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Interspecific Competition of a New Invasive Mosquito, *Culex coronator*, and Two Container Mosquitoes, *Aedes albopictus* and *Cx. quinquefasciatus* (Diptera: Culicidae), Across Different Detritus Environments

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Interspecific Competition of a New Invasive Mosquito, *Culex coronator*, and Two Container Mosquitoes, *Aedes albopictus* and *Cx. quinquefasciatus* (Diptera: Culicidae), Across Different Detritus Environments

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Abstract

The mosquito *Culex coronator* (Dyar and Knab) (Diptera: Culicidae) has undergone rapid range expansion in the United States since 2003, with its historical distribution in the southwest expanding eastward to the Atlantic coast. Although Cx. coronator nominally use small natural aquatic habitats for development, the use of containers (e.g., tires) makes it potentially important as container invasive. To determine the potential ecological effects of *Cx. coronator* on resident container species, we conducted a laboratory experiment to assess its competitive ability with two common tire-inhabiting species, *Aedes albopictus* (Skuse) and *Culex quinquefasciatus* (Say) (Diptera: Culicidae). Larvae were reared under a factorial design with each species alone and in combination (*Cx. coronator* + *Ae. albopictus*, *Cx. coronator* + *Cx. quinquefasciatus*) across three different resource environments (leaf detritus only, animal detritus only, animal + leaf). Mosquito performance (survival, adult male and female mass, and development time) was measured for each species across treatments. Female *Cx. coronator* developed slowest when grown with *Ae. albopictus*, or when grown with leaves only regardless of species combinations; similar patterns emerged for males although species effects were restricted to mass. Few differences were evident in performance for male and female *Cx. coronator* across detritus environments when grown with *Cx. quinquefasciatus*. *Cx. quinquefasciatus* did not vary in mass or development time in the presence of *Cx. coronator* compared with when grown alone. *Ae. albopictus* female mass was 15% lower in the presence of *Cx. coronator*. Survival of *Cx. coronator* was highest in animal and leaf detritus containers, although survival was generally lower when larvae were grown with *Ae. albopictus*. These findings suggest that the performance of *Cx. coronator* is similar to that of *Cx. quinquefasciatus* but it suffers in the presence of *Ae. albopictus* under some resource environments.

Keywords

Aedes; competition; container; *Culex*; range expansion

The United States has experienced several introductions of mosquitoes over the past half century, including the introduction of perhaps the most important nonindigenous species, the Asian tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae; Hawley et al. 1987). Invasive species (i.e., those that show considerable rapid spread into novel environments, Lounibos 2002) within the United States appear to take two forms, including those that cross large inhospitable distances (e.g., oceans) and those that exhibit range expansion from an

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otherwise restricted range; both types are often aided by humans. The former category includes the aforementioned *Ae. albopictus* as well as a more recent invader, *Aedes japonicus* (Theobald), with both species arriving from southeast Asia in shipments of vehicle tires (Hawley et al. 1987, Peyton et al. 1999). A historical invasive, *Aedes aegypti* (L.) also fits this broader invasive category, likely having arrived aboard slave ships from Africa in the 1500s (Tabachnick 1991). The second category includes species that may simply experience expansion within an existing geographic area, which may or may not be aided by human activities. *Aedes atropalpus* (Coquillett) was restricted to rock pools located along shorelines of lakes and streams in the eastern United States but exhibited range expansion into the midwest (e.g., Illinois, Indiana) after starting to use vehicle tires for oviposition and larval development (Berry and Craig 1984). Movement patterns for all these species are relatively well documented; however, the effects that these new arrivals have on resident mosquito communities and changes to patterns of disease resulting from their presence are of the utmost importance to fully understand their effect on humans and other organisms.

Culex coronator (Dyar and Knab), part of a larger complex of six species (Bram 1967), is common in south and central America and often uses small water bodies to complete its life cycle (Dyar and Knab 1906, Carpenter and LaCasse 1955, Heinemann and Belkin 1977, Pecor et al. 2002). This species has been known from the southwestern United States from the early 20th century, with populations in southern Texas (Dyar 1921, Randolph and O'Neill 1944, Rueger and Druce 1950, Eads et al. 1951, Hill et al. 1958), Arizona (Richards et al. 1956), and New Mexico (Wolff et al. 1975). Over the past several years, *Cx. coronator* has undergone range expansion and, since 2003, has increased its range both east and north. Specifically, this species is now documented in Louisiana (Debboun et al. 2005), Oklahoma (Bradley 2004), Mississippi (Varnado et al. 2005, Goddard et al. 2006), Alabama (McNelly et al. 2007), Georgia (Gray et al. 2008, Moulis et al. 2008), Florida (Smith et al. 2006), South Carolina (Moulis et al. 2008), and North Carolina (Harrison 2009).

