Larval Mosquito Habitat Utilization and Community Dynamics of *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae)

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ABSTRACT *Aedes albopictus* (Skuse) and *Ae. japonicus* (Theobald) are important container-inhabiting mosquitoes that transmit disease agents, outcompete native species, and continue to expand their range in the United States. Both species deposit eggs in natural and artificial containers and thrive in peridomestic environments. The goal of our study was to examine the types and characteristics of containers that are most productive for these species in the northeastern United States. In total, 306 containers were sampled in urban, suburban, and rural areas of New Jersey. Multiple biotic and abiotic factors were recorded in an attempt to identify variables associated with the productivity of each species. Based on pupal abundance and density of container types, results showed that tires, trash cans, and planter dishes were the most important containers for *Ae. albopictus*, while planter dishes were the most important containers for *Ae. japonicus*. Container color (black and gray), material (rubber), and type (tires) were correlated with species presence for *Ae. albopictus* and *Ae. japonicus*. These factors may play a role in the selection of oviposition sites by female mosquitoes or in the survival of their progeny. Differences in species composition and abundance were detected between areas classified as urban, suburban, and rural. In urban and suburban areas, *Ae. albopictus* was more abundant in container habitats than *Ae. japonicus*; however, *Ae. japonicus* was more abundant in rural areas, and when water temperatures were below 14°C. Our results suggest many variables can influence the presence of *Ae. albopictus* and *Ae. japonicus* in container habitats in northeastern United States.

KEY WORDS larval survey, container-inhabiting, larval-pupal productivity, New Jersey

The invasion of two exotic container-inhabiting mosquitoes in the United States, *Aedes albopictus* (Skuse) (Sprenger and Wuithiranyagool 1986) and *Aedes japonicus* (Theobald) (Peyton et al. 1999) has attracted considerable attention among mosquito ecologists and mosquito control agencies because of the numerous small container habitats these species may use. The problem with rapid accumulation of disposable containers (i.e., bottles, cups, and cans) in urban and suburban developments increases the difficulties of efficacious and sustainable control measures by local mosquito abatement districts. These species possess desiccation-resistant eggs, a biological mechanism that facilitated their introduction into the United States, likely from shipments of used tires (Lounibos 2002). Both species occupy similar natural and artificial containers throughout their native and introduced areas.

Ae. albopictus and *Ae. japonicus* are competent vectors for a number of temperate and tropical disease-causing pathogens, such as West Nile virus (Turell et al. 2001). *Ae. albopictus* is a major human biting pest and is considered second only to *Ae. aegypti* in its importance as a disease vector of dengue and dengue hemorrhagic fever (Estrada-Franco and Craig 1995, Knudsen et al. 1996). *Ae. albopictus* was solely responsible from the outbreak of dengue fever in Hawaii during 2001 (Effler et al. 2005). *Ae. albopictus* is also a potential vector of Venezuelan equine encephalitis virus (Beaman and Turell 1991), Rift Valley fever virus (Turell et al. 1988), and chikungunya virus (Turell et al. 1992). *Ae. japonicus* is a laboratory vector of Japanese encephalitis virus, a pathogen not yet found in the United States (Tanaka et al. 1979). The introduc-

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tion of these two species into North America increases the human health threat, because these species may serve as bridge vectors in existing mosquito-disease cycles (Juliano and Lounibos 2005).

Ae. albopictus is considered to have evolved along forest-fringed areas in tropical regions of Southeast Asia, but its range extends considerably farther into northern Japan and southern Siberia where populations overwinter in the egg stage (Hawley 1988). *Ae. japonicus* is native to northern Asian countries that include Japan and Korea (Tanaka et al. 1979), and does not occur in the tropics. New Jersey's climate resembles that of Korea and northern Japan where the two species co-occur naturally. As *Ae. albopictus* and *Ae. japonicus* adapt locally in New Jersey, the relationship of the two species to each other and to native container-inhabiting mosquitoes is an open question worth studying from the standpoint of invasion biology and of practical mosquito control. New Jersey's climate and biogeography provides an excellent opportunity to study the habitat utilization of these two species.

Ae. albopictus has been shown to have a competitive advantage over *Ae. japonicus* in artificial container habitats (Armistead et al. 2008). In Connecticut, where *Ae. albopictus* has not become established, *Ae. japonicus* outcompetes native artificial and natural container species (Andreadis and Wolfe 2010). In New Jersey, *Ae. albopictus* has been increasing its range since 1995, yet it has failed to become established in the northwestern part of the state (Farajollahi and Nelder 2009), a cooler and more rural region where *Ae. japonicus* now occurs. As both *Ae. albopictus* and *Ae. japonicus* become established in different parts of the country, any shifts in competitive advantage in different regions, habitats, and climates become important topics for investigation.

Both *Ae. albopictus* and *Ae. japonicus* larvae use a wide range of containers. Natural and artificial container habitats are heterogeneous with the environment, temporal and spatial fluctuations in temperature, water volume, nutrient conditions, and other factors (Sota et al. 1994, Sunahara and Mogi 1997). All these factors may have an effect on oviposition selection, survival, and fitness of progeny. Previous studies have shown niche segregation among container-inhabiting mosquitoes based on container type selection (Sota et al. 1994, Sunahara et al. 2002). This paper focuses on investigation of the container habitat usage of two invasive species (*Ae. albopictus* and *Ae. japonicus*) in northeastern United States.

Since the introduction of *Ae. albopictus* and *Ae. japonicus* into the United States, the significance of artificial containers as habitats for larvae has drawn increased interest from mosquito control agencies. Traditional *Stegomyia* indices measure abundance of container-inhabiting mosquitoes using house-to-house surveys, which reflect the proportion of mosquito-positive and mosquito-negative containers in an area (Chan et al. 1971, Focks and Chadee 1997). These indices assign equal importance to each container without taking into account the variation in produc-tivity of container habitats. Since the survivorships of pupae and emerging adults are directly related, an approach that involves estimating the mosquito production potential of different types of containers based on their density and standing crop of pupae provides valuable information for directing control efforts (Strickman and Kittayapong 2003, Richards et al. 2008).

