

Spatial and temporal patterns of abundance of *Aedes aegypti* L. (*Stegomyia aegypti*) and *Aedes albopictus* (Skuse) [*Stegomyia albopictus* (Skuse)] in southern Florida

M. H. REISKIND and L. P. LOUNIBOS

Department of Entomology and Nematology, Florida Medical Entomology Laboratory, Vero Beach, FL, U.S.A.

Abstract. Invasion by mosquito vectors of disease may impact the distribution of resident mosquitoes, resulting in novel patterns of vectors and concomitant risk for disease. One example of such an impact is the invasion by *Aedes albopictus* (Skuse) [*Stegomyia albopictus* (Skuse)] (Diptera: Culicidae) of North America and this species' interaction with *Aedes aegypti* L. (*Stegomyia aegypti* L.). We hypothesized that *Ae. aegypti* would be found in urban, coastal areas that experience hotter and drier conditions, whereas *Ae. albopictus* would be more commonly found in suburban and rural areas that are cooler and wetter. In addition, we hypothesized that *Ae. aegypti* would be more abundant early in the wet season, whereas *Ae. albopictus* would be more abundant later in the wet season. Urban areas were drier, hotter and contained more *Ae. aegypti* than suburban or rural areas. *Aedes aegypti* was relatively more abundant early in the wet season, whereas *Ae. albopictus* was more abundant in both the late wet season and the dry season. The spatial patterns of inter- and intraspecific encounters between these species were also described. The distribution of these mosquitoes is correlated with abiotic conditions, and with temperature, humidity and the relative availability of rain-filled containers. Understanding the ecological determinants of species distribution can provide insight into the biology of these vectors and important information for their appropriate control.

Key words. *Aedes aegypti*, *Aedes albopictus*, dengue fever, fundamental niche, urban–rural gradients, realized niche.

Introduction

The risk for infection by a mosquito-transmitted pathogen is directly related to the vectorial capacity of the population of mosquitoes (Dye, 1992). Major components of vectorial capacity can be species-specific, including vector competence, adult longevity, abundance and host biting rate. As such, understanding the landscape distribution of different mosquitoes and the determinants of that distribution is critical to the effective prevention of disease (Reisen, 2010). This has become extremely important in heavily populated areas of southern

Florida, U.S.A., in the wake of a dengue outbreak in Key West, because of the landscape-level co-occurrence and habitat segregation of two dengue vectors, the naturalized *Aedes aegypti* L. (*Stegomyia aegypti* L.) and the invasive *Aedes albopictus* (Skuse) [*Stegomyia albopictus* (Skuse)] (Rey *et al.*, 2006; Radke *et al.*, 2012). The presence in Florida of a naturalized and a recently invading vector mosquito represents an opportunity to gain insight into the factors that determine the distribution of vectors across a landscape.

When a species invades a new area, it interacts with ecologically similar resident organisms; this may generate

Correspondence: Dr Michael H. Reiskind, Department of Entomology, North Carolina State University, Box 7613, Raleigh, NC 27695, U.S.A. Tel.: +1 919 515 0719; Fax: +1 919 515 7746; E-mail: mhreiski@ncsu.edu

a novel pattern of the invasive and resident species in the landscape, which provides insight into the nature of the interaction. For species that have little to no interaction, there may be no change in the resident species' distribution. When there is an interaction, invasions can result in a change in the distribution of the resident species or even the complete extirpation of resident species in the case of an invasive competitor or consumer (Mooney & Hobbs, 2000). When a successful invasion does not result in local extirpation of resident species, some form of habitat segregation or niche partitioning may develop (Gause, 1932). There is also an intermediate result in which the range or abundance of one species is diminished; this is called 'competitive reduction' (Lounibos, 2007). However, longterm field studies of invasion dynamics that might describe such an equilibrium state have been lacking, which limits examination of what happens after the initial spread of an invader (Strayer *et al.*, 2006).

Human-dominated landscapes are often associated with invasive species (Mooney & Hobbs, 2000), including mosquito vectors of disease. For example, *Culex pipiens s.l.* L. (Diptera: Culicidae) and *Ae. aegypti* L., both of which are anthropophilic species, have been spread around the world since at least the 16th century by human travel (Lounibos, 2002). In the 20th century, *Anopheles gambiae* Giles (Diptera: Culicidae), the most important vector of malaria in Africa, invaded Brazil (Harrison, 1978; Lounibos, 2002) and in the latter half of the 20th century *Ae. albopictus* (Skuse), the Asian tiger mosquito, invaded Europe, and North and South America (Hawley, 1988).

The invasion of North America by *Ae. albopictus* was predicted to lead to the decline of *Aedes triseriatus* Say based upon laboratory competition experiments (Livdahl & Willey, 1991), an event that has not occurred, possibly as a result of complex interactions with predators (Griswold & Lounibos, 2005; Kesavaraju *et al.*, 2008) or changes in phenology or habitat use (Swanson *et al.*, 2000; Joy *et al.*, 2003; Joy & Sullivan, 2005). The predicted effect of *Ae. albopictus* on *Ae. aegypti*, a resident exotic in the southern U.S.A., was less clear (Livdahl & Willey, 1991). In larval competition experiments, *Ae. aegypti* and *Ae. albopictus* varied in competitive superiority, with *Ae. aegypti* proving superior in experiments with artificial diet and *Ae. albopictus* superior under conditions of natural leaf litter resources (Juliano, 2010). This result may have suggested their coexistence if larval competition were the only important factor in competitive displacement. Empirical observations from field surveys demonstrated a clear decline in *Ae. aegypti* as *Ae. albopictus* invaded many parts of the southern U.S.A. (O'Meara *et al.*, 1995; Moore, 1999). However, the decline in *Ae. aegypti* with the invasion of *Ae. albopictus* was incomplete. *Aedes aegypti* populations persisted in urban areas of south Florida 25 years after the invasion (Braks *et al.*, 2003; Rey *et al.*, 2006; Britch *et al.*, 2008).

