Weak Larval Competition Between the Invasive Mosquito *Aedes japonicus japonicus* (Diptera: Culicidae) and Three Resident Container-Inhabiting Mosquitoes in the Laboratory

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ABSTRACT The spread of exotic mosquito species into new environments can introduce shifts in mosquito populations and potentially alter public health risks to mosquito-borne diseases. The successful establishment of exotic species may occur due to their competitive advantage over other cohabitating species. We hypothesized that the recently introduced exotic mosquito *Aedes japonicus japonicus* (Theobald) would be a more effective competitor than *Aedes atropalpus* (Coquillett) and *Aedes triseriatus* (Say), and an equal competitor to *Culex pipiens* (L.) based on larval abundance data within tire habitats. Impacts of competition were measured using the larval developmental rate and survival of larvae, adult mortality, wing length, and sex ratio. We found that intraspecific competition acted strongest against *Ae. japonicus* versus the other three resident mosquito species by delaying larval development and increasing adult mortality. Interspecific competition was generally weak and significant main effects were only detected for species and density. Overall, our results show that larval competition between *Ae. japonicus* and the three resident species was weak when present, indicating that other ecological or behavioral factors may be influencing the invasion success for *Ae. japonicus* in North America.

KEY WORDS invasion biology, exotic mosquito, density dependence

The spread of exotic mosquito species into new geographic areas can introduce shifts in mosquito populations. Uncovering factors that influence the population and invasion dynamics of exotic mosquito species are crucial for addressing potential changes in ecological composition and consequently, public health risk to mosquito-borne disease where the mosquito species serve as effective vectors (Andreadis and Wolfe 2010). Larval competition can be a significant stressor for container-inhabiting mosquito species because their breeding sites fluctuate in size, water volume, food availability, and oviposition quality. Thus, competition within and between mosquito species is an important factor that probably regulates invasion success and population dynamics (Barrera 1996, Juliano and Lounibos 2005).

It is hypothesized that successful establishment by exotic species occurs due to the competitive advantage of the invasive species over the native species particularly when subject to interspecific conditions. For example, field observations have attributed the decline of *Aedes aegypti* (L.) in the southern United States as a product of being outcompeted by the more recently introduced *Aedes albopictus* (Skuse) (Juliano and Lounibos 2005), an observation that has been supported by laboratory experiments (Livdahl and Willey 1991, Costanzo et al. 2005).

Aedes japonicus (Theobald) is an invasive rock hole and container-breeding mosquito native to Japan, Korea, and eastern China (Tanaka et al. 1979). It was first detected in 1998 in the eastern United States (Peyton et al. 1999, Andreadis et al. 2001). It has since rapidly spread along the East Coast and into the Midwest and is currently established in 31 states. Successful population establishments have also been noted in Canada (Thielman and Hunter 2006) and Europe (Schaffner et al. 2003, Schaffner et al. 2009, Versteirt et al. 2009). *Ae. japonicus* has been implicated as a potential bridge vector of West Nile virus to humans (Turell et al. 2005, Molaei et al. 2009), and laboratory studies have shown it is a competent vector of eastern equine encephalitis (Sardelis et al. 2002a), Japanese encephalitis (Takashima and Rosen 1989), LaCrosse (Sardelis et al. 2002b), St. Louis encephalitis (Sardelis et al. 2003), and West Nile (Turell et al. 2001) viruses.

Due to the diversity of oviposition sites *Ae. japonicus* uses, it can be found alone or co-occurring with other mosquito species (Andreadis et al. 2001, Bevins 2007). Mosquito surveys in tire piles have indicated that both *Aedes atropalpus* (Coquillett), a rock hole mosquito; and *Aedes triseriatus* (Say), a tree hole mosquito and the primary vector of LaCrosse virus (Pantuwatana et

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Table 1. Life-history parameter measurements from intraspecific competition treatments for *Ae. japonicus*, *Ae. atropalpus*, *Ae. triseriatus*, and *Cx. pipiens*

Parameter and species	Density cohort		
	Low (20:0)	Medium (40:0)	High (60:0)
Larval development (days ± SEM)*			
Ae. japonicus	9.2 ± 0.1a	9.8 ± 0.2b	10.1 ± 0.2b
Ae. atropalpus	9.2 ± 1.1	9.2 ± 0.4	8.7 ± 0.3
Ae. triseriatus	11.7 ± 0.9	13.5 ± 0.9	11.9 ± 0.2
Cx. pipiens	7.7 ± 0.3	8.7 ± 0.3	8.7 ± 0.3
Wing length (mm ± SEM)			
Ae. japonicus	3.45 ± 0.06	3.40 ± 0.01	3.41 ± 0.02
Ae. atropalpus	3.14 ± 0.10	3.24 ± 0.09	3.20 ± 0.07
Ae. triseriatus	2.83 ± 0.02	3.01 ± 0.07	2.95 ± 0.07
Cx. pipiens	3.21 ± 0.14	3.14 ± 0.07	3.22 ± 0.03
Adult mortality (% ± SEM)			
Ae. japonicus	0.31 ± 0.06a	0.47 ± 0.06ab	0.61 ± 0.04b
Ae. atropalpus	0.80 ± 0.09	0.83 ± 0.10	0.86 ± 0.05
Ae. triseriatus	0.57 ± 0.04	0.67 ± 0.01	0.61 ± 0.11
Cx. pipiens	0.68 ± 0.03	0.67 ± 0.08	0.65 ± 0.05

