

ABSTRACT

Title of Thesis: RELATIVE ROLES OF AGGREGATION,
COMPETITION, AND PREDATION IN THE NORTH
AMERICAN INVASION OF THE ASIAN BUSH
MOSQUITO, *Aedes japonicus*.

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The success of an invasion can be mediated by biological interactions (e.g. competition and predation). The newly invasive mosquito *Aedes japonicus* has established in the range of the competitively superior resident mosquito *Aedes albopictus* and the predatory indigenous mosquito *Toxorhynchites rutilus*. I tested the hypotheses that intraspecific aggregation, fluctuating resources, or keystone predation are facilitating the invasion of *A. japonicus* into the range of *A. albopictus*. Populations of *A. japonicus* and *A. albopictus* were negatively correlated with each other and intraspecifically aggregated in field studies, suggesting that aggregation is facilitating coexistence. Resources showed a high amount of spatial variability, and *A. japonicus* populations were strongly associated with resource-rich containers, providing evidence for the fluctuating resource hypothesis. A laboratory experiment showed that predation suppresses *A. japonicus* populations to a greater extent than interspecific competition when all three species co-occur, and provided no evidence for keystone predation.

RELATIVE ROLES OF AGGREGATION, COMPETITION, AND PREDATION IN
THE NORTH AMERICAN INVASION OF THE ASIAN BUSH MOSQUITO,
AEDES JAPONICUS.

By

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Chapter 1: Introduction

Importance of studying invasions.

Globalization of trade, increased international transportation, and land use change has increasingly facilitated introduction and spread of species beyond their indigenous range (Vitousek et al. 1997, Kolar and Lodge 2001). Introduced species that establish self-sustaining populations and negatively affect native species, ecosystems, or human health are considered 'invasive' (Juliano and Lounibos 2005). Biological invasions are the second most common cause of extinctions following habitat loss (Vitousek 1996). Biodiversity loss, often due to competition with or predation of indigenous species by invasive species (Mack et al. 2000), can have significant impacts on ecosystem properties such as food web structure, disturbance regime, and productivity by altering functional traits of the resident community (Hooper et al. 2005). Invasive species are estimated to cause more than \$137 billion per year in agricultural and environmental losses, damages, and related control costs in the United States (Pimentel 2000). Additionally, there can be costs associated with human health impacts due to invasive species (Mack et al. 2000). For example, the invasion of *Anopheles* mosquitoes into Brazil in 1938 and concurrent malaria epidemic is thought to have caused incidences of mortality as high as 10-25% (Lounibos 2002). Understanding the patterns and processes related to invasions is important to the mitigation of these ecological, economic, and human health impacts. Biological invasions provide ecologists with the opportunity to study nonequilibrium systems and test our understanding of how biotic interactions such as predation and competition can affect populations and communities (Lodge 1993, Leibold and McPeck

2006). In this paper, I study how biological interactions in patchy environments can affect an invasion.

The influence of biological interactions and patchy habitats on invasions.

Biological invasions are affected by the interaction of traits of the invader, of the resident community, and the environment (Shea and Chesson 2002), and there are conceptual connections between ecological processes which influence coexistence and diversity among resident species and those that facilitate or impede the spread of invaders (Stohlgren et al. 1999, Shea and Chesson 2002). The spread of an invasive species can be facilitated or impeded by biological interactions with resident communities such as competition and predation (Lodge 1993, Simberloff 2006). In the simplest cases, the presence of a resident competitor or predator directly affects the invasibility of a community. When invasive and resident species share the same resources, competitive asymmetry has a strong influence on invasion success (Seabloom et al. 2003). If the invasive species is competitively inferior to a co-occurring resident species, competition could act as a barrier to invasion (Case 1991). On the other hand, competitive superiority of an invasive species can facilitate its establishment and spread and potentially lead to competitive exclusion of the resident species (Simberloff and Boecklen 1991). Predation can also affect invasion success. Species that spread beyond the geographic range of their natural predators have a greater chance to become invasive, e.g. enemy release hypothesis (Maron and Vila 2001, Keane and Crawley 2002). Alternatively, invasive species that spread into the range of novel resident predators may not have the behavioral

adaptations necessary to avoid resident predators, and can be disproportionately impacted by their presence than resident prey (Lodge 1993).

In more complex cases, interactions between predators and competitors can indirectly affect invasion success. For example, keystone predation, wherein a predator maintains greater diversity in a community by preying disproportionately on competitively dominant prey, is a process that can relieve the competitive effect on inferior competitors (Paine 1966, Blaustein and Chase 2007). In a landmark study, Paine (1966) showed that invertebrate diversity in tidal pools was higher when a starfish predator was present, and that competition without the starfish predator resulted in the exclusion of inferior competitors. Preferential predation can be caused by behavioral differences between prey species (Kesavaraju et al. 2008), body size (Alto et al. 2009), gender (Alto et al. 2005), prey density (Krebs et al. 1978; Werner and Hall 1979), or utilization of refugia (Sih and Kats 1991). Keystone predation can alter the outcome of competition, which can affect invasion success or change the impact of an invader on a community (Shea and Chesson 2002). Keystone predation can act as a barrier to invasion of a competitively superior species (Garvey et al. 2003, Kesavaraju et al. 2008), or it can potentially facilitate the invasion of a competitively inferior species (Leibold 1996, Veiga et al. 2011).

Species interactions and their impact on invasions can also be affected by the distribution of habitats and resources in the introduced range (Shea and Chesson 2002). Patchy habitat or resource availability can influence the success of invasions by altering the distribution of interacting species, thereby mediating the effect of biological

interactions. When competitively asymmetric species co-occur, ecological theory predicts that the competitively inferior species will be excluded (Gause 1932; Hardin 1960).

Predators can also influence the population growth and abundance of prey species in co-occurring habitats (Lodge 1993). However, when competitors and predators are distributed among patchy habitats, their overlap can be at a value less than unity, reducing the impact of biological interactions (Shorrocks et al. 1979).

Mosquito invasions.

Mosquitoes are the most important insect vectors of disease and the rate of mosquito invasions has increased in the last three decades (Lounibos 2002). The most common invasive mosquito species utilize discrete, ephemeral container habitats as larval development sites (Juliano and Lounibos 2005). Containers can be natural (e.g. treeholes, plant axils) or artificial (e.g. tires, birdbaths, trash receptacles), and mosquitoes that utilize artificial containers are often found in urban settings in close proximity with humans. Epidemiological studies have shown that invasions by exotic mosquitoes can increase the prevalence of endemic diseases, introduce a novel disease, and/or establish a host infrastructure for the future invasion of a novel disease (Deane 1988, Kilpatrick 2011, and Gubler and Clark 1995). In addition to affecting human disease epidemiology, many mosquitoes transmit economically damaging livestock diseases such as eastern equine encephalitis and act as biting pests (Lounibos 2002).

Most species interactions between container utilizing mosquitoes and other species occur at the larval stage and affect the abundance, fitness, and vectorial capacity of emerging adults (Juliano and Lounibos 2005, Alto et al. 2005, Alto et al. 2008).

Container habitats are patchy and ephemeral and mosquito colonization is dependent upon precipitation (Leonard and Juliano 1995). The energetic basis of these habitats is the allochthonous input of senesced leaves and other organic detritus, which are colonized by microbes that are consumed by mosquito larvae (Carpenter 1983). Container habitats usually have limiting nutrients (Carpenter 1983), and bottom-up effects are often very strong (Kitching 2001). Containers can also be the habitat of predatory dipteran larvae such as other mosquitoes or midges that feed upon mosquito larvae (Grill and Juliano 1996). Due to the resource-limited systems and relatively few trophic levels of the habitat, container-breeding mosquitoes have been used as model species for testing behavioral, population, and community ecology (Juliano 2009).

The Asian bush mosquito, *Aedes japonicus* (Theobald), invaded North America in the late 1990s via the used tire trade from Japan (Peyton et al. 1999). Genetic analyses indicate that there have probably been multiple introduction events since the first invasion with different source populations in the subsequent years (Fonseca et al. 2001). Since its introduction, *A. japonicus* has spread to at least 29 other states and Canada in the past decade (Fonseca et al. 2010). In addition to its invasion into North America, *A. japonicus* has invaded other countries and is the first invasive mosquito that has established and spread in Central Europe (Schaffner et al. 2009). The larvae of *A. japonicus* has been found in both natural and artificial containers (Bevins 2007). *Aedes japonicus* adults are known to aggressively blood feed on mammals during the day, including humans (Apperson et al. 2004, Molaei et al. 2008). *Aedes japonicus* is predominantly found in forests and artificial containers (Tanaka et al. 1979). *A. japonicus*

adults have been identified as competent laboratory vectors of La Crosse encephalitis (Sardelis et al. 2002a), Eastern equine encephalitis (Sardelis et al. 2002b), St. Louis encephalitis (Sardelis et al. 2003), and West Nile viruses (Sardelis and Turell 2001). In the eastern United States, *A. japonicus* commonly co-occurs with resident competitor *Aedes albopictus* and indigenous predator *Toxorhynchites rutilus* in water-holding containers (Yee 2008).

The Asian tiger mosquito, *Aedes albopictus* (Skuse), invaded the United States through Houston in the mid-1980s via used tire shipments from Japan (Hawley et al. 1987). *Aedes albopictus* is prevalent in most types of urban container habitats such as tires and has become the most dominant species in the southeastern United States (Juliano and Lounibos 2005). *Aedes albopictus* is a known vector for several arboviruses, including dengue, eastern equine encephalitis, LaCrosse encephalitis, and West Nile virus (Ibáñez-Bernal et al. 1997, Gerhardt et al. 2001, Turell et al. 2005). The dominance of *A. albopictus* is largely attributed to its superior ability to compete for food resources compared to co-occurring resident species (Juliano and Lounibos 2005). The invasion of *A. albopictus* has caused the decline and even local extinctions of resident mosquitoes, such as *Aedes aegypti* in the southeastern U.S. (Juliano 1998). Consistent with its strong competitive ability, one study demonstrated that *A. albopictus* is competitively superior to *A. japonicus* (Armistead et al. 2008b), but more studies are needed to confirm this. Despite competitive inferiority, *A. japonicus* has continued to co-exist with and invade into the range of *A. albopictus*, indicating that competitive exclusion is being prevented.

Toxorhynchites rutilus (Coquillett) is a common predator in container habitats in the eastern United States that preys upon aquatic invertebrates, including mosquito larvae (Steffan and Evenhuis 1981; Campos and Lounibos 2000). Mortality due to predation by *T. rutilus* can strongly suppress the abundance of prey populations in container systems (Lounibos et al. 1993). However, populations of *T. rutilus* are generally patchy among containers, resulting in a variable distribution of top-down effects (Lounibos et al. 1997). *Toxorhynchites rutilus* commonly preys upon co-occurring *A. japonicus* and *A. albopictus* (Farajollahi et al. 2009).

A number of hypotheses could explain the continued invasion of *A. japonicus* into the range of *A. albopictus* and *T. rutilus* which involve the roles of competition and predation among patchy habitats. In this study, I test three alternative (but not mutually exclusive) hypotheses using field data on the distribution and abundance of each species and a controlled experimental manipulation of the relative roles of competition and predation. The first hypothesis is that abundances of *A. japonicus* and *A. albopictus* are strongly intraspecifically aggregated and have relatively weak interspecific aggregation among containers, minimizing competition and promoting regional coexistence—known as the aggregation model of coexistence. The second hypothesis is that spatially or temporally fluctuating resource amounts relieve the competitive effect in some patches in which *A. japonicus* and *A. albopictus* co-occur, providing refuge for *A. japonicus*. The third hypothesis is that keystone predation by *Toxorhynchites rutilus* is facilitating the invasion of *A. japonicus* into the range of *A. albopictus* where all three mosquitoes co-occur.