The incomplete displacement of *Ae. aegypti* set up a pattern of habitat segregation between *Ae. aegypti* and *Ae. albopictus* in urban and rural areas in Brazil (Braks *et al.*, 2003), south and west Florida, U.S.A. (Rey *et al.*, 2006) and Thailand (Tsuda *et al.*, 2006) in which *Ae. aegypti* is dominant in urban areas and *Ae. albopictus* is dominant in rural areas.

Other researchers have noted habitat segregation along a rainfall gradient in Madagascar (Fontenille & Rodhain, 1989) and among cemeteries in Florida which differ in microclimates, with *Ae. albopictus* favouring cooler, wetter areas, and *Ae. aegypti* in hotter, drier areas (Juliano *et al.*, 2004; Lounibos *et al.*, 2010). The mechanisms behind the observed habitat segregation are not well understood, although the competitive outcomes of cage replacement experiments under simulated dry vs. wet conditions suggest the importance of two factors: the larval competitive superiority of *Ae. albopictus*, and the superior desiccation resistance of *Ae. aegypti* eggs (Juliano *et al.*, 2004; Costanzo *et al.*, 2005; Lounibos *et al.*, 2010). The relative adult longevity of these two species in response to dry conditions may also contribute (Mogi *et al.*, 1996; Reiskind & Lounibos, 2009).

The phenology of *Ae. aegypti* and *Ae. albopictus* in areas in which they coexist has been described in studies of oviposition carried out in Chiang Mai, Thailand (Mogi *et al.*, 1988) and Tampa, Florida (Leisnham & Juliano, 2009). Both of these studies examined the seasonal egg abundance of these two species and found that eggs of *Ae. albopictus* became more numerous as the wet season progressed. However, the timeframes over which these populations were examined were limited [1 year in Thailand (Mogi *et al.*, 1988) and June and September of 1 year in Florida (Leisnham & Juliano, 2009)] and their conclusions should be interpreted in light of the limited observation time. Furthermore, Mogi *et al.* (1988) recognized significant problems in the handling of eggs between oviposition and rearing for identification that may have biased their results towards *Ae. aegypti*, which has more desiccation-resistant eggs (Mogi *et al.*, 1996; Juliano *et al.*, 2004). Both studies suggest the late season predominance of *Ae. albopictus* may reflect larval competition, the same mechanism invoked in early explanations for the rapid decline of *Ae. aegypti* in response to the invasion of *Ae. albopictus* (O'Meara *et al.*, 1995). However, the phenology of *Ae. albopictus* shows a late wet season surge in the absence of competition from *Ae. aegypti* in Florida tree holes (Lounibos & Escher, 2008). Furthermore, recent work has suggested larval competition may not be the only or best explanatory factor, and reproductive competition may be as or more important in explaining the decline (Kaplan *et al.*, 2010; Tripet *et al.*, 2011).

Based upon a wet-dry seasonality in south Florida (Myers & Ewel, 1990), previous work demonstrating the importance of drying as a potential mechanism of coexistence (Costanzo *et al.*, 2005), and previous observations in Thailand and Tampa, Florida (Mogi *et al.*, 1988; Leisnham & Juliano, 2009), we hypothesized that the coexistence of *Ae. aegypti* and *Ae. albopictus* observed at the landscape scale in south Florida would be demonstrated by differences in seasonal abundances and distributions between these two species. To test this hypothesis, we conducted a 25-month survey of relative abundances of *Ae. aegypti* and *Ae. albopictus* over replicated transects along an urban-suburban-rural gradient in Palm Beach County, Florida. We predicted that *Ae. aegypti* would be more abundant at the beginning of the wet season and in urban areas as a result of higher egg survivorship during the dry season, whereas *Ae. albopictus* would be

more abundant later in the wet season and in less urban areas. As we used an explicit spatial sample design over an urban–rural/coastal–inland gradient, we were also able to examine the landscape distributions of both species over time and to describe the geographic patterns of inter- and intraspecific co-occurrences for both species.

Materials and methods

Sites

During May 2006, six east–west road transects were chosen in Palm Beach County based upon their distance apart (4.7–10.0 km) and their path (from the urbanized east coast to the suburban/rural west), in consultation with the Palm Beach County mosquito control district authority. Five sampling locations were established on each transect, beginning as close as possible to the Atlantic Intracoastal Waterway, an estuarine lagoon (Fig. 1). The sampling sites on each transect were located at the Intracoastal Waterway (0 km) and at 1 km, 3 km, 8 km and 15 km west of the Intracoastal Waterway. Keeping within 250 m of the transect road and the allotted distance from the Intracoastal Waterway, trapping sites were located in parks, vacant lots or behind businesses or government offices. Residences were not used to sample mosquitoes despite their likely role as a major source of mosquitoes in order to avoid selection bias associated with differences in socioeconomic status among neighbourhoods or houses. Effort was made to locate all sites in considerable shade. As residences were not used in this study, the haphazard nature of the exact sampling location was imposed by necessity in the context of working in a human-dominated landscape.

Sampling methodology

At each site, three black plastic oviposition cups (475 mL total volume; www.printappeal.com) were attached to existing plant or man-made (e.g. fences) structures to give a total of 15 cups per transect. Cups were printed with explanatory and contact information in English and Spanish and set at 0.12–1.00 m (average: 0.45 m) above the ground, at least 3.0 m apart (average: 5.7 m). Cups were kept in place throughout the survey, unless a site needed to be relocated or a cup was missing or had been destroyed (an average of 1.2 cups, or 1.3%, were lost per week). An overflow hole was drilled into each cup so that the maximum possible volume of water contained in each cup was 350 mL. Sampling took place over a 2-week period and sampling periods were separated by intervals of 2 weeks. At the beginning of each sampling period, any water accumulated was collected with all detrital material in the container. At the same time, cups were baited with 200 mL of 3-day-old oak leaf infusion (5 g/L) and a strip (7 × 15 cm) of seed germination paper was placed in each cup for oviposition (Seedburo Equipment Co., Des Plaines, IL, U.S.A.). After a week in the field, egg papers and the aquatic fraction (water remaining from the 200 mL of bait water plus any rainfall accumulated) were collected. The cup was again baited with 200 mL of 3-day-old

