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# **Habitat Segregation of Mosquito Arbovirus Vectors in South Florida**

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# **Abstract**

Oviposition traps set in rural to urban environments in three south Florida counties were colonized predominantly by *Culex quinquefasciatus* Say (35.1%), *Aedes albopictus* (Skuse) (34.5%), *Aedes aegypti* (L.) (23.8%), and *Culex nigripalpus* Theobald (6.6%) during 1 yr of monthly sampling. Significant differences were detected among counties for abundances of *Cx. quinquefasciatus* and for percentage composition of that species and *Ae. albopictus*. Aerial images of habitats around each collection site were digitized, and coverages by each of 16 habitat variables were recorded. Abundances of *Ae. aegypti* were positively related to habitat variables associated with urbanization and negatively correlated to those reflecting rural characteristics. Multiple regression models of habitat selection explained similar proportions of variances in abundance of *Ae. aegypti* and *Ae. albopictus*, but signs of significant variables were opposite for these two species. No consistent trends of habitat associations were observed among counties for the two *Culex* spp. Co-occurrences of the four species in individual traps depended on container type (tub versus cup), and, for *Aedes* spp. with *Culex* spp., county. The results underscore the importance of scale in evaluating habitat selection and the utility of quantifiable habitat characteristics of intermediate scale to identify site characteristics favored by the arboviral vectors *Ae. aegypti* and *Ae. albopictus*.

# **Keywords**

*Aedes*; *Culex*; Florida; rural; urban

The geographic distributions of *Aedes aegypti* (L) and *Aedes albopictus* (Skuse) overlap in tropical Asia, North and South America, and a few African nations. Spatial segregation because of differences in habitat preferences by the two species has been proposed as one mechanism promoting geographical coexistence (Hawley 1988, O'Meara et al. 1995, Thavara et al. 2001). Typically, *Ae. aegypti* predominates in urban areas, and *Ae. albopictus* predominates in rural areas; however, our knowledge of habitat preferences of these species remains qualitative and subjective because the environmental determinants have not been identified or quantified. The latter information is essential for predicting *Ae. aegypti* and *Ae. albopictus* incidence and abundance, and for risk assessment of disease transmission.

Furthermore, although the level of urbanization seems to be an important factor influencing the relative abundance of the two species, we do not have information on the influence of intermediate scale (hundreds of meters) habitat characteristics on mosquito presence and abundance, and data on micro-habitat (less than a meter) discrimination by the two species is scant.

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*Ae. aegypti* is the primary vector of dengue, and *Ae. albopictus* also may play a role in the transmission of dengue in its native and invaded range (Effler et al. 2005). Although many species of North American mosquitoes have been detected infected with West Nile virus or resolved as competent laboratory vectors, the available evidence suggests that *Culex* spp., especially *Culex nigripalpus* Theobald, *Culex salinarius* Co-quillett, *Culex restuans* Theobald, *Culex pipiens* L., and *Culex quinquefasciatus* Say, are likely involved in bird to human transmission of the virus (Sardelis et al. 2002, Rutledge et al. 2003, Turell et al. 2005). In many peri-domestic environments in the southeastern United States, *Ae. albopictus* accounts for a high proportion of mosquito–human contacts, and, because of its broad host range, cannot be ruled out as a West Nile virus vector.

This contribution investigates habitat factors that are associated with the spatial distributions of *Ae. aegypti, Ae. albopictus,* and *Culex* species in three populated counties of peninsular Florida: Miami-Dade, Palm Beach, and Manatee counties (Fig. 1). Relationships between habitat variables at several scales and mosquito presence and abundance are investigated, and co-occurrences are examined to detect spatial and trap influences on interspecific associations between *Ae. aegypti* and *Ae. albopictus* and between *Aedes* spp. and *Culex* spp.