Knowing the most productive container habitats can be used for targeted vector control interventions, which reduces the use of larvicides and pupicides and eventual adulticides. This information can also be used to answer fundamental research questions, and increase efficiency of education and control efforts. The aim of this study, regarding *Ae. albopictus* and *Ae. japonicus*, was to 1) identify the most productive container types in urban, suburban, and rural settings, 2) determine which environmental variables contribute to increased pupal productivity within containers, and 3) compare and contrast the overlap of the two species in natural and artificial container habitats.

Materials and Methods

Site Selection. To characterize container characteristics for *Ae. albopictus* and *Ae. japonicus*, we selected towns or cities where both species are present. In previous studies, *Ae. albopictus* was found to be abundant and widespread in suburban and urban sites (Farajollahi and Nelder 2009). Definitions from the U.S. Census Bureau (2010) were used to classify urban, suburban, and rural sites. However, because there is currently no definition for suburban, for this study, we classified suburban as urban sites that are not part of urbanized areas. Urban sites (classified under the U.S. Census Bureau's term "urbanized area" as having >50,000 residents and over 1,000 persons per 2.59 km^2) were located in Trenton, Mercer County. The suburban site (classified under the U.S. Census Bureau's term "urban" as having >2,500 residents, and over 1,000 persons per 2.59 km^2) was located in Keyport, Monmouth County, where *Ae. albopictus* was first collected in New Jersey during 1995 (Crans et al. 1996). Three rural sites (classified under the U.S. census bureau's term "rural" as having <1,000 persons per square mile) were selected within Monmouth, Middlesex, and Mercer counties. Cheesequake State Park (Middlesex County) is a diverse habitat primarily made up of forested hardwood deciduous habitat, along with salt water marsh, cedar hardwoods, and Pine Barrens, which is ≈3.2 km^2, and is located 2.3 km from the suburban location. Turkey Swamp Wildlife Management area, which is mainly coniferous forest, is located in Freehold (Monmouth County) is ≈4.1 km^2, and is 27 km from the study area. In Mercer County, a rural parcel in Pennington Boro, served as our rural residential area.

Urban and suburban sites were divided into 25 blocks (≈30 homes each). A single block was selected at random for each site. Each residence within a designated block was sampled, skipping and recording those residences where permission was not granted.

Our goal was to sample at least 25 homes in both the urban and suburban areas. We continued to randomly select blocks until enough homes were sampled. Rural sites were divided into 25 transects ($\approx$1.5 km), each extending from west to east. A single transect was randomly chosen and all tree holes and containers discovered along the transect were sampled. We continued to randomly select transects until at least 30 tree holes were sampled. In rural areas, a transect was chosen instead of a block to test a hypothesis that *Ae. albopictus* decreases in tree holes as you transition from residential areas to forested regions.

Sampling Procedure. Containers were defined as anything natural or artificial that in its present state was holding water, and was capable of holding water for three or more days. All artificial and natural containers were sampled by pouring the contents through a four-tier sieve (4, 2, 0.5, and 0.25 mm). A 30 ml turkey baster was used to extract all water from inaccessible containers (tires and tree holes) and the contents were resuspended into an enamel pan using deionized water. All larvae and pupae were placed in individual 500 ml cups with caps, labeled (date and sample number), and transported to the laboratory. The sampling variables recorded for each container included container type, material (aluminum, brass, cellophane, cement, ceramic, cloth, copper, fiberglass, glass, granite, unknown metal, plastic, pvc, rubber, Styrofoam, and wood), color, dimensions (height, length, width, and diameter), surface area, water depth, water volume, location characteristics (grass, bare soil, pavement, groundcover, bush, porch, pile, and tree), height of base of container from ground, sun exposure (full sun, partial sun, and full shade), types of detritus within the water (leaves, grass, trash, dirt, sand, and nothing), water condition as a measure of water cleanliness (polluted, organic detritus only, and clean with no detritus), water color (clear, light, and dark), presence of leaves, presence and abundance of mosquito species, and presence and abundance of predators, such as *Toxorhynchites rutilus septentrionalis* (Dyar and Knab). The temperature and pH were recorded for each container before sampling using a Symphony electric meter (VWR International, LLC, Batavia, IL). For each container, the address and global positioning system (GPS) coordinates were recorded. In the urban sites, the GPS coordinates were taken for the house level only. Whereas in the suburban and rural sites, we obtained GPS coordinates for each specific container.

All larvae and pupae were collected and counted; pupae were allowed to emerge as adults, all of which were identified to species. Early instar larvae were reared to third and fourth instars for more accurate identification. Larval specimens were preserved in 90% ethanol. The majority of containers (57%) had <40 larvae, which were all identified to species. The remaining containers had $\approx$100 larvae. From these containers, a subsample of 30 larval specimens were randomly selected and identified to species (Stojanovich 1961, Darsie and Ward 2005). Damaged larval specimens were identified to genus only. Given that

Culex mosquitoes were not the primary focus of our study, we combined them into *Culex* species for comparison against container *Aedes*.

Statistical Analysis. A principal component analysis was used to condense variables (temperature, pH, shade level, water color, height, depth, surface area, and volume) into factor groups (SPSS version 18; IBM Corporation, Armonk, NJ). We chose pupal abundance, because pupal survival is considered a good estimate of emerging adults (Focks and Chadee 1997), and we wanted to determine which factors are predictors of suitable habitat. A logistic regression was performed to compare presence and absence of species (*Ae. albopictus* and *Ae. japonicus*) to all variables (container type, water condition, container color, container material, presence of leaves, surface area, temperature, pH, volume, shade, water color, depth, height, and whether it was artificial or natural) (SPSS version 18). Chi-square tests were conducted to further examine significant categorical variables. The Mann–Whitney *U* test was performed to compare mean values for *Ae. albopictus* and *Ae. japonicus* (surface area, depth, volume, temperature, pH, and height). Spatial variation in temperature for the suburban and rural sites were mapped using ArcMAP 10 GIS, North American Datum 1983, using inverse distance weighted mapping tools. The urban site was excluded from the analysis, because we did not have coordinates for each specific container. A geographically weighted regression was used to correlate spatially the variation in temperature with potential covariates (shade, volume, leaves, surface area, and time of sampling) using ArcMAP 10 GIS. The Index of Container Importance (ICI), which accounts for pupal and container abundance was calculated for rural, suburban, and urban containers (Richards et al. 2008). The ICI values were only performed on *Ae. albopictus* and *Ae. japonicus* because they were the most common in all three study areas, and were the focus of this study. Mean densities of *Ae. albopictus* versus *Ae. japonicus* were compared for each container type using analysis of variance (ANOVA) (SPSS version 18). Mean crowding (Bradshaw 1983) was calculated for *Ae. albopictus* and *Ae. japonicus* for total numbers of immature in all containers, total numbers in tires only, number of immature per liter, and number of immature per square meter surface area. To determine the likelihood of emergence before evaporation in each of the container types, we modeled evaporation rates based on a previous formula (Bartlett–Healy et al. 2011). The evaporation model enabled us to examine the mean number of days to evaporation in containers inhabited by the most common species collected.