Lowercase letters denote significant differences between density cohorts within a species.

al. 1972), have declined in abundance in these tire habitats and may be competitively displaced by *Ae. japonicus* (Scott et al. 2001, Andreadis and Wolfe 2010). Conversely, the relative abundance in tire habitats of *Culex pipiens* (L.), which is distributed worldwide (Barr 1957, Vinogradova 2000), does not seem to have shifted since the invasion of *Ae. japonicus* (Andreadis and Wolfe 2010).

Little is known about the competitive status of *Ae. japonicus.* In a previous study, *Ae. japonicus* population performance was negatively impacted when placed under intraspecific conditions (Armistead et al. 2008b), but under interspecific conditions, *Ae. japonicus* was able to maintain positive population growth (Armistead et al. 2008a). To further define the competitive capabilities of *Ae. japonicus,* we conducted a controlled laboratory experiment with a working hypothesis that intraspecific and interspecific larval rearing conditions impact the larval development of *Ae. japonicus* and other resident container-inhabiting mosquito species of the northeastern United States.

Materials and Methods

Mosquitoes. Mosquitoes were reared in an environmental chamber at 25°C, 80% RH, and a photoperiod of 14:10 (L:D) h. These environmental parameters produced laboratory mosquitoes similar in size to those collected from the field (female wing length; data not shown). We used *Ae. japonicus* eggs originally collected from artificial containers in Ocean and Sommerset counties, NJ, that were colonized at Rutgers University in 2000 by forced mating (Williges et al. 2008). Due to the possibility of laboratory-adapted behaviors of the *Ae. japonicus* colony, we used similarly colonized and laboratory reared mosquitoes of *Ae. atropalpus* (collected in 2005 from natural rock holes located at Stevenson Dam in Oxford, CT), *Ae. triseriatus* (collected in 1995 from discarded tires in Waterford, CT), and *Cx. pipiens* (collected as field egg rafts from New Haven, CT, in 2000). Use of laboratory colonies allowed for concurrent egg hatch and identical larval feeding regimes (1:1 ratio of lactalbumin: brewer's yeast) to minimize experimental variability.

Experimental Setup. Mosquito eggs were synchronously hatched and introduced into the experiment as 24-h larvae. Larvae were placed into containers (473.2 ml, Newspring Packaging, Kearny, NJ) containing 250 ml of distilled water and 20 mg of mosquito food every other day. For each species, newly hatched larvae were placed into a density cohort and treatment group. Density cohorts were assigned as low ($n = 20$), medium ($n = 40$), and high ($n = 60$). Competition treatment groups referred to a species being placed with conspecifics (intraspecific) or in a 1:1 ratio with the competitor (interspecific). Experimental cups were randomly rotated every day to prevent any positional affects within the chamber.

Larval competition was investigated by monitoring larval and adult life-history parameters of each species in the density × competitor treatment combinations. Larvae were examined daily, and mortality and pupation were recorded for a maximum of 20 d. Pupae were collected from each cup daily and placed into individual test tubes until adult emergence. All mosquitoes were scored by replicate, density cohort, competition treatment, species, sex, and female wing length (Nasci 1990). Mosquito wing length determinations were made using a Discovery.V12 SteREO dissecting microscope equipped with an AxioCam HRc camera (AxioVision v.4.8.1.0; Carl Zeiss Inc., Thornwood, NY). All species × density × competition treatment combinations were replicated three times, except *Ae. japonicus* intraspecific treatments, which were replicated nine times.

Data Analysis. Intraspecific competition effects were determined by comparing life-history parameters from the intraspecific treatments for a single species across the three increasing density levels (low, medium, and high). Interspecific competition effects were determined by comparing a species' life-history parameters in the intraspecific versus interspecific