# **Materials and Methods**

In each county, 15 stations were selected to include rural, urban, suburban, and industrial/ commercial settings. Each station was sampled for mosquitoes once per month from March 2002 to February 2003. At each sampling, oviposition traps for *Aedes* and *Culex* mosquitoes (O'Meara et al. 1989, Reiter et al. 1991, Service 1993, Rawlings et al. 1998) were deployed in the shade (in Florida, eggs exposed to the sun exhibit very poor survival; L.P.L., unpublished data.).

The *Aedes* traps were black plastic cups (400 ml) with (2- by 10-cm) masonite paddles immersed in a dilute (10%) oak infusion (O'Meara et al. 1989). Each cup had holes near the lip to prevent overflowing. Three cups were set at each station during each sampling. The *Culex* traps consisted of plastic tubs (32 by 23 by 17 cm) half-filled with undiluted oak infusion. The tubs also had holes near the lip on the shorter dimension to prevent overflowing. The traps were left in the field for 1 wk, after which time all the contents were collected and returned to the laboratory, where all immature mosquitoes were hatched and/or reared, identified to species, and counted. When >100 larvae were collected, all larvae were counted, but a random subset of 100 was chosen for identification and the species composition extrapolated to the total number of larvae.

Georeferenced aerial imagery for each site was obtained either commercially (Miami-Dade and Palm Beach counties) or from county geographical information system (GIS) facilities (Manatee Co.). A 100-m-diameter buffer was constructed around each site by using ArcGIS, and cover within this 100-m buffer was hand digitized and assigned to one of 17 cover categories (Table 1). Compound cover categories, made up of simple combinations of the measured variables, also were computed for each site (Table 1). Digitizing was simplified because we were familiar with all of the sites due to frequent sampling visits to each site. Problems with features that were unidentifiable or whose boundaries were not clear from the images were resolved by direct inspection/measurement at the site. In a few cases, access to such questionable features was not possible, in which case the feature was assigned to the "unknown" category. The resulting data include information on areal coverage, frequency, and distribution of each cover type at each site. The coverage data were imported into Statistica (StatSoft, Tulsa OK) or SAS (SAS Institute, Cary, NC) statistical packages for analysis.

## **Statistical Analyses**

One-way analyses of variance of the total mosquito catch of each species (log transformed to achieve normality) and percentage of composition (arcsine square root transformed) against county were computed using the General Linear Models module of Statistica. Tukey's honestly significant difference (HSD) post hoc test was used to identify significant individual comparisons. Similar analyses also were performed for the compound cover variables by county. Comparison of measured habitat variables between counties was accomplished via Kruskal–Wallis tests followed by multiple comparisons of mean ranks for each pair of groups via normal z-values, with post hoc probabilities corrected for the number of comparisons as per Siegel and Castellan (1988). Nonparametric tests were used for these analyses because of violations of assumptions for parametric analysis of variance (ANOVA) by some of the variables that could not be eliminated with data transformations.

Forward stepwise multiple regressions of (log) total mosquito abundance against the measured habitat variables were performed for each county and for the three counties combined using the Multiple Regression module of Statistica. Variables contributing significantly to the regression models were determined by significant F statistics and significant *t*-tests for standardized regression coefficients (β, Iles 1993)

Principal component analyses (PCAs) based on covariances were computed (PCA and Classification module, Statistica) for the same groups mentioned above, and the relative abundance and percentage of composition of the major mosquito species at each station were then plotted against the station's factor coordinates for every combination of the first three principal components. Multiple regressions of total numbers of *Ae. aegypti* and *Ae. albopictus* versus site coordinates for the first two principal components also were calculated.

For analyses of co-occurrences, monthly samples were regarded as independent because traps were removed and replaced with new traps each month. Individual containers also were treated independently. Because of major differences in trap size, presence/absence data were analyzed, instead of absolute abundances, as contingency tables with the CATMOD procedure in SAS, with container type (cup or tub) and county  $(n = 3)$  as independent variables in maximum likelihood analyses of variance.