The 'aggregation model of coexistence' postulates that if intraspecific aggregation is greater than interspecific aggregation then species coexistence can be facilitated (Ives 1988a, Ives 1988b, Sevenster 1996). If a population is aggregated intraspecifically among patches, then its overlap with competitors within patches is reduced and it is more likely to be limited by intraspecific competition than interspecific competition (Sevenster 1996). For example, Ives (1991) found that intraspecific aggregation among carrion fly communities on patches of dung reduced the importance of interspecific competition sufficiently to allow coexistence between two competitors. Intraspecific aggregation of competing species is generally due to attraction to different environmental cues and has been observed in a number of experimental and empirical studies (Sevenster and van Alphen 1996, Woodcock et al. 2002, Takahashi et al. 2005, Abós et al. 2006, Leisnham and Juliano 2009), and has been applied in models to explain the invasion of a competitively inferior species (Amarasekare and Nisbet 2001). Similarly, predator-induced mortality is reduced when prey are aggregated independently of a predator, regardless of how the predator is aggregated (Nachman 2006). Thus, intraspecific aggregation of an invader is desirable if predation suppresses their population, but detrimental for a competitively inferior invader if it were relying on keystone predation to facilitate coexistence with a superior competitor. *Aedes albopictus* has been shown to be aggregated among individual containers independently of the resident inferior competitor *Aedes aegypti*, and this has been proposed as one mechanism facilitating its persistence after the invasion of *A. albopictus* in some areas of Florida (Leisnham and Juliano 2009). Intraspecific aggregation of *A. albopictus* and *A. japonicus* may be facilitating their

coexistence in the northeastern United States. Because larvae cannot move between containers, aggregation of mosquitoes must be due to oviposition by adults. Aggregation of the larval competing stages could result from either aggregation of female oviposition visits or deposition of eggs aggregated in clutches (Hartley and Shorrocks 2002).

Following prior studies, this paper does not attempt to separate aggregation of oviposition visits from aggregation due to multi-egg clutches, but accounts only for aggregation of competing stages (see Hartley and Shorrocks 2002, Leisnham and Juliano 2008).

Environmental cues affecting aggregation of *Aedes* mosquitoes could include resource levels within a patch, the type of container (i.e. tree holes or tires), prevalence of hosts, or other factors.

The fluctuating resource hypothesis predicts that highly variable pulses of resources relieve the competitive effect in some individual containers or patches of containers in which *A. japonicus* and *A. albopictus* co-occur, providing spatial or temporal refuge for *A. japonicus*. In some cases, organisms or populations may escape competitive exclusion when they co-occur within habitats that have a variable distribution of resources or rate of resource inputs, which can facilitate invasions of competitively inferior species (Huston and DeAngelis 1994, Jiang and Morin 2004, Stachowicz and Byrnes 2006). The ‘fluctuating resource availability theory of invasibility’ states that variability in pulses of resources can establish spatial or temporal refugia from competition, increasing the invasibility of the high-resource patches (Davis et al. 2000). This theory was first recognized after a study comparing the effects of disturbance and soil fertility on invasibility of plants found that, when propagule pressure

was constant, invasion success was highest in the most variable patches (Davis et al. 2000). Opportunistic, competitively inferior invasive species can utilize the high-resource patches if they are better able to respond to the presence of these patches than a competitively superior resident species (Schoolmaster and Snyder 2007). The response is often manifested either by more efficient utilization of increased per-capita resources or quicker colonization of patches with high resources (Calcagno et al. 2006).

Keystone predation by *T. rutilus* could be relieving the effect of competition on *A. japonicus* if *A. albopictus* is preferentially preyed upon. Past studies have shown that predation by *T. rutilus* on competing mosquito communities can alter the outcome of competition (Griswold and Lounibos 2005; Griswold and Lounibos 2006), but the relative impact of predation of *T. rutilus* and its effect on competition between *A. albopictus* and *A. japonicus* has not yet been examined. The highly active foraging behavior characteristic of *A. albopictus* allows it to be competitively superior to many other mosquito species, but increases the amount of encounters with *T. rutilus* (Kesavaraju et al. 2011), which likely makes it more susceptible to predation.

In this paper, I test whether the spatial distribution and relative roles of predation and competition of *A. japonicus* and *A. albopictus* are consistent with these three hypotheses. The co-occurrence patterns of *A. japonicus*, *A. albopictus*, and *T. rutilus* were observed in field surveys in tree holes and tires containers among eleven sites in the metropolitan Washington D.C. area, and data of physiochemical variables within containers was collected. A laboratory experiment directly tested the presence of keystone predation and the roles of competition and predation on the population

performance of *A. albopictus* and *A. japonicus*. All of the hypotheses predict competitive superiority of *A. albopictus* over *A. japonicus*, but each hypothesis has distinct testable predictions about the distribution and abundance of these mosquitoes in the field and relative impacts of *T. rutilus*. There are testable predictions related to each proposed hypothesis:

- 1) The aggregation hypothesis predicts that abundances of *A. japonicus* and *A. albopictus* will be aggregated intraspecifically, and interspecific aggregation will be weak or nonexistent. One or both of the species may be aggregated by the presence or absence of *T. rutilus*.
- 2) The fluctuating resource availability hypothesis predicts spatial variation in food resources among field containers or sites, and that *A. japonicus* has a stronger relationship with resources than *A. albopictus*. This study only attempts to account for spatial variance in resource amounts, not temporal.
- 3) Keystone predation predicts that abundances of *A. japonicus* will be negatively correlated with abundances of *A. albopictus* and positively associated with the presence of *T. rutilus* in the field survey. Abundance of *A. albopictus* will be negatively associated with the presence of *T. rutilus*. In the laboratory experiment, population performance and fitness correlates of *A. japonicus* will be higher in the presence of both *A. albopictus* and predator *T. rutilus* compared to *A. albopictus* only.

Chapter 2: Materials and Methods

Field Study.

Aedes japonicus, *A. albopictus*, and *T. rutilus* were sampled from five tree hole sites, six tire sites, and three rock pool sites during summer 2011 in the metropolitan Washington D.C. area. Tree holes were sampled from five forested sites in the southern Maryland and Washington DC area (Watkin's Park, Prince George's County; Walker Mill Park, Prince George's County; Indian Creek, College Park; and two geographically distinct [>1 km apart] sites in Patuxent Wildlife Research Refuge, Laurel), the tire samples were collected from six used tire deposits (Upper Marlboro, Silver Spring, two sites in College Park, and two sites in Beltsville), and the rock pools were sampled from three locations along the Potomac River (Plummers Island, Cabin John; two sites in C&O Canal National Park). Tree hole sites were located in heavily forested areas and all containers sampled were at least 50m into the forest to control for edge effects. Used tires were sampled in suburban or urban areas. Each sampling session occurred between 2 and 7 days after a rainfall event of at least 6 mm. Between 6 and 18 containers were destructively sampled from each site. All contents of each container (i.e. water, detritus, and all biota) were collected. Detritus and biota in each sample were sieved through a 0.125 mm mesh and separated. Detritus was dried at 35° C for at least 48 hours and weighed as a measure of resource quantity. All mosquitoes were identified down to the species level and counted. The container water was measured for volume and pH, and a 75 mL subsample was acidified at pH 2.0 and refrigerated for later analysis of total nitrogen and total phosphorus using Hach test kits (TNT826 and TNT844 respectively)

and Hach spectrophotometer (Hach Company, Colorado). The only two species found in rock pools (*Culex pipiens* and *Aedes atropalpus*) were not related to the hypotheses; thus, the rock pool data was not included in analyses or conclusions.

Aggregation of mosquito abundances in containers was assessed following the procedure of Ives (1991). The index of intraspecific aggregation J is the proportionate increase in the average number of conspecifics found in a patch relative to the number expected of a random distribution:

$$J_1 = \frac{V_1}{m_1^2} - \frac{1}{m_1}$$

where m_1 is the mean and V_1 is the variance of species 1 per patch. At $J = 0$, species 1 is randomly distributed among patches, and at $J > 0$ species 1 is aggregated. The index of interspecific aggregation C is the proportionate increase in the average number of heterospecifics found in a patch relative to the number expected of a random distribution:

$$C_{12} = \frac{\text{Cov}_{12}}{(m_1 * m_2)}$$

where Cov_{12} is the covariance between species 1 and species 2. At $C = 0$ the two species are independently distributed, at $C > 0$ the two species are positively associated, and at $C < 0$ the two species are negatively associated. The index of relative aggregation A is the relative strength of intraspecific versus interspecific aggregation:

$$A_{12} = \frac{(J_1 + 1)(J_2 + 1)}{(C_{12} + 1)^2}$$

where intraspecific aggregation and interspecific aggregation are equally strong at $A = 1$, interspecific aggregation dominates at $A < 1$, and the species are intraspecifically aggregated at $A > 1$. Although A_{12} is considered to be a necessary condition for

coexistence between competitors, another index T_{12} is both necessary and sufficient for coexistence (Sevenster 1996). In this case, results were identical between A_{12} and T_{12} , so only A_{12} is presented.

Competition and predation experiment.

Eggs of *A. japonicus* and *A. albopictus* were synchronously hatched in a solution of .3g/L brewer's yeast/distilled water 24 hours prior to the addition of larvae. One of five population densities of *A. japonicus* : *A. albopictus* were established per container (150:0, 300:0, 150:150, 0:300, and 0:150) in order to test intra- and interspecific competition at low and high levels of per-capita resources. Hereafter, treatments are referred to as low-density conspecific (150:0 or 0:150), high-density conspecific (300:0 or 0:300), or heterospecific (150:150). One first-instar *T. rutilus* was added to predator treatments three days after the establishment of the prey species. Predator or control treatments were crossed with each of the five density combinations and replicated three times for a total of 30 replicated units (2 x 5 x 3). The containers were 800-mL tri-pour beakers filled to and maintained at 720 mL with distilled water. The containers were initially stocked with 3 grams of senesced *Quercus alba* leaves and inoculated with 200 μ L of pond water four days prior to the addition of larvae to accelerate microbial activity. One gram of additional leaf litter from the same collection date and location was added on day 7 of the experiment and every 14 days thereafter until the conclusion of the experiment, imitating the periodic addition of leaf litter in natural systems. All containers were kept in a Percival I-36VL growth chamber (Percival, Perry, IA) for the duration of the experiment at 26.0° C and 14:10 (L:D) photoperiod cycle. The containers were

rotated within the incubator daily to minimize chamber effects. Pupae were removed from containers daily and placed into separate 15-mL vials until they eclosed as adults. Upon eclosion, adults were sexed, identified, and dried in a warming oven. After being dried for at least two weeks, adults were weighed and females' wings were dissected and measured. Female wing lengths were measured to estimate fecundity, which is possible by using empirically-derived formulas developed in prior studies (Lounibos 2002; Armistead et al. 2008b).

Aedes japonicus larvae were harvested from eggs obtained from colonies maintained at the Center for Vector Biology, Mosquito Research Unit at Rutgers University in New Brunswick, NJ. *Aedes albopictus* larvae were from an F₁ generation colony originally collected in the towns of College Park, MD and Hyattsville, MD. *Toxorhynchites rutilus* larvae were sourced from a colony maintained at Illinois State University.