The potential for *Cx. coronator* to be an important vector is undetermined, although the invasion by a new vector species always has the potential to affect patterns of arbovirus transmission. In its native range, *Cx. coronator* been found to be naturally infected with the St. Louis encephalitis (Hammon et al. 1943, Anderson et al. 1957) and Venezuelan equine encephalitis (Scherer et al. 1971, Burguete et al. 1973) virus. Examinations within the United States have led to the possibility of this species as a West Nile virus threat (Centers for Disease Control [CDC] 2005). *Cx. coronator* primarily feeds on mammals, including humans in Brazil (Roberts and Hsi 1979) and will freely take human blood meals in the lab (J.F.S., unpublished data). Recent work in Louisiana shows that the white tailed deer (*Odocoileus virginianus*) were a common blood source, although birds and medium sized mammals are occasional hosts as well (MacKay et al. 2010).

Several natural and artificial habitats have been reported to be used by *Cx. coronator,* including swales, ditches, animal water troughs, forest ponds, and rock pools (Dyar and Knab 1906, Varnado et al. 2012); artificial systems such as abandoned swimming pools in Florida (G. O'Meara, personal communication) and trash cans (Varnado et al. 2005, Gray et al. 2008) also appear to be a common larval habitat. In 2009, Yee et al. (2012) found *Cx. coronator* larvae in vehicle tires at a large automobile salvage business in Forrest County, MS, during the late summer. Specifically, of the 48 tires surveyed, four contained *Cx. coronator,* of which two also contained *Cx. quinquefasciatus* and one contained *Ae. albopictus* and *Cx. quinquefasciatus* (Yee et al. 2012). Subsequent sampling in tires at this site and others in the state have continued to find larvae of this species (D.A.Y., unpublished data). For instance, 81 tires were surveyed across the summer of 2012 in Ohol, MS, with 25 positive for *Cx. coronator.* Of these, two tires were also positive for *Cx. quinquefasciatus,*

and all 25 tires were positive for *Ae. albopictus* (D.A.Y., unpublished data). This indicates that at least in our study area, *Cx. coronator* commonly encounters these other two dominant species. Moreover, the fact that *Cx. coronator* colonizes small volumes of water for larval development in its native range (e.g., rock pools, tree holes; Heinemann and Belkin 1977, Pecor et al. 2002) and tires (Lopez 1997) makes tires potentially an important but understudied factor in its recent range expansion. Tires in Mississippi, and more widely in the southern United States, are dominated by *Ae. albopictus* (Yee 2008, Yee et al. 2012), with *Culex quinquefasciatus* (Say) also appearing in high abundance in tires in our study area (Yee et al. 2012). Although *Cx. coronator* occurs at lower densities in tires compared with these species (Yee et al. 2012), the effect of this new invasive on the dominant resident species has the potential to affect disease dynamics, potentially via ecological effects on the current vector community (Juliano and Lounibos 2005). We measured the performance of *Cx. coronator* across different resource environments and assessed the potential competitive effects of *Ae. albopictus* and *Cx. quinquefasciatus* on *Cx. coronator* under controlled laboratory conditions.

Materials and Methods

Mosquitoes

Cx. coronator larvae (F_3) came from egg rafts produced from colonies established from larvae collected from Indian River County, FL. *Ae. albopictus* eggs (F_1) were obtained from a laboratory colony that originated from Hattiesburg, MS. Six egg rafts of *Cx. quinquefasciatus* were collected from tires and storm drains on the USM campus. To avoid contamination of the experiment with rafts from species other than *Cx. quinquefasciatus*, each raft was used for one replicate. We set aside 10 first instar larvae from each raft and reared them using a 1:1 lactalbumin:yeast diet. The species identification for fourth instars and adults from these samples were confirmed using Darsie and Ward (2005) (all larvae and adults were *Cx. quinquefasciatus*). Egg rafts and eggs were hatched using a solution of 0.33 g of nutrient broth (Difco, Detroit, MI) in 750 ml of reverse osmosis (RO) water and first instar larvae were rinsed to remove the nutrient broth before being added to beakers.