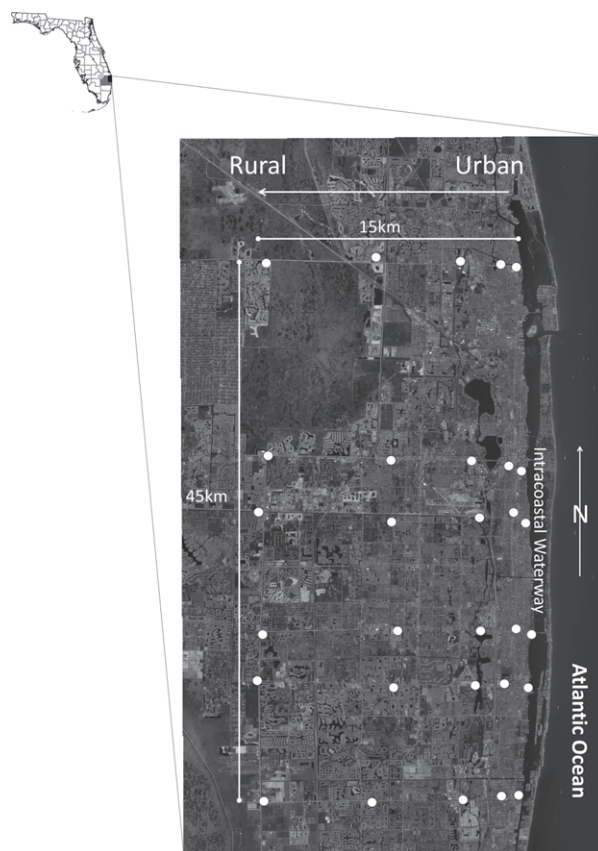


Fig. 1. Aerial image of sampling transects in Palm Beach County, FL, U.S.A. ○, sampling points.

oak leaf infusion and a strip of seed germination paper, and collected after another week in the field.

Processing of field samples

Aquatic samples were taken in Whirl-Pak® bags (Nasco Co., Fort Atkinson, WI, U.S.A.) back to the laboratory. Each sample was qualitatively scored for the presence or absence of vegetable material (leaf, fruit, flower, woody tissue), carcasses of invertebrates, presence of living invertebrates, and presence of mosquito larvae. All mosquito larvae were reared to fourth-instar or pupal stage for identification. Eggs on papers were also brought back to the laboratory, allowed to dry overnight, and were counted and hatched in 300 mL of tap water with 0.15 g/L of 1 : 1 yeast : albumin in groups of ≤ 30 eggs. Hatched larvae were reared to fourth-instar or pupal stage for identification. All larval mosquitoes were enumerated (unhatched eggs were counted but not included in the count of mosquitoes). The total number of mosquitoes counted included larvae from the aquatic samples plus larvae hatched from eggs.

Collection of environmental data

Temperature and humidity data were recorded every 10 min at 11–15 sites throughout the sampling period. Sites were sampled in a stratified, random design, such that nine sites were randomly selected from the 18 located at 0 km, 1 km and 3 km from the Intracoastal Waterway, and six from the 12 located at 8 km and 15 km from the Intracoastal Waterway. The variable number of sites monitored reflected the loss of sampling units during the survey period, primarily through the loss of cups. Weather data were collected using iButton data loggers (Maxim Corp., Dallas, TX, U.S.A.), glued (using silicone caulk) to the bottom of one cup in each designated site. The percentage of containers holding water was also determined for each sampling period, based upon our collection data.

Sampling period

Samples were taken for 27 4-week periods from 6 June 2006 to 14 July 2008. In order to examine the yearly pattern of environmental variables, each period was assigned to the month in which the majority of days in the period fell (i.e. if 15 of 28 days of the period fell in December, the period was assigned 'December'), which led to there being two samples for each month, taken from different years, except for May (two samples in 2007), December (two samples in 2007) and June and July (2006, 2007 and 2008), when there were three. All results are reported by period as the sum of all data for that period in a given site. Although summing of data for a given site loses some measurement of within-site variability, it minimizes variability resulting from missing data, a common occurrence caused by disturbance.

Mosquito variables

To normalize these data, all abundances were \log_{10} transformed. As we had three containers at each site, we were able to calculate a mean crowding index (M_w) for both intraspecific and interspecific encounters at each site for each time period (Lloyd, 1967).

Statistical analysis

Environmental variables. We examined temperature and relative humidity (RH) over the same time period. Independently collected environmental data were analysed for each month (all years were combined for each month) separately by linear regression of average RH and temperature on distance from the coast. Although there is considerable year-to-year variation in environmental variables, combining the data from different years into the same month and examining averages avoids the impacts of one extreme year, while losing some of the variance. Variation in sample size for each month arose from loss and the irregular replacement of data loggers in the field. June and July were sampled three times, whereas all other months were sampled only twice. The percentage of wet containers

per site in each month was calculated and examined as a linear function of distance from the coast.

Temporal pattern of mosquito abundance. We examined the temporal distributions of each species, the proportion of mosquitoes that were *Ae. aegypti* and the proportion of wet containers over the whole landscape. We also examined correlations between the log abundance of each species for the 27 4-week periods using Pearson correlations in SAS Version 9.3 (SAS Corp., Cary, NC, U.S.A.) over the entire sampling area. To examine seasonality in abundances of the two species, we considered each transect and each sampling period as an independent unit of analysis. We then separated the year into three biologically meaningful seasons of 4 months each (Myers & Ewel, 1990): dry (January–April, $n = 48$); early wet (May–August, $n = 60$), and late wet (September–December, $n = 54$) and compared the difference between normalized variables of *Ae. aegypti* and *Ae. albopictus* abundance. These variables were normalized against the mean abundance within each species across all transects and all periods. A positive difference variable means relatively more *Ae. albopictus* in a given season, whereas a negative difference variable means relatively more *Ae. aegypti* in a given season. As this difference variable was not normal, we used the non-parametric Wilcoxon's test to compare relative abundances of *Ae. albopictus* and *Ae. aegypti* in different seasons. Following a significant Wilcoxon's test, pairwise differences between each season were made, with an alpha adjusted by the number of comparisons ($\alpha_{\text{adjusted}} = 0.0183$).