Mean values of each response variable (survivorship, development time, and mass) were calculated for each species in each container. These demographic values were used to estimate the finite rate of population increase (λ') for each species (Livdahl and

Sugihara 1984):

$$\lambda' = \exp \left[\frac{\ln \left[(1/N_0) \sum_x A_x f(w_x) \right]}{D + \left[\frac{\sum_x x A_x f(w_x)}{\sum_x A_x f(w_x)} \right]} \right]$$

Where N_0 is the initial number of females (assumed to be 50%), x is the median days to eclosion, A_x is the mean number of females eclosing on day x , and w_x is the mean wing

length on day x . The function $f(w_x)$ is the species-specific relationship between fecundity and female wing length. For *A. albopictus*, $f(w_x) = .5 * (78.02 * w_x - 121.24)$ (Lounibos 2002). For *A. japonicus*, $f(w_x) = (53.078 * w_x) - 113.91$ (Armistead et al. 2008b). D is the time from eclosion to reproduction, which is estimated to be 14 days for *A. albopictus* (Lounibos 2002) and 12 days for *A. japonicus* (Armistead et al. 2008b).

Statistical Analysis.

To determine if abundances of *A. japonicus* and *A. albopictus* varied with respect to habitat type, resources, and the presence of a predator, I performed three separate multivariate ANOVA tests (MANOVA) using SAS PROC GLM and a logistic regression using PROC LOGISTIC.

The first MANOVA analyzed abundances of *A. japonicus* and *A. albopictus* from a container as dependent variables and site as an independent variable. The second MANOVA analyzed detritus (grams dry weight), volume of water, total nitrogen (mg/L), and total phosphorus (mg/L) as dependent variables and site as an independent variable to determine if physiochemical characteristics varied by habitat type. I tested for significant differences among sites, including mean differences between tire and tree hole sites, using pairwise contrasts with sequential Bonferroni correction for all possible comparisons within each analysis. A logistic regression tested the effect of site on presence or absence of *T. rutilus* (SAS PROC LOGISTIC). A correlation matrix of the physiochemical characteristics revealed that volume covaried with detritus amount (Table 5), and thus was not included in the model for the third MANOVA. Independent variables in the third MANOVA were presence or absence of *T. rutilus*, detritus amount,

total nitrogen, total phosphorus, and all two-way interactions, and dependent variables were abundances of *A. japonicus* and *A. albopictus*. In all MANOVAs, standardized canonical coefficients (SCCs; Schiener 2001) were used to analyze correlations of mean abundances of the dependent variables and to determine the relative contribution of the dependent variables to significant differences among the independent variables. To test for independent aggregation, Wilcoxon signed rank tests were used to test the null hypotheses that $J = 0$, $C = 0$, and $A = 1$. For all statistical analyses, P is evaluated at $\alpha = 0.05$.

To account for assumptions of normality and homogeneity of variances, all abundances of *A. japonicus* and *A. albopictus* were $\log_{10}(y+1)$ transformed. Sites in this survey were not randomly selected, so I treated site as a fixed effect and all statistical inferences are restricted to the sites chosen. This strategy is consistent with past studies (e.g. Reznick et al. 2001, Leisnham et al. 2009, Leisnham and Juliano 2010) and follows a strict interpretation of random effects in linear models.

One-way analyses of variance (ANOVA) were used to measure the effects of competition on λ' and survivorship (PROC GLM, SAS 9.32). Residual variances of λ' and survivorship ANOVAs were dramatically and systematically different between predation treatments and could not be improved by transforming the data, so I tested effects of competition on λ' and survivorship independently for each predator treatment. Two-way analyses of variance (ANOVA) were used to measure the effect of predation and competition on median development time to adulthood (male and female) and median mass (male and female) (PROC GLM, SAS 9.32).

Chapter 3: Results

Field Survey.

There was an effect of site on mosquito abundances (Pillai's Trace $F = 7.07$, $df = 20$, $p < 0.0001$). SCCs indicated that *A. japonicus* (SCC = -1.15) and *A. albopictus* (SCC = 1.44) both contributed strongly to this association but were negatively correlated among sites. Mean abundances among tire sites and tree hole sites were different (Pillai's Trace $F = 21.88$, $df = 2$, $p < 0.0001$), signifying that *A. japonicus* and *A. albopictus* abundances vary by site type (Fig. 1). Abundances of both *A. albopictus* and *A. japonicus* were higher in tire sites than in tree hole sites (Table 1). SCCs indicate that the site type mean abundances of *Aedes japonicus* (SCC = -0.20) was negatively correlated with the site type mean abundance of *A. albopictus* (SCC = 1.44), and *A. albopictus* abundance explained most of the difference between tires and tree holes. Mean abundances of both species were higher in tire sites than tree hole sites (Fig. 1).

There was an effect of site on physiochemical properties (Pillai's Trace $F = 3.45$, $df = 40$, $p < 0.0001$). SCCs showed that detritus (SCC = -1.44) and volume (SCC = 3.06) contributed most strongly to this effect, while total nitrogen (SCC = -0.15) and total phosphorus (SCC = 0.37) had weak contributions. Mean physiochemical properties varied between tires and tree holes (Pillai's Trace = 39.28, $df = 4$, $p < 0.0001$). Tire sites had more detritus and a greater volume, but lower concentrations of total nitrogen and total phosphorus than tree hole sites (Table 1). Presence of *T. rutilus* did not vary by site or between tire sites and tree hole sites, indicating a relatively even geographic distribution of *T. rutilus* larvae (Appendix A, Table 3).

There was a positive association of detritus and a marginally positive association of phosphorus with mosquito abundances (Table 2). *Aedes japonicus* contributed more strongly than *A. albopictus* to the effect of detritus (SCC = 1.47 vs. 0.35) and phosphorus (SCC = 1.37 vs. 0.46), and they were both positively correlated to increasing detritus amounts (Fig. 2). Total nitrogen and presence of *T. rutilus* did not affect abundances of mosquitoes. There was an interaction of detritus X presence of *T. rutilus* (Table 2). *Toxorhynchites rutilus* were found in containers that showed a stronger effect of detritus on *A. japonicus* and a weaker effect of detritus on *A. albopictus* (Fig. 2).

Aedes japonicus ($J_j=2.89$, $p=0.002$) and *A. albopictus* ($J_a=1.51$, $p=0.004$) abundances were aggregated among all containers, and the index of aggregation was greater than parity ($A_{ja}=24.7$, $p=0.002$), indicating that intraspecific aggregation is stronger than interspecific aggregation (Fig. 3). The index of aggregation was marginally significantly different from parity in tires ($A_{ja}=9.03$, $p=0.06$) and tree holes ($A_{ja}=40.4$, $p=0.06$) (Fig. 3). Interspecific aggregation (C_{ja}) was never significantly different from zero, indicating that interspecific aggregation is weak among all sites and site types.

Competition and predation experiment.

Survival and λ' . *Toxorhynchites rutilus* had a strong negative effect on λ' of *A. japonicus* in all competition treatments and negatively affected λ' of *A. albopictus* in two of the three treatments (Fig. 4a and 5a), presumably because of the low survival (Fig. 4b and 5b). There were no effects of competition on λ' or survival for either species in predator treatments (Table 3). In no-predator treatments, there was an effect of competition on λ' and survival of *A. japonicus* and *A. albopictus* (Table 3). *Aedes japonicus* had the highest

λ' and survival in low density conspecific treatments and the lowest λ' and survival in heterospecific treatments, suggesting that interspecific competition has a greater negative impact than intraspecific competition (Fig. 4a and b). *Aedes albopictus* populations had the highest λ' and survival in low density conspecific treatments and the lowest λ' and survival in high density conspecific treatments, indicating that intraspecific competition has a greater negative impact than interspecific competition (Fig. 5a and b). Within predator treatments, *A. albopictus* had consistently higher λ' and survival than *A. japonicus* across all competition treatments, suggesting that it is less impacted by predation. Both *A. japonicus* and *A. albopictus* had the highest λ' in heterospecific treatments when a predator was present, but post-hoc pairwise comparisons do not reveal a significant difference compared to conspecific treatments (Fig. 4a and Fig. 5a).

Dry mass. The median dry mass of *A. japonicus* females was affected by competition and the competition X predation interaction (Table 4). *Aedes japonicus* females in the high-density heterospecific competition treatments with a predator had the least mass and mosquitoes in the low-density conspecific competition treatments with a predator had the most mass, but the differences were not significant (Fig. 4c). Competition did not have an effect on *A. japonicus* males (Table 4). The median dry mass of *A. albopictus* females was affected by competition, predation, and the competition X predation interaction (Table 4). In no-predator treatments, median mass of *A. albopictus* females was highest in the low-density conspecific treatment and lowest in the high-density conspecific treatments (Fig. 5c). In the predator treatments, the median mass of *A. albopictus* females was highest in high-density conspecific treatments and lowest in low density conspecific

treatments (Fig. 5c). There was no effect of competition or predation on *A. albopictus* males (Table 4).

Development time. The median development time of *A. japonicus* females was affected by competition and predation (Table 4). In no-predator treatments, *A. japonicus* females had the longest development time in the high-density heterospecific competition treatment and the shortest development time in the high density conspecific treatment (Fig. 4e). The addition of a predator decreased development time among all treatments (Fig. 4e). The development time of *A. japonicus* males was affected by competition (Table 4). *Aedes japonicus* males had the longest development time in high density heterospecific treatments (Fig. 4f). The development time of *A. albopictus* females was also affected by competition (Table 4). In no-predator treatments, the longest female development times occurred in high-density conspecific competition and shortest in low-density conspecific treatments (Fig. 5e). Development time of *A. albopictus* females was affected by the presence of a predator (Table 4). *Aedes albopictus* females in predator treatments had shorter development times than those in no-predator treatments (Fig. 5e). There was an interaction of competition X predator treatments for *A. albopictus* females (Table 4). The development time of *A. albopictus* males was affected by competition treatments, presence of a predator, and the competition X predation interaction (Table 4). *Aedes albopictus* males had a longer time to development in high density conspecific treatments without a predator than any other treatment (Fig. 5f). Predation decreased development time of *A. albopictus* males (Fig. 5f).

Chapter 4: Discussion

Aedes japonicus has invaded into the range of competitor *A. albopictus* and continues to coexist despite evidence from at least one study that it is an inferior resource competitor (Armistead et al. 2008a). Consistent with Armistead et al. (2008a), results of this study found *A. albopictus* to be competitively superior to *A. japonicus* but spatial patterns of these species among containers are consistent with predictions of the aggregation model of coexistence and the fluctuating resource availability hypothesis for *A. japonicus* invasion. This study also indicated that populations of *A. japonicus* are impacted to a greater extent by predation of *T. rutilus* than populations of *A. albopictus*, which is inconsistent with prior studies which suggested that *A. japonicus* is less vulnerable to predation (Kesavaraju et al. 2011).

