Asymmetrical Competition and Patterns of Abundance of *Aedes albopictus* and *Culex pipiens* (Diptera: Culicidae)

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ABSTRACT   We tested for competitive advantage among larvae of *Aedes albopictus* (Skuse) and *Culex pipiens* L. in a laboratory experiment and determined the frequency and spatial and temporal patterns of co-occurrence in the field in East St. Louis, IL. In a laboratory competition experiment at multiple combined densities of *Ae. albopictus* and *Cx. pipiens* larvae, *Ae. albopictus* survivorship and developmental times were significantly affected by conspecific densities but not by *Cx. pipiens* densities. In contrast, *Cx. pipiens* survivorship and developmental times were significantly affected by both conspecific and *Ae. albopictus* densities. Per capita rate of increase (r') for *Ae. albopictus* cohorts declined significantly due to density of conspecifics, but not density of *Cx. pipiens*. Interspecific competition between *Ae. albopictus* and *Cx. pipiens* under these laboratory conditions was strong and asymmetrical, with the effect of *Ae. albopictus* on *Cx. pipiens* much stronger than the reverse. In monthly samples from tire sites in East St. Louis, *Ae. albopictus* was highly seasonal, occurring in relatively low abundance from early May to July and increasing in abundance in August and September. Co-occurrence corresponded to the seasonality of *Ae. albopictus*, with *Cx. pipiens* encountering *Ae. albopictus* in more tires and at higher numbers within a tire, in August and September. Abundance of both species was high in residential areas and was unrelated to overstory cover, total nitrogen, and total phosphorus. Abundance of *Ae. albopictus*, but not of *Cx. pipiens*, was positively associated with conductivity. We expect *Cx. pipiens* to suffer from the effects of interspecific competition in tires in which it encounters *Ae. albopictus*. Interspecific competition between these species may be of both ecological and medical importance.

COMPETITIVE INTERACTIONS BETWEEN two species are often asymmetrical, so that the effect of one of the species on the other is much more prominent than the reverse (Lawton and Hassell 1981). Competitive asymmetry has important consequences for competitors. With high competitive asymmetry, the competitively superior species is expected to eliminate the competitively weaker species unless other processes (e.g., disturbance and predation) intervene to facilitate coexistence (Lawton and Hassell 1981, Connell 1983).

The Asian tiger mosquito, *Aedes albopictus* (Skuse), was introduced into the United States in the mid-1980s through tire shipments from Asia (Sprenger and Wuithranyagool 1986). It has become the most abundant container-dwelling mosquito in many regions of the country (Moore and Mitchell 1997). *Ae. albopictus* is medically important because it is a vector of arboviruses, including dengue, La Crosse encephalitis, eastern equine encephalitis, and West Nile virus (WNV) (Ibañez-Bernal et al. 1997; Mitchell et al. 1992; Gerhardt et al. 2001; Turell et al. 2001, 2005). Invasion by *Ae. albopictus* also had an ecological impact and has been associated with declines in abundance and local extinction of other North American mosquitoes (Hobbs et al. 1991, McHugh 1993, Hornby et al. 1994, Mekuria and Hyatt 1995, O'Meara et al. 1995).

There have been numerous studies on the competitive interactions of larval *Ae. albopictus* with container-dwelling aedine mosquitoes, particularly *Ochlerotatus triseriatus* (Say) and *Aedes aegypti* L. In most instances, *Ae. albopictus* proves the superior competitor, notably when resources are limiting (Livdahl and Willey 1991, Edgerly et al. 1993, Barrera 1996, Juliano 1998, Daugherty et al. 2000, Teng and Apperson 2000, Braks et al. 2004).

Culex pipiens L., the northern house mosquito, is established throughout the northern United States and southern Canada (Darsie and Ward 1981). Recently, interest in the ecology of *Cx. pipiens* has increased because laboratory and field studies implicate it as an important vector of WNV (Kulasekera et al. 2001; Spielman 2001; Turell et al. 2001, 2005; Fonseca et al. 2004). There have been relatively few studies of competitive interactions of larvae of this species (but see Carrieri et al. 2003).

The distribution of *Cx. pipiens* is largely associated with development and urbanization (Vinogradova 2000, Fonseca et al. 2004). *Cx. pipiens* is ecologically

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associated with humans and shows high ecological and physiological flexibility, with larvae inhabiting containers with high levels of organic and industrial pollution, drainage canals, and other highly contaminated bodies of water (Vinogradova 2000). Laboratory and field data indicate that the larvae of *Cx. pipiens* are eurytopic, tolerating extreme values of pH, high organic material, high temperatures, and high salinity (Vinogradova 2000).

Ae. albopictus and *Cx. pipiens* encounter one another in their shared artificial habitats, and their distributions overlap in much of North America (Hawley 1988, Vinogradova 2000). The larvae of both these species can occur in natural and artificial containers, and they share similar feeding habits such as filtering and browsing (Hawley 1988, Vinogradova 2000). In Italy, *Ae. albopictus* and *Cx. pipiens* commonly co-occur in artificial containers in the field, and in competition in the laboratory, *Ae. albopictus* is more successful at high combined densities with low food availability than is *Cx. pipiens* (Carrieri et al. 2003). Carrieri et al. (2003) worked with a single strain of each species from southern Europe, and geographic variation in larval growth and development is well known in both species (Vinogradova 2000; P. Armbruster and J. Conn, unpublished data). Furthermore, interpretation of the experiment by Carrieri et al. (2003) is complicated by their use of highly artificial food substrates (cat biscuits). Outcome of competition among mosquito larvae, including *Ae. albopictus*, is well known to be sensitive to larval food substrates (Barrera 1996, Daugherty et al. 2000). Thus, results from Carrieri et al. (2003) cannot be assumed to apply to all populations of these species, and more realistic food substrates may yield very different results.