Results

Seven larval surveys (September and October) were conducted during peak mosquito activity in 2009 in Mercer, Monmouth, and Middlesex counties in New Jersey. During these surveys, 50 houses (25 urban, 25 suburban), two junkyards, and two forests were surveyed. In total, 9,909 mosquito larvae and pupae, rep-
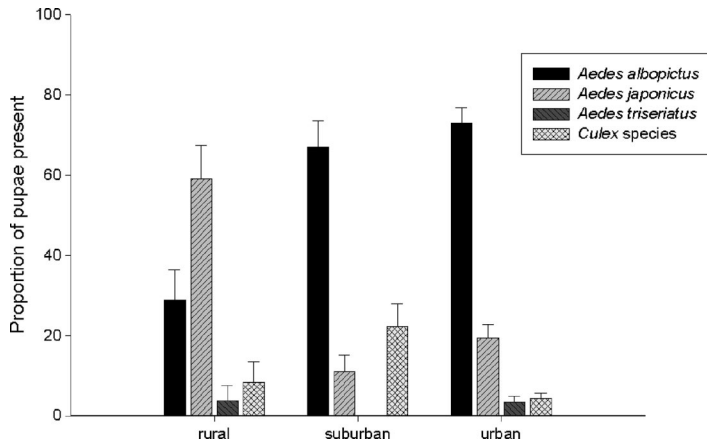
Fig. 1. The mean proportion of pupae collected in containers in urban, suburban, and rural areas of New Jersey.

resenting 11 species from six genera were collected from 306 containers. Of the 80 containers sampled in rural habitats, 56% contained larvae or pupae. Of the 116 and 110 containers sampled in suburban and urban sites, 34.5 and 68.2% contained immature mosquitoes. *Ae. albopictus* was collected in 41.2% of containers sampled, with *Ae. japonicus* present in 28.7% of those sampled. *Culex* species (14.4%), *Ae. triseriatus* (8.8%), *Tx. r. septentrionalis* (7.2%), *Orthopodomyia signifera* (Coquillett) (1.0%), *Culiseta melanura* (Coquillett) (0.6%), *Anopheles punctipennis* (Theobald) (0.6%), and *Aedes vexans* (Meigen) (0.3%) were also collected. In urban and suburban sites, *Ae. albopictus* was the most common species collected (making up 43.9 and 51.6% of the total specimens collected in those areas). However, in rural sites, *Ae. japonicus* (41.9% of total specimens) was slightly more abundant than *Ae. albopictus* (39.5% of total specimens) (Fig. 1). A number of *Culex* species were also collected from containers that were composed of *Cx. pipiens* (60.3%), *Cx. restuans* Theobald (28.3%), *Cx. salinarius* Coquillett (0.4%), and unidentified *Culex* species (11.0%).

In total, 276 artificial containers were sampled, consisting mainly of tires (10.0%), buckets (8.7%), trashcans (8.3%), planter dishes (8.0%), tarps (5.0%), and trashcan lids (4.7%). The majority of containers had few (2.9 ± 0.5) species present. The highest diversity of species occurred in tires (nine species), trash cans (six species), tree holes (five species), and large plastic buckets and trays (four species). The height of artificial containers ranged from 10 cm below to 245.6 cm above ground. Most of the artificial containers sampled were on ground level (61.3%). *Ae. albopictus* was collected in containers as high as 151 cm, whereas *Ae. japonicus* was found as high as 101 cm. There was no significant difference ($P = 0.618$) between mean container heights for *Ae. albopictus* (15.6 ± 2.9 cm) compared with those of *Ae. japonicus* (14.6 ± 3.2 cm). Over 69% of the artificial containers sampled held leaf litter. *Ae. albopictus* was collected more often in containers with leaf litter (79%) than those without leaf litter (21%). A similar pattern was found with *Ae. japonicus*, which was more frequent in containers with

leaf litter (86%), compared with those without (14%). There was no significant difference for mean surface area of containers ($P = 0.24$) for *Ae. albopictus* (0.09 ± 0.01 m²) or *Ae. japonicus* (0.1 ± 0.02 m²), mean depth of water ($P = 0.7$) (0.07 ± 0.01 m, 0.08 ± 0.01 m), mean volume of water ($P = 0.32$) (8.2 ± 1.8, 10.2 ± 2.6), and mean pH ($P = 0.42$) (7.4 ± 0.07, 7.5 ± 0.06) for containers with *Ae. albopictus* versus those with *Ae. japonicus*.

Water temperature ranged from 9.7 to 33.0°C, with a mean of 18.6°C, and median of 18.7°C (Table 1). The majority of species were collected in containers with a mean water temperature below 18.6°C, including *Ae. albopictus* (17.2°C ± 0.3), *Ae. japonicus* (16.4°C ± 0.4), *Ae. triseriatus* (16.5°C ± 0.4), *Culex* species (18.0°C ± 0.5), and *Tx. r. septentrionalis* (17.6°C ± 1.2). The mean temperature for containers lacking mosquito larvae was 19.7°C ± 0.3. *Ae. albopictus* was present in the greatest range of temperatures (12 to 33°C). When comparing the proportion of *Ae. albopictus* and *Ae. japonicus* at increasing container temperatures, we found the highest proportion of *Ae. japonicus* in cooler temperatures, especially during October (Fig. 2).