Intraspecific aggregation is stronger than interspecific aggregation for both species among all containers and among tire sites and tree hole sites separately, fulfilling the necessary conditions for coexistence due to aggregation (Fig. 3) (Sevenster and Van Alphen 1996). Interspecific aggregation (C_{ja}) was weak or non-existent (Fig. 3), which is consistent with past studies of freshwater invertebrates in patchy habitats (e.g. Murphy et al. 1998, Schmera 2004, Abós et al. 2006) and is probably due to differences in species-specific traits like range of mobility, oviposition cues, or avoidance of pre-colonized patches (Williams et al. 1993). The results of this study are consistent with prior empirical (Leisnham and Juliano 2008) and experimental (Fader and Juliano 2010) studies that showed *A. albopictus* larvae were aggregated independently of a competitor. Abundances of both species were higher in tires than in tree holes (Table 1), providing no

evidence for spatial segregation between these habitat types. However, there were distinct differences of the aggregation index A_{ja} among tires vs. among tree holes, indicating that container type affects intra- and interspecific aggregation. Despite having a higher index of aggregation A_{ja} , both intra- and interspecific aggregation were lower in tree holes than in tires (Fig. 3). This indicates that abundances of both species among tree holes are more randomly distributed than in tires. Most likely, the difference in aggregation is due to an effect of container type on the environmental factors by which the two species aggregate. Neither species was associated with the presence of *T. rutilus*, indicating that they are distributed independently of the predator. This is consistent with past studies that have shown that distributions of *T. rutilus* are patchy compared to distributions of prey species (Lounibos et al. 1997). Nachman (2006) shows that when prey species are aggregated independently of a predator, the influence of predation on community structure is diminished.

One limitation to measuring the aggregation of larvae is that biological interactions may have impacted abundances before they were measured. In some cases, for example, *A. japonicus* larvae may have already experienced mortality due to competition with *A. albopictus* or predation by *T. rutilus*, which would artificially decrease measurements of interspecific aggregation C_{ja} . Although prior studies have measured aggregation using competing stages (see Abós et al. 2006 and Fader and Juliano 2010), the potential impact on interspecific aggregation should be recognized. Due to the nature of the methodology used in this study, the impact of biological interactions confounding aggregation measurements should be minimized due to

sampling shortly after containers were flooded and thus shortly after the mosquito larvae hatched. This timetable leaves little room for competition or predation to occur.

Additionally, it would be extremely difficult to measure aggregation of the eggs in containers without experimentally placing oviposition traps.

Abundances of both *A. japonicus* and *A. albopictus* are positively affected by increasing detritus amount and marginally positively affected by increasing concentration of total phosphorus (Table 2). Consistent with predictions associated with the fluctuating resource hypothesis, SCCs show that *A. japonicus* contributes to the significant effect more strongly than *A. albopictus* in both cases, indicating that *A. japonicus* abundances are more reliant upon high resource patches than *A. albopictus* (Table 2). Detritus amount and total phosphorus concentration vary by site (Appendix A, Table 2), fulfilling another condition of the fluctuating resource hypothesis. Pairwise contrasts show that there were significant differences in the physiochemical factors among tire sites and between tire sites and tree hole sites, but not among tree hole sites (Appendix A, Table 2). This reflects a greater variability of physiochemical factors within tires compared to tree holes. Additionally, there is a higher variance of mean detritus and total phosphorus among tires than tree holes (Table 1). This indicates that invasion of *A. japonicus* may be more successful when it establishes in tires than in tree holes. The laboratory experiment confirms that *A. albopictus* has a stronger competitive response to increased resources than *A. japonicus* does, as indicated by the difference in lambda between the high density conspecific and the low density conspecific treatments (Fig. 4a and 5a). This means that *A. japonicus* must take advantage of fluctuating resources in some other fashion, such as

quicker colonization. Mosquito colonization can be dependent upon the recognition of chemical cues in a container by the ovipositing female, and the sensitivity to the chemical cues of high-detritus containers is species-specific (Blaustein and Kotler 1993, Bond et al. 2005). Future research should target whether or not *A. japonicus* is quicker to colonize or better at detecting high-resource habitats than *A. albopictus*.

The results of the lab experiment and the field study provide no evidence for keystone predation, but reveal information on the relative effects of predation and competition on the invasion of *A. japonicus*. Predator treatments generally decreased λ , survivorship, and development time and increased or did not affect mass (Figs. 4 and 5). In most cases, the effects of competition were only apparent in treatments without a predator, indicating that predation by *T. rutilus* does relieve prey larvae of the competitive effect. In no-predator treatments, high levels of competition decreased λ , survivorship, and mass and increased development time. Interspecific competition had the strongest effect on *A. japonicus* (Fig. 4), while intraspecific competition had the strongest effect on *A. albopictus* (Fig. 5), which is consistent with my predictions and the results of a previous competition study (Armistead et al. 2008a). The population performance of *A. japonicus* in heterospecific competition treatments with a predator was lower than it was in heterospecific competition treatments without a predator, which does not support the hypothesis of keystone predation (Fig. 4a).

Predation treatments negatively affected the λ' of both species, but the negative effect was greater for *A. japonicus*. The presence of *T. rutilus* strongly impacted survival of *A. japonicus*, with no females emerging from the high density conspecific treatment

and very few emerging from the other treatments (Fig. 4b). Across all predator treatments, there were no *A. japonicus* males to emerge, possibly indicating sex-specific preferential predation. One study by Alto et al. (2005) found evidence of sex-specific predation on mosquito larvae, though their results suggested that females are more susceptible to predation which conflicts with the results of this study. In contrast with competition, predation treatments generally increased mass and decreased development time (Fig. 4c, d, e, f; Fig. 5c, d, e, f), which is consistent with past studies of predation on mosquito larvae (Alto et al. 2005, Griswold and Lounibos 2006, Costanzo et al. 2011). Several hypotheses have been proposed to account for the increased mass of mosquitoes in the presence of predators. One hypothesis is that surviving larvae will have a greater amount of per-capita resources to consume due to predator-induced mortality (Griswold and Lounibos 2006). A second, non-mutually exclusive hypothesis is that predation on other mosquitoes within a container releases nutrients to the water column (Costanzo et al. 2011). Past studies have shown that 1) decay of invertebrate carcasses is more nutritious to the microbes that mosquitoes feed upon than leaf litter is (Yee and Juliano 2006), 2) mosquito larvae preferentially feed upon the microbes associated with decaying invertebrate carcasses (Kesavaraju et al. 2007), and 3) that fitness parameters of mosquito larvae are higher in containers with invertebrate detritus than in containers with leaf litter (Murrell and Juliano 2008). These conclusions suggest that the addition of nutrients related to predator-induced mortality can have disproportionate effects on the development of mosquito larvae. Additionally, a study by Alto et al. (2005) proposes that since slow developing larvae are subjected to a predator for longer, they are associated

with an innately higher chance of predator encounters than larvae that emerge quicker, biasing the mean development time. Past research suggests that *A. albopictus* engages in risky behavior in the presence of a predator (Kesavaraju et al. 2008), but it performed better than *A. japonicus* in predation treatments.

The field study showed that there was an interaction between detritus amount and the presence of a predator on abundances of *A. albopictus* and *A. japonicus* (Fig. 2). This may indicate that the effect of predation on *A. albopictus* becomes more important as competition is relieved, a hypothesis consistent with ecological theory (Juliano 2009). However, the opposite trend is present for *A. japonicus*. One hypothesis for these findings is that *T. rutilus* may preferentially oviposit in containers with *A. japonicus* due to chemical cues, which would be consistent with past studies regarding oviposition of the *Toxorhynchites* genus (e.g. Trimble 1978, Benzou et al. 1988). However, if preferential oviposition due to prey abundances was occurring, it should be positively related to abundances of *A. albopictus* as well. It is possible that the chemical cues released by *A. albopictus* and *A. japonicus* may differ, causing *T. rutilus* to aggregate among sites with high abundances of *A. japonicus* but not among sites with high abundances of *A. albopictus*. Another hypothesis for the interaction between detritus and *T. rutilus* is that greater amounts of organic matter in containers may provide physical refuge for the prey species. Previous studies have shown that *A. albopictus* does not alter its active foraging behavior in the presence of a predator (Kesavaraju et al. 2008), so *A. japonicus* may be more effective at utilizing refuge in the presence of a predator than *A. albopictus*. Although this hypothesis is consistent with my results, it conflicts with results of another

study that demonstrated no effect of habitat structure on the predation rates of *T. rutilus* (Alto et al. 2005).

The results of the laboratory experiment indicate that the top-down effect of predation could be a stronger impediment to the invasion of *A. japonicus* than the bottom-up effect of competition in containers with all three species co-occurring. However, the results of the field study showed that the presence of *T. rutilus* was patchy and infrequent, and that *A. japonicus* was aggregated independently of the predator. This suggests that, on a regional scale, the impact of predation on *A. japonicus* invasion is limited by the distribution of *T. rutilus*. This study found evidence that intraspecific aggregation and fluctuating resources are facilitating the invasion of *A. japonicus* into the range of *A. albopictus*, but no evidence to support keystone predation. Future research should target the effect of temporal variation in resource abundance due to allochthonous inputs of organic matter, the relative ability of *A. japonicus* and *A. albopictus* to colonize high-resource patches, and the ability of *A. japonicus* to utilize detritus as refuge from predation.

Conclusions.

I found that the invasion of *A. japonicus* is impeded by competition with *A. albopictus* and predation by *T. rutilus*. Results from a laboratory experiment show that *A. albopictus* is competitively superior to *A. japonicus* and that *A. japonicus* is strongly negatively impacted by the presence of a predator. Distributions of mosquitoes sampled in a field survey show that *A. japonicus* and *A. albopictus* are more abundant in tires than

in tree holes, and that *T. rutilus* larvae are evenly distributed. I found no evidence from either the laboratory or field survey to support the hypothesis that keystone predation is facilitating invasion of *A. japonicus*; however, data from the field survey are consistent with predictions associated with the aggregation model of coexistence and the fluctuating resources hypothesis. This indicates that the patchy characteristics of container habitats may reduce the importance of biological interactions in determining the fate of an invasion.

Table 1: Means and standard error of species abundance and physiochemical characteristics among tires and among tree holes.

	Tires		Tree Holes	
	Mean	SE	Mean	SE
<i>A. japonicus</i>	8.67	2.50	0.82	0.27
<i>A. albopictus</i>	66.4	16.7	4.35	1.94
Detritus (g dry weight)	6.53	0.91	3.89	0.75
Volume (mL)	1948	193	136.6	14.9
Total Nitrogen (mg/L)	11.0	2.99	41.5	12.5
Total Phosphorus (mg/L)	3.03	0.93	4.44	0.93

Table 2: MANOVA on the effect of physiochemical container characteristics and presence or absence of *T. rutilus* on log₁₀(y+1) transformed abundances of *A. japonicus* and *A. albopictus*. Significant and marginally significant effects are indicated in bold.

Source of Variation	Multivariate Statistics			Standardized Canonical Coefficients	
	Pillai's Trace (F)	<i>df</i>	<i>P</i>	<i>Aedes japonicus</i>	<i>Aedes albopictus</i>
Detritus	11.19	2, 61	<0.0001	1.47	0.35
Total Nitrogen	1.15	2, 61	0.32	0.46	1.03
Total Phosphorus	2.80	2, 61	0.07	1.37	0.46
<i>T. rutilus</i>	0.42	2, 61	0.66	-0.38	1.18
Detritus * Total Nitrogen	0.23	2, 61	0.80	-0.73	1.16
Detritus * Total Phosphorus	1.61	2, 61	0.21	1.50	0.32
Detritus * <i>T. rutilus</i>	4.20	2, 61	0.02	1.71	-0.44
Total N * Total P	0.74	2, 61	0.48	1.72	-0.28
Total N * <i>T. rutilus</i>	0.24	2, 61	0.79	-0.15	1.17
Total P * <i>T. rutilus</i>	0.07	2, 61	0.94	-0.16	1.17

Table 3. ANOVA results of effect of competition on λ' and survivorship of *A. japonicus* and *A. albopictus* with and without the predator *T. rutilus*. Predator treatments were analyzed separately due to homogeneity of variances. Significant effects are indicated in bold.