Spatial pattern of mosquito abundance. We used correlation analysis (Pearson's correlation) to examine the effect of distance from the coast on the \log_{10} -transformed abundance of both species of mosquito. We compared indices of intra- and interspecific encounter rates based on mean crowding (Lloyd, 1967), across distance from the coast using a generalized linear model with a negative binomial error distribution (parameters estimated by maximum likelihood) and determined the best fit to the data according to the Pearson chi-squared statistic divided by the degrees of freedom being close to 1 (PROC GENMOD). The significance of distance from the coast was assessed by likelihood ratio analysis (in SAS Version 9.3). Post hoc comparisons between each distance were made with contrasts in the generalized linear model with an adjusted alpha ($\alpha_{\text{adjusted}} = 0.0045$) to create homogeneous groups.

Spatiotemporal pattern of mosquito abundance. The effects of space and time were examined using correlation coefficients from Spearman rank correlations between distance from the coast and rank of mosquito abundance and were compared within each month examined. A significant correlation for a given month, considering all the data for that month (at least two samples were taken in each month and three were taken in May, June and July), suggests the existence of a spatial correlation with relation to distance from the coast.

Table 1. Parameter estimates, degrees of freedom and associated *P*-values for average daily relative humidity, temperature and percentage of wet containers based on a linear regression with distance (km) from the coast.

Month	Parameter estimate, relative humidity, %	d.f. (<i>P</i> -value)	Parameter estimate, temperature	d.f. (<i>P</i> -value)	Parameter estimate, % wet containers	d.f. (<i>P</i> -value)
January	0.4293	23 (0.003)	−0.1475	23 (<0.0001)	1.23	58 (0.0327)
February	0.4134	24 (0.0042)	−0.1239	24 (0.0365)	1.36	58 (0.0079)
March	0.3947	23 (0.0275)	−0.1083	23 (<0.0001)	1.48	58 (0.0231)
April	0.4059	24 (0.0007)	−0.1051	24 (0.001)	1.10	58 (0.0293)
May	0.2529	22 (0.0339)	−0.0759	22 (0.0035)	1.34	88 (0.0027)
June	0.2605	38 (0.0239)	−0.0705	38 (0.005)	1.25	88 (0.0059)
July	0.2829	37 (0.0165)	−0.0924	37 (0.0021)	1.76	58 (0.0009)
August	0.5533	26 (0.0002)	−0.1115	26 (<0.0001)	1.55	58 (0.0031)
September	0.5017	26 (0.0005)	−0.1099	26 (<0.0001)	1.01	58 (0.0097)
October	0.3513	23 (0.0863)	−0.0842	23 (0.009)	1.40	58 (0.065)
November	0.5174	22 (<0.0001)	−0.0949	22 (0.0015)	2.21	58 (0.0001)
December	0.3671	23 (<0.0001)	−0.0962	23 (<0.0001)	1.37	88 (0.0028)
Mean parameter estimate:	0.3941	—	−0.1017	—	1.42	—

Results

Environmental variables: spatiotemporal variation

Average daily RH was significantly positively correlated with distance from the coast in every month, except October (Table 1, first column). The average parameter estimate for the linear coefficient of distance from the Intracoastal Waterway for the percentage RH was 0.3942% (range: 0.2529–0.5533%), meaning that for each kilometre west from the coast, RH increased by approximately 0.4% or about 6% over each east–west transect. Average daily temperature was significantly negatively correlated with distance from the

coast in every month (Table 1, second column). The average parameter estimate for temperature was -0.1017°C (range: -0.0705°C to 0.1475°C), meaning that for each kilometre west from the coast, the temperature dropped by an average of approximately 0.1°C or by 1.5°C across each transect. The average percentage of wet containers per site was significantly positively correlated with distance from the coast in all months except October (Table 1, third column). The average parameter estimate for number of containers was 1.42%, meaning that for each kilometre west from the coast, a site is predicted to have a 1.5% increase in wet containers so that there will be about 20% more wet containers at 15 km from the coast relative to the number at the coast.

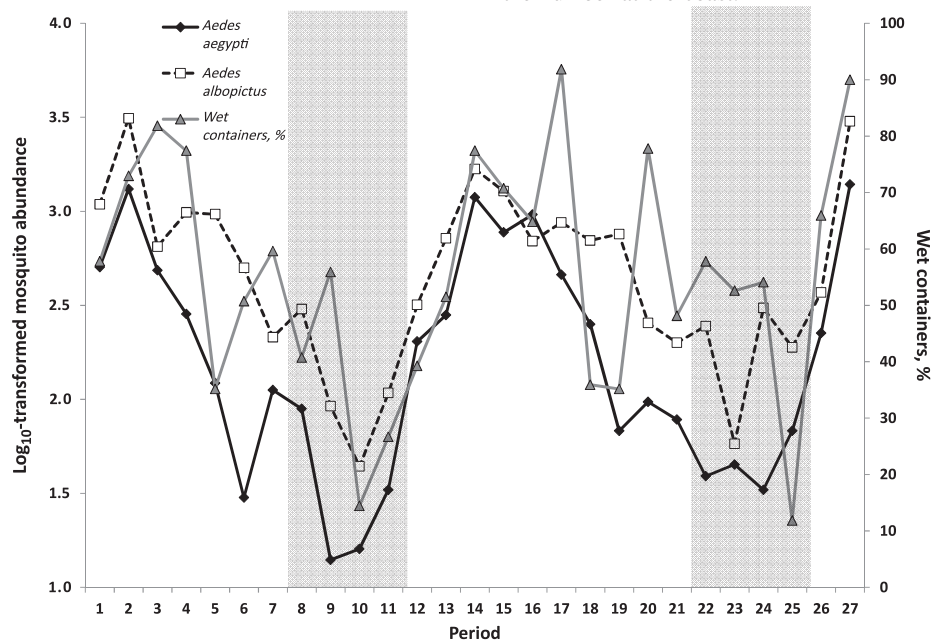
**Fig. 2.** Total abundance (\log_{10}) of *Aedes albopictus* and *Aedes aegypti* and percentage of containers with water from June 2006 to July 2008. Dry season (January–April; Myers & Ewel, 1990) is shaded light grey.