# **Results**

#### **Mosquito Abundances**

In total, 49,525 mosquitoes were collected in the traps during the study. More than 99% of these mosquitoes belonged to the following four species: *Cx. quinquefasciatus* (17,393; 35.1%), *Ae. albopictus* (17,077; 34.5%), *Ae. aegypti* (11,774; 23.8%), and *Cx. nigripalpus* (3,248; 6.6%). Incidental species also collected included *Toxorhynchites rutilus* (Coquillett), *Culex biscaynensis* Zavortink & O'Meara, *Cx. salinarius, Culex territans* Walker as well as midges in the genus *Corethrella* (Corethrellidae). Analyses of variance indicate significant differences in overall abundance of *Cx. quinquefasciatus* and of percentage of composition of *Ae. albopictus* and *Cx. quinquefasciatus* (Table 2) among counties (Fig. 2). A posteriori comparisons of these data indicated that *Cx. quinquefasciatus* abundance was highest in Miami-Dade Co. and lowest in Manatee Co., whereas the percentage of composition of *Ae. albopictus* was greater in Manatee Co. than in Miami-Dade Co., and the opposite was true for *Cx. quinquefasciatus.*

## **Habitat Variables**

There were few significant overall differences among counties in the measured habitat variables. Kruskal–Wallis tests revealed significant variation in the variables mixed vegetation

 $(H_2 \le 8.164, P = 0.02, n = 44)$ , open building  $(H_2 = 23.379, P \le 0.001, n = 44)$ , and unknown  $(H_2 = 12,314, P \le 0.005, n = 44)$ . Multiple comparison of these variables indicate that for mixed vegetation, Miami-Dade Co. had significantly higher cover than Manatee Co.; for open building, the rankings were Miami-Dade > Manatee > Palm Beach and for unknown Palm Beach > Manatee. The only significant difference between counties in coverage by the different compound variables was in the "other" category, where Miami-Dade had significantly higher cover than Palm Beach (Table 3).

## **Habitat and Mosquitoes**

For *Ae. aegypti,* only an urbanization-related variable (building) contributed positively to the mosquito abundance regression equations (Table 4), whereas variables related to more rural or open settings (bare, canopy vegetation, mixed vegetation, and unpaved road) made significant negative contributions. The only exception was the variable open building, which was (negatively) significant in the equation for Manatee Co. The converse was true for *Ae. albopictus,* with significant urbanization-related variables (building, raved road, and open building) exhibiting negative coefficients, and ground vegetation, unpaved road, and bare exhibiting positive coefficients (Table 4). Unpaved lot, however, exhibited a significant negative coefficient in Manatee Co. For *Ae. aegypti,* regression equations explain (*R* 2 ) from 80.7% of the variation in mosquito abundance in Miami-Dade and Manatee counties to 51.2% for all counties combined. The amount of variation explained by the first variable entering the equations range from 56.8% (building in Palm Beach Co.) to 33.3% (open building in Manatee Co.; Table 4). For *Ae. albopictus,* variation explained by the regressions range from 83.2% in Palm Beach Co. to 37.4% in Miami-Dade Co. First variables explain from 56.7% (building, Palm Beach Co.) to 31.7% (building, all counties combined).

The regressions for *Cx. nigripalpus* and *Cx. quinquefasciatus* (Table 4) did not exhibit consistent patterns. For *Cx. nigripalpus,* more variables contributed significantly to the regression equations than for the other three species (six in Miami-Dade and Palm Beach counties, three in Manatee Co., and one for all sites combined). *Cx. quinquefasciatus,* however, had the fewest significant variables (none in Miami-Dade Co., one in Palm Beach Co., and two each in Manatee Co. and all sites combined). The only consistent pattern for the *Culex* species with respect to urban- and rural-related variables was that canopy vegetation did not enter significantly in any of the regressions. For *Cx. nigripalpus,* regression equations explain from 99.3% of the variation in mosquito abundance in Palm Beach Co. to 41.2% for all counties combined. The amount of variation explained by the first variable entering the equations range from 50.1% (ground vegetation in Palm Beach Co.) to 26.9% (building in Manatee Co.; Table 4). For *Cx. quinquefasciatus,* variation explained by the regressions range from 56.0% in Palm Beach Co. to 0% in Miami-Dade Co. First variables explain from 56.0% (mixed vegetation, Palm Beach) to 11.9% (paved lot, all counties combined).