	λ'						Survivorship					
	<i>A. japonicus</i>			<i>A. albopictus</i>			<i>A. japonicus</i>			<i>A. albopictus</i>		
	F	df	<i>P</i>	F	df	<i>P</i>	F	df	<i>P</i>	F	df	<i>P</i>
No Predator	5.93	2,6	0.04	35.36	2,6	0.0005	30.43	2,6	0.0007	71.79	2,6	<0.0001
Predator	1.43	2,6	0.31	0.53	2,6	0.62	0.80	2,6	0.49	1.25	2,6	0.35

Table 4. ANOVA results on *A. japonicus* and *A. albopictus* male and female mass and development time. Significant effects are indicated in bold. Due to total mortality in predator treatments, *A. japonicus* males only have competition effects.

Effect	Mass			Development Time		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<i>A. albopictus</i>						
Male						
Competition	1.82	2,11	0.20	62.21	2,11	<0.0001
Predation	2.69	1,11	0.13	47.29	1,11	<0.0001
Competition X predation	3.14	2,11	0.08	22.12	2,11	0.0001
Female						
Competition	11.84	2,10	0.002	46.28	2,10	<0.0001
Predation	103.05	1,10	<0.0001	87.81	1,10	<0.0001
Competition X predation	27.98	2,10	<0.0001	26.11	2,10	0.0001
<i>A. japonicus</i>						
Male						
Competition	0.18	2,6	0.83	19.84	2,6	0.002
Female						
Competition	5.45	2,7	0.04	9.14	2,7	0.01
Predation	2.40	1,7	0.16	27.66	1,7	0.001
Competition X predation	7.95	1,7	0.03	0.71	1,7	0.43

Table 5: Correlation matrix of physiochemical container characteristics. Significant correlations are indicated in bold.

	Detritus (g)	Total Nitrogen (mg/L)	Total Phosphorus (mg/L)	Volume (mL)
Detritus (g) <i>P</i> =		-0.09 0.42	0.06 0.61	0.79 <0.0001
Total Nitrogen (mg/L) <i>P</i> =			0.03 0.80	-0.20 0.08
Total Phosphorus (mg/L) <i>P</i> =				-0.03 0.81

Figure 1. Species abundances among site and habitat type. Filled in shapes indicate tire sites, while outlined shapes indicate tree hole sites. Abundances are $\log_{10}(y+1)$ transformed and means are \pm SE.

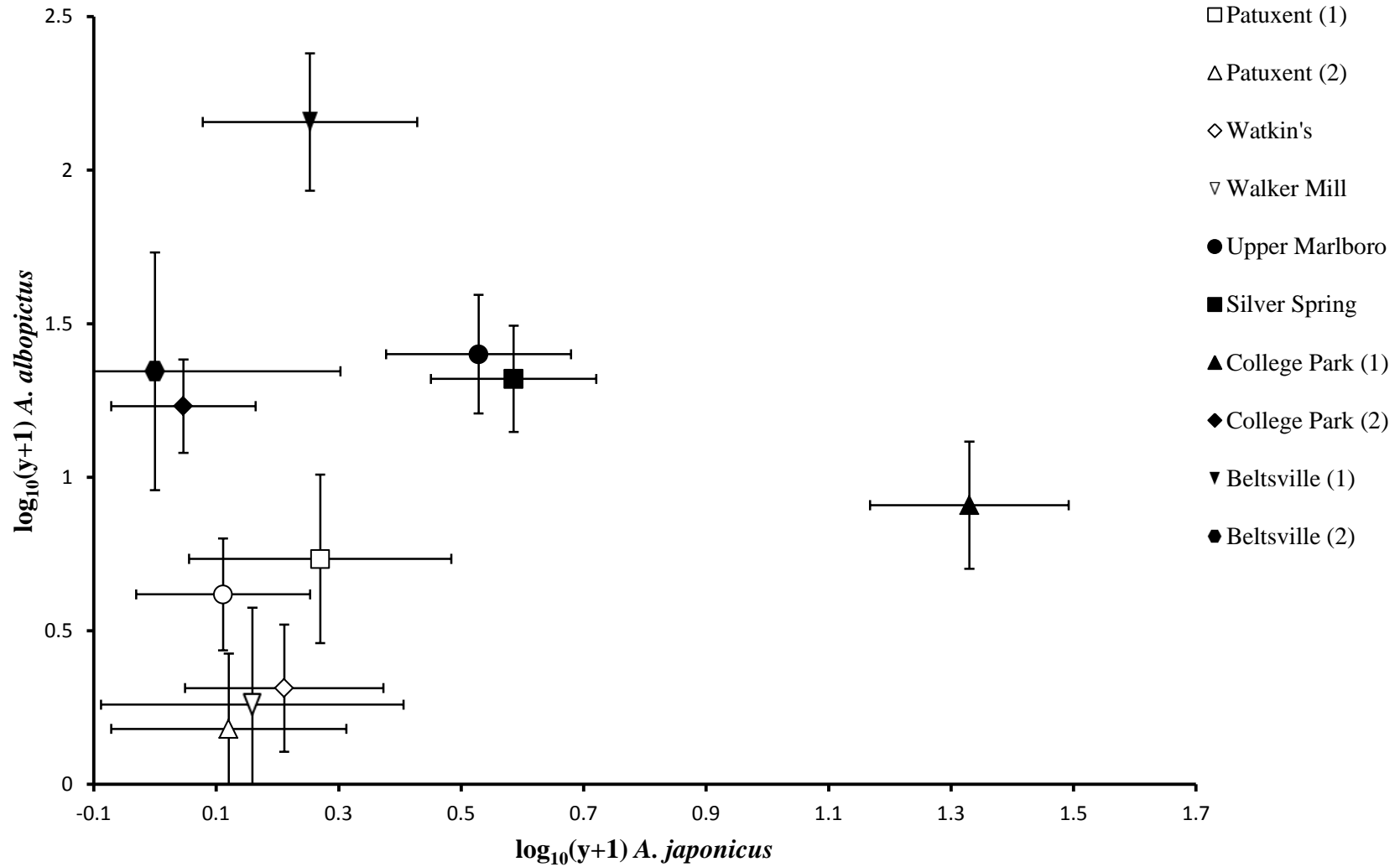
Figure 2. The interaction between detritus and presence or absence of *T. rutilus* on abundances of *A. japonicus* (A) and *A. albopictus* (B). Solid lines show the regression of mosquito abundances with detritus when a predator is present, and dashed lines show the regression of mosquito abundances with detritus when a predator is absent. Each point represents total abundance within a single container. Data are $\log_{10}(y+1)$ transformed.

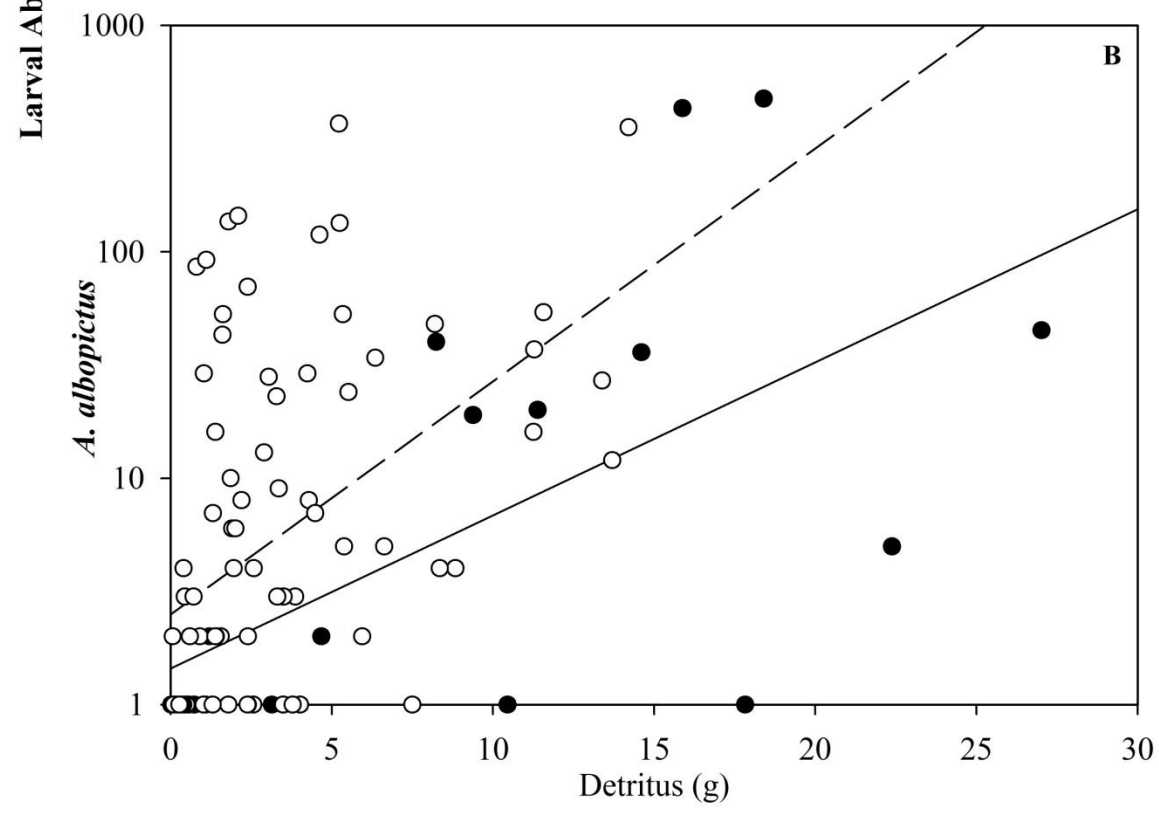
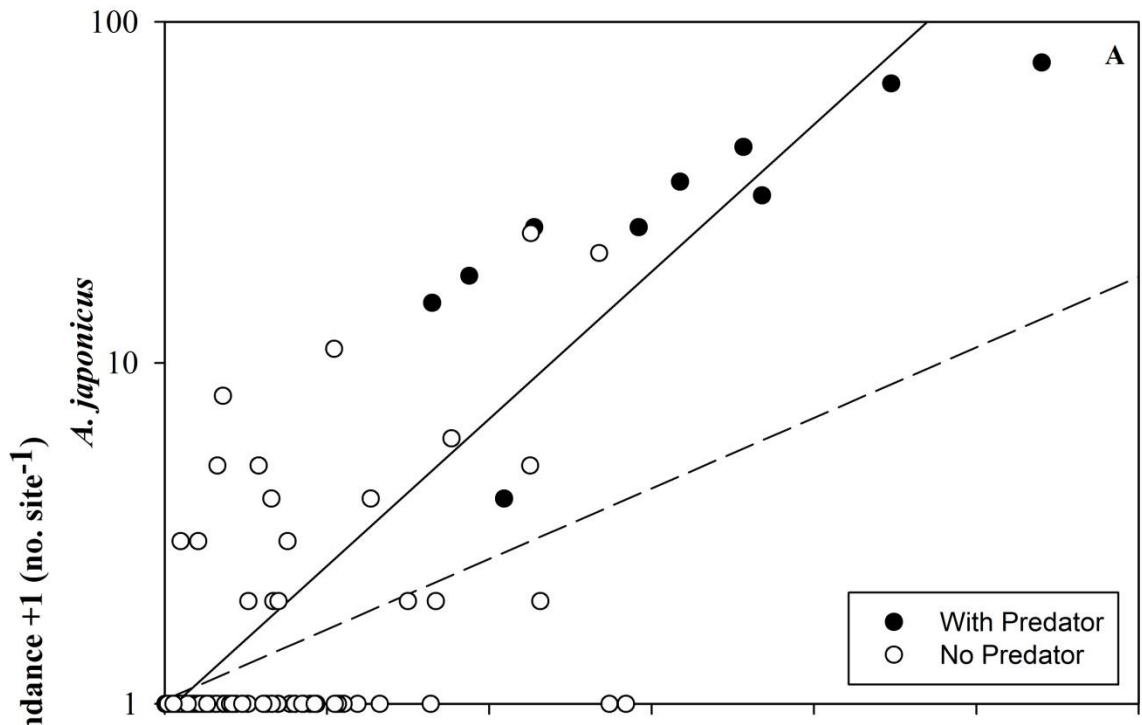
Figure 3. The values of the intraspecific aggregation index J for *A. japonicus* and *A. albopictus*, the interspecific aggregation index C_{ja} , and the index of relative aggregation A_{ja} among all sites, tire sites only, and tree holes only. Significance is evaluated as marginally significant (* $P < 0.10$) or significant (** $P < 0.05$) (see Methods for null hypotheses).