Experimental Design

Our experiment involved a factorial design using different combinations of species (hereafter species combination) and food resources (hereafter detritus). Before the addition of larvae (24 h), 400-ml tripour beakers were filled with 199 ml of RO water, detritus, and 1 ml of field collected tire water that served as an inoculum of microorganisms. Inoculum was collected from several field tires and thoroughly mixed and strained before being added to the beakers. Beakers contained either 1.00 g of leaves (senescent *Acer rubrum* [red maple] collected at the Lake Thoreau Center, Hattiesburg, MS, and dried at 60°C for 48 h), 0.20 g of animal detritus (freeze dried decorated crickets [*Gryllodes sigillatus* Walker, Fluker Farms, Port Allen, LA]), or both detritus types (1.00 g leaves and 0.20 g animal detritus, hereafter animal + leaf). These types of detritus are naturally found in containers (Yee et al. 2007, 2012) and have been shown to have species specific effects on container mosquitoes (Yee and Juliano 2007, Murrell and Juliano 2008). For our species comparisons, we added all species singly as well as two treatment levels involving two species: *Cx. coronator + Ae. albopictus*, *Cx. coronator + Cx. quinquefasciatus*. In all cases, larvae of each species were added at densities of 20 per cup (i.e., two species cups contained 20 of each species). These densities are similar to those used in other studies on competitive interactions among container mosquitoes (Costanzo et al. 2005, Yee et al. 2007, Reiskind and Wilson 2008) and to densities from field surveys in our study area (Yee et al. 2012). This design allowed us to understand any additive effects of interspecific competition, although it precludes any assessment of intraspecific effects (Goldberg and Scheiner 2001). Detritus (3) and species

combination (5) treatment levels were replicated 6 times for a total of 90 experimental units. All beakers were housed in an environmental chamber set at 27°C and a photoperiod of 12:12 (L:D) h. Beakers were placed into several large tubs that were rotated daily to reduce any within chamber variation. We also added RO water as needed to maintain water levels.

After adults began to emerge, we noticed that one replicate of *Ae. albopictus* grown in leaf only was improperly stocked with *Cx. quinquefasciatus,* and thus this entire replicate was dropped from the analyses. In addition, we noted a few instances of containers that had one ($n=5$) or two ($n=1$) nontarget species, which likely occurred during allocating first instar larvae to beakers. In these cases, we assumed that the contribution of these larvae to experimental outcomes was minimal and therefore we retained these replicates after dropping data for nontarget species. We calculated dependant variables after readjusting for the reduced totals.

Pupae were removed every day, isolated, and adults were allowed to eclose in individual glass shell vials. Adults were identified to species, sexed, dried at 50°C for 48 h, and weighed to the nearest 0.0001 mg using an ultramicrobalance (Mettler-Toledo, Columbus, OH). Mean mass and development time (from egg to adult) for each sex were generated from each replicate and represented the dependent variables for each beaker. In addition, we calculated survival as the number of adults produced from each beaker.

Statistical Analyses

We analyzed mosquito mass and development time for each sex separately using multivariate analysis of variance (ANOVA; MANOVA) with detritus type (3), species combinations (5), and their interactions as independent variables. Significant MANOVA effects were interpreted using standardized canonical coefficients (SCCs; Scheiner 2001). These coefficients allowed us to quantify the magnitude of the contributions of the individual dependent variables in producing significant multivariate differences. Several transformations of raw data were necessary to meet assumptions of MANOVA (i.e., *Cx. coronator* male mass [Log_x], male development time [$1/x$]; *Ae. albopictus* male mass [x^2], female development time [x^{-3}]; *Cx. quinquefasciatus* female development time [x^{-2}]). Survival was analyzed using two-way ANOVA for each species separately, with detritus type (3), species combinations (5), as well as their interactions as independent variables. Survival for *Cx. quinquefasciatus* was arcsine square root transformed to meet assumptions of this test. All analyses were conducted in SAS (2004).

Results

Cx. coronator female mass and development times varied with detritus, species combination, and their interaction (Table 1). In all cases, development time contributed more to the significant multivariate effects (Table 1). Specifically, females took significantly longer to develop into adults in the presence of *Ae. albopictus* compared with either when alone or in combination with *Cx. quinquefasciatus* in animal only detritus (Fig. 1). Other detritus types yielded similar development times among species combinations. In addition, *Cx. coronator* developed significantly faster in animal and animal + leaf treatment levels compared with other leaf only (Fig. 2). *Cx. coronator* developed faster in animal + leaf detritus when paired with *Ae. albopictus* compared with other detritus types (Fig. 3).