Spatial analysis of the suburban site showed that the southeast quadrant had containers with the highest recorded temperatures; whereas the southwest quadrant had the lowest temperatures (Fig. 3). Collections of *Ae. albopictus* and *Ae. japonicus* pupae also occurred in these areas of cooler temperatures. Air temperatures during suburban sampling ranged from 21 to 23°C, although water temperatures ranged from 17.6

Table 1. Mean temperatures (°C), surface area (m²) and pH for the most frequently collected container inhabiting mosquitoes in urban, suburban, and rural areas in New Jersey

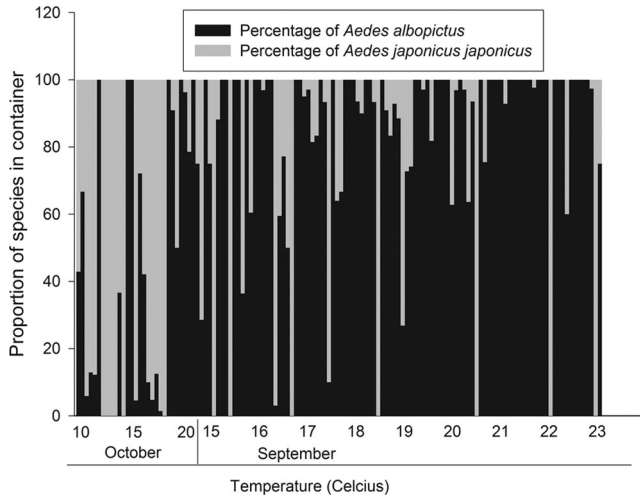| Species	Temperature (mean ± SE)	Surface area (mean ± SE)	pH (mean ± SE)
Ae. albopictus	17.2 ± 0.3	0.09 ± 0.01	7.4 ± 0.1
Ae. japonicus	16.4 ± 0.4	0.10 ± 0.02	7.5 ± 0.1
Cx. species	18.0 ± 0.5	0.17 ± 0.04	7.3 ± 0.2
Ae. triseriatus	16.5 ± 0.4	0.09 ± 0.02	7.3 ± 0.1
Tx. r. septentrionalis	17.6 ± 1.2	0.02 ± 0.01	6.8 ± 0.2

Fig. 2. Proportion of *Ae. albopictus* and *Ae. japonicus* at increasing temperatures in artificial containers for September and October 2009, New Jersey.

to 33.0°C. Geographically weighted regression analysis of the suburban site showed that water temperature was strongly correlated with shade ($R^2 = 0.51$), with weaker correlations with leaves ($R^2 = 0.45$), water volume ($R^2 = 0.45$), water surface area ($R^2 = 0.39$), or time of sampling ($R^2 = 0.32$). We found similar geographically weighted regression results for the ru-

ral residential site, with water temperatures correlating strongest with shade ($R^2 = 0.43$), with weaker correlations with surface area ($R^2 = 0.37$), leaves ($R^2 = 0.33$), volume ($R^2 = 0.33$), and time of sampling ($R^2 = 0.33$).

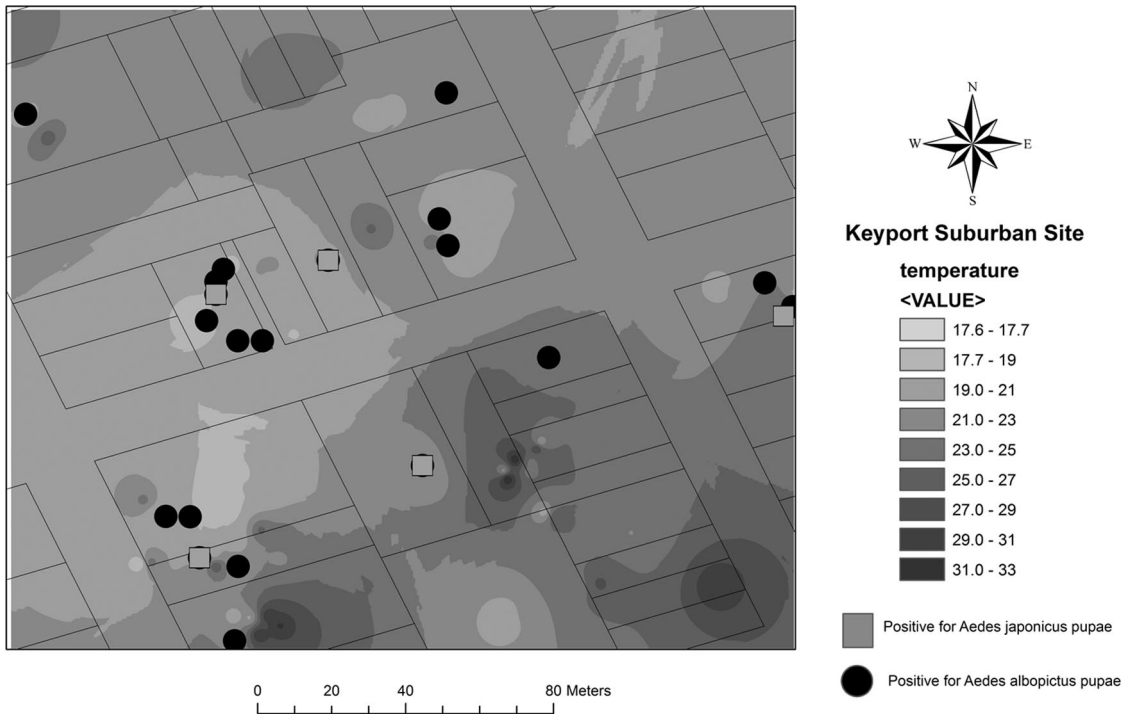In total, 34 tree holes, containing 54 larvae and pupae, were sampled from the rural sites in Cheese-

Fig. 3. Spatial interpolation of container water temperatures within the Keyport, NJ, suburban site, 14 September 2009. Interpolation goes from light (cool) to dark (warm). Locations where *Ae. albopictus* pupae were collected are indicated with black circles. Locations where *Ae. japonicus* pupae were collected are indicated with the gray squares. Air temperatures during sampling ranged from 21 to 23°C.

quake (30), Turkey Swamp (2), Pennington (1), and the suburban Keyport site (1). The tree holes sampled were predominantly found in *Acer rubrum* L. (50%) and *Quercus prinus* L. (23.5%). Other tree species containing holes that were sampled included *Prunus serotina* Ehrh, *Fagus grandifolia* Ehrh, *Ulmus* species, *Carya* species, *Quercus alba* L., and *Acer platanoides* L. Two *Ae. albopictus* pupae were collected in a *Q. prinus* tree hole (0.21 km from closest residential area), which also contained *Tx. r. septentrionalis*. *Tx. R. septentrionalis* was detected in half of the tree holes examined, and were abundant in *A. rubrum* (58.8%), *Q. prinus* (29.4%), *P. serotina* (5.9%), and *Carya* species (5.9%). When collected in tree holes, *Tx. r. septentrionalis* occurred concurrently with *Ae. triseriatus* (17.6%), *Or. signifera* (11.8%), *Cs. melanura* (11.8%), and *Ae. albopictus* (5.8%). No *Ae. japonicus* were found in tree holes.