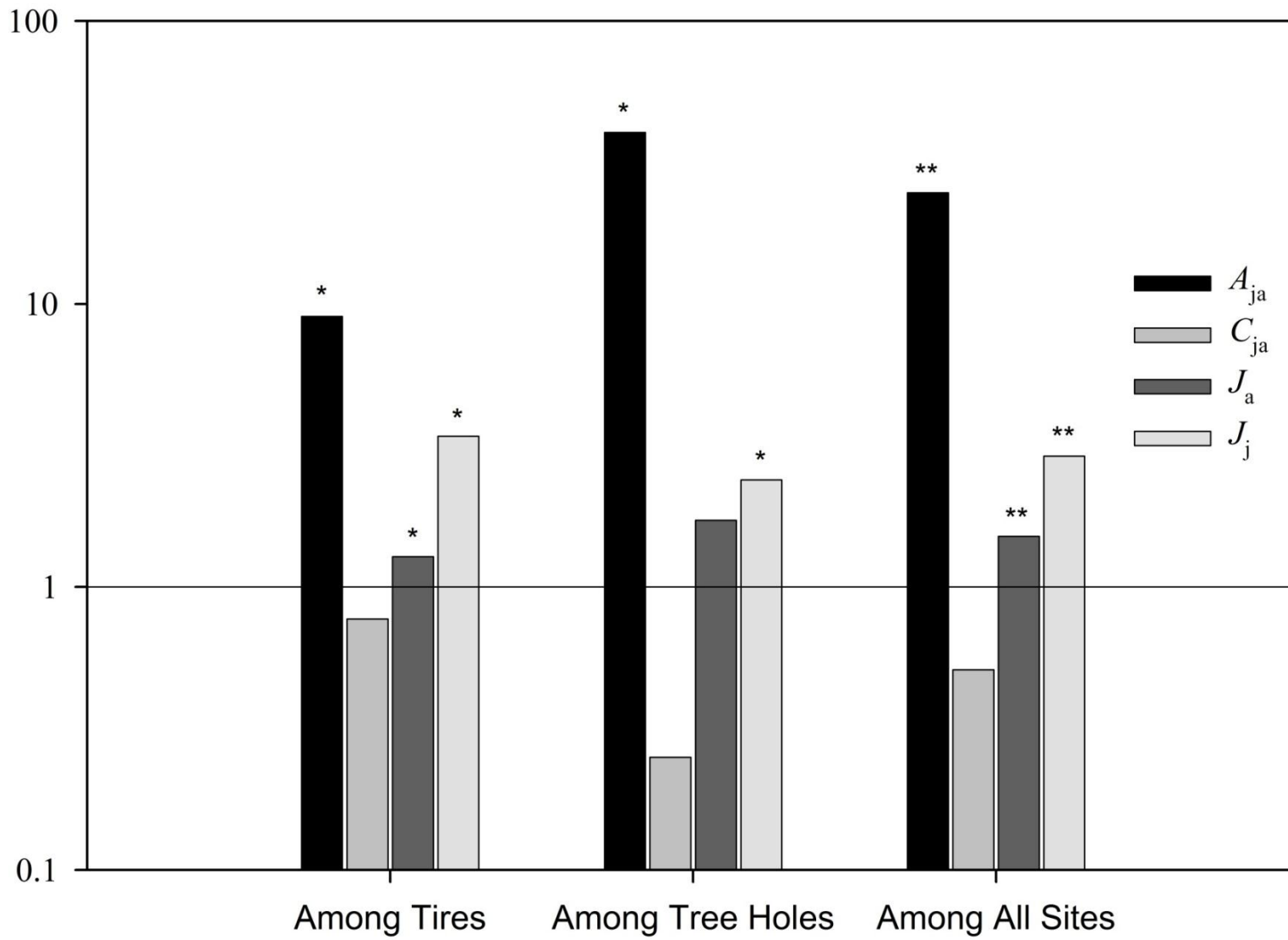
Figure 4. The effects of competition densities and presence or absence of a predator on finite rate of population increase (λ') (A), total survivorship (B), female and male mass (C and D), and female and male development time (E and F) of *Aedes japonicus*. Significant differences in pairwise comparisons are indicated with letters. Graphs with capital and lowercase letters reflect separate analyses for predator and no-predator treatments. Least squares means are \pm SE.

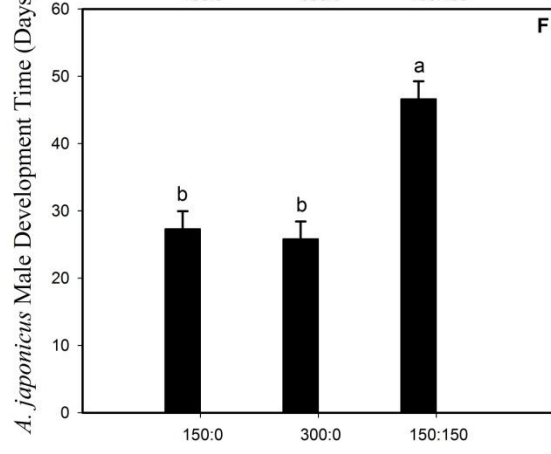
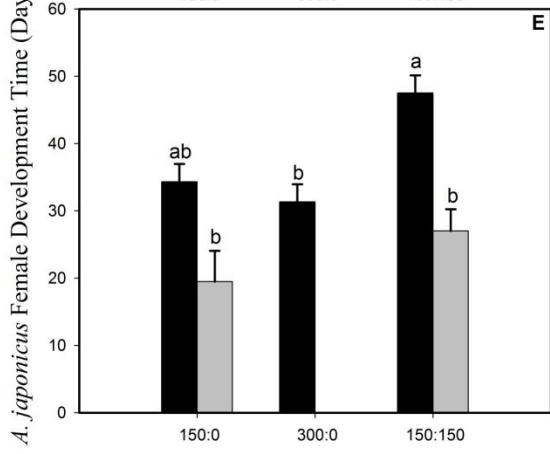
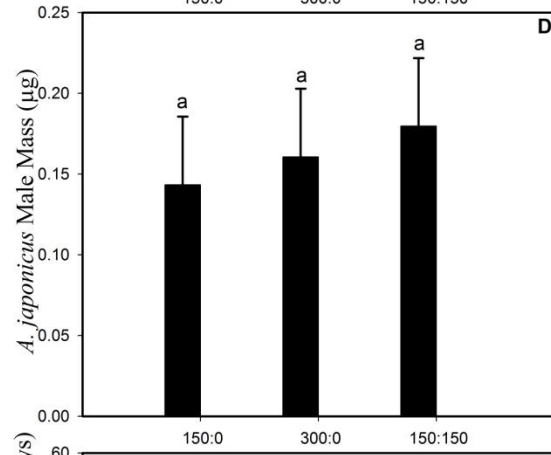
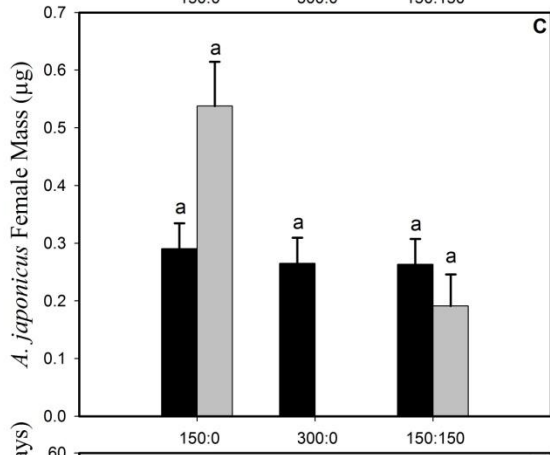
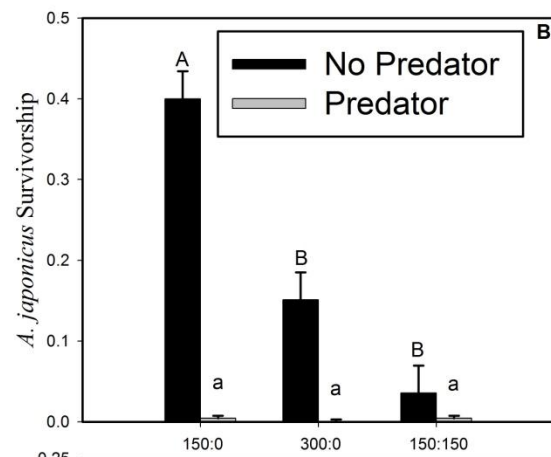
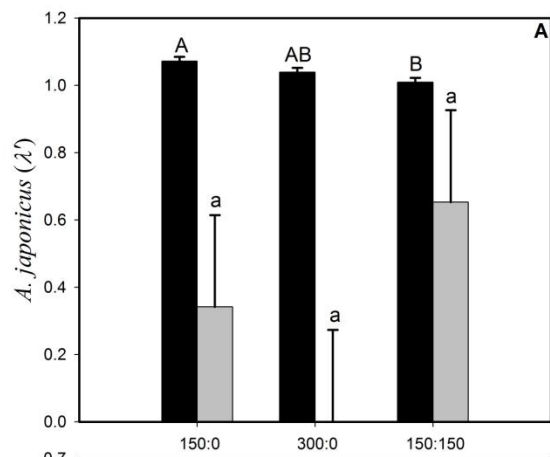
Figure 5. The effects of competition densities and presence or absence of a predator on finite rate of population increase (λ') (A), total survivorship (B), female and male mass (C and D), and female and male development time (E and F) of *Aedes albopictus*. Significant differences in pairwise comparisons are indicated with letters. Graphs with capital and lowercase letters reflect separate analyses for predator and no-predator treatments. Least squares means are \pm SE.