Analysis resulted in significant effects of detritus and species combination but not their interaction for male *Cx. coronator* (Table 1). In both cases, SCCs for mass and development were similar, suggesting that both were important for explaining multivariate effects. Males were larger but developed more quickly in animal and animal + leaf containers compared

with leaf only environments (Fig. 2a). In addition, males were significantly lighter in the presence of *Cx. quinquefasciatus* compared with *Ae. albopictus* (Fig. 2b).

Ae. albopictus females and males both exhibited a significant effect of detritus, whereas females alone displayed a significant effect of species combination; neither sex exhibited a significant interaction between treatments (Table 1). For detritus, mass and development time contributed to the significant effect, whereas only mass was large and positive for males. Females were larger and took less time to develop in containers with animal and animal + leaves compared with leaf only containers (Fig. 3a). Males displayed a similar response to detritus, although differences in development time were not significant (Fig. 3b). Females were ≈15% smaller (0.610 ± 0.066 mg) when grown with *Cx. coronator* compared with when grown alone (0.717±0.050 mg). Development time contributed little to the significant effect of species combination.

Cx. quinquefasciatus females and males displayed a significant effect of detritus but did not vary between species combinations or their interaction between detritus and species combination (Table 1). For both sexes, mass and development were large and positive. Development times for females (Fig. 4a) and males (Fig. 4b) were longer in leaf only containers compared with other detritus types; female mass, but not male mass, also differed in similar ways (Fig. 4a and b).

Survival for *Cx. coronator* significantly differed among detritus levels ($F_2 = 39.19$; $P < 0.001$), species combination ($F_2 = 4.24$; $P = 0.021$), and their interaction ($F_4 = 2.90$; $P = 0.033$). When grown alone, survival was significantly higher in animal + leaf containers compared with leaf only containers, with animal detritus intermediate (Fig. 5a). The addition of *Ae. albopictus* did have a significant negative effect on survival within detritus levels (Fig. 5a); adding *Cx. quinquefasciatus* to *Cx. coronator* in animal only and leaf only beakers reduced survival significantly compared with animal + leaf (Fig. 5a). Survival of *Ae. albopictus* did not vary among detritus levels ($F_2 = 0.352$; $P=0.706$), species combination ($F_1=2.40$; $P= 0.132$), or their interaction ($F_2=2.468$; $P=0.102$). *Cx. quinquefasciatus* survival did vary among detritus levels ($F_2 = 35.48$; $P < 0.001$) but not with species combination ($F_1 = 0.151$; $P = 0.700$) or the interaction ($F_2=0.241$; $P=0.788$). More larvae survived to adults in containers with animal detritus alone or in combination with leaves compared with leaf only containers (Fig. 5b).

Discussion

Based on our laboratory study, *Cx. coronator* and *Cx. quinquefasciatus* exhibited similar levels of larval performance, at least under the resources conditions used and the density tested. All detritus environments proved similar in their effect on both species, either alone or in combination, with leaf only beakers producing the lowest mass and longest development times (Figs. 1, 2, and 4). The only negative effect was seen on male *Cx. coronator* mass, which was significantly lower in the presence of *Cx. quinquefasciatus* (Fig. 2b). Given that survival and female attributes were largely unaffected by interactions between *Culex* species, we conclude that these species are similar in terms of the life history values measured, and therefore displacement of *Cx. quinquefasciatus* by *Cx. coronator* may be unlikely in tires. We note that our findings are incomplete, as both species are known to occupy larger bodies of water (Dyar and Knab 1906, Siverly 1972), and thus the entire extent of their potential ecological interactions remains untested. Ecological interactions between different containers inhabiting *Culex* species are less well known than those among different *Aedes*. For example, Reiskind and Wilson (2008) showed that although there was a small competitive advantage of *Cx. restuans* (Theobald) over *Cx. pipiens* (L), these species were ecologically similar. Other work has shown large negative effects of interacting *Culex*,

with *Cx. quinquefasciatus* displacing *Cx. tarsalis* (Coquillett) in laboratory containers (Smith et al. 1995). Containers in the current distribution of *Cx. coronator* contain several other *Culex* (e.g., *Cx. salinarius, Cx. restuans,* and *Cx. Territans;* Yee et al. 2012), and thus it remains a possibility that this species could negatively affect congenerics; given the relatively low abundances of these other *Culex,* any negative effects on community patterns are likely to be modest.