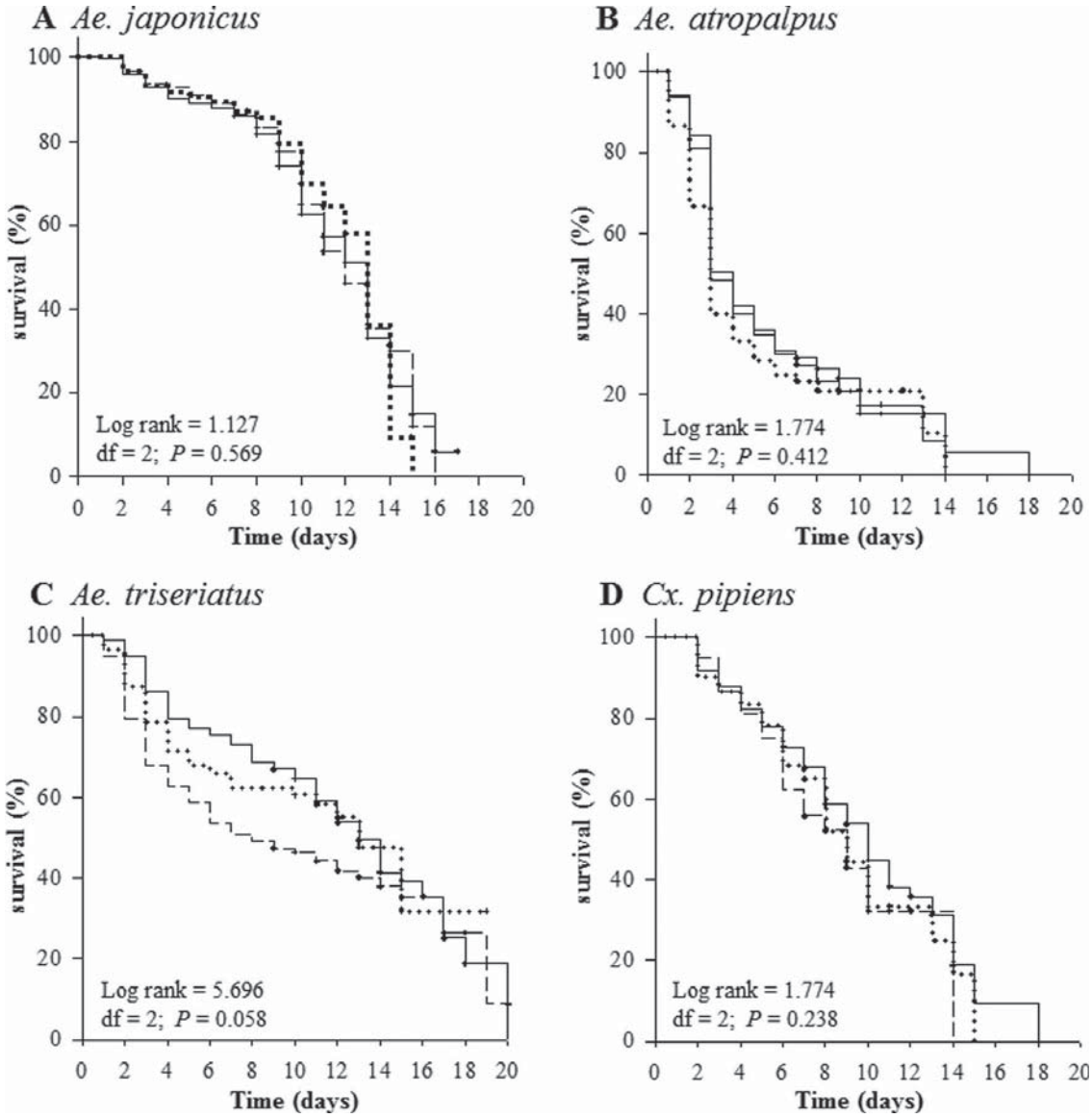

Fig. 1. Larval survival curves of *Ae. japonicus* (A), *Ae. atropalpus* (B), *Ae. triseriatus* (C), and *Cx. pipiens* (D) from intraspecific competition treatments at the low (20:0, dotted line), medium (40:0, dashed line), and high (60:0, solid line) density levels.

treatment within each density. Life-history parameter measurements included larval development (days from hatch to pupation) and larval survival (median age, age at which 50% of the population is still alive) obtained from curves generated using the Kaplan–Meier method and log rank statistics. For survival curves, death was considered an event and pupation or larvae alive at the end of the experiment were treated as censored data. Adult life-history parameter measurements included wing length, sex ratio, and mortality. All data were transformed, if necessary, to meet assumptions of normality and homogeneity of variances or for statistical analysis (i.e., arcsine transformation of mortality data). Intraspecific competition differences were analyzed by one-way analysis of variance (ANOVA). Interspecific competition differences were evaluated for each species by using pairwise comparisons with Bonferroni correction for experiment wise $\alpha = 0.05$ between competition treatments within a density (Systat Software, Inc. 2010). A three-way multivariate ANOVA (MANOVA) was performed on the life-history parameter data. The effects of mosquito species, competition treatment, and density treatment and their interactions, on larval development, sex ratio, and wing length were investigated. Univariate ANOVAs for each dependent variable were conducted as follow-up tests to the MANOVA (R Statistical Computing 2011).