Our overall objective was to test the hypothesis that invading North American *Ae. albopictus* affects *Cx. pipiens* through interspecific competition. We tested this by evaluating two predictions of this hypothesis: 1) interspecific competition among larvae yields strong effects of *Ae. albopictus* on *Cx. pipiens*, and 2) co-occurrence of *Ae. albopictus* and *Cx. pipiens* within containers is common in the field in our study area in southern Illinois. We tested the first prediction in a laboratory experiment testing the effects of increased densities of larvae of *Ae. albopictus* or *Cx. pipiens* upon the performance of the other species. We expected that *Ae. albopictus* would be the superior competitor to *Cx. pipiens*, just as *Ae. albopictus* is superior in competition with other container-dwelling mosquitoes (Ho et al. 1989, Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004) and with *Cx. pipiens* in Europe (Carrieri et al. 2003). We tested the second prediction by assessing the relative abundance and co-occurrence of these species in tire habitats in East St. Louis, IL, from late spring to fall 2003, determining the frequency of co-occurrence in the field. Preliminary sampling indicated that *Ae. albopictus* and *Cx. pipiens* are two dominant species in urban tires in this area (S.A.J., unpublished data). We also were interested in identifying any spatial and temporal patterns of co-occurrence in the field, specifically asking: In

what types of macro- and microhabitats, and in what season, are these two species are most likely to co-occur? Because *Cx. pipiens* has a high tolerance for organic pollution (Vinogradova 2000), we tested whether variation in dissolved nutrients across tires is associated with distribution and abundance of *Ae. albopictus* and *Cx. pipiens.* We also examined land use associated with the urban tires occupied by these species.

Materials and Methods

Rearing. Individuals used in this experiment were first generation progeny of individuals collected from discarded tires in East St. Louis. *Cx. pipiens* co-occurs with *Cx. quinquefasciatus* in East St. Louis, and these species produce hybrids in regions of co-occurrence (Brogdon 1984, Vinogradova 2000, Fonseca et al. 2004). Field-collected larvae were sorted based on a siphonal index (Brogdon 1984), which can typically separate pure populations of these species (Brogdon 1984, Vinogradova 2000). We cannot, however, separate hybrids reliably; hence, our laboratory population probably included individuals carrying genes of *Cx. quinquefasciatus.* Approximately 90% of field-collected individuals from our East St. Louis site were morphologically consistent with *Cx. pipiens.* We regard our laboratory population as a representative sample of the interbreeding members of the *Cx. pipiens* complex from our field site and therefore the relevant population for evaluation of effects of competition from *Ae. albopictus.* We will refer to them as *Cx. pipiens* for simplicity.

Larvae of both species were reared to adulthood at 25°C under a photoperiod of 16:8 (L:D) h and then released into 0.6-m² cages. Larvae of *Ae. albopictus* were fed bovine liver powder (ICN Biochemicals, Cleveland, OH), and larvae of *Cx. pipiens* were fed an artificial diet comprised of bloodmeal, powdered milk, yeast, and wheat flour (see Copeland 1987 for details). Adult females of both species were housed in an insectary at 22–26°C under a photoperiod of 16:8 (L:D) h and blood fed on anesthetized laboratory mice to obtain eggs used to produce larvae for this study. Adult female *Cx. pipiens* were provided with a 500-ml black cup filled with 400 ml of deionized (DI) water and several blades of foxtail grass, *Setaria faberi* Herrmann, as an oviposition stimulant. Egg rafts of *Cx. pipiens* were collected within 24 h of oviposition, hatched in pans, and larvae were transferred to the experiment. Eggs of *Ae. albopictus* were hatched synchronously in five by 40-mm glass tubes filled with a solution of 0.33 g of nutrient broth in 750 ml of DI water. After 24 h, larvae were rinsed and transferred to the experiment. Starting hatchling larvae in synchrony, rather than giving one species a head start, was done for simplicity, as has been the case in previous experiments on these species (Carrieri et al. 2003).

Laboratory Experiment. The experiment consisted of the following initial combinations of larvae (*Ae. albopictus:Cx. pipiens*): 0:10, 0:20, 0:40, 10:10, 10:20, 10:40, 20:10, 20:20, 20:40, 40:10, 40:20, 10:0, 20:0, and

40:0. We did not include a 40:40 treatment because preliminary runs of this experiment indicated that the highest densities included in this experiment were severely detrimental. Therefore, the addition of the 40:40 treatment would not provide additional information on the effects of density. Each combination was replicated six times, yielding 84 experimental units. This design enabled us to determine the relative magnitudes of intra- and interspecific competition (Goldberg and Scheiner 2001). The experiment was executed in 250-ml cups (79 by 70 mm, height by depth) with 160 ml of DI water. At the beginning of the experiment, each cup received its assigned larval cohorts, 1 ml of water field collected from tires for microbial inoculum, and a mixture of field-collected senescent elm leaves/grass (0.15 g:0.05 g dry mass). The leaves used in this experiment were a mix of American elm, *Ulmus americana* L., and slippery elm, *Ulmus rubra* Muhl., and the grass was foxtail.

Eggs of *Cx. pipiens* cannot be held without hatching; hence, we set up the experiment in a blocked design as *Cx. pipiens* eggs became available. Each block was one replicate of each combination. We collected *Cx. pipiens* egg rafts 4 d after adult blood feeding and eggs hatched 1–2 d after oviposition. We flooded *Ae. albopictus* eggs (deposited on paper and stored dry) 1 d after we collected *Cx. pipiens* egg rafts to synchronize species' hatching.

The experiment was housed in an environmental chamber at 25°C under a photoperiod of 16:8 (L:D) h. Treatments were randomly assigned to cups. Cup position within the chamber was shuffled daily. There were elm/grass additions (0.15 g:0.05 g dry mass) to each cup at 7 and 14 d after the start of each replicate to minimize resource depletion. Each day, we collected pupae and placed them in individual vials with water until adult emergence. We recorded the date of emergence, sex, species, species combination, and replicate for each adult. On the day of emergence, adults were killed by drying, and the size of the adult was quantified as wing length, determined using a dissecting microscope and image analysis system (ImagePro Plus 6.0). We used wing length as a measure of size to use a regression of fecundity versus wing length (Lounibos et al. 2002) to estimate fecundity of *Ae. albopictus* for calculation of r' (Livdahl and Sugihara 1984).