Cx. coronator did not perform as well when grown with the dominant container species, *Ae. albopictus.* Specifically, survival decreased by ≈50% in the presence of *Ae. albopictus,* especially in single detritus environments (Fig. 5a). Moreover, there were other negative effects, especially on development time for females (Fig. 1), with male mass actually benefiting from *Ae. albopictus* presence. Since its introduction, *Ae. albopictus* has been shown to have negative ecological effects on other container species, including *Ae. triseriatus* (Livdahl and Willey 1991, Yee et al. 2007), *Cx. pipiens* (Costanzo et al. 2005), and *Ae. aegypti* (Hobbs et al. 1991, O'Meara et al. 1995, Reiskind and Lounibos 2009). The latter species is thought to have gone extinct from much of its historic range after the introduction of *Ae. albopictus,* likely because of intense resource competition (Juliano 1998, Lounibos et al. 2002), although other mechanisms may exist (Lounibos 2002, Tripet et al. 2011). The reduction in female *Ae. albopictus* mass when grown with *Cx. coronator* is potentially important because mass has generally been shown to be a good predictor of egg production in mosquitoes, particularly in *Ae. albopictus* (Lounibos et al. 2001). Thus, our data suggest that *Ae. albopictus* may exhibit some reduced fecundity as the result of interactions with *Cx. coronator,* although the profound negative effects of *Ae. albopictus* on *Cx. coronator,* especially on survival and female mass, are likely to decrease the potential success of *Cx. coronator* in tires, given the dominance of *Ae. albopictus* in these containers throughout the current range of *Cx. coronator* (Yee 2008).

All species varied in performance with detritus, either alone or with different species combinations (Table 1). Sexes of both species of *Culex* were generally larger and took less time to develop in animal and animal + leaf detritus environments, whereas the effect of animal detritus was less pronounced for *Ae. albopictus,* especially for adult mass. Dead insects are a better resource for mosquitoes compared with plant material, often producing larger adults with more rapid development times (Yee and Juliano 2006, Murrell and Juliano 2008). The highest amount of detrital mass used in the animal + leaf treatment level (1.20 g) may help to explain some of the results seen here, although it must be noted that the fivefold higher amount of leaves (1.00 g) compared with animal detritus (0.20 g) actually produced smaller mosquitoes who did not survive as well. This apparent benefit of animal detritus to mosquitoes is related to higher nutrient content (i.e., nitrogen; Winters and Yee 2012) and perhaps a lack of secondary compounds that may negatively affect larval growth (Yee and Juliano 2006).

Currently, the mechanism for range expansion of *Cx. coronator* is unknown, but hypotheses include an increase in mean annual temperatures (Goddard et al. 2006, McNelly et al. 2007), movement via recent hurricane activity (McNelly et al. 2007), and human aided movement (Goddard et al. 2006); combinations of these and other factors have potentially aided and continue to aid this species expansion. We suggest that the use of tire habitats, which have frequently facilitated movement of mosquitoes (Yee 2008), may also have contributed to the movement of this species, or at the very least has expanded the potential habitats where this species can be found. We have shown that *Cx. coronator* is unlikely to outcompete the two most common container species in tires in our area, but it remains possible that this species can become a commonly encountered tire-inhabiting species, especially when it can avoid habitats with *Ae. albopictus.* Future work with a greater response surface design conducted at more densities may reveal other patterns in the interactions among these species.