Results

Intraspecific Competition. Significant effects of increased density (Table 1) resulted in lengthened time to pupation ($F_{2,26} = 7.292$; $P = 0.003$) and increased adult mortality ($F_{2,26} = 6.874$; $P = 0.004$) for *Ae. japonicus.* However, there were no significant effects of

Table 2. Results of MANOVA for effects and interactions of species (*Ae. japonicus* and *Ae. atropalpus*), competition treatment (intraspecific and interspecific), and density cohort (low, medium, and high) on larval development, sex ratio, and wing length

Variable	df_1, df_2	Pillai's trace	*P*	Follow-up ANOVA *P* values		
				Development	Sex	Wing length
Species (S)	3, 364	0.512	**<0.0001**	**<0.0001**	**0.038**	**<0.0001**
Competition (C)	3, 364	0.009	0.372	0.540	0.110	0.080
Density (D)	6, 730	0.182	**<0.0001**	**<0.0001**	0.963	**0.016**
S × C	3, 364	0.031	**0.010**	**0.011**	0.367	0.066
S × D	6, 730	0.032	0.068	0.109	0.241	0.058
C × D	6, 730	0.032	0.067	**0.039**	0.257	0.641
S × C × D	6, 730	0.043	**0.015**	0.385	0.141	0.711

Significant effects are in bold.

density on *Ae. japonicus* larval survival (Fig. 1A) or on female wing length (Table 1). No significant differences across density treatments were detected for any of the measured life-history parameters (Table 1) of *Ae. atropalpus* (Fig. 1B), *Ae. triseriatus* (Fig. 1C), and *Cx. pipiens* (Fig. 1D).

Interspecific Competition Between *Ae. japonicus* and *Ae. atropalpus*. Mosquito species and density cohort were significant as well as the interactions of species × competition and species × competition × density (Table 2). Significant univariate main effects for species were obtained for larval development to pupation, sex ratio and wing length, whereas univariate main effects for density were obtained for larval development and wing length (Table 2). The survival of *Ae. japonicus* larvae significantly increased when