Analyses. We analyzed five population growth correlates for cohorts of each species within each replicate: mean size at adulthood for each sex (wing length in millimeters), median development time (days from hatching to adulthood) for each sex, and survivorship (number of adults/initial number of larvae) for each species. We also calculated the composite index of mosquito population performance (r') for *Ae. albopictus* for each container. This estimates the realized per capita rate of population change ($dN/N\,dt = r$) for each cohort and thus provides an overall synthesis of performance for that cohort (Livdahl 1984, Livdahl and Sugihara 1984). We calculated r' for each cohort as follows:

$$r' = \left(D + \frac{\left(\ln(1/N_o) \sum_x A_x f(w_x) \right)}{\left(\sum_x x A_x f(w_x) / \times \sum_x A_x f(w_x) \right)} \right)$$

where N_o is the initial number of females in a cohort (assumed to be 50% of the initial cohort); A_x is the number of females eclosing on day x; w_x is a measure of mean female size per replicate; $f(w_x)$ is a function relating fecundity to female size; and D is the time (in days) required for a newly eclosed female to mate, obtain a bloodmeal, and oviposit. D is assumed to be 14 d for *Ae. albopictus* (Juliano 1998). The fecundity–size relationship for *Ae. albopictus* was $f(w_x) = 78.02\,w_x - 121.240$ ($r^2 = 0.173$, $n = 91$, $P < 0.000$; Lounibos et al. 2002) with w_x representing wing length in millimeters. Very few female *Cx. pipiens* emerged from the experiment (see *Results*); hence, we were unable to calculate r' for this species.

To determine the intra- and interspecific effects for both species, we analyzed r' and population growth correlates (development time, size, and survivorship) for each species by multiple regression (PROC GLM, SAS Institute 1989) with the densities of *Ae. albopictus* and *Cx. pipiens* as dependent variables. Raw data met assumptions of homogeneous variance and normality. We tested block and its interactions in all analyses, omitting the interaction from the final analysis if it was not significant. Block was retained in the analysis regardless of significance, although tests of significance for block are not reported. Because we ran regressions for 11 dependent variables for two independent variables, we used a sequential Bonferroni adjustment for 22 tests, with experimentwise $\alpha = 0.05$.

Field. Samples from East St. Louis were collected monthly from May through September 2003, from multiple tire sites. Each month, we collected at five sites and randomly chose five tires from each site. For each tire, we determined percentage of overstory cover by using a densiometer. We also determined land use category (e.g., urban, residential, transportation, industrial, or open-land) for each site by obtaining the latitudinal and longitudinal coordinates with a hand-held global positioning system (GPS) unit (eTrex Venture, Garmin Corp., Olathe, KS) and then referencing those coordinates on geographic information system (GIS) maps of East St. Louis (Geographic Community International Corp. 2004). After recording data in the field, we collected container contents and brought them back to the laboratory, where we sorted, identified, and counted mosquitoes. For the water in each sampled container, we determined conductivity, total inorganic nitrogen (includes nitrite, nitrate, and ammonia), and total phosphorous by using a DR/850 colorimeter (Hach Company, Loveland, CO) and appropriate reagent kits.

Analyses. We used multivariate analysis of variance (MANOVA, PROC GLM, SAS Institute 1989) of abundance of *Ae. albopictus* and *Cx. pipiens* (log transformed to meet the assumptions of homogeneity of

Table 1. Slopes ± SE, R^2, and tests of significance for relationships of survivorship, developmental times, and wing lengths for *Ae. albopictus* and *Cx. pipiens*, and *r'* for *Ae. albopictus* only

			Independent variable			
			Ae. albopictus density		*Cx. pipiens* density	
Dependent variable	df error	R^2	Slope ± SE	P	Slope ± SE	P
Ae. albopictus						
Survivorship	48	0.2685	**−0.0053 ± 0.0014**	**0.0004**	0.0002 ± 0.0012	0.8753
Female dev. time	48	0.5358	**0.2570 ± 0.0364**	**<0.0001**	0.0292 ± 0.0321	0.3599
Male dev. time	47	0.5175	**0.1690 ± 0.0257**	**<0.0001**	0.0159 ± 0.0222	0.4786
Female wing length	45	0.4286	**−0.0061 ± 0.0004**	**0.0006**	**−0.0062 ± 0.0015**	**0.0002**
Male wing length	40	0.5616	**−0.0072 ± 0.0029**	**<0.0001**	**−0.0039 ± 0.0011**	**0.0016**
r'	48	0.5970	**−0.0018 ± 0.0002**	**<0.0001**	−0.0004 ± 0.0002	0.0163
Cx. pipiens						
Survivorship	48	0.4427	**−0.0101 ± 0.0020**	**<0.0001**	**−0.0105 ± 0.0023**	**0.0001**
Female dev. time	27	0.6039	**0.2531 ± 0.0447**	**<0.0001**	0.1392 ± 0.0502	0.0100
Male dev. time	28	0.5782	**0.1688 ± 0.0351**	**0.0002**	−0.1315 ± 0.0355	0.0174
Female wing length	6	0.8401	0.0128 ± 0.0253	0.7837	−0.0233 ± 0.0060	0.0083
Male wing length	26	0.6688	−0.0151 ± 0.1635	0.0250	−0.0092 ± 0.0200	0.0151

Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.

variances and normality) to test for effects of site and date as main effects. We interpreted the relative contribution of abundance of each species by using standardized canonical coefficients (SCC) as described by Scheiner (2001). Interaction of date and site could not be assessed because we were unable to sample each site on all dates due to cleanup of tires by the local health district. We performed a contingency table test for independence of the presence and absence of these species (PROC FREQ, SAS Institute 1989). We also calculated mean crowding for all tires within each site. This indicates the average number of *Ae. albopictus* that one *Cx. pipiens* individual encounters within a tire (Bradshaw 1983). This index was calculated as follows:

$$\text{Mean crowding} = \sum_{i=1}^{5}(a_i * c_i) / \sum_{i=1}^{5} c_i$$

where *a* is total number of *Ae. albopictus* larvae found within a tire and *c* is total number of *Cx. pipiens* found within a tire. We did not include volume in this calculation; hence, mean crowding is expressed per tire, regardless of volume (Bradshaw 1983). Although calculating mean crowding per liter would provide information on the actual densities of the two species, our calculation of mean crowding per tire is indicative of the interspecific encounter, or how many heterospecific individuals one of the species encounters. We then calculated the means for each month (averaging across sites) and ran a Kruskal–Wallis test for monthly differences in mean crowding.