Species abundance by habitat type



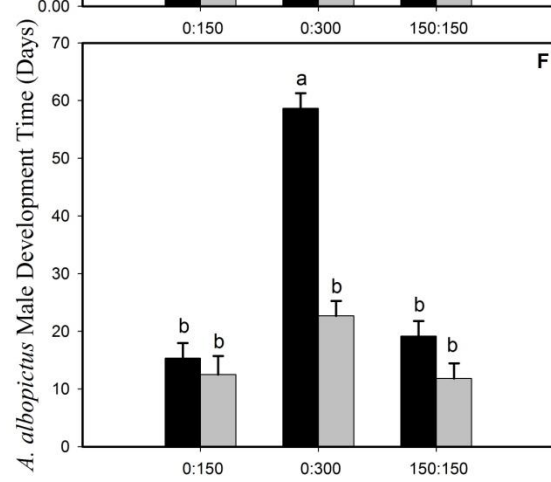
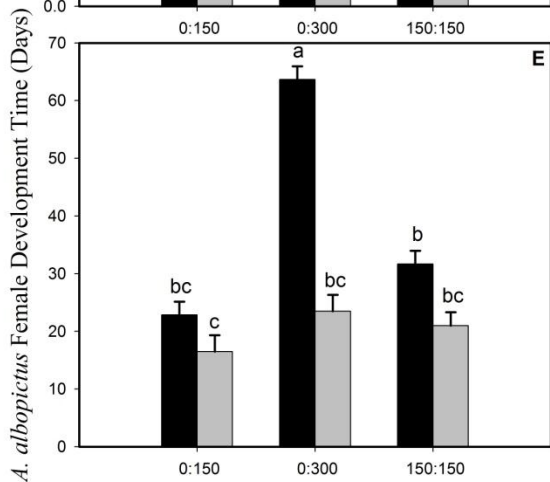
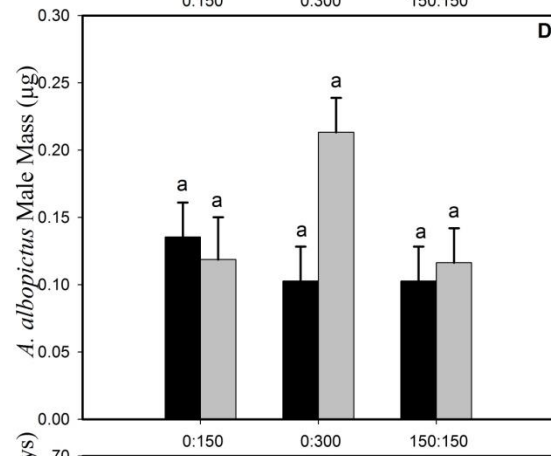
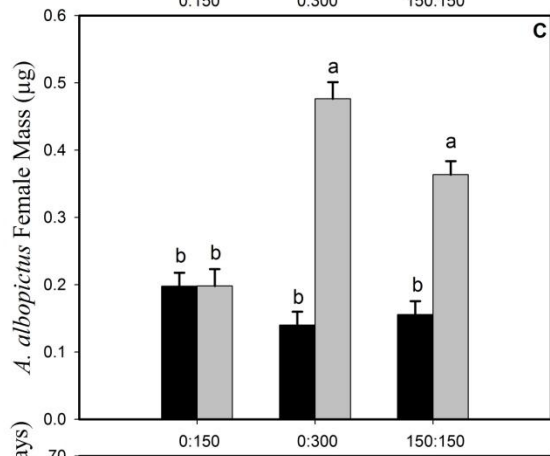
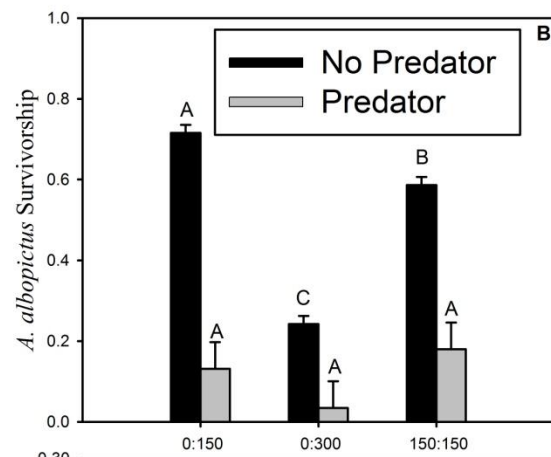
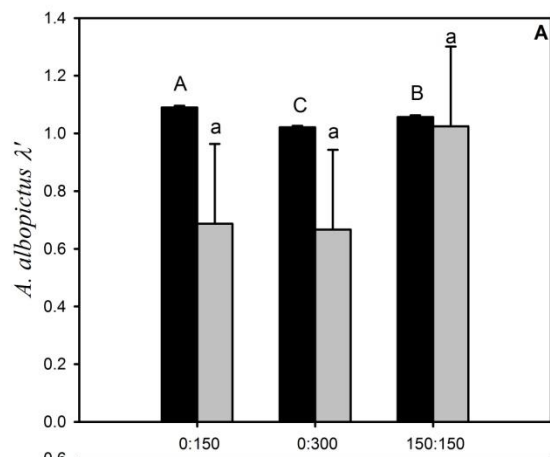






Population Density (*A. japonicus* : *A. albopictus*)

Population Density (*A. japonicus* : *A. albopictus*)



Population Density (*A. japonicus* : *A. albopictus*)

Population Density (*A. japonicus* : *A. albopictus*)

Appendix A. Table 1: MANOVA results and standardized canonical coefficients for the effect of habitat type and site on $\log_{10}(y+1)$ transformed abundances of *A. japonicus* and *A. albopictus*. Multivariate pairwise contrasts are sequential Bonferroni comparisons. Significant effects are indicated in bold.

Source of Variation	Multivariate Statistics			Standardized Canonical Coefficients	
	Pillai's Trace (F)	df	P	<i>Aedes japonicus</i>	<i>Aedes albopictus</i>
Site	7.07	20, 126	<0.0001	-1.15	1.44
Tires vs. Tree holes	21.88	2, 62	<0.0001	-0.20	1.44
Indian Creek vs. Patuxent 1	0.19	2, 62	0.83	1.21	0.13
Indian Creek vs. Patuxent 2	1.38	2, 62	0.26	-0.75	1.55
Indian Creek vs. Watkins	1.27	2, 62	0.28	-1.06	1.49
Indian Creek vs. Walker Mill	0.76	2, 62	0.47	-0.89	1.54
Indian Creek vs. Upper Marlboro	4.43	2, 62	0.01	0.31	1.16
Indian Creek vs. Silver Spring	4.50	2, 62	0.01	0.57	0.94
Indian Creek vs. College Park 1	17.67	2, 62	<0.0001	1.44	-0.52
Indian Creek vs. College Park 2	5.00	2, 62	0.01	-0.86	1.54
Indian Creek vs. Beltsville 1	16.58	2, 62	<0.0001	-0.58	1.55
Indian Creek vs. Beltsville 2	2.31	2, 62	0.11	-0.92	1.54
Patuxent 1 vs. Patuxent 2	1.15	2, 62	0.32	-0.25	1.47
Patuxent 1 vs. Watkins	0.84	2, 62	0.43	-0.50	1.53
Patuxent 1 vs. Walker Mill	0.66	2, 62	0.51	-0.32	1.49
Patuxent 1 vs. Upper Marlboro	1.94	2, 62	0.15	-0.00	1.35
Patuxent 1 vs. Silver Spring	1.68	2, 62	0.19	0.31	1.15
Patuxent 1 vs. College Park 1	9.04	2, 62	0.0004	1.45	-0.61
Patuxent 1 vs. College Park 2	3.12	2, 62	0.05	-1.14	1.45
Patuxent 1 vs. Beltsville 1	10.70	2, 62	0.0001	-0.74	1.55
Patuxent 1 vs. Beltsville 2	2.03	2, 62	0.13	-1.13	1.45
Patuxent 2 vs. Watkins	0.10	2, 62	0.90	0.58	0.93
Patuxent 2 vs. Walker Mill	0.02	2, 62	0.98	0.21	1.22
Patuxent 2 vs. Upper Marlboro	7.54	2, 62	0.001	-0.11	1.41
Patuxent 2 vs. Silver Spring	7.09	2, 62	0.002	0.04	1.32
Patuxent 2 vs. College Park 1	11.44	2, 62	<0.0001	1.29	-0.05
Patuxent 2 vs. College Park 2	9.50	2, 62	0.0003	-0.82	1.55
Patuxent 2 vs. Beltsville 1	21.32	2, 62	<0.0001	-0.63	1.55
Patuxent 2 vs. Beltsville 2	4.83	2, 62	0.01	-0.86	1.55
Watkins vs. Walker Mill	0.02	2, 62	0.98	0.94	0.52
Watkins vs. Upper Marlboro	7.36	2, 62	0.001	-0.21	1.44
Watkins vs. Silver Spring	6.83	2, 62	0.002	-0.03	1.37
Watkins vs. College Park 1	11.84	2, 62	<0.0001	1.33	-0.14
Watkins vs. College Park 2	10.66	2, 62	0.0001	-0.94	1.53
Watkins vs. Beltsville 1	23.16	2, 62	<0.0001	-0.69	1.56
Watkins vs. Beltsville 2	4.78	2, 62	0.01	-0.96	1.53
Walker Mill vs. Upper Marlboro	4.69	2, 62	0.01	-0.14	1.41
Walker Mill vs. Silver Spring	4.25	2, 62	0.02	0.03	1.33
Walker Mill vs. College Park 1	7.75	2, 62	0.001	1.32	-0.11
Walker Mill vs. College Park 2	5.85	2, 62	0.005	-0.87	1.55
Walker Mill vs. Beltsville 1	14.71	2, 62	<0.0001	-0.65	1.55
Walker Mill vs. Beltsville 2	3.75	2, 62	0.03	-0.91	1.54
Upper Marlboro vs. Silver Spring	0.17	2, 62	0.84	-1.24	1.37
Upper Marlboro vs. College Park 1	14.55	2, 62	<0.0001	1.39	-1.16
Upper Marlboro vs. College Park 2	3.29	2, 62	0.04	1.41	-0.38
Upper Marlboro vs. Beltsville 1	7.16	2, 62	0.002	-1.09	1.48
Upper Marlboro vs. Beltsville 2	1.47	2, 62	0.24	1.46	-0.67
Silver Spring vs. College Park 1	13.10	2, 62	<0.0001	1.40	-1.13
Silver Spring vs. College Park 2	5.20	2, 62	0.008	1.45	-0.61
Silver Spring vs. Beltsville 1	10.05	2, 62	0.0002	-1.11	1.47
Silver Spring vs. Beltsville 2	2.10	2, 62	0.13	1.46	-0.82
College Park 1 vs. College Park 2	32.88	2, 62	<0.0001	1.45	-0.97
College Park 1 vs. Beltsville 1	36.22	2, 62	<0.0001	-1.28	1.32
College Park 1 vs. Beltsville 2	12.92	2, 62	<0.0001	1.43	-1.02
College Park 2 vs. Beltsville 1	6.09	2, 62	0.004	-0.34	1.49
College Park 2 vs. Beltsville 2	0.09	2, 62	0.92	-1.11	1.46
Beltsville 1 vs. Beltsville 2	1.64	2, 62	0.20	-0.16	1.43

Appendix A. Table 2: MANOVA results and standardized canonical coefficients for the effect of habitat type and site on detritus, volume, total nitrogen, and total phosphorus. Multivariate pairwise contrasts are sequential Bonferroni comparisons. Significant effects are indicated in bold.