Acknowledgments

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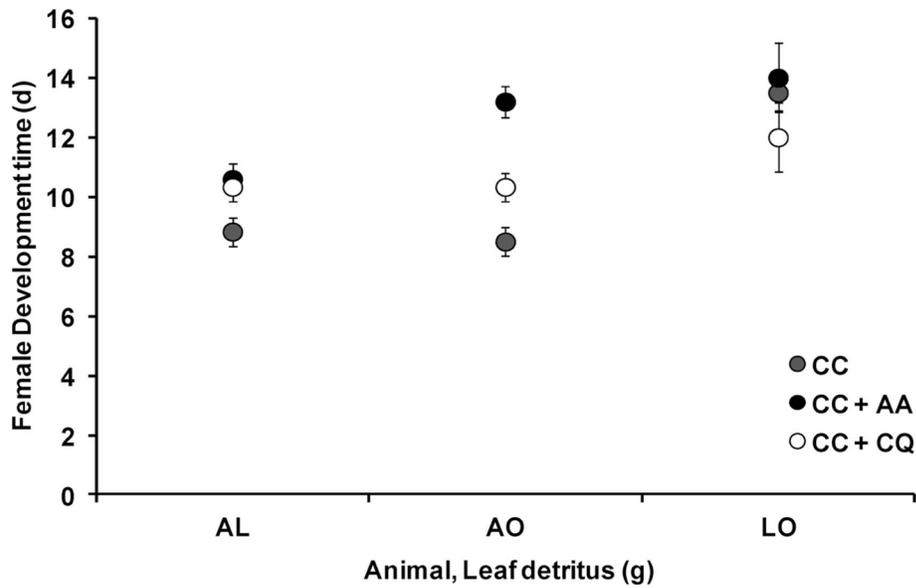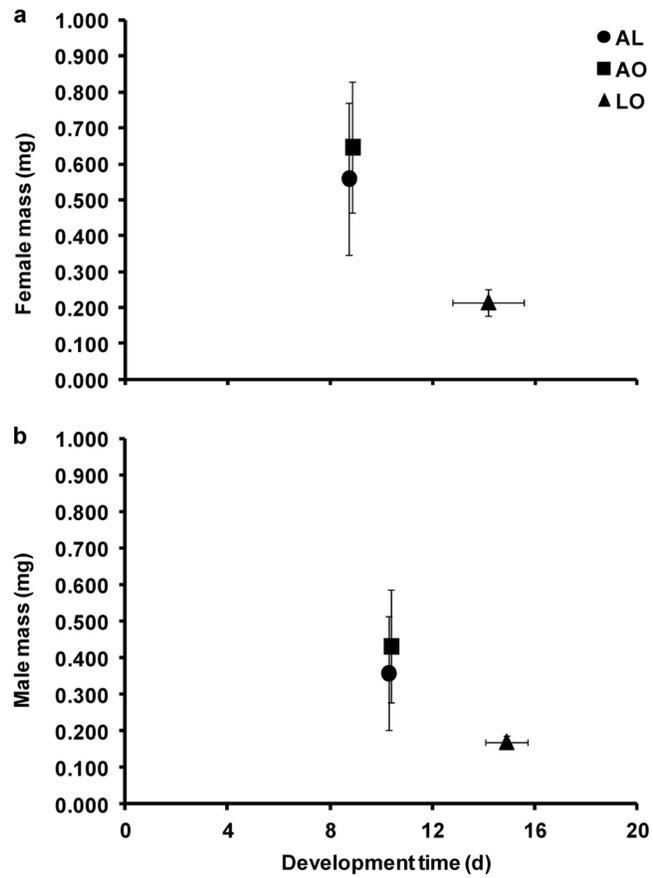
Fig. 1.
Interaction of detritus types and species combination on *Cx. coronator* female development time (means ± SE). Detritus types are animal + leaf (AL), animal only (AO), and leaf only (LO). Species combinations are *Cx. coronator* alone (CC), *Cx. coronator + Aedes albopictus*(CC + AA), and *Cx. coronator + Cx. quinquefasciatus* (CC + CQ).
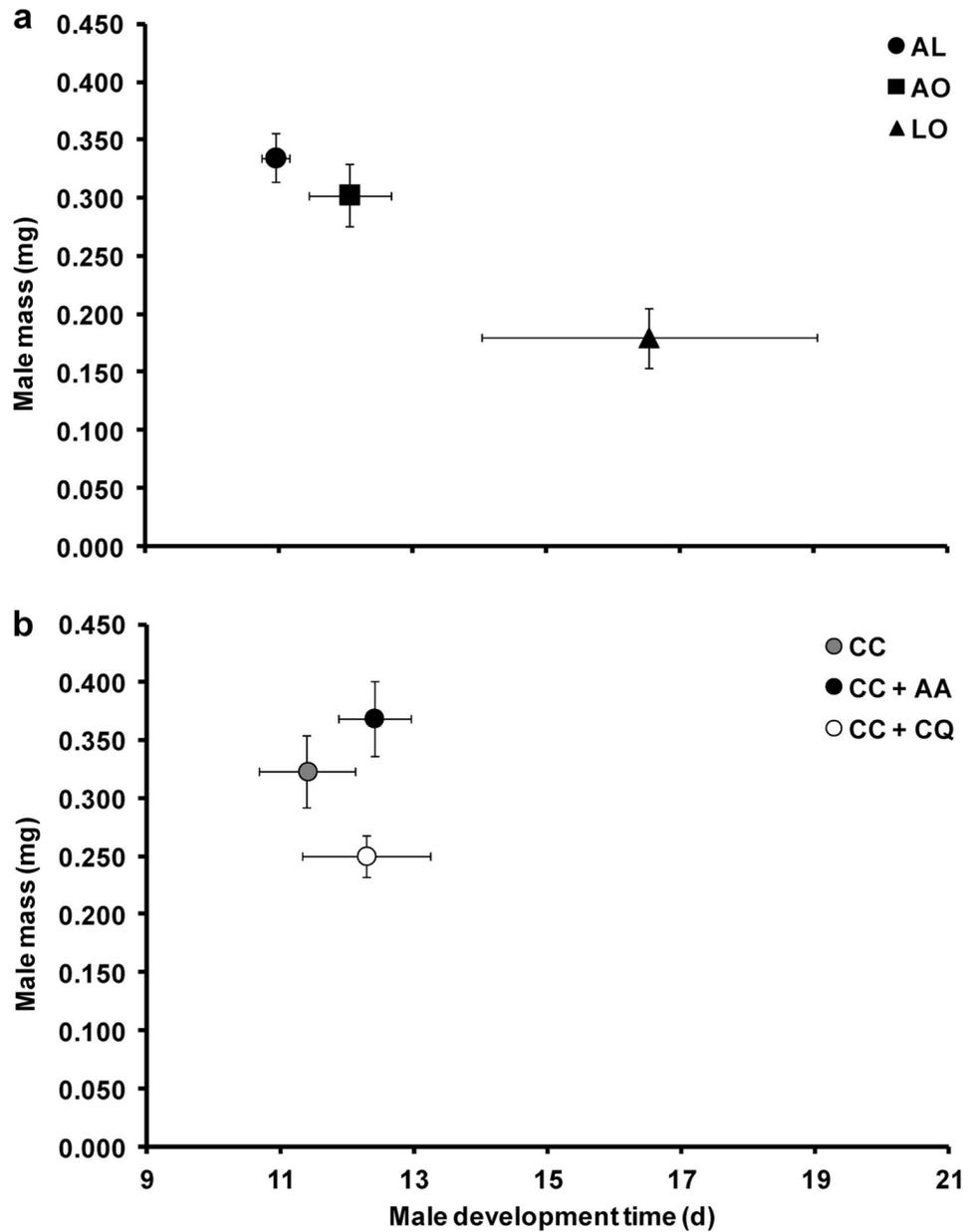
Fig. 2.
Bi-plots of *Cx. coronator* mean male mass and development type (±SE) for the significant effects of (a) detritus type and (b) species combination. Detritus types are animal + leaf (AL), animal only (AO), and leaf only (LO). Species combinations are *Cx. coronator* alone (CC), *Cx. coronator +Aedes albopictus* (CC+AA), and *Cx. coronator + Cx. quinquefasciatus* (CC + CQ).
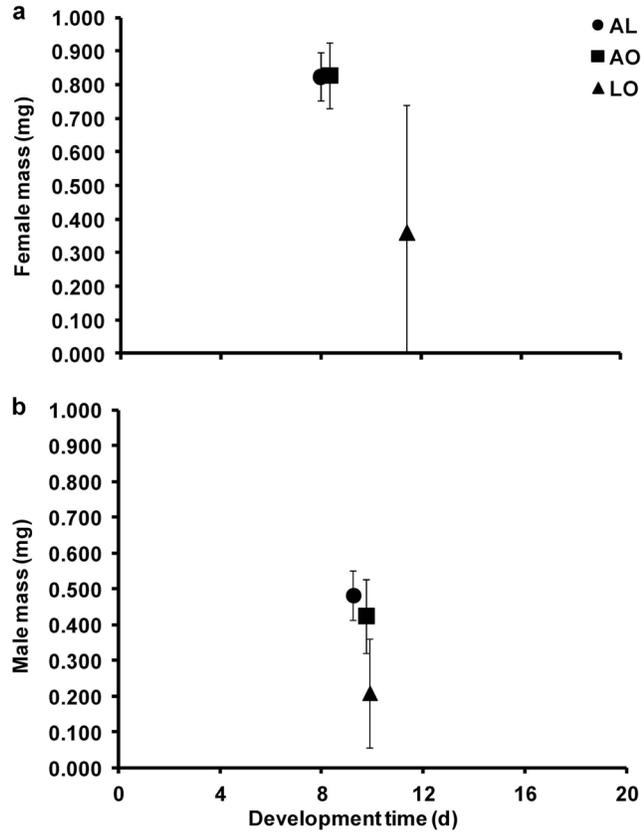
Fig. 3.
Bi-plots of *Ae. albopictus* mean mass and development type (±SE) for the significant effects of detritus type on (a) females and (b) males. Detritus types are animal + leaf (AL), animal only (AO), and leaf only (LO).