In total, 28 tires were sampled from the rural (8), suburban (1) and urban (19) sites. In total, 2,122 larvae (23.8% of total), and 196 pupae (19%) were collected from these tires. The most common mosquito collected was *Ae. albopictus* (25 tires, 89.3%). Within the tires, *Ae. albopictus* coexisted with *Ae. japonicus* (72%), and *Ae. triseriatus* (20%), and *Tx. r. septentrionalis* (4%). All sampled tires supported mosquito larvae with the exception of one, which was tipped on its side, had a temperature of 12.6°C, pH of 7.3, and a depth of 3.8 cm. Other tires had similar pH, and depth, but had cooler water temperatures (11.4–12.5°C).

The logistic regression showed that the presence of *Ae. albopictus* had a positive correlation with container color ($\chi^2 = 46.2$; df = 14; $P = 0.001$), container type ($\chi^2 = 47.4$; df = 18; $P < 0.001$), container material ($\chi^2 = 43.5$; df = 15; $P = 0.002$), the presence of leaves ($\chi^2 = 5.8$; df = 1; $P = 0.016$), water color ($\chi^2 = 14.6$; df = 3; $P < 0.001$), and increase in shade ($\chi^2 = 8.7$; df = 1; $P = 0.003$). There was a negative correlation with water temperature ($\chi^2 = 12.8$; df = 1; $P < 0.001$). Of all container colors sampled, presence of *Ae. albopictus* had positive correlations with containers being black ($\chi^2 = 22.6$; df = 1; $P < 0.001$) or gray ($\chi^2 = 9.4$; df = 1; $P = 0.002$), but not with blue, brown, clear, green, metallic, orange, pink, purple, red, tan, white, or yellow. Of all container types sampled, only tires ($\chi^2 = 29.3$; df = 1; $P < 0.001$) had positive correlations with the presence of *Ae. albopictus*. Rubber ($\chi^2 = 25.2$; df = 1; $P < 0.001$) was the only container material to positively correlate with the presence of *Ae. albopictus*.

The logistic regression showed that the presence of *Ae. japonicus* had a positive correlation with container color ($\chi^2 = 49.7$; df = 14; $P < 0.001$), container type ($\chi^2 = 57.2$; df = 18; $P < 0.001$), container material ($\chi^2 = 40.0$; df = 15; $P = 0.005$), the presence of leaves ($\chi^2 = 12.8$; df = 1; $P < 0.001$), surface area ($\chi^2 = 8.9$; df = 1; $P = 0.003$), and water color ($\chi^2 = 16.6$; $P < 0.001$). The presence of *Ae. japonicus* had a negative correlation with water temperature ($\chi^2 = 13.1$; df = 1; $P < 0.001$). Of all container colors sampled, presence of *Ae. japonicus* had positive correlations with containers being black ($\chi^2 = 18.3$; df = 1; $P < 0.001$) or

Table 2. Rotated factor pattern scores from eight principal components of containers collected from urban, suburban, and rural areas of New Jersey

Variable	PC1	PC2	PC3	PC4	PC5
Water temp	−9	−85[a]	−6	−14	3
Water pH	−21	−3	2	95[a]	−2
Shade	−1	80[a]	−18	−12	−15
Water color	−28	60[a]	47	−22	−3
Depth	93[a]	3	10	−9	−3
Surface area	30	−7	86[a]	6	−5
Volume	92[a]	−4	15	−16	−3
Height	−4	−14	−5	−2	98[a]

[a] Scores >50 that account for the most variation in principal component. The percent variation for each component is as follows: PC1 (27.0%), PC2 (23.7%), PC3 (13.0%), PC4 (11.0%), and PC5 (9.3%).

gray ($\chi^2 = 11.0$; df = 1; $P = 0.001$), but not with blue, brown, clear, green, metallic, orange, pink, purple, red, tan, white, or yellow. Of all container types sampled, only tires ($\chi^2 = 27.3$; df = 1; $P < 0.001$) and buckets larger than five gallons ($\chi^2 = 10.0$; df = 1; $P = 0.002$) correlated with the presence of *Ae. japonicus*. Rubber ($\chi^2 = 15.5$; df = 1; $P < 0.001$) and polyvinyl-chloride ($\chi^2 = 6.5$; df = 1; $P = 0.011$) were the only container materials to have positive correlations with the presence of *Ae. japonicus*.

The principal component (PC) analysis resulted in five factors that explained >83% of the variation in the data (Table 2). Factors included associations with water depth and volume (PC1), shade, water color, and temperature (PC2), surface area (PC3), water pH (PC4), and height (PC5). *Ae. albopictus* pupal abundance was significantly associated with PC3 ($R^2 = 0.02$; $F = 3.9$; df = 1, 258; $P = 0.05$) indicating that its numbers increased with an increase in surface area. *Ae. japonicus* pupal abundances were significantly associated with PC2 and PC3 ($R^2 = 0.2$; $F = 28.9$; df = 1, 258; $P < 0.001$) indicating that their abundances increased with increasing surface area, shade and water color and decreasing temperature. The pupal abundance of *Culex* species was significantly associated with PC3 and PC1 ($R^2 = 0.44$; $F = 194.0$; df = 1, 258; $P < 0.001$) indicating that it increased with increase in surface area, depth, and volume. *Ae. triseriatus* pupal abundances were significantly associated with PC1 ($R^2 = 0.03$; $F = 7.1$; df = 1, 258; $P = 0.008$) indicating that their abundances increased with increasing depth and volume.

For *Ae. albopictus*, artificial container habitats became an increasingly important variable as population density increased (Table 3). This was particularly evident for tires, which were over seven times more important in urban than rural settings. Although not sampled in all three settings, trash cans had the highest ICI for *Ae. albopictus* (ICI = 66). For *Ae. japonicus*, tires were the most important container type in rural (ICI = 18.75) and urban settings (ICI = 17.04). *Ae. japonicus* was rare in suburban sites.