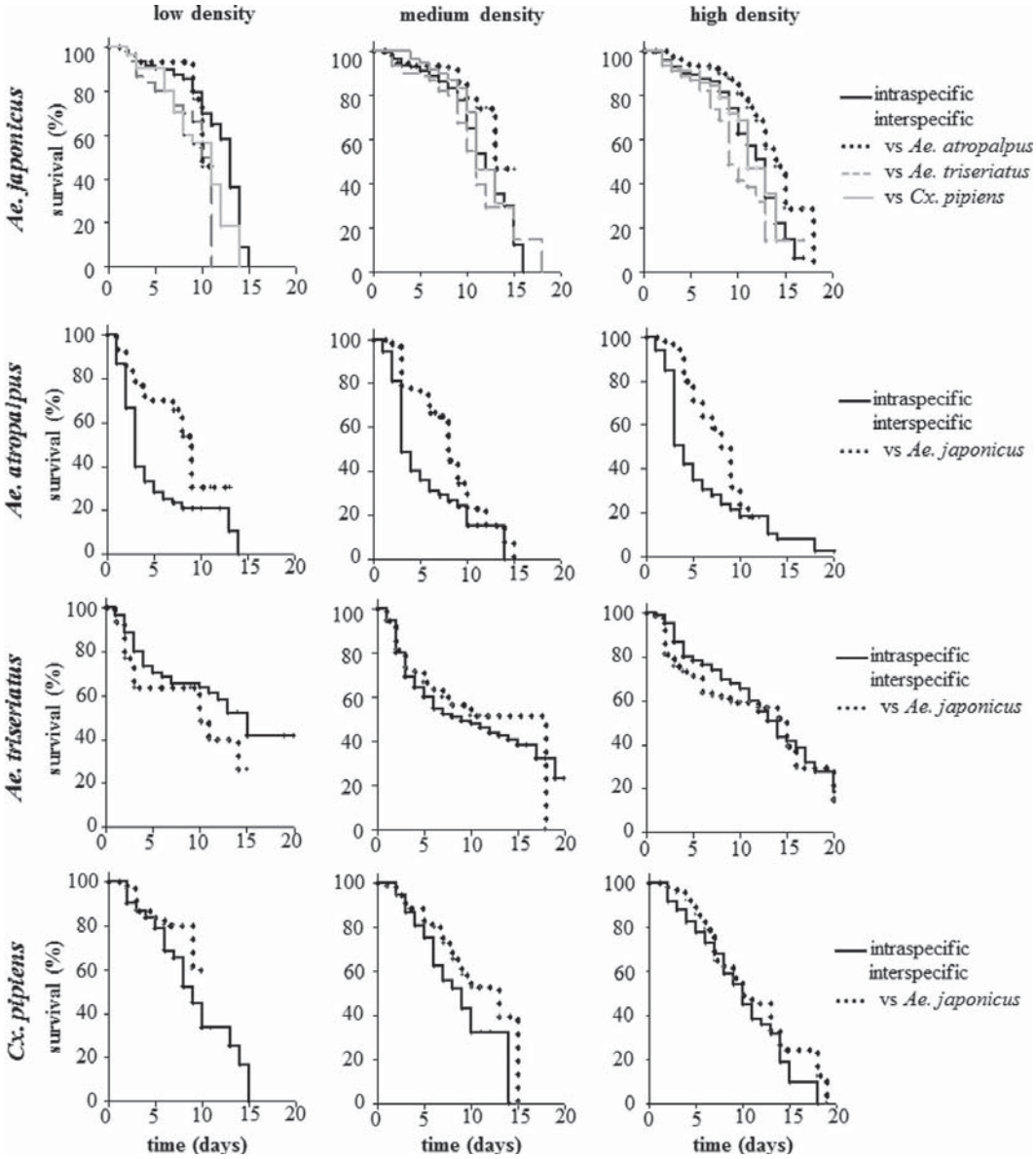

Fig. 2. Larval survival curves of *Ae. japonicus*, *Ae. atropalpus*, *Ae. triseriatus*, and *Cx. pipiens* from competition treatments at the low-, medium-, and high-density levels. Interspecific competition was determined using log rank survival analysis at each density by comparing the species in the intraspecific treatment to the same species in the interspecific treatment.

placed with *Ae. atropalpus* compared with when placed with other *Ae. japonicus* in the medium (median age: interspecific, 12.6 ± 0.5 d; intraspecific, 11.5 ± 0.2 d; log rank = 5.296, df = 1, $P = 0.021$) and high (median age: interspecific = 13.6 ± 0.6 d, intraspecific = 11.4 ± 0.2 d, log rank = 11.756, df = 1, $P < 0.001$) density treatments (Fig. 2). No significant effects on *Ae. japonicus* larval development (Fig. 3A), wing length (Fig. 3B), or adult mortality (Fig. 3C) were associated with the competition treatment. *Ae. atropalpus* had more robust life-history parameter measurements when placed in the interspecific condition with *Ae. japonicus* than when in the intraspecific condition. The larval survival of *Ae. atropalpus* significantly increased when placed with *Ae. japonicus* (Fig. 2) in all three density treatments (median age in low density: interspecific, 8.1 ± 0.9 d; intraspecific, 5.2 ± 0.6 d; log rank = 9.014, df = 1, $P = 0.003$; median age in medium density: interspecific, 8.2 ± 0.6 d; intraspecific, 5.7 ± 0.4 d; log rank = 11.767, df = 1, $P < 0.001$; median age in high density: interspecific, 7.9 ± 0.3 d; intraspecific, 6.1 ± 0.4 d; log rank = 17.0, df = 1, $P < 0.001$). Wing length of *Ae. atropalpus* females was significantly increased in the high-density 30:30 cohort compared with the high-density 60:0 cohort ($t = 2.944$, df = 4, $P = 0.042$). No significant effects of competition treatment were detected for *Ae. atropalpus* larval development (Fig. 3A) or adult mortality (Fig. 3C).

Interspecific Competition Between *Ae. japonicus* and *Ae. triseriatus*. Mosquito species and competition treatment were significant as well as the interaction of species × density (Table 3). Significant univariate main effects for species were obtained for larval development and wing length, whereas univariate main effects for competition were obtained for larval development (Table 3). The larval survival of *Ae. japonicus* significantly decreased when placed with *Ae. triseriatus* compared with when placed with other *Ae. japonicus* in the low (median age: interspecific, 8.8 ± 0.6 d; intraspecific, 11.5 ± 0.3 d; log rank = 5.759, df = 1, $P = 0.016$) and high (median age: interspecific, 10.1 ± 0.5 d; intraspecific, 11.4 ± 0.2 d; log rank = 14.724, df = 1, $P < 0.001$) density treatments (Fig. 2). No significant effects on *Ae. japonicus* larval development (Fig. 4A), wing length (Fig. 4B), or adult mortality (Fig. 4C) were associated with the competition treatment. *Ae. triseriatus* developed significantly more quickly (Fig. 4A) when placed in competition with *Ae. japonicus* than when placed in the intraspecific condition at the medium ($t = 2.887$, df = 4, $P = 0.045$) and high ($t = 2.820$, df = 4, $P = 0.048$) density levels. No significant effects of competition treatment were detected for *Ae. triseriatus* larval survival (Fig. 2), larval development in the low density (Fig. 4A), wing length (Fig. 4B), or adult mortality (Fig. 4C).

Interspecific Competition Between *Ae. japonicus* and *Cx. pipiens*. Mosquito species and density were significant, but competition and the interactions were not (Table 4). Significant univariate main effects for species were obtained for larval development and wing length, whereas univariate main effects for density were obtained for larval development (Table 4).