Source of Variation	Multivariate Statistics			Standardized Canonical Coefficients			
	Pillai's Trace (F)	df	P	Detritus	Volume	Total N	Total P
Site	3.45	40, 248	<0.0001	-1.44	3.06	-0.15	0.37
Tires vs. Tree holes	39.28	4, 59	<0.0001	-1.56	3.06	-0.26	0.20
Indian Creek vs. Patuxent 1	0.54	4, 59	0.71	0.61	-0.54	1.00	0.19
Indian Creek vs. Patuxent 2	1.88	4, 59	0.13	-1.27	1.71	0.70	0.60
Indian Creek vs. Watkins	1.34	4, 59	0.26	-1.81	2.33	0.46	0.51
Indian Creek vs. Walker Mill	1.38	4, 59	0.25	-1.77	2.12	0.57	0.29
Indian Creek vs. Upper Marlboro	7.94	4, 59	<0.0001	-1.50	3.09	0.07	0.22
Indian Creek vs. Silver Spring	15.64	4, 59	<0.0001	-1.74	3.17	-0.04	0.45
Indian Creek vs. College Park 1	40.66	4, 59	<0.0001	-1.31	2.98	-0.00	0.48
Indian Creek vs. College Park 2	15.28	4, 59	<0.0001	-2.03	3.11	-0.13	0.12
Indian Creek vs. Beltsville 1	10.89	4, 59	<0.0001	-1.85	3.18	-0.12	0.18
Indian Creek vs. Beltsville 2	4.99	4, 59	0.002	-2.07	3.09	-0.13	0.11
Patuxent 1 vs. Patuxent 2	0.85	4, 59	0.50	-1.99	2.50	0.16	0.61
Patuxent 1 vs. Watkins	0.97	4, 59	0.43	-2.15	2.59	-0.27	0.35
Patuxent 1 vs. Walker Mill	0.95	4, 59	0.44	-2.22	2.55	0.00	0.20
Patuxent 1 vs. Upper Marlboro	5.77	4, 59	0.0005	-1.59	3.07	-0.22	0.15
Patuxent 1 vs. Silver Spring	10.68	4, 59	<0.0001	-1.77	3.10	-0.27	0.38
Patuxent 1 vs. College Park 1	27.19	4, 59	<0.0001	-1.36	3.01	-0.14	0.44
Patuxent 1 vs. College Park 2	10.79	4, 59	<0.0001	-1.98	2.94	-0.34	0.07
Patuxent 1 vs. Beltsville 1	8.73	4, 59	<0.0001	-1.82	3.02	-0.34	0.12
Patuxent 1 vs. Beltsville 2	4.98	4, 59	0.002	-2.00	2.91	-0.34	0.06
Patuxent 2 vs. Watkins	0.25	4, 59	0.91	0.31	-0.17	0.91	0.55
Patuxent 2 vs. Walker Mill	0.18	4, 59	0.95	1.33	-1.12	0.29	0.73
Patuxent 2 vs. Upper Marlboro	4.58	4, 59	0.003	-0.92	2.46	-0.34	-0.11
Patuxent 2 vs. Silver Spring	7.90	4, 59	<0.0001	-1.43	2.90	-0.40	0.23
Patuxent 2 vs. College Park 1	25.02	4, 59	<0.0001	-1.10	2.83	-0.19	0.37
Patuxent 2 vs. College Park 2	8.35	4, 59	<0.0001	-1.63	2.61	-0.49	-0.16
Patuxent 2 vs. Beltsville 1	6.82	4, 59	<0.0001	-1.42	2.66	-0.47	-0.09
Patuxent 2 vs. Beltsville 2	3.48	4, 59	0.01	-1.69	2.61	-0.49	-0.16
Watkins vs. Walker Mill	0.13	4, 59	0.97	-1.28	1.19	0.69	-0.27
Watkins vs. Upper Marlboro	4.67	4, 59	0.002	-0.92	2.63	-0.14	0.02
Watkins vs. Silver Spring	8.76	4, 59	<0.0001	-1.44	3.03	-0.24	0.35
Watkins vs. College Park 1	29.66	4, 59	<0.0001	-1.08	2.83	-0.09	0.42
Watkins vs. College Park 2	8.41	4, 59	<0.0001	-1.75	2.88	-0.36	-0.07
Watkins vs. Beltsville 1	6.67	4, 59	0.0002	-1.50	2.90	-0.33	0.01
Watkins vs. Beltsville 2	3.06	4, 59	0.02	-1.82	2.88	-0.35	-0.06
Walker Mill vs. Upper Marlboro	2.87	4, 59	0.03	-0.64	2.33	-0.29	0.07
Walker Mill vs. Silver Spring	4.98	4, 59	0.002	-1.21	2.80	-0.36	0.40
Walker Mill vs. College Park 1	17.93	4, 59	<0.0001	-0.96	2.71	-0.15	0.44
Walker Mill vs. College Park 2	4.26	4, 59	0.004	-1.56	2.74	-0.50	-0.01
Walker Mill vs. Beltsville 1	4.07	4, 59	0.006	-1.28	2.71	-0.46	0.06
Walker Mill vs. Beltsville 2	2.20	4, 59	0.08	-1.64	2.75	-0.49	-0.02
Upper Marlboro vs. Silver Spring	1.63	4, 59	0.18	-1.64	2.19	-0.30	0.79
Upper Marlboro vs. College Park 1	12.50	4, 59	<0.0001	-1.09	2.75	-0.06	0.64
Upper Marlboro vs. College Park 2	2.63	4, 59	0.04	1.73	-1.16	0.42	0.14
Upper Marlboro vs. Beltsville 1	1.06	4, 59	0.39	-1.91	-1.99	0.55	0.01
Upper Marlboro vs. Beltsville 2	1.11	4, 59	0.36	1.76	-1.18	0.39	0.13
Silver Spring vs. College Park 1	9.81	4, 59	<0.0001	-0.67	2.48	0.05	0.46
Silver Spring vs. College Park 2	2.63	4, 59	0.04	0.41	0.72	0.19	0.89
Silver Spring vs. Beltsville 1	0.87	4, 59	0.49	0.11	0.50	0.27	1.04
Silver Spring vs. Beltsville 2	0.90	4, 59	0.47	0.61	0.52	0.19	0.83
College Park 1 vs. College Park 2	19.54	4, 59	<0.0001	-0.36	2.08	0.10	0.64
College Park 1 vs. Beltsville 1	10.60	4, 59	<0.0001	-0.54	2.25	0.11	0.67
College Park 1 vs. Beltsville 2	6.91	4, 59	0.0001	-0.28	1.99	0.10	0.63
College Park 2 vs. Beltsville 1	0.41	4, 59	0.80	0.72	0.80	0.00	0.33
College Park 2 vs. Beltsville 2	0.01	4, 59	1.00	1.86	-1.26	0.13	0.03
Beltsville 1 vs. Beltsville 2	0.23	4, 59	0.92	1.01	0.35	0.02	0.27

Appendix A. Table 3: Logistic regression results for the effect of habitat type and site on presence or absence of *T. rutilus*. Multivariate pairwise contrasts are sequential Bonferroni comparisons. There were no significant effects.

Multivariate Statistics			
Source of Variation	Wald Chi-Square	<i>df</i>	<i>P</i>
Site	9.31	10	0.50
Tires vs. Tree holes	0.00	1	0.99
Indian Creek vs. Patuxent 1	0.00	1	0.95
Indian Creek vs. Patuxent 2	1.86	1	0.17
Indian Creek vs. Watkins	0.16	1	0.69
Indian Creek vs. Walker Mill	0.00	1	0.96
Indian Creek vs. Upper Marlboro	0.02	1	0.89
Indian Creek vs. Silver Spring	0.01	1	0.91
Indian Creek vs. College Park 1	5.12	1	0.02
Indian Creek vs. College Park 2	0.01	1	0.91
Indian Creek vs. Beltsville 1	0.01	1	0.94
Indian Creek vs. Beltsville 2	0.00	1	0.97
Patuxent 1 vs. Patuxent 2	0.00	1	0.94
Patuxent 1 vs. Watkins	0.00	1	0.95
Patuxent 1 vs. Walker Mill	0.00	1	1.00
Patuxent 1 vs. Upper Marlboro	0.00	1	0.95
Patuxent 1 vs. Silver Spring	0.00	1	0.95
Patuxent 1 vs. College Park 1	0.01	1	0.94
Patuxent 1 vs. College Park 2	0.00	1	1.00
Patuxent 1 vs. Beltsville 1	0.00	1	1.00
Patuxent 1 vs. Beltsville 2	0.00	1	1.00
Patuxent 2 vs. Watkins	2.41	1	0.12
Patuxent 2 vs. Walker Mill	0.00	1	0.95
Patuxent 2 vs. Upper Marlboro	1.51	1	0.22
Patuxent 2 vs. Silver Spring	2.20	1	0.14
Patuxent 2 vs. College Park 1	0.96	1	0.33
Patuxent 2 vs. College Park 2	0.02	1	0.90
Patuxent 2 vs. Beltsville 1	0.01	1	0.93
Patuxent 2 vs. Beltsville 2	0.00	1	0.96
Watkins vs. Walker Mill	0.00	1	0.96
Watkins vs. Upper Marlboro	0.26	1	0.61
Watkins vs. Silver Spring	0.09	1	0.76
Watkins vs. College Park 1	5.50	1	0.02
Watkins vs. College Park 2	0.01	1	0.92
Watkins vs. Beltsville 1	0.01	1	0.94
Watkins vs. Beltsville 2	0.00	1	0.98
Walker Mill vs. Upper Marlboro	0.00	1	0.96
Walker Mill vs. Silver Spring	0.00	1	0.96
Walker Mill vs. College Park 1	0.00	1	0.95
Walker Mill vs. College Park 2	0.00	1	1.00
Walker Mill vs. Beltsville 1	0.00	1	1.00
Walker Mill vs. Beltsville 2	0.00	1	1.00
Upper Marlboro vs. Silver Spring	0.06	1	0.80
Upper Marlboro vs. College Park 1	4.56	1	0.03
Upper Marlboro vs. College Park 2	0.01	1	0.91
Upper Marlboro vs. Beltsville 1	0.01	1	0.94
Upper Marlboro vs. Beltsville 2	0.00	1	0.97
Silver Spring vs. College Park 1	5.64	1	0.02
Silver Spring vs. College Park 2	0.01	1	0.91
Silver Spring vs. Beltsville 1	0.01	1	0.94
Silver Spring vs. Beltsville 2	0.00	1	0.97
College Park 1 vs. College Park 2	0.02	1	0.89
College Park 1 vs. Beltsville 1	0.01	1	0.92
College Park 1 vs. Beltsville 2	0.00	1	0.96
College Park 2 vs. Beltsville 1	0.00	1	1.00
College Park 2 vs. Beltsville 2	0.00	1	1.00
Beltsville 1 vs. Beltsville 2	0.00	1	1.00

Appendix B: Calculated values of aggregation indices among tires, among tree holes, and among all sites.

	J_j	J_a	C_{ja}	A_{ja}
Tires	3.41	1.28	0.77	9.03
Tree Holes	2.39	1.72	0.25	40.4
All Sites	2.89	1.51	0.51	24.7

Appendix C: Mean site characteristics, mosquito abundances, and sampling dates.

Site	<i>A. japonicus</i>	<i>A. albopictus</i>	Detritus (g dry weight)	Volume (mg/L)	Total Phosphorus (mg/L)	Total Nitrogen (mg/L)	Date
Indian Creek	0.55	4.55	5.19	151.1	3.08	16.7	7/19/11
Patuxent (1)	1.50	14.5	5.84	170.0	3.82	54.4	8/5/11
Patuxent (2)	0.60	0.80	2.91	115.0	6.68	64.4	9/14/11
Watkin's	1.00	2.28	2.76	137.1	5.10	42.0	8/12/11
Walker Mill	0.66	1.00	1.61	83.33	4.09	59.1	8/24/11
Upper Marlboro	8.50	122	7.92	1763	1.68	28.1	8/5/11
Silver Spring	7.30	37.5	6.26	1805	5.81	11.3	8/12/11
College Park (1)	34.7	15.8	14.9	4014	8.20	13.6	7/19/11
College Park (2)	0.23	29.1	2.61	1277	0.38	4.80	7/25/11
Beltsville (1)	2.00	191	5.40	1728	0.81	2.99	8/24/11
Beltsville (2)	0	37.5	1.85	1200	0.36	4.41	9/5/11

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