We analyzed the relationship of species abundance to environmental variables by using a canonical correlation analysis, with redundancy analysis (PROC CANCOR, Lindeman et al. 1980, SAS Institute 1989). This technique is used to test for a significant multivariate relationship between two sets of variables and is often used to assess correlations of organisms' traits and abundance with environmental data (Scheibe 1987). In our study, "species" variables were *Ae. al-bopictus* and *Cx. pipiens* abundance and "environment" variables were phosphorus, total inorganic nitrogen, conductivity, total canopy cover, and month. Canonical correlation first finds the linear combinations of the original variables that result in maximum correlation between the two sets, and tests whether the correlation is significantly different from 0. Second, it finds the next most highly correlated linear combinations from each set that are orthogonal to the first pair of canonical variates. For further details, see Lindeman et al. (1980).

Results

Laboratory Experiment. *Survivorship.* Block and its interactions were not significant for all survival data, so we omitted the interaction from the analyses. *Ae. albopictus* survivorship declined significantly with increasing conspecific density, but it did not decline with increasing *Cx. pipiens* density (Table 1; Fig. 1A). *Cx. pipiens* survivorship declined significantly, and based on the slopes, at a similar rate, with either increasing *Ae. albopictus* or conspecific densities (Table 1; Fig. 1B).

Developmental Time. Block and its interactions were not significant for all developmental time data, so we omitted the interaction from the analyses. Developmental times of *Ae. albopictus* females and males (Fig. 2A and B) increased significantly with increasing *Ae. albopictus* density but not with *Cx. pipiens* density (Table 1). *Cx. pipiens* female and male development times increased significantly with *Ae. albopictus* and *Cx. pipiens* density (Fig. 3A and B).

Wing Length. For all wing length variables, interactions were not significant and were omitted. For *Ae. albopictus*, female and male wing lengths declined significantly with increasing densities of both *Ae. albopictus* and *Cx. pipiens* (Table 1; Fig. 4A and B). For *Cx. pipiens* female and male wing lengths, there were significant effects of density of both species (Table 1; graphs not shown).
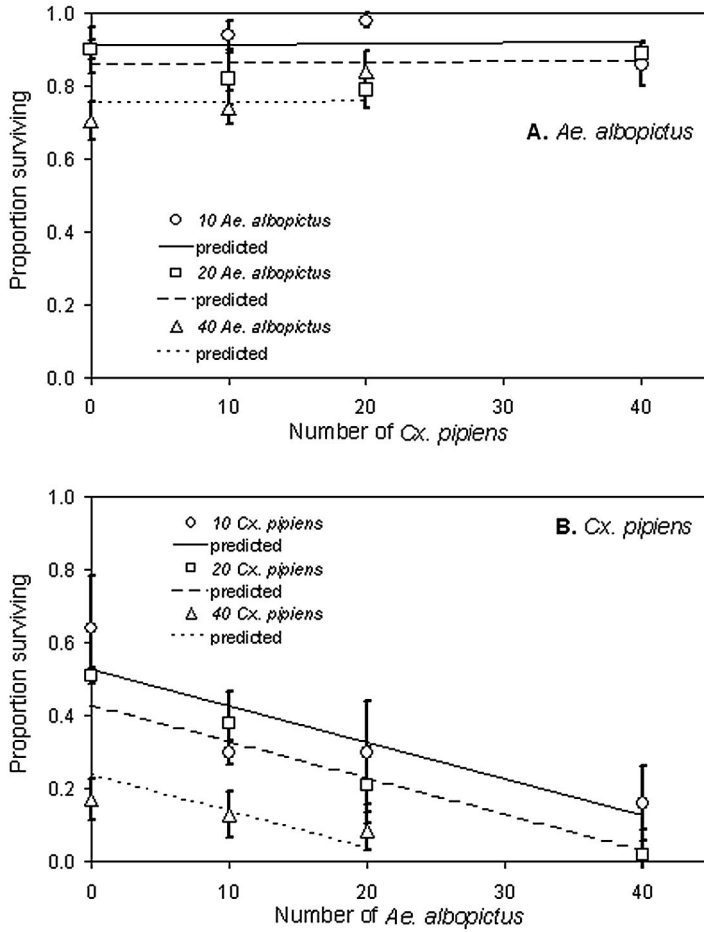
Fig. 1. Means (± 1 SE) of *Ae. albopictus* (A) and *Cx. pipiens* (B) survival to adulthood across larval density treatments. Significance tests and slope estimates in Table 1.

Composite Index (r'). For *Ae. albopictus*, estimated rate of increase (r') there were no significant interactions with block. *Ae. albopictus* r' decreased significantly with conspecific density but not with *Cx. pipiens* density (Table 1; Fig. 5). Thus, intraspecific competition had a much greater impact on *Ae. albopictus* cohort rate of increase than did interspecific competition with *Cx. pipiens.*

Field Study. There were significant effects of both date ($F_{8, 186} = 5.63; P < 0.0001$) and site ($F_{16, 186} = 1.74$; $P = 0.0424$) on *Ae. albopictus* and *Cx. pipiens* abundance in the field. SCCs indicate that *Ae. albopictus* contributed most (SCC = 1.23), and *Cx. pipiens* contributed little (SCC = 0.06) to the date effect. In contrast, *Cx. pipiens* contributed more (SCC = 0.97) to the site effect than did *Ae. albopictus* (SCC = 0.057), with positive values indicating that across sites, abundance of these species was positively correlated. We compared months by using multivariate pairwise comparisons (Sequential Bonferroni, $\alpha = 0.05$) (Fig. 6). Early months (May through July) did not differ significantly in the abundance of the two species. However, August was significantly different from all of the

earlier months, primarily due to a large increase in *Ae. albopictus'* abundance in August (Fig. 6). As indicated by the significant date effect, the abundance of *Ae. albopictus* was highly seasonal, increasing dramatically in late summer (Fig. 6).