The highest pupal densities for *Ae. albopictus* occurred in planter dishes (5.9 pupae per liter), trash cans (4.3 pupae per liter), lids (2.9 pupae per liter), and large buckets (1.8 pupae per liter) (Table 4). *Ae.*

Table 3.   ICI from the most common containers found in urban, suburban, and rural areas of New Jersey

Container	*Ae. albopictus*			*Ae. japonicus*		
	Rural	Suburban	Urban	Rural	Suburban	Urban
Bag	0.0	0.8	0.0	0.0	0.3	0.0
Bucket	0.0	11.5	11.2	1.5	0.1	1.3
Cup/bowl	0.0	0.3	0.0	0.0	0.0	0.0
Lid	2.5	1.1	4.5	0.5	0.0	0.0
Planter dish	0.0	1.3	8.1	0.0	0.0	11.1
Plastic tray	0.0	0.0	2.0	0.0	0.0	0.0
Tarp	0.2	0.0	4.0	0.0	0.0	0.3
Tire	4.4	18.0	34.6	18.8	0.0	17.0
Toy	0.0	0.3	0.0	0.0	0.0	0.0
Trashcan[a]	n/a	5.5	66.0	n/a	0.1	0.4
Treehole[a]	0.1	0.0	n/a	0.03	0.0	n/a
Other[a]	0.2	2.4	20.6	0.4	0.1	6.6
Overall	2.5	20.7	180.0	7.0	0.2	26.7

[a] Not sampled in each of the three zones.

ICI, a measure of mean standing crop of pupae per container times the density of the container.

albopictus larval densities were also high in these container types ranging from 1.4 to 236.9 larvae per liter. For *Ae. japonicus* the highest pupal densities occurred in flexible drain pipes (6.0 pupae per liter), and planter dishes (0.7 pupae per liter), with larval densities in these artificial containers ranging from 0.2 to 41.5 larvae per liter (Table 5). For *Ae. japonicus* the greatest larval densities occurred in large buckets (41.5 larvae per liter) and tires (19.2 larvae per liter). Although tree holes were sampled most frequently, only one contained *Ae. albopictus*. However, out of 28 tires sampled, we collected *Ae. albopictus* from 25, with an average of 0.9 pupae and 236.9 larvae per liter. In individual container types, there was no significant difference between densities of *Ae. albopictus* and *Ae. japonicus*. However, overall artificial containers had higher densities of *Ae. albopictus* larvae ($F = 3.95$; df = 1, 270; $P = 0.04$) and pupae ($F = 10.6$; df = 1, 270; $P = 0.001$) per liter compared with *Ae. japonicus*.

Ae. albopictus and *Ae. japonicus* co-occurred in 25% of the containers sampled across all locations. χ^2 tests showed that the presence of *Ae. japonicus* was a strong predictor of the presence of *Ae. albopictus* ($\chi^2 = 10.0$; df = 1; $P = 0.002$). Mean crowding of these two species was similar in both rural and suburban areas, and was much higher in urban areas (Table 6).

To determine the likelihood of emergence before evaporation in each of the container types, we modeled evaporation rates based on a previous formula (Bartlett–Healy et al., 2011). Using the average July temperature of 23°C (when *Ae. albopictus* become abundant, and when temperature and evaporation rates are at their highest), and a standard wind speed of 1 m/s, we estimated the number of days until evaporation for common container types for both full sun and 50% shade cover (Fig. 4). Buckets and tires provided the longest duration of available habitat for small volume containers. From these data, we can infer that tires provide protection from sun and wind, thereby reducing overall evaporation rates compared with containers with exposed surfaces. The evaporation model also allowed us to examine the mean number of days to complete evaporation in containers inhabited by the most common species collected, using the mean temperature of 18.6°C during sampling (Table 7). Because *Ae. albopictus* may undergo larval development rapidly (5–7 d), our data suggests that survival of this species in containers that are susceptible to higher rates of evaporation may be greater than other container-inhabiting mosquitoes such as *Cx pipiens*.

Discussion

In suburban and urban sites, *Ae. albopictus* were the most frequently collected container-inhabiting mosquito immatures; whereas *Ae. japonicus* and *Ae. albopictus* were equally frequent in rural containers. *Ae. triseriatus* was less abundant in container hab-

Table 4.   *Ae. albopictus* container densities

Container type	Number present	*Ae. albopictus*			
		Mean larvae per liter	Mean larvae per m² surface	Mean pupae per liter	Mean pupae per m² surface
Bag	8	1.4 ± 1.1	0.4 ± 0.3	0.3 ± 0.3	12.9 ± 12.9
Bird bath	6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Bottle	3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Small bucket	24	12.1 ± 6.2	7.8 ± 4.7	1.5 ± 1.5	134 ± 94.2
Can	5	31.4 ± 15.8	9.9 ± 5.5	0.0 ± 0.0	0.0 ± 0.0
Cooler	4	18.1 ± 15.1	6.5 ± 5.9	1.5 ± 1.5	58.1 ± 58.1
Cup	14	3.5 ± 3.4	0.5 ± 0.4	0.3 ± 0.3	3.3 ± 3.2
Drain pipe	2	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	17.5 ± 17.5
Large bucket	4	51.3 ± 45.1	10.1 ± 8.5	1.8 ± 1.8	46.0 ± 46.0
Lid	15	13.4 ± 4.9	3.7 ± 1.7	2.9 ± 1.7	62.7 ± 42.6
Planter dish	22	20.1 ± 11.7	7.7 ± 4.1	5.9 ± 2.8	264.4 ± 174.8
Tarp	14	38.6 ± 21.7	6.5 ± 2.8	0.4 ± 0.3	21.5 ± 18.6
Tire	28	236.9 ± 230.2	32.2 ± 29.2	0.9 ± 0.4	26.2 ± 13.7
Toy	6	7.5 ± 7.5	0.8 ± 0.7	0.6 ± 0.6	5.7 ± 5.7
Trash can	23	42.2 ± 33.7	3.5 ± 1.9	4.3 ± 3.2	63.0 ± 26.1[a]
All artificial	271	62.2 ± 27.2[a]	11.1 ± 3.7[a]	2.1 ± 0.5[a]	60.7 ± 17.6[a]

[a] Values for *Ae. albopictus* and *Ae. japonicus* are significantly different at $P = 0.05$ using ANOVA (SPSS version 18).