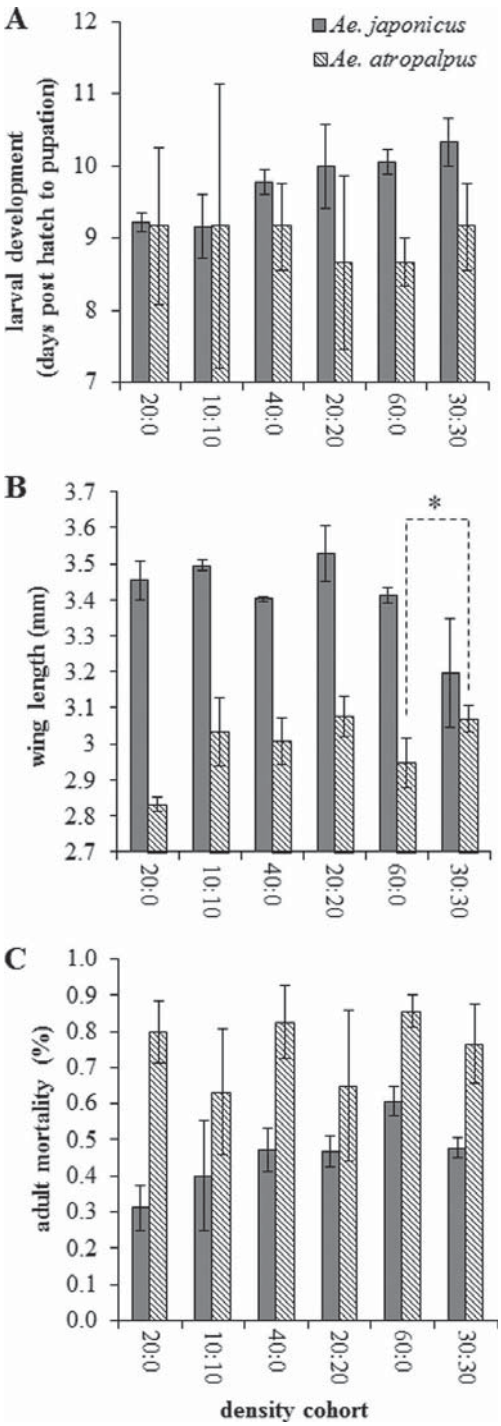

Fig. 3. Outcomes of interspecific competition between *Ae. japonicus* (gray bars) and *Ae. atropalpus* (banded bars) on life-history parameters: larval development (±SEM; A), female wing length (±SEM; B), and adult mortality (±SEM; C). Significant differences are denoted with an asterisk (*).

The survival of *Ae. japonicus* larvae significantly decreased when placed with *Cx. pipiens* (Fig. 2) compared with the intraspecific condition in the low-density treatment (interspecific, 9.6 ± 0.8 d; intraspecific, 11.5 ± 0.3 d; log rank = 7.450, df = 1, $P = 0.006$). There were no significant effects on *Ae. japonicus* larval development (Fig. 5A), wing length

Table 3. Results of MANOVA for effects and interactions of species (*Ae. japonicus* and *Ae. triseriatus*), competition treatment (intraspecific and interspecific), and density cohort (low, medium, and high) on larval development, sex ratio, and wing length

Variable	df_1, df_2	Pillai's trace	*P*	Follow-up ANOVA *P* values		
				Development	Sex	Wing length
Species (S)	3, 453	0.582	**<0.0001**	**<0.0001**	0.632	**<0.0001**
Competition (C)	3, 453	0.063	**<0.0001**	**<0.0001**	0.725	0.720
Density (D)	6, 908	0.025	0.076	**0.027**	0.289	0.754
S × C	3, 453	0.006	0.443	0.193	0.986	0.798
S × D	6, 908	0.034	**0.017**	0.098	0.957	0.279
C × D	6, 908	0.015	0.321	0.395	0.134	0.122
S × C × D	6, 908	0.010	0.623	0.628	0.784	0.363

Significant effects are in bold.

(Fig. 5B), or adult mortality (Fig. 5C) associated with the competition treatment. Larval survival of *Cx. pipiens* (Fig. 2) was significantly increased when the interspecific condition (median age, 10.7 ± 0.7 d) was compared with the intraspecific condition (median age, 8.8 ± 0.4 d) in the medium-density treatment (log rank = 4.864, df = 1, $P = 0.027$). Adult mortality of *Cx. pipiens* (Fig. 5C) was significantly decreased in the low-density 10:10 cohort compared with the low-density 20:0 cohort ($t = 7.432$, df = 4, $P = 0.002$). No significant effects of competition treatment were detected for *Cx. pipiens* larval development (Fig. 5A) or wing length (Fig. 5B).

Discussion

Larval competition has been shown to be an important determinant in successful invasions by exotic mosquito species (Juliano and Lounibos 2005). The establishment and spread of *Ae. japonicus* in North America have coincided with a reduction of other container-inhabiting mosquitoes in used tire and rock-hole habitats (Andreadis and Wolfe 2010). Under our experimental conditions, we observed that significant effects of intraspecific and interspecific competition were weakly evident for *Ae. japonicus* and often favored the resident species. Thus, contrary to the results expected based on field observations where decreased abundance of *Ae. atropalpus* and *Ae. triseriatus* in discarded tires has been observed in several geographic regions (Joy and Sullivan 2005, Andreadis and Wolfe 2010), it was the survival of *Ae. japonicus* that was negatively affected by the concurrent presence of an equal number of competitor larvae. However, our results show that interspecific competition with *Ae. japonicus* does not strongly act on *Cx. pipiens,* corresponding well with the comparatively stable abundance of this species in discarded tire habitats in Connecticut (Andreadis and Wolfe 2010). Therefore, further exploration of the ecology or behavior patterns of *Ae. japonicus* may provide insight into how it can successfully co-occur with other container-breeding mosquitoes.