Co-occurrence. We collected from a total of 119 tires throughout the season. Contingency table tests for independence of the presence and absence of these species were not significant across all months ($P > 0.05$). Across the whole season, *Cx. pipiens* co-occurred with *Ae. albopictus* in 64.7% of the tires in which it occurred. In July, August, and September, when *Ae. albopictus* was common, *Cx. pipiens* encountered *Ae. albopictus* in 50, 91, and 100%, respectively, of the tires it inhabited (Table 2). There was a significant effect of month on mean crowding across sites (Kruskal–Wallis $\chi^2 = 11.5322$, df = 4, $P = 0.0212$). In May, June, and July, *Cx. pipiens* larvae encountered an median of <6 *Ae. albopictus* larva per tire, but in August and September, *Cx. pipiens* larvae encountered >25 *Ae. albopictus* larvae per tire (Table 2).

Environmental Data. Five of nine sites sampled were within a residential land use category. Although
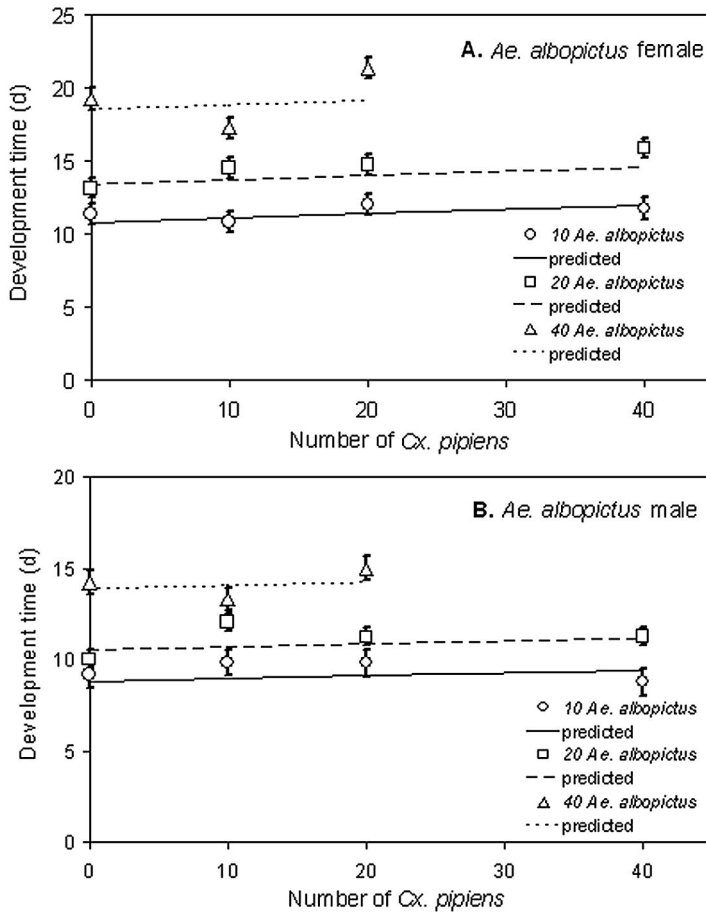
Fig. 2. Means of developmental times to adulthood (±1 SE) for *Ae. albopictus* females (A) and males (B) across larval density treatments. Significance tests and slope estimates in Table 1.

the GPS coordinates for 39th Street fell within a transportation category, this site was on the border of a highway and a residential area. Mean abundance per tire for both species was greatest in residential areas compared with urban and transitional sites (Fig. 7).

The first canonical correlation of 0.4809 was significant ($F_{10, 104} = 2.13$; $P = 0.0283$) and accounted for 23.1% of the variation in canonical space. The first species canonical variate was positively related to *Ae. albopictus* abundance (SCC = 1.0095) and negatively related to *Cx. pipiens* abundance (SCC = −0.7321). The first environment canonical variate was positively related to month (SCC = 0.6878) and conductivity (SCC = 0.7321) and only weakly related to phosphorus, total inorganic nitrogen, and total canopy cover (SCCs with magnitudes <0.1000). Overall, abundance and dominance of *Ae. albopictus* increased later in the season and with greater solute concentration. Canonical redundancy analysis indicated that the environment canonical variate was able to predict only 11.25% of the variance in the individual original species variables. The second canonical correlation was not significant ($F_{4, 53} = 1.53$; $P = 0.2055$) and only explained 10.3% of the variation in canonical space. The overall

model accounted for 72.2% of the variance and was significant ($F_{10, 106} = 2.13$; $P = 0.0278$).

Discussion

The laboratory experiment supported our prediction that interspecific competition between larvae of *Ae. albopictus* and *Cx. pipiens* is strong and highly asymmetrical, with *Ae. albopictus* clearly superior to *Cx. pipiens* under these conditions. Competitive asymmetry was most apparent for survivorship. Survivorship of *Ae. albopictus* was strongly affected by intraspecific competition but unaffected by intraspecific competition from *Cx. pipiens.* In contrast, both intra- and interspecific competition affected *Cx. pipiens* survivorship. Overall survivorship of *Cx. pipiens* was low relative to that for *Ae. albopictus* (Fig. 1), despite the fact that the temperature chosen for this experiment is described as ideal for *Cx. pipiens,* producing maximum survival (Vinogradova 2000). Wing length and developmental time provided less evidence of competitive asymmetry.