Table 5. *Ae. japonicus* container densities

Container type	Number present	*Ae. japonicus*			
		Mean larvae per liter	Mean larvae per m^2 surface	Mean pupae per liter	Mean pupae per m^2 surface
Bag	8	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	4.3 ± 4.3
Bird bath	6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Bottle	3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Small bucket	24	16.1 ± 15.6	13.3 ± 12.7	0.1 ± 0.1	7.1 ± 4.3
Can	5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Cooler	4	6.1 ± 6.1	2.3 ± 2.3	0.5 ± 0.5	19.4 ± 19.4
Cup	14	0.8 ± 0.8	0.6 ± 0.6	0.0 ± 0.0	0.0 ± 0.0
Drain pipe	2	0.9 ± 0.9	0.4 ± 0.4	6.0 ± 6.0	228 ± 228
Large bucket	4	41.5 ± 29.6	7.5 ± 5.6	0.0 ± 0.0	0.0 ± 0.0
Lid	15	16.8 ± 9.8	6.6 ± 4.6	0.8 ± 0.8	21.5 ± 21.5
Planterdish	22	2.5 ± 2.3	0.6 ± 0.6	0.7 ± 0.4	49.7 ± 39.8
Tarp	14	2.0 ± 1.5	0.3 ± 0.1	0.1 ± 0.1	1.2 ± 1.2
Tire	28			19.2 ± 16.4	3.6 ± 2.1
Toy	6			0.9 ± 0.9	0.1 ± 0.1
Trash can	23		0.5 ± 0.3	0.3 ± 0.1	
All artificial	271		7.7 ± 2.5^a	2.8 ± 1.2^a	

[a] Values for *Ae. albopictus* and *Ae. japonicus* are significantly different at $P = 0.05$ using ANOVA (SPSS version 18).

itats in all three sites, and most commonly collected in tires and tree holes. Livdahl and Willey (1991) demonstrated that *Ae. albopictus* outcompetes *Ae. triseriatus* in most container habitats, except in tree holes, where they predicted a stable coexistence. Tires and tree holes are more likely to support more complex communities, including mosquito predators, such as *Toxorhynchites rutilus* (Coquillett) (Campos and Lounibos 2000). Our data supports this, with our highest diversity of species occurring in tires, trash cans, and tree holes. All three habitat types also had at least one collection of *Tx. rutilus.* Yee (2008) provided a detailed review of tire habitats, examining the environmental factors contributing to species presence, including leaf litter, temperature, and community structure. Vegetation cover around tires can greatly affect mosquito larval distribution, by increasing the nutrient load (Kling et al. 2007), and lowering the water temperature (Beier et al. 1983).

Tires were an important habitat in rural, suburban, and urban sites for both *Ae. albopictus* and *Ae. japonicus.* The ICI showed that as human population density increased, the importance of tires as an *Ae. albopictus* habitat increased as well. Richards et al. (2008) re-

Table 6. Mean crowding and overlap of *Ae. albopictus* and *Ae. japonicus* in rural, suburban, and urban areas in New Jersey

Characteristic	Rural	Suburban	Urban
Neither species	52	80	36
Ae. albopictus only	6	21	22
Ae. japonicus only	6	3	2
Both species	16	11	50
Mean crowding (total)	3.7	3.7	23.9
Mean crowding (tires)	8.9	0	11.1
Mean crowding (per liter)	7.8	3.3	277.4
Mean crowding (per 100 cm^2 surface area)	3.0	0.5	36.9

Species counts indicate the no. of times occurring from the total of 305 containers sampled.

ported that ICI values of tires in their suburban North Carolina sites were much lower than other container habitats, including planter dishes, buckets, and trash cans. Unlike the North Carolina study, we only collected one tire in the suburban site. However, because there was an abundance of pupae in this container type, the ICI value was also high. Our results were similar to Richards et al. (2008), demonstrating that planter dishes, buckets, and trash cans were important artificial containers for *Ae. albopictus* in suburban habitats. Planter dishes, buckets, and tires were also important habitats for *Ae. japonicus.* We anticipate that *Ae. albopictus* and *Ae. japonicus* are opportunistic in their selection of oviposition sites, and expect to find year-to-year variability similar to Richards et al. (2008).

Ae. albopictus and *Ae. japonicus* were collected more often in cooler containers, compared with those with higher temperatures. A closer spatial examination showed that these areas with highest temperatures had reduced tree cover when compared with other parts of the study area. Therefore, our temperature data may be confounded by container location, considering a higher proportion of both *Ae. albopictus* and *Ae. japonicus* were found in shaded or partially shaded containers (86.1 and 90.5%, respectively). Principal component two was comprised of water temperature, shade, and water color, which correlated with *Ae. japonicus* containers. Beier et al. (1983), determined differences in species composition and larval density between exposed and shaded tires. Their results demonstrated that *Ae. triseriatus* had distinct preference for shaded tires in tire yards in Indiana. Containers found in shaded areas provide ideal habitats for developing mosquito larvae. Natural shade not only lowers water temperatures, but often provides a bacterial food source for mosquito larvae from fallen leaves and debris that subsequently collects in containers (Eaton et al. 1973). Abundance of *Ae. albopictus* and *Ae. japonicus* larva in shaded or partially shaded areas may
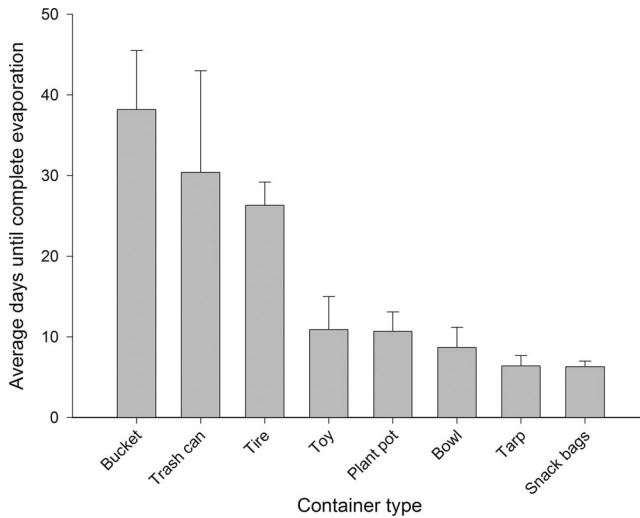
Fig. 4. Evaporation rates in common container types sampled as part of the urban, suburban, and rural larval surveillance in New Jersey.

be attributed in part to abundant food resources in shaded containers. Shade and cooler temperature also reduce container evaporation rates (Bartlett–Healy et al. 2011). Delatte et al. (2009) found *Ae. albopictus* survival in La Reunion was much greater at 15°C than 35°C, contradicting other studies. Therefore, containers with extremely high water temperatures are suboptimal larval habitats.