#### **Habitat Components**

The percentage of variance in measured habitat variables by county explained by the first principal component ranged from 74.2% in Palm Beach Co. to 47.2% in Miami-Dade Co. Cumulative variance explained by the first three components ranged from 96.6% in Palm Beach Co. to 99.1% in Miami-Dade Co. (Table 5). For all sites combined, the first component explained 57.3% of the variance, and the first three components 97.4%. Four compound variables–canopy, A&C, dirt, and ground vegetation–accounted for most of the variance in the sites across the three counties.

Plots of factor coordinates of each station versus principal components (PC) 1 and 2 for all stations combined with mosquito relative abundance reveal that stations where *Ae. albopictus* was abundant tended to fall on the negative side of the PC1 axis, and their PC2

coordinates increased almost linearly with increases in the PC1 coordinates (Fig. 3). Sites with abundant *Ae. aegypti,* however, tended to have positive PC1 coordinates and showed a decrease in PC2 coordinates with an increase in PC1 coordinates. Regressions of *Ae. aegypti* and *Ae. albopictus* abundances at each station with station coordinates for PC1 and PC2 were highly significant (*Ae. aegypti:*  $F_{1, 41} = 9.065, P \le 0.0006$ ; and *Ae. albopictus:*  $F_{1, 41} = 12.140, P \le$ 0.0001).

No distinct patterns, however, were evident for *Culex* spp. (Fig. 4). At the county level, patterns were similar, but reflected the loadings at each county. For example, at Palm Beach Co., PC1 and PC2 loadings were similar to the loadings for all counties combined, and the site coordinates reflected mosquito relative abundances similarly. In Manatee Co., however, ground vegetation had a high negative loading for PC2 (positive for all counties and Palm Beach).

## **Co-occurrences**

Among all cups in which one or more *Aedes* spp. were recovered, *Ae. aegypti* and *Ae. albopictus* were found together in 22.7% (Table 6). In tubs, the two species together represented 33.3% of all *Aedes*-positive occurrences, which accounted for a significant container effect on *Aedes* spp. co-occurrences (Table 7). Although no significant county effect was detected, a significant county  $\times$  container interaction (Table 7) was associated with an unexpectedly low rate of co-occurrences of the two *Aedes* spp. in Manatee tubs (18.4%).

Co-occurrences of *Aedes* spp. with *Culex* spp. represented only 5.7% of all cups that harbored one or more species from these two genera, but they accounted for 45.4% of all *Culex*-positive plus *Aedes*-positive tubs, which produced a highly significant container effect (Table 7). The significant county effect in maximum likelihood ANOVA (Table 7) was associated with much higher levels of co-occurrences in both container types in Miami-Dade Co. (Table 6).

