populated cities.

The results of this field study suggest seasonal condition-specific competition, aggregation among individual containers, and spatial partitioning by land use may all foster the coexistence of *A. albopictus* and *A. aegypti* in Tampa, Florida. Identifying habitat distribution patterns and environmental variation associated with land uses within cities may help the management of key vector species and influence the spread of disease in many regions.

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