Fig. 4.
Bi-plots of *Cx. quinquefasciatus* mean mass and development type (±SE) for the significant effects of detritus type on (a) females and (b) males. Detritus types are animal + leaf (AL), animal only (AO), and leaf only (LO).
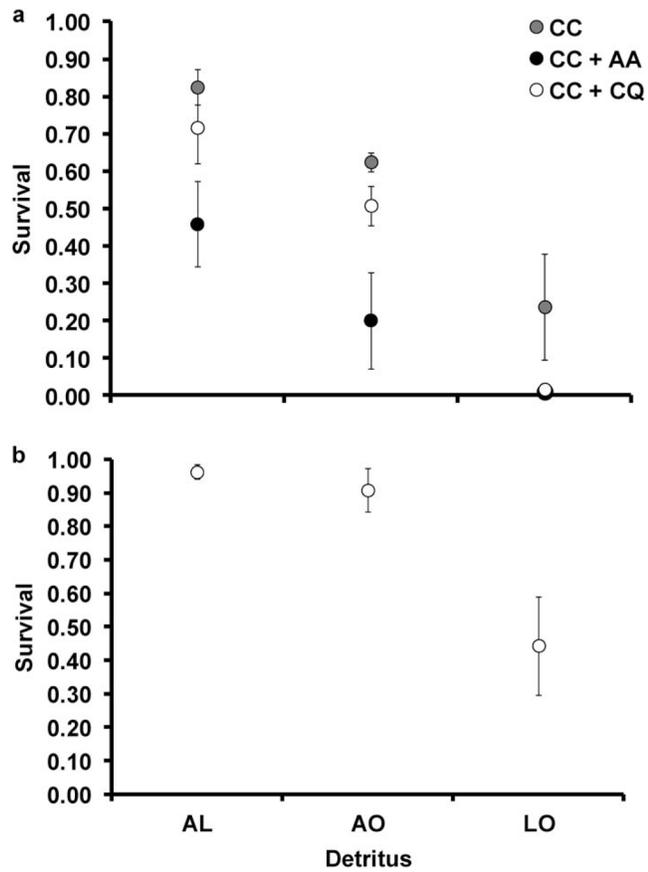
Fig. 5.
Effects of treatments on survival of container mosquitoes. (a) Interaction of detritus types and species combination on *Cx. coronator* survival (means ± SE). (b) Significant effect of detritus type on *Cx. quinquefasciatus*. Detritus types are animal + leaf (AL), animal only (AO), and leaf only (LO). Species combinations are *Cx. coronator* alone (CC), *Cx. coronator + Aedes albopictus* (CC + AA), and *Cx. coronator + Cx. quinquefasciatus* (CC + CQ).