# **Discussion**

Results from this study indicate that factors at several scales, ranging from county to trap type, affected the abundance of *Culex* and *Aedes* mosquitoes at our sites. For example, *Cx. quinquefasciatus* is a predominantly urban mosquito whose larvae can be found in water containing a high degree of organic pollution and close to human habitation and whose females bite mammals in preference to birds (Cornel et al. 2003). The abundance of this species in the three counties (Miami-Dade > Palm Beach > Manatee; Table 2) probably reflects the relative abundance of highly urbanized habitats in each (average housing units per square kilometer at Miami-Dade, Palm Beach, and Manatee counties are 174.3, 112.7, and 76.2, respectively; U.S. Census statistics, 2000 and 2002). Although all three counties have significant urban coverage, urban sprawl in Miami-Dade Co. has left only pockets of green habitat throughout the county. Palm Beach Co. is similar to Miami-Dade Co., but it still has significant undeveloped acreages in the western portions of the county, whereas in Manatee Co. there is significant undeveloped coverage with interspersed highly urbanized areas. These differences occurred in spite of the fact that the only consequential difference in coverage between counties at our particular study sites was the opposite of what you would expect from the above county wide patterns (mixed vegetation cover was greater at our sites in Miami-Dade Co. than at our sites in Manatee Co.; see Results and Table 3). Although a high percentage of the variation in *Cx. nigripalpus* abundance was explained by the stepwise regressions for Dade and Palm Beach counties (to be expected, given the large number of significant variables), the *Culex* species did not exhibit consistent patterns among counties in terms of which habitat variables entered into the regressions equations and their signs (Table 4).

*Aedes* mosquitoes, however, seemed to respond more to intermediate scale factors, such as measures of habitat cover within a 100-m-diameter of each sampling site (Table 1). Thus, results of the multiple regressions of mosquito abundance with the measured habitat variables indicated a positive association by *Ae. aegypti* with urbanization-related variables such as building coverage and a negative association with variables more commonly associated with rural areas such as canopy and mixed vegetation coverage, whereas the opposite was true for *Ae. albopictus* (Table 4).

When the arrangement of sites along principal component axes is combined with the relative abundance of the four major species at each site, it is evident that *Aedes* abundances reflect the site's characteristics as represented by their factor coordinates (Fig. 3). Sites where *Ae. aegypti* was abundant clustered on the positive side of PC1, which had a high positive loading for A&C, a variable associated with urbanization, and on the negative side of PC2, which had a high negative loading for dirt, which reflects a rural setting. Conversely, sites where *Ae. albopictus* was abundant clustered along the negative side of PC1, where canopy vegetation (normally associated with rural-forested areas) had a high loading. The first principal component alone, with high loadings for canopy at one end and A&C at the other end can separate the majority of sites where either *Ae. aegypti* or *Ae. albopictus* predominate.

The PC2 axis has high negative loadings for dirt and high positive loadings for ground vegetation. It is interesting to note the patterns of changes in PC2 coordinates with changes in PC1 coordinates for both *Ae. aegypti-* and *Ae. albopictus-*rich sites. For the former species, PC2 coordinates tend to increase with decreases in PC1 coordinates, whereas for the latter, PC2 coordinates increase with increases in PC1. Regressions of the abundance of both species with PC1 and PC2 coordinates are highly significant (see Results). Ground vegetation can reflect a suburban setting (lawns and gardens) or a rural setting (low growing crops or pastures), but ground vegetation cover associated with asphalt and concrete (A&C) (*Ae. aegypti*) is usually mostly lawns, whereas ground vegetation associated with canopy vegetation (*Ae. albopictus*) normally indicates pastures and low-growing crops.

*Culex* species, however, did not show such distinct patterns (Fig. 4). Stations with high relative abundance of *Cx quinquefasciatus* showed considerable spread along both axes, whereas *Cx. nigripalpus* predominated in only a few stations with no consistent pattern.

The overall frequency of co-occurrence of *Ae. aegypti* and *Ae. albopictus* in cups in three counties (22.7%) was less than reported for West Palm Beach (48%) but more than Boca Raton (13%), based on much briefer surveys of these cities (Braks et al. 2003). The significantly higher frequency of co-occurrence of these species in tubs may be related to the much larger volume of the latter trap type. Tubs in Manatee Co. registered fewer co-occurrences than the other two counties, because of the relative scarcity of *Ae. aegypti* in that county (Fig. 2), leading to the significant county  $\times$  container interaction. The co-occurrences of these species suggest that interspecific larval competition, thought to account for the range reduction of *Ae. aegypti* by *Ae. albopictus* in Florida and elsewhere (Juliano 1998, Braks et al. 2004), is probable in nature.