Most hypotheses on the role of interspecific competition among container-inhabiting mosquitoes come from extensive research on *Ae. albopictus* that

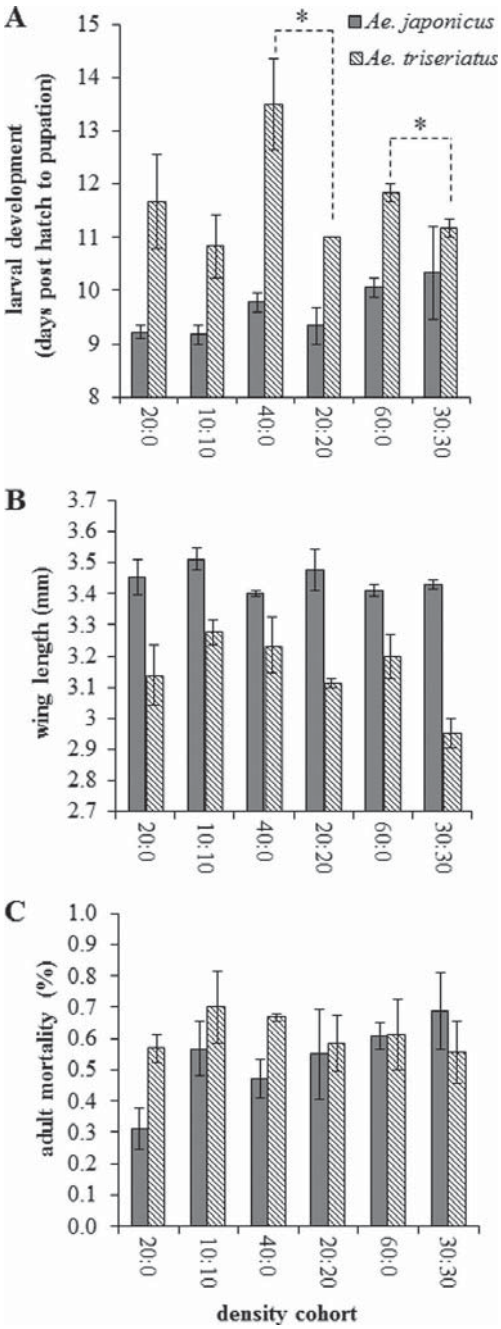

Fig. 4. Outcomes of interspecific competition between *Ae. japonicus* (gray bars) and *Ae. triseriatus* (banded bars) on life-history parameters: larval development (±SEM; A), female wing length (±SEM; B), and adult mortality (±SEM; C). Significant differences are denoted with an asterisk (*).

indicate that this exotic mosquito is often superior to other mosquitoes in resource competition (Ho et al. 1989; Livdahl and Willey 1991; Novak et al. 1993; Barrera 1996; Juliano 1998; Daugherty et al. 2000; Teng and Apperson 2000; Lounibos et al. 2001; Braks et al. 2004; Juliano et al. 2004; Costanzo et al. 2005, 2011; Armistead et al. 2008b; Bevins 2008; Murrell and Juliano 2008; Reiskind et al. 2009). Although many invasive species are categorized as dominant competitors that can quickly adapt to their new environment

Table 4. Results of MANOVA for effects and interactions of species (*Ae. japonicus* and *Cx. pipiens*), competition treatment (intraspecific and interspecific), and density cohort (low, medium, and high) on larval development, sex ratio, and wing length

Variable	df_1, df_2	Pillai's trace	*P*	Follow-up ANOVA *P* values		
				Development	Sex	Wing length
Species (S)	3, 438	0.303	**<0.0001**	**<0.0001**	0.522	**0.0002**
Competition (C)	3, 438	0.009	0.280	0.110	0.130	0.349
Density (D)	6, 878	0.114	**<0.0001**	**<0.0001**	0.494	0.075
S × C	3, 438	0.003	0.772	0.335	0.441	0.587
S × D	6, 878	0.016	0.327	0.595	0.219	0.768
C × D	6, 878	0.004	0.927	0.564	0.831	0.860
S × C × D	6, 878	0.007	0.781	0.811	0.984	0.717

Significant effects are in bold.