Competition from *Cx. pipiens* only affected *Ae. albopictus* through size at adulthood. *Ae. albopictus* fe-
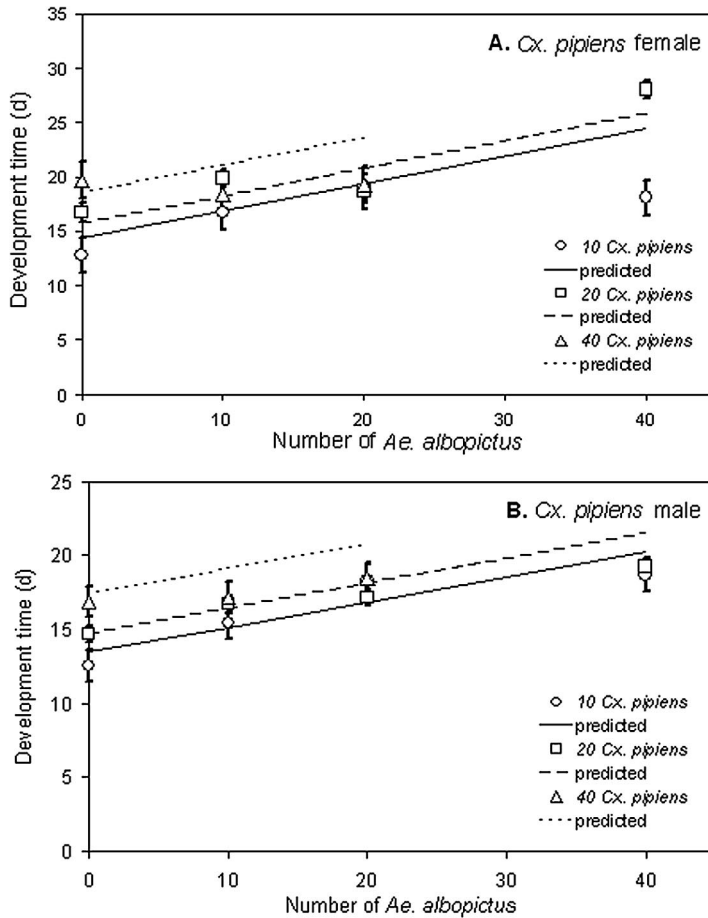
Fig. 3. Means of developmental times to adulthood (± 1 SE) for *Cx. pipiens* females (A) and males (B) across larval density treatments. Significance tests and slope estimates in Table 1.

male and male wing lengths significantly decreased in treatments of higher densities of both conspecifics and *Cx. pipiens.* Even if the (nonsignificant) effect of *Cx. pipiens* density on r' were regarded as real, the decline due to *Ae. albopictus* density was more severe (by a factor of ≈ 4) than the decline due to *Cx. pipiens* density (Table 1).

In aggregate, this laboratory experiment provides compelling evidence indicating that *Ae. albopictus* is the superior competitor to *Cx. pipiens* with leaves and grass as a substrate. Such competitive asymmetry results in *Ae. albopictus* cohorts apparently maintaining positive population growth (estimated by r'), even under conditions that probably yielded declines for cohorts of *Cx. pipiens.* This result suggests that under these conditions, competitive exclusion is possible, if there are no other mechanisms for coexistence (e.g., spatial or temporal refuges). Our results are consistent with the findings of competitive interactions of these two species in Italy at 25°C. Our combined densities bracket that used by Carrieri et al. (2003).

Although we, like Carrieri et al. (2003), show highly asymmetric competition between these two species,

Carrieri et al. (2003) provide more direct evidence that the mechanism is specifically resource competition. Previous studies on *Ae. albopictus* in interspecific competition indicate *Ae. albopictus* is often superior in resource competition (Ho et al. 1989, Livdahl and Willey 1991, Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004). In our study, *Cx. pipiens* had a very low survivorship relative to *Ae. albopictus*, even in the low-density treatments. This may indicate that resources in the experiment were limited and insufficient to produce maximal success of *Cx. pipiens.* Carrieri et al. (2003) found in populations from Italy that *Cx. pipiens* survivorship was relatively low at low food levels compared with *Ae. albopictus* and that *Ae. albopictus* was better able to exploit resources and was more efficient at converting food to biomass. *Ae. albopictus* may be more efficient at resource acquisition and spend more time behaviorally actively foraging or feeding than other container-dwelling mosquitoes (Juliano 1998, Daugherty et al. 2000, Braks et al. 2004, Yee et al. 2004). The competition experiment between *Ae. albopictus* and *Cx. pipiens* in Italy tested for resource competition through manipulations of re-
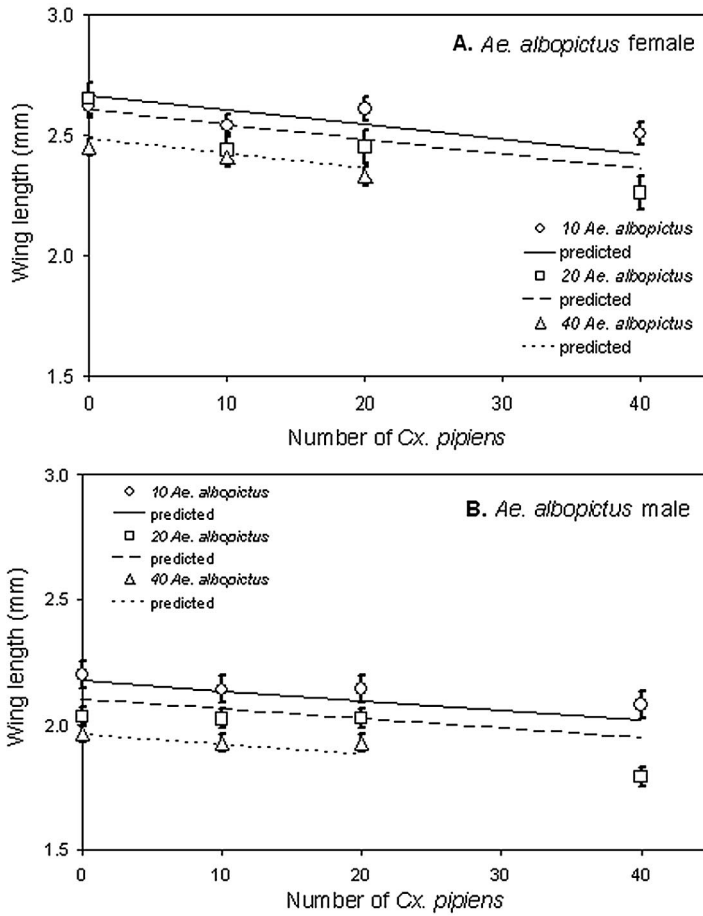
Fig. 4. Means of wing lengths (±1 SE) for *Ae. albopictus* females (A) and males (B) across larval density treatments. Significance tests and slope estimates in Table 1.
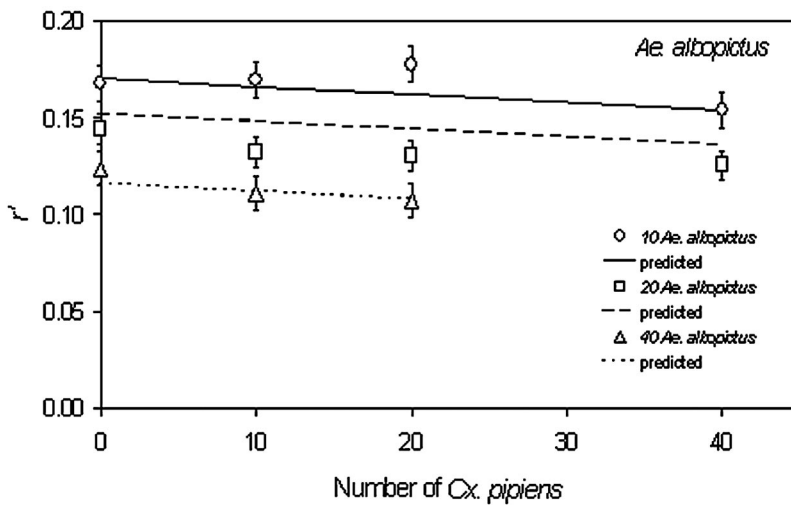