The high frequency of co-occurrences of *Aedes* spp. with *Culex* spp. in tubs, but not in cups, is facilitated by the predilection of Florida *Culex* (*Culex*) spp., particularly *Cx. nigripalpus,* to oviposit in the larger container type (O'Meara et al. 1989). Based on results of the competitive superiority of *Ae. albopictus* larvae co-occurring with *Cx. pipiens* (Costanzo et al. 2005), *Culex* spp. in tubs in Florida may suffer competitively in the presence of *Aedes* spp. larvae. Among our study areas, such competitive interactions were most likely in Miami-Dade Co., where the frequencies of inter-generic co-occurrence were highest.

It should be emphasized that the current study addresses only oviposition habitats of these mosquito species, which may differ from habitats used for other activities, such as host seeking. These data do show the general preference of *Ae aegypti* and *Ae albopictus* for different habitats and container types.

In the New World, most oviposition by *Ae. aegypti* occurs outdoors (Braks et al. 2003, Honório et al. 2003), whereas more domesticated populations of this species usually oviposit indoors in parts of Asia (Thavara et al. 2001) and Africa (Lounibos 2003).

Although habitat segregation between *Ae. aegypti* and *Ae. albopictus* is well established in the Old World (Fontenille and Rodhain 1989), some of the habitat variables used in the current study, such as paved surfaces, will not be present in undeveloped sites. Thus, a further challenge may be elucidation of the underlying cues used by these species for habitat selection and segregation (Juliano et al. 2004).

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**Fig. 1.** Location of Miami-Dade, Palm Beach, and Manatee counties.



**Fig. 2.** Total numbers of mosquitoes collected in oviposition traps per county.



# **Fig. 3.**

Factor coordinates of all stations plotted against PC1 and 2 of the compound habitat variable and *Aedes* mosquito relative abundance at each station. Boxes identify variables with high loadings in the corresponding sides of the axes.



#### **Fig. 4.**

Factor coordinates of all stations plotted against PC1 and 2 of the compound habitat variable and *Culex* mosquito relative abundance at each station. Boxes identify variables with high loadings in the corresponding sides of the axes.

Habitat variables used in this study (first column) and composition of derived compound variables



<sup>*a*</sup> Compound variables are a simple sums of the coverage in those habitat variables marked with a 1 and 50% of the coverage in those marked with 1/2 under their respective columns.

Results of analysis of variance for differences in abundance and percent composition of the major mosquito species by county



*a* Significant (*P* ≤ 0.05) individual differences determined a posteriori (Tukey's HSD test).

*<sup>b</sup>*MD, Miami-Dade; MNT, Manatee; PB, Palm Beach.

# **Table 3** Results of analysis of variance for differences in coverage by county



*a* Significant (*P* ≤ 0.05) individual differences determined a posteriori (Tukey's HSD test).

*<sup>b</sup>*MD, Miami-Dade; MNT, Manatee; PB, Palm Beach.

Significant ( $P \le 0.05$ ) contributions to forward stepwise multiple regressions of *Aedes* spp. and *Culex* spp. abundance with compound habitat categories by county



Variables to include in the model were determined by significant F statistics and significant *t*-tests for standardized regression coefficients.

*a* Cumulative *R* 2.

# **Table 5** Factor loadings for the first three PCs of the compound cover variables



Numbers in parentheses indicate the percentage of the variance explained by the factor or by the first three factors if next to a county name. Loadings > 0.8 are shown in bold.

Numbers of co-occurrences and occurrences alone in traps



Maximum likelihood ANOVA for co-occurrences of *Ae. aegypti* and *Ae. albopictus* and *Aedes* spp. and *Culex* spp. in relation to trap type and county