Table 1

Multivariate analysis of variance results for male and female container mosquito mass (mg) and development time (d) across different detritus and species combinations

Factor	Females			SCC		Males			SCC	
	df	Pillai's trace	P value	Mass	Development time	df	Pillai's trace	P value	Mass	Development time
Culex coronator										
Detritus (D)	4, 62	0.455	**0.003**	−0.14	1.72	4, 48	0.838	**<0.001**	1.01	1.48
Combination (C)	4, 62	0.460	**0.002**	−0.20	1.68	4, 48	0.871	**<0.001**	0.93	1.54
D × C	8, 62	0.419	**0.055**	−0.19	1.69	6, 48	0.350	0.143	0.90	1.56
Aedes albopictus										
Detritus (D)	4, 58	1.088	**<0.001**	1.92	1.79	4, 44	1.164	**<0.001**	3.68	−0.04
Combination (C)	2, 28	0.300	**0.008**	3.02	−0.62	2, 21	0.023	0.781	1.43	1.26
D × C	4, 58	0.250	0.098	2.79	0.51	4, 44	0.340	0.079	3.27	−0.45
Cx. quinquefasciatus										
Detritus (D)	4, 50	1.040	**<0.001**	1.64	0.91	4, 50	1.091	**<0.001**	1.74	1.14
Combination (C)	2, 24	0.21	0.063	0.06	1.86	2, 24	0.193	0.076	1.33	1.48
D × C	4, 50	0.10	0.632	2.31	−1.03	4, 50	0.190	0.278	1.90	−1.08

Significant effects are shown in bold. The size of the standardized canonical coefficients (SCC) are used to indicate the dependent variable important for significant multivariate effects.