Fig. 5. Means of the composite index of population performance (r') (±1 SE) for *Ae. albopictus* across larval density treatments. Significance tests and slope estimates in Table 1.
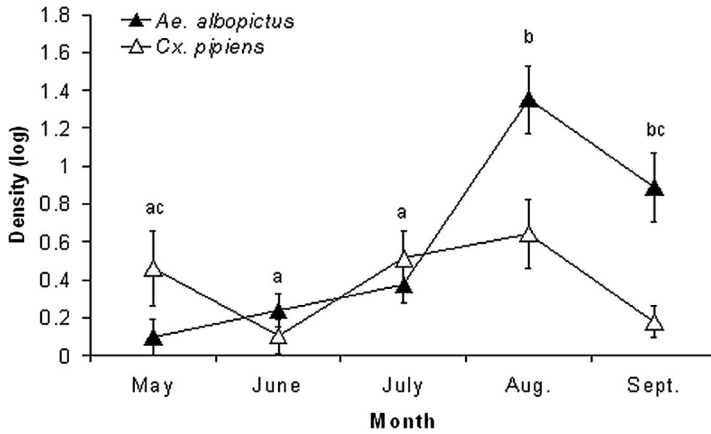
Fig. 6. Means (± 2 SE) of the abundance of *Ae. albopictus* and *Cx. pipiens* per tire across all months sampled. Months with the same letter indicate no significant differences between the combined abundance of both species.

source levels by using an artificial diet (cat biscuits; Carrieri et al. 2003). The similarity of our results, using more realistic substrates, to those of Carrieri et al. (2003) suggests that *Ae. albopictus* is generally superior to *Cx. pipiens* in competition at 25°C.

Asymmetrical competition is ecologically important only if the potential competitors encounter one another in nature. Our field data show that *Cx. pipiens* encounters *Ae. albopictus* in urban tires, suggesting that competitive superiority of *Ae. albopictus* could affect populations of *Cx. pipiens.* The abundance of *Ae. albopictus* was highly seasonal, with relatively low abundance early in the season (May–July), increasing abundance in August, and continuing high abundance in September. The co-occurrence data correspond to the seasonality of *Ae. albopictus*' abundance; later in the season, *Cx. pipiens* encountered *Ae. albopictus* in tires more frequently. As the abundance of *Ae. albopictus* increased later in the season, the proportion of tires in which *Cx. pipiens* encountered *Ae. albopictus* increased as well. In addition, the mean crowding of *Ae. albopictus* on *Cx. pipiens* within a tire also corresponded to the seasonality of *Ae. albopictus*' abundance. Thus, we expect that if competition from *Ae. albopictus* is important for field populations of *Cx. pipiens,* it will be important in late summer and early fall.

Although *Ae. albopictus* and *Cx. pipiens* co-occur in these container habitats, these two species differ in patterns of oviposition and egg hatch. *Ae. albopictus* oviposits on the walls of containers, above the water line, and hatching is induced by submergence of the eggs (Hawley 1988). During periods of low precipitation, *Ae. albopictus*' hatching is low and eggs accumulate. Species in the *Cx. pipiens* complex deposit egg rafts on the surface of the water, and these hatch 1–2 d later, without the requirement of additional water input into the container (Vinogradova 2000). This asynchrony in hatching may result in tires where *Cx. pipiens* larvae hatch and reside during periods of low precipitation in the absence of *Ae. albopictus,* thus providing *Cx. pipiens* with a refuge from competition. However, when a container goes dry for a period, *Ae. albopictus* eggs may remain on the walls. These eggs would hatch shortly after flooding of the container. In this situation, *Cx. pipiens* would oviposit after this flooding, with the recently hatched larvae of *Cx. pipiens* encountering late-stage larvae of *Ae. albopictus.* Thus, stage dependence of competitive interactions of these species may be very important in nature, and additional investigation of competition among asynchronous cohorts of *Ae. albopictus* and *Cx. pipiens* is needed.