Table 2. Effect of season on difference in normalized abundance of *Aedes aegypti* to *Aedes albopictus*.

Source	Median	Observed rank-sum	Expected rank-sum	Kruskal–Wallis χ^2 /Wilcoxon normal approx.	d.f.	P-value
Season	—	—	—	7.3615	2	0.0252
Dry	−0.08174	3934.5	3912.0	—	—	—
Early	−0.2162	4200.0	4890.0	—	—	—
Late	0.04282	5068.5	4401.0	—	—	—
Dry vs. early	—	—	—	2.8914	1	0.0891
Dry vs. late	—	—	—	2.8674	1	0.0904
Early vs. late	—	—	—	5.5471	1	0.0185

Significant differences are shown in bold ($\alpha_{\text{adjusted}} = 0.0183$).

Temporal pattern of mosquito abundance

At the landscape level, both mosquito species showed similar patterns in abundance over time ($r = 0.82$, $n = 27$; $P < 0.0001$) (Fig. 2). There was also a significant correlation between the abundances of both species and the percentage of wet containers [*Ae. aegypti*: $r = 0.56$, $n = 27$ ($P < 0.01$); *Ae. albopictus*: $r = 0.54$, $n = 27$ ($P < 0.01$)] (Fig. 2). For both species, there were significant correlations between mosquito abundance and the percentage of wet containers one and two periods earlier when the entire landscape was considered [*Ae. aegypti* (n_{-1}): $r = 0.60$, $n = 27$ ($P < 0.05$); *Ae. aegypti* (n_{-2}): $r = 0.42$, $n = 27$ ($P < 0.05$); *Ae. albopictus* (n_{-1}): $r = 0.48$, $n = 27$ ($P < 0.05$); *Ae. albopictus* (n_{-2}): $r = 0.47$, $n = 27$ ($P < 0.05$)]. No other lags up to six prior periods were significant. The *Ae. aegypti* : *Ae. albopictus* ratios over the whole landscape were highest in period 3 (*Ae. aegypti* : total: 486 : 1135, 1–29 August 2006), period 16 (*Ae. aegypti* : total: 962 : 1656, 8 August to 5 September 2007), and period 23 (*Ae. aegypti* : total: 78 : 136, 6 March to 3 April 2008). The lowest *Ae. aegypti* : *Ae. albopictus* ratios were found in period 6 (*Ae. aegypti* : total: 30 : 531, 1–28 November 2006), period 19 (*Ae. aegypti* : total: 68 : 825, 7 November to 5 December 2007), and period 24 (*Ae. aegypti* : total: 33 : 339, 13 March to 10 April 2008). When the data were classified by season, significant differences in the relative abundance of *Ae. aegypti* emerged (Table 2). The relative abundance of *Ae. aegypti* to *Ae. albopictus* showed a trend towards being higher early in the wet season relative to later in the wet season, with no differences in relative abundances between either parts of the wet season and the dry season.

Spatial pattern of competition

Distance from the coast explains a significant amount of variation in abundances of both species of mosquito, but in opposite directions. An analysis of the total abundance of each species over the 27 4-week periods shows that *Ae. aegypti* was found in greater abundance closer to the Intracoastal Waterway ($r = -0.71$, $n = 30$; $P < 0.0001$) (Fig. 3), whereas the opposite pattern was observed for *Ae. albopictus* ($r = 0.76$, $n = 30$; $P < 0.0001$) (Fig. 3). Examination of inter- and intraspecific mean crowding (M_w) showed the pattern of co-occurrence for each species (Fig. 4). For *Ae. aegypti*,

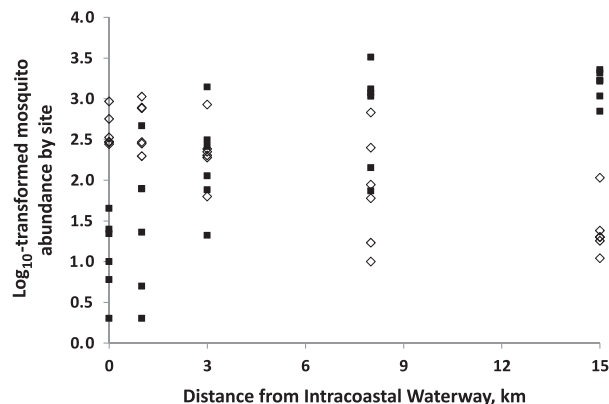


Fig. 3. Total abundance (\log_{10} , June 2006 to July 2008) of *Aedes albopictus* (■) and *Aedes aegypti* (◇) in each site by distance from the Intracoastal Waterway.

intraspecific M_w was highest at 1 km from the coast and significantly lower at 8–15 km from the coast. Interspecific M_w for *Ae. aegypti* was highest at 8 km from the coast. For *Ae. albopictus*, intraspecific M_w was equally high at 8 km and 15 km from the coast, whereas interspecific M_w was highest at 3 km from the coast.

Spatiotemporal pattern of mosquitoes

The significant correlation of mosquito species abundance with distance from the coast over the whole sampling period was also observed in most individual months, except in January, March and December for *Ae. aegypti* (Table 3).

Discussion

Transects from the urbanized coast to the suburban or rural inland areas of Palm Beach County, Florida demonstrated significant variation in species distribution, wetness (percentage of wet containers), temperature and humidity. As we did not explicitly quantify urbanization and all of the transects ran from the coast inland, we cannot rule out the possibility that this pattern in abiotic conditions is a coastal–inland pattern. However, temperature gradients similar to those we observed (e.g. urban