Ae. albopictus and *Ae. japonicus* were common in containers with leaf litter. Leaf litter provides an important nutrient source for bacteria, which in turn are the primary food source for mosquito larvae (Merritt et al. 1992). Different types of detritus can also affect microbial composition, which in turn might affect species distributions (Yee and Juliano 2006). Studies have shown that *Ae. albopictus* prefers to oviposit in containers with leaves (Dieng et al. 2003). Additionally, Lounibos et al. (2002) demonstrated that *Ae. albopic-*

tus development was enhanced in containers with leaves, and Tsuda et al. (1994) demonstrated a propensity for *Ae. albopictus* inhabiting open containers with leaf litter compared with closed containers. Although not significant, our data show that *Ae. albopictus* and *Ae. japonicus* were twice as abundant in containers with leaves. In future studies, we hope to quantify and identify leaves as part of our larval surveillance procedure.

Ae. albopictus and *Ae. japonicus* were common in containers having high evaporation rates, such as buckets, trash cans, discarded snack bags, and Styrofoam cups and bowls. Evaporation analyses showed that *Culex* species were more common in containers that are less influenced by evaporation. These containers, which remain flooded longer, have ample amounts of leaf litter and slightly higher temperatures, providing a more nutritive environment for mosquito larvae. Conversely, *Ae. albopictus* was found in containers that were influenced by dry and wet cycles. Edgerly et al. (1993) determined that a reduction in dissolved oxygen, because of microbial action, is a hatching stimulus for most container *Aedes* species and eggs are only induced to hatch after heavy rains. However, they determined that because *Ae. albopictus* eggs hatch immediately after flooding, they could feed immediately on the microbes present, increasing the dissolved oxygen content. Moreover, the authors determined this behavior inhibited eggs of other species from hatching, providing a competitive advantage to *Ae. albopictus* in container habitats.

Higher number of mosquito species coexisted in tires, trash cans, and tree holes compared with other container types. *Ae. albopictus* and *Ae. japonicus* co-occurred in 71.4% of the 28 tires sampled. In addition, the presence of both species correlated with the colors black and gray, containers made of rubber, and tire

Table 7. Average no. of days until evaporation of containers surveyed in the field

Species	Average days to evaporation	Development times[a]
Culex species		
Larvae or pupae	47.5 + 4.2SE	24d[b]
Pupae only	51.5 + 4.3SE	
Ae. triseriatus		
Larvae or pupae	31.6 + 3.3SE	16–18d[c]
Pupae only	41.6 + 3.9SE	
Ae. japonicus		
Larvae or pupae	25.3 + 2.2SE	19–31d[d]
Pupae only	27.5 + 1.9SE	
Ae. albopictus		
Larvae or pupae	23.5 + 2.1SE	14.4d[e]
Pupae only	23.3 + 2.2SE	

[a] Mean water temp 18.6.
[b] Vinogradova (2000).
[c] Teng and Apperson (2000).
[d] Scott (2003).
[e] Delatte et al. (2009).

habitats. Tires are less susceptible to water loss, because of their shape. Tires shield the water surface from wind and sunlight, resulting in slower evaporation rates. Even though tires and tree holes hold relatively small amounts of water, evaporation is reduced, thereby supporting an array of mosquito species, even during summer months. Increased amounts of leaf litter deposited in these containers provide optimum sites for other mosquito species. *Tx. rutilus,* a large predatory mosquito, is abundant in both tires and tree hole habitats (Campos and Lounibos 2000). The increased abundance of predators within these two habitats reduces the competitive advantage of *Ae. albopictus,* which has not evolved similar anti-predatory responses, like those observed in *Ae. triseriatus* (Kesavaraju and Juliano 2009). This may have contributed to the greater diversity we observed in tire and tree hole habitats.

Our mosquito larval survey occurred during a season of intense rainfall. Between August and October the region received the fifth highest rainfall on record since 1895, receiving 48.7 cm (19.6 cm above the average) over the 3 mo period (Office of the NJ State Climatologist 2010). Alto and Juliano (2001) demonstrated that *Ae. albopictus* development was influenced by temperature and precipitation, with higher temperatures and drying contributing to increased mortality. Furthermore, Vitek and Livdahl (2009) demonstrated that eggs were subjected to fewer hatching stimuli (rain events) and are more likely to hatch between rain events.

Our data suggest that tires are numerous and productive habitats for *Ae. albopictus* in all study habitats, along with buckets, trash cans, and plant receptacles. Although slightly less abundant, *Ae. japonicus* prefers similar habitats. Our data collections show that *Ae. albopictus* and *Ae. japonicus* occur more often together in urban and rural areas than they do alone. In suburban areas, *Ae. albopictus* was most commonly found alone. However, *Ae. japonicus* was more common with *Ae. albopictus,* than alone. Mean crowding of these two species was also substantially higher in urban areas, compared with rural and suburban containers. There were higher densities of *Ae. albopictus* in artificial containers compared with *Ae. japonicus.* Given that our study sites were located at the northern most distribution of overwintering for *Ae. albopictus,* future monitoring is warranted to determine how these two species interact and compete for similar larval habitats, as their populations continue to increase throughout the state. It is also worth noting that *Aedes atropalpus* (Coquillett) was not collected during this study. *Ae. atropalpus* was readily found before 2005 in Mercer County and was the dominant species at some locations in Trenton (A. Farajollahi, personal communication). We anticipate conducting future studies to determine if increasing *Ae. albopictus* and *Ae. japonicus* populations are contributing to the decline of *Ae. atropalpus* in New Jersey.

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