(Mooney and Cleland 2001, Sakai et al. 2001, Reitz and Trumble 2002, Levine 2008), and despite growing research examining the competitive mechanisms that further confirm that *Ae. albopictus* is a highly competitive species (Juliano and Lounibos 2005) in container habitats, caution must be used in suggesting the same is true for the invasion success of *Ae. japonicus.*

Our results do not clearly implicate interspecific competition as a strong factor promoting the spread of *Ae. japonicus* in artificial container habitats in North America. A complementary laboratory study (Armistead et al. 2008b) that examined interactions between *Ae. japonicus* and *Ae. atropalpus* at the high-density equivalent ($n = 60$) reported a decline in *Ae. japonicus* survival when placed in the interspecific condition with *Ae. atropalpus.* This finding is contradictory to the results of our study that found that the survival of both species at the high-density level increased when in the interspecific condition. In addition, we observed a significant effect on the wing length of female *Ae. atropalpus* in the interspecific treatment at high density but Armistead et al. (2008b) did not.

A recently completed study examining the effects of interspecific competition between *Ae. japonicus* and *Ae. triseriatus* (Alto 2011) provided an overall conclusion that both species perform poorly at higher larval densities and that performance is negligibly altered by the relative ratios of the two species. Alto (2011) did not observe a significant treatment or species combination effect on *Ae. japonicus* female body size. They found that body size did not significantly differ when *Ae. triseriatus* were reared on a high-nutrition diet. They suggest that these results indicate that both species are equally affected by intraspecific and interspecific competition (Alto 2011). Similarly, we observed weak intraspecific effects for *Ae. japonicus* due to slowed larval development and increased adult mortality, and *Ae. japonicus* was negatively affected by the interspecific interactions with *Ae. triseriatus.* Contrasting Alto (2011), we did not observe intraspecific competition for *Ae. triseriatus,* and *Ae. triseriatus* was positively affected by interspecific interactions with *Ae. japonicus.*

Various ecological or behavior characteristics may be influencing the invasion success for *Ae. japonicus*

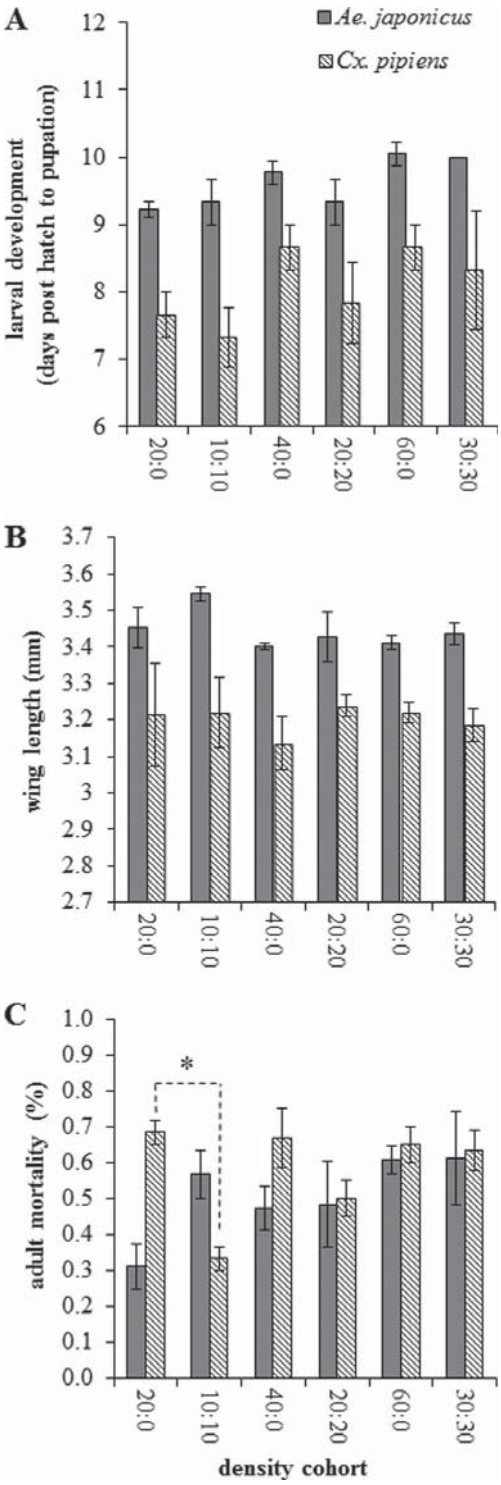

Fig. 5. Outcomes of interspecific competition between *Ae. japonicus* (gray bars) and *Cx. pipiens* (banded bars) on life-history parameters: larval development (±SEM; A), female wing length (±SEM; B), and adult mortality (±SEM; C). Significant differences are denoted with an asterisk (*).

(Teng and Apperson 2000, Armistead et al. 2008a). These characteristics could include habitat alteration (Lounibos 2007), behavioral differences (Holway and Suarez 1999), female oviposition preferences, overwintering success, and egg desiccation resistance

(Costanzo et al. 2005, Leisnham and Juliano 2009). Because this experiment uses laboratory colonies and artificial diet, effects associated with competition which might have been evident under more natural conditions may have been weakened going undetected in our analyses. Alternatively, competitive displacement could be playing a particularly significant role (Lounibos 2007), and the effects may only be evident under different environmental conditions (Kesavaraju et al. 2010).

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