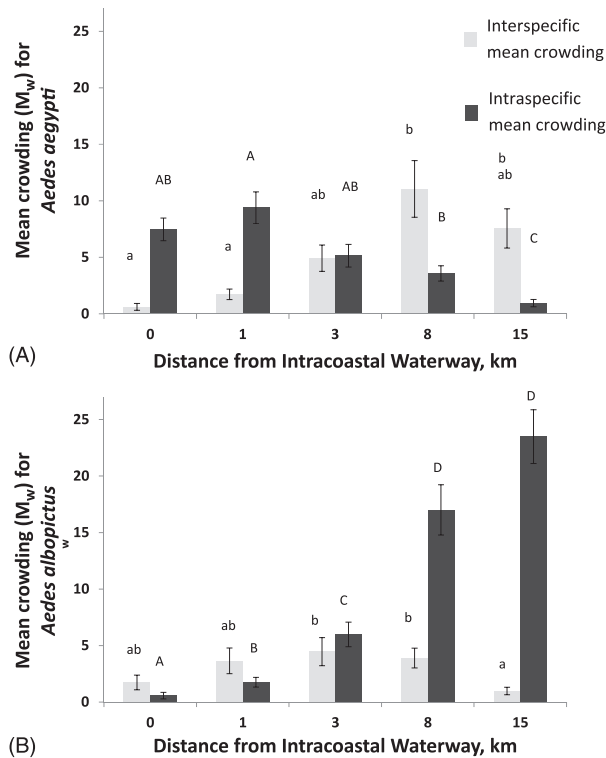


Fig. 4. Intraspecific and interspecific encounter rates (number of individuals encountered by one individual) by distance from the coast for (A) *Aedes aegypti* [interspecific: $\chi^2_{(d.f. = 4)} = 30.20$ ($P < 0.0001$); intraspecific: $\chi^2_{(d.f. = 4)} = 46.68$ ($P < 0.0001$)] and (B) *Aedes albopictus* [interspecific: $\chi^2_{(d.f. = 4)} = 11.14$ ($P = 0.0254$); intraspecific: $\chi^2_{(d.f. = 4)} = 154.74$ ($P < 0.0001$)]. Letters within case denote homogeneous groups by pairwise contrasts with a corrected alpha ($\alpha_{\text{adjusted}} = 0.0045$).

Table 3. Spearman correlation coefficients between distance from the coast (km) and rank of mosquito abundance.

Month	r_s <i>Aedes aegypti</i>	n (P -value)	r_s <i>Aedes albopictus</i>	n (P -value)
January	-0.2322	60 (0.0741)	0.5924	60 (<0.0001)
February	-0.3339	60 (0.0091)	0.4729	60 (<0.0001)
March	0.0806	60 (0.5401)	0.4690	60 (0.0002)
April	-0.3259	60 (0.011)	0.3691	60 (0.0037)
May	-0.2644	90 (0.0118)	0.6047	90 (<0.0001)
June	-0.5819	90 (<0.0001)	0.6746	90 (<0.0001)
July	-0.5599	60 (<0.0001)	0.7649	60 (<0.0001)
August	-0.4908	60 (<0.0001)	0.6997	60 (<0.0001)
September	-0.4184	60 (0.0009)	0.6233	60 (<0.0001)
October	-0.2963	60 (0.0215)	0.6723	60 (<0.0001)
November	-0.2712	60 (0.0361)	0.6321	60 (<0.0001)
December	-0.1995	90 (0.0588)	0.5426	90 (<0.0001)
All months	-0.2888	810 (<0.0001)	0.5381	810 (<0.0001)

heat islands) are commonly seen in tropical and subtropical urban landscapes (Roth, 2007). In addition, urban areas may increase precipitation for areas downwind through increased convection or particulate matter (Burian & Shepherd, 2005).

However, winds in Palm Beach County are more likely to come from the west, making this explanation less compelling (Green *et al.*, 1982). Regrettably, we know of no recent or concurrent meteorological studies of this area at a sufficiently fine scale that might corroborate our measurements of temperature, humidity and wetness in this landscape.

These abiotic factors may have a direct effect on mosquitoes; previously published papers show a strong association between urban landscape variables (e.g. impermeable surfaces) and the relative abundance of *Ae. aegypti* to *Ae. albopictus* in south Florida (Braks *et al.*, 2003; Rey *et al.*, 2006). The spatial distribution identified in our study confirms these previously described patterns with regard to urbanized areas, and demonstrates relationships between temperature, humidity and wetness and the relative abundance of the two species. Costanzo *et al.* (2005) showed the importance of habitat drying in competition between *Ae. aegypti* and *Ae. albopictus* in an elegant laboratory study, but the parameters used in their study are difficult to relate to our observed environmental conditions. Nevertheless, the gradients in temperature, humidity and wet containers suggest that the spatial distributions of each species are indeed enforced through a similar mechanism of non-competing life history stages, whereby *Ae. aegypti* survives in drier, hotter microclimates relative to *Ae. albopictus*, in agreement with other field studies (Mogi *et al.*, 1996; Juliano *et al.*, 2004).

We described significant variations over time and space in the abundances and distributions of the invasive *Ae. albopictus* and the resident *Ae. aegypti*. We found a significant effect of season on relative abundances of the two mosquito species, with a trend towards a lower relative abundance of *Ae. aegypti* in the late wet season than in the early dry season, as predicted in our hypothesis. The difference in relative abundances of *Ae. aegypti* and *Ae. albopictus* between the early and late wet season was non-significant because we adopted a conservative correction factor (α -value per three comparisons). We did not see any difference in relative abundances in the dry season relative to the early or late wet season. Although we did not make specific *a priori* predictions about the relative abundance of each species during the dry season, we might have expected to find a high ratio of the desiccation-resistant *Ae. aegypti* (Mogi *et al.*, 1996; Reiskind & Lounibos, 2009), which we did not observe. As there are anthropogenic water sources around households during the dry season and *Ae. albopictus* has a greater abundance over these transects, the lack of difference in relative abundance between *Ae. albopictus* and *Ae. aegypti* during the dry season may indicate the presence of mosquitoes from anthropogenically (e.g. as a result of lawn watering) wet areas.

The ability of *Ae. aegypti* to increase early in the wet season suggests this species may be able to move out of its current distribution in the absence of *Ae. albopictus*. This is supported by the observation that *Ae. aegypti* was found in both urban and rural areas in Florida prior to the invasion of *Ae. albopictus*. Control strategies that are targeted at *Ae. albopictus* may therefore have the unfortunate result of allowing *Ae. aegypti* to reinvade areas (Lounibos, 2007; Kaplan, *et al.*, 2010). Likewise, control of *Ae. aegypti* has allowed *Ae. albopictus* to invade more urban areas (Lounibos,

2007). However, studies of the tolerances of *Ae. albopictus* in both the egg and adult stages suggest it is limited by dry conditions, possibly to the point that drier, urban areas fall outwith its fundamental niche (Hutchinson, 1957; Mogi *et al.*, 1996; Juliano *et al.*, 2002; Reiskind & Lounibos, 2009). We suggest that planners of targeted control of *Ae. albopictus* should consider the longterm dynamics of both species to mitigate the reinvasion of areas by *Ae. aegypti*.