Table 2. Co-occurrence and mean crowding data across the entire season (May–September)

Date	Neither species	Only *Ae. albopictus*	Only *Cx. pipiens*	Both species	Median mean crowding (n)	Minimum, maximum
Entire season	59	26	12	22	1.00 (18)	0, 88.23
May	21	1	3	0	0 (4)	0, 0
June	19	5	1	1	5.50 (2)	0, 11.00
July	8	5	7	7	2.96 (5)	0, 3.35
Aug.	3	6	1	10	25.29 (4)	2.96, 52.98
Sept.	8	9	0	4	73.82 (3)	1.00, 88.23

Reported are the number of tires yielding neither *Ae. albopictus* nor *Cx. pipiens, Ae. albopictus* and no *Cx. pipiens, Cx. pipiens* and no *Ae. albopictus,* or both species co-occurring. Mean crowding of *Ae. albopictus* larvae on *Cx. pipiens* is averaged across sites (n is number of sites) within each month.
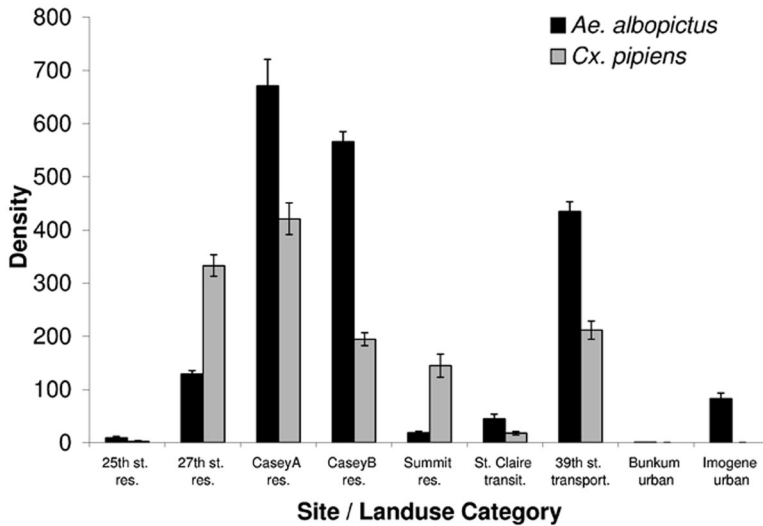
Fig. 7. Means (± 2 SE) of the abundance of *Ae. albopictus* and *Cx. pipiens* per tire across all sites sampled with land use categories: res, residential; transit, transitional; transport, transportation; and urban, urban.

Our field data establish co-occurrence and thus show that an impact of interspecific competition is possible, but we have not determined the actual impact of competition from *Ae. albopictus* in the field. We found no negative correlation of these species in the field. A better test of the impact of competition in the field would be to determine how production of pupae or adults is related to density of a potential competitor. As with studies of competition between *Ae. albopictus* and *Ae. aegypti* (Juliano 1998, Braks et al. 2004, Juliano et al. 2004), there is a need for field experiments on interspecific competition between *Ae. albopictus* and *Cx. pipiens.*

Although we sampled a limited number of sites, our data provide a preliminary description of macro- and microhabitat characteristics associated with high abundance and co-occurrence of *Ae. albopictus* and *Cx. pipiens.* These two species co-occur in high abundance in tires in residential areas. Canonical correlation analysis of environmental and abundance data yielded no strong evidence that the abundance and co-occurrence of these two species are related to environmental variables at the microhabitat level. The abundance of *Ae. albopictus,* but not *Cx. pipiens,* was strongly associated with month and conductivity, and total inorganic nitrogen and phosphorus were not strongly related to the abundance of either species. Although canonical correlation was significant, redundancy analysis indicated that the environment canonical variate predicted relatively little of the variance in the individual species variates, indicating little predictive power from these environmental variables. The absence of significant correlations of nutrient availability with abundance may be a result of low variation of nitrogen and phosphorus among tires. Across a wider range of habitats (e.g., catch basins and storm drains), greater tolerance of *Cx. pipiens* for more eutrophic waters may be more important.

Cx. pipiens is a habitat generalist, not confined to container habitats, and often resides in stagnant pools of water, marshes, drainage ditches, and canals (Vinogradova 2000). For such a generalist, the competition with *Ae. albopictus* in urban tires may not result in drastic overall reductions in overall *Cx. pipiens* numbers. The interaction of these species in urban tires may nevertheless be ecologically and medically important. Many of our tire sites were in proximity to residential areas (four-eighths sites within ≈50 m of residences), and both species occurred in relatively high abundance in residential areas. These peridomestic containers may be particularly important sources of *Cx. pipiens* and *Ae. albopictus* that are likely to carry arboviruses to humans. Members of the *Cx. pipiens* complex are considered the primary vectors of WNV in North America (Kulasekera et al. 2001; Spielman 2001; Turell et al. 2001, 2005; Fonseca et al. 2004). The adults are primarily bird feeders, but North American *Cx. pipiens* also feed avidly on humans (Vinogradova 2000, Fonseca et al. 2004). In contrast, *Ae. albopictus* adults primarily feed on mammals, including humans, and often take meals from birds (Hawley 1988). Competition between *Ae. albopictus* and *Cx. pipiens* in residential tires has the potential to affect the epidemiology of WNV because of effects on population dynamics and life history traits of *Cx. pipiens* in peridomestic containers but also because *Ae. albopictus* from these same containers may act as a bridge vector of WNV (Sardelis et al. 2002, Turell et al. 2005).

This is the first study of competitive interactions of *Cx. pipiens* and *Ae. albopictus* in North America and is consistent with results for these species in southern Europe (Carrieri et al. 2003). In the field, we found spatial and temporal patterns in the co-occurrence of these two species in across macrohabitat and season. We conclude that the interaction may be important in tires in residential areas in late summer and fall. Thus,

the impact of competition from the recent invader *Ae. albopictus* on *Cx. pipiens* could be ecologically important. Because both species are thought to have a role in transmission of WNV (Turell et al. 2005), their co-occurrence and interactions in areas of relatively high human population also could be medically important. There is a clear need for field investigations of both the ecological effects and epidemiological consequences of competition between these species.

Acknowledgments

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