The pattern of mean crowding indices suggests that the potential for interspecific competition peaks at different distances from the coast for each mosquito species. *Aedes aegypti* has the highest interspecific mean crowding (encounters the most *Ae. albopictus*) at 8 km from the coast, whereas interspecific mean crowding for *Ae. albopictus* peaks at 3 km from the coast. This may again reflect a broader fundamental niche for *Ae. aegypti* because it can colonize at greater distance from its core areas, whereas *Ae. albopictus* is more limited in its ability to colonize the hotter, drier coastal–urban zone. Consistent with the general pattern of species abundance, intraspecific mean crowding is highest near the coast for *Ae. aegypti* and inland for *Ae. albopictus*.

In addition to the abiotic gradient of conditions, urban and rural areas may also vary in biotic factors that might impact mosquitoes. A previous study along these same transects showed variations in the diversity of plant material within mosquito habitats, which may influence the productivity of those habitats for mosquitoes (Reiskind *et al.*, 2010). Other urban–rural gradients have also shown differences in plant diversity and growth, which may affect the quality of container habitats and insect and bird diversity, and thus the presence of predators and bloodmeal sources (Clergeau *et al.*, 1998; Niemela *et al.*, 2002; Pautasso, 2007). These biotic influences were not examined in this study, but they may provide important further information explaining the distribution of *Ae. aegypti* and *Ae. albopictus* in south Florida. The impact of all of these factors may influence the transmission of mosquito-borne infectious disease in a given area, as has been shown for West Nile virus in the southern U.S.A. (Bradley *et al.*, 2008).

The abiotic conditions associated with the urban–rural gradient are sufficient to maintain the regional coexistence of these species, demonstrating the impact of urbanization on ecological interactions. Consequently, as parts of the world, particularly tropical and subtropical areas, become increasingly urbanized, a better understanding of how local fauna will respond is necessary to predict the risk for disease transmission and to inform the control of important vectors of disease. As *Ae. aegypti* is generally considered to have a higher vectorial capacity than *Ae. albopictus* for certain pathogens (dengue and yellow fever), its predilection for more urban areas may suggest an increase in disease risk for humans in subtropical urbanizing areas in the future.

Acknowledgements

The authors wish to thank Krystle Green, Naoya Nishimura, Cathy Westbrook, and Kendra Pesko, of the Florida Medical Entomology Laboratory in Vero Beach, FL for assistance in

the field or in the rearing and identifying of field material. This work was supported by a National Institutes of Health grant (R01-AI044793) to LPL. We also wish to thank two anonymous reviewers for their helpful input.

References

- Bradley, C.A., Gibbs, S.E.J. & Altizer, S. (2008) Urban land use predicts West Nile virus exposure in songbirds. *Ecological Applications*, **18**, 1083–1092.
- Braks, M.A.H., Honorio, N.A., Lourenco-De-Oliveira, R., Juliano, S.A. & Lounibos, L.P. (2003) Convergent habitat segregation of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in southeastern Brazil and Florida. *Journal of Medical Entomology*, **40**, 785–794.
- Britch, S.C., Linthicum, K.J., Anyamba, A., Tucker, C.J. & Pak, E.W., Mosquito Surveillance Team (2008) Longterm surveillance data and patterns of invasion by *Aedes albopictus* in Florida. *Journal of the American Mosquito Control Association*, **24**, 115–120.
- Burian, S. & Shepherd, J. (2005) Effect of urbanization on the diurnal rainfall pattern in Houston. *Hydrological Processes*, **19**, 1089–1103.
- Clergeau, P., Savard, J., Mennechez, G. & Falardeau, G. (1998) Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. *Condor*, **100**, 413–425.
- Costanzo, K.S., Kesavaraju, B. & Juliano, S.A. (2005) Condition-specific competition in container mosquitoes: the role of non-competing life-history stages. *Ecology*, **86**, 3289–3295.
- Dye, C. (1992) The analysis of parasite transmission by bloodsucking insects. *Annual Review of Entomology*, **37**, 1–19.
- Fontenille, D. & Rodhain, F. (1989) Biology and distribution of *Aedes albopictus* and *Aedes aegypti* in Madagascar. *Journal of the American Mosquito Control Association*, **5**, 219–225.
- Gause, G.F. (1932) Experimental studies on the struggle for existence: mixed population of two species of yeast. *Journal of Experimental Biology*, **9**, 389–402.
- Green, A.E.S., Schwartz, J.M., Singhal, R.P. & Bolch, W.E. (1982) Wind roses for Florida. *Journal of the Air Pollution Control Association*, **32**, 822–825.
- Griswold, M.W. & Lounibos, L.P. (2005) Does differential predation permit invasive and native mosquito larvae to coexist in Florida? *Ecological Entomology*, **30**, 122–127.
- Harrison, G.A. (1978) *Mosquitoes, Malaria, and Man: A History of the Hostilities since 1880*. J. Murray, London.
- Hawley, W. (1988) The biology of *Aedes albopictus*. *Journal of the American Mosquito Control Association*, (Suppl. 1), 1–40.
- Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.
- Joy, J.E. & Sullivan, S.A. (2005) Occurrence of tyre-inhabiting mosquito larvae in different geographic regions of West Virginia. *Journal of the American Mosquito Control Association*, **21**, 380–386.
- Joy, J.E., Hanna, A.A. & Kennedy, B.A. (2003) Spatial and temporal variation in the mosquitoes (Diptera: Culicidae) inhabiting waste tyres in Nicholas County, West Virginia. *Journal of Medical Entomology*, **40**, 73–77.
- Juliano, S.A. (2010) Coexistence, exclusion, or neutrality? A meta-analysis of competition between *Aedes albopictus* and resident mosquitoes. *Israel Journal of Ecology and Evolution*, **56**, 325–351.
- Juliano, S.A., O'Meara, G.F., Morrill, J.R. & Cutwa, M.M. (2002) Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes. *Oecologia*, **130**, 458–469.

- Juliano, S.A., Lounibos, L.P. & O'Meara, G.F. (2004) A field test for competitive effects of *Aedes albopictus* on *Ae. aegypti* in south Florida: differences between sites of coexistence and exclusion? *Oecologia*, **139**, 583–593.
- Kaplan, L., Kendell, D., Robertson, D., Livdahl, T. & Khatchikian, C. (2010) *Aedes aegypti* and *Aedes albopictus* in Bermuda: extinction, invasion, invasion and extinction. *Biological Invasions*, **12**, 3277–3288.
- Kesavaraju, B., Damal, K. & Juliano, S.A. (2008) Do natural container habitats impede invader dominance? Predator-mediated coexistence of invasive and native container-dwelling mosquitoes. *Oecologia*, **155**, 631–639.
- Leishnam, P.T. & Juliano, S.A. (2009) Spatial and temporal patterns of coexistence between competing *Aedes* mosquitoes in urban Florida. *Oecologia*, **160**, 343–352.
- Livdahl, T.P. & Willey, M.S. (1991) Prospects for an invasion—competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science*, **253**, 189–191.
- Lloyd, M. (1967) Mean crowding. *Journal of Animal Ecology*, **36**, 1–30.
- Lounibos, L.P. (2002) Invasions by insect vectors of human disease. *Annual Review of Entomology*, **47**, 233–266.
- Lounibos, L.P. (2007) Competitive displacement and reduction. *Journal of the American Mosquito Control Association*, **23**, 276–282.
- Lounibos, L.P. & Escher, R.L. (2008) Sex ratios of mosquitoes from longterm censuses of Florida tree holes. *Journal of the American Mosquito Control Association*, **24**, 11–15.
- Lounibos, L.P., O'Meara, G.F., Juliano, S.A. *et al.* (2010) Differential survivorship of invasive mosquito species in south Florida cemeteries: do site-specific microclimates explain patterns of coexistence and exclusion? *Annals of the Entomological Society of America*, **103**, 757–770.
- Mogi, M., Khamboonruang, C., Choochote, W. & Suwanpanit, P. (1988) Ovitrap surveys of dengue vector mosquitoes in Chiang Mai, northern Thailand—seasonal shifts in relative abundance of *Aedes albopictus* and *Aedes aegypti*. *Medical and Veterinary Entomology*, **2**, 319–324.
- Mogi, M., Miyagi, I., Abadi, K. & Syafruddin. (1996) Inter- and intraspecific variation in resistance to desiccation by adult *Aedes* (*Stegomyia*) spp. (Diptera: Culicidae) from Indonesia. *Journal of Medical Entomology*, **33**, 53–57.
- Mooney, H.A. & Hobbs, R.J. (2000) *Invasive Species in a Changing World*. Island Press, Washington, DC.
- Moore, C.G. (1999) *Aedes albopictus* in the United States: current status and prospects for further spread. *Journal of the American Mosquito Control Association*, **15**, 221–227.
- Myers, R.L. & Ewel, J.J. (1990) *Ecosystems of Florida*. University of Central Florida Press, Orlando, FL.
- Niemela, J., Kotze, D., Venn, S. *et al.* (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: an international comparison. *Landscape Ecology*, **17**, 387–401.
- O'Meara, G.F., Evans, L.F., Gettman, A.D. & Cuda, J.P. (1995) Spread of *Aedes albopictus* and decline of *Aedes aegypti* (Diptera, Culicidae) in Florida. *Journal of Medical Entomology*, **32**, 554–562.
- Pautasso, M. (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters*, **10**, 16–24.
- Radke, E.G., Gregory, C.J., Kintziger, K.W. *et al.* (2012) Dengue outbreak in Key West, Florida, U.S.A., 2009. *Emerging Infectious Diseases*, **18**, 135–137.
- Reisen, W.K. (2010) Landscape epidemiology of vector-borne diseases. *Annual Review of Entomology*, **55**, 461–483.
- Reiskind, M. & Lounibos, L. (2009) Effects of intraspecific larval competition on adult longevity in the mosquitoes *Aedes aegypti* and *Aedes albopictus*. *Medical and Veterinary Entomology*, **23**, 62–68.
- Reiskind, M.H., Zarrabi, A.A. & Lounibos, L.P. (2010) Invasive leaf resources alleviate density dependence in the invasive mosquito, *Aedes albopictus*. *Biological Invasions*, **12**, 2319–2328.
- Rey, J.R., Nishimura, N., Wagner, B., Braks, M.A.H., O'Connell, S.M. & Lounibos, L.P. (2006) Habitat segregation of mosquito arbovirus vectors in south Florida. *Journal of Medical Entomology*, **43**, 1134–1141.
- Roth, M. (2007) Review of urban climate research in (sub)tropical regions. *International Journal of Climatology*, **27**, 1859–1873.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the longterm effects of species invasions. *Trends in Ecology & Evolution*, **21**, 645–651.
- Swanson, J., Lancaster, M., Anderson, J., Crandell, M., Haramis, L., Grimstad, P. & Kitron, U. (2000) Overwintering and establishment of *Aedes albopictus* (Diptera: Culicidae) in an urban La Crosse virus enzootic site in Illinois. *Journal of Medical Entomology*, **37**, 454–460.
- Tripet, F., Lounibos, L.P., Robbins, D., Moran, J., Nishimura, N. & Blosser, E.M. (2011) Competitive reduction by satyriization? Evidence for interspecific mating in nature and asymmetric reproductive competition between invasive mosquito vectors. *American Journal of Tropical Medicine and Hygiene*, **85**, 265–270.
- Tsuda, Y., Suwonkerd, W., Chawprom, S., Prajakwong, S. & Takagi, M. (2006) Different spatial distribution of *Aedes aegypti* and *Aedes albopictus* along an urban–rural gradient and the relating environmental factors examined in three villages in northern Thailand. *Journal of the American Mosquito Control Association*, **22**, 222–228.

Accepted 15 October 2012

First published online 27 December 2012