The Effects of Interspecific Courtship on the Mating Success of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) Males

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ABSTRACT Satyrization, a form of asymmetric reproductive interference, has recently been shown to play a role in competitive displacements of *Aedes aegypti* (L.) by *Aedes albopictus* (Skuse). Furthermore, female *Ae. aegypti* from populations in sympatry with *Ae. albopictus* have evolved reproductive character displacement and changes in mating behavior to reduce interspecific mating. In this article, we examine evolutionary responses of males to interspecific mating and show that satyrization has also evoked reproductive character displacement in males. We demonstrate that the presence of heterospecific females negatively influences conspecific mating success in male *Ae. aegypti*, most likely due to misdirected courting or mating efforts, and that males of this species from populations in sympatry with *Ae. albopictus* have evolved to be less influenced by the presence of heterospecific females than their allopatric counterparts. Conversely, we suggest that the presence of conspecifics may, in some circumstances, increase interspecific mating. This study demonstrates that co-occurrences of these two invasive species may lead to evolution and adaptation of reproductive behaviors to changing circumstances. Understanding the processes driving development of mate choice preferences or avoidance mechanisms may help predict future changes in the distribution and abundance of insect vectors or pests.

KEY WORDS satyrization, interspecific courtship, *Aedes aegypti*, *Aedes albopictus*, male

Aedes aegypti (L.) and *Aedes albopictus* (Skuse) are considered the most invasive vectors in history (Juliano and Lounibos 2005) and, owing to their wide dispersal, often come in contact in their invasive ranges. Both species belong to the subgenus *Stegomyia* and share similar life histories and mating habits. Males and females aggregate at vertebrate hosts during similar diurnal peak activity periods (Hartberg 1971, Gubler and Bhattachaya 1972) and initiate mating in flight by following visual and auditory cues (Roth 1948, Cator et al. 2009). These common behaviors may contribute to interspecific mating between these two species, particularly after successful establishments lead to first encounters of invasive and resident populations. Interspecific matings, however, do not produce viable offspring (Leahy and Craig 1967, Lee et al. 2009) and leave females of *Ae. aegypti*, but not *Ae. albopictus*, refractory to further mating (Tripet et al. 2011). This satyrizing effect may be a powerful mechanism (Ribeiro and Spielman 1986, Ribeiro 1988, Nasci et al. 1989, Lounibos 2007, Tripet et al. 2011, Bargielowski et al. 2013, Bargielowski and Lounibos 2014) in the displacement of *Ae. aegypti* populations by invading *Ae. albopictus*. Furthermore, recent work has shown bidirectional mating in this species pair to be asymmetrical, with *Ae. aegypti* females being more susceptible to interspecific insemination than *Ae. albopictus* females (Nasci et al. 1989, Bargielowski et al. 2013, Bargielowski and Lounibos 2014). The selection pressure for *Ae. aegypti* females to avoid such errant mating is therefore great, and rapid evolution of resistance to satyrization has been documented in previous studies (Bargielowski et al. 2013, Bargielowski and Lounibos 2014). Female *Ae. aegypti* from populations allopatric to *Ae. albopictus* in the field were more susceptible to interspecific mating than females from sympatric populations, and selection experiments in cages confirmed the rapid development of resistance to satyrization in the laboratory, as well as changes in behavior toward conspecifics associated with increased satyrization resistance (Bargielowski and Lounibos 2014). In contrast, little is known about male mating behavior of these species in relation to interspecific encounters.

In this article, we examine evolutionary responses of both *Ae. aegypti* and *Ae. albopictus* males to interspecific mating by measuring whether the presence of heterospecific females may impact conspecific mating success in cages.

The mating systems of *Ae. aegypti* and *Ae. albopictus* have traditionally been thought to be governed largely by male scramble competition. However, recent findings suggest female mate choice (at least in *Ae. aegypti*) to be important in these species (Cator and Harrington 2011, Bargielowski et al. 2013, Bargielowski and Lounibos 2014). Males may therefore not only need to reach a female before their competitors, but also elicit female acceptance once they have located a potential mate.

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Furthermore, studies suggest males may be limited in the number of females they can inseminate in a day and over a lifetime (Bargielowski et al. 2011). Interspecific courtship will therefore waste time, energy, and possibly gametes, as well as exposing males to increased predation risk or host defenses. Male courtship costs have been established in a number of arthropods (e.g., fruit flies (Cordts and Partridge 1996), drumming wolf spiders (Mappes et al. 1996), tsetse flies (Clutton-Brock and Parker 1992), dobsonflies (Hayashi 1993), and crickets (Sakaluk 1985)) as well as for the mosquitoes *Sabethes cyaneus* (South et al. 2009) and *Anopheles freeborni* (Yuval and Bouskila 1993, Yuval et al. 1993). From an evolutionary perspective, it is therefore important for males, as well as females, to direct their courtship toward conspecifics instead of incompatible heterospecifics.

In this article, we test two predictions, that—1) the presence of heterospecific females will impact the success of conspecific mating (as males will waste reserves courting and possibly mating heterospecific females) and 2) adaptations in male behavior will have evolved, analogous to those in female behavior established by our earlier work (Bargielowski et al 2013, Bargielowski and Lounibos 2014), when comparing males from sympatric and allopatric populations. Since mating "errors" as predicted in 1) are costly to males, we expect males from sympatric populations to avoid such behavior and therefore to have higher intraspecific mating success than males from allopatric populations.

Furthermore, we examine the effect that the presence of conspecifics has on the rate of interspecific insemination. To date, interspecific mating has commonly been assessed in nonchoice trials (i.e., female *Ae. aegypti* caged with male *Ae. albopictus*, or vice versa). However, it is possible that the presence of conspecifics may influence the dynamics of interspecific interactions and change the frequency of interspecific courtship and mating.

Methods

Laboratory and Rearing Conditions. *Ae. aegypti* and *Ae. albopictus* colonies were established in 2011 from field collections of aquatic immatures from artificial containers, such as discarded tires or cemetery vases. Sympatric lines were derived from collections at a salvage yard in Vero Beach (VB), FL, where the two species have co-occurred for at least two decades (O'Meara et al. 1993), while the allopatric line of *Ae. aegypti* was collected in Key West (KW), FL, and the allopatric line of *Ae. albopictus* was established from collections in East St. Louis (ESL), IL. Adults used in the experiments had spent three to five generations in the laboratory ($F_{3–5}$), except for the allopatric strain of *Ae. albopictus*, which was F_9. Experiments were carried out in screened, plastic Bug Dorm (Bioquip) cages (30 by 30 by 30 cm^3) in an insectary maintained at 27 (±0.62)°C and 89 (±5.28)% relative humidity (RH) under a photoperiod of 14:10 (L:D) h. Larvae were reared from hatch to pupation in pans containing one liter of tap water (100 larvae per pan) and provided 0.6 g of a 1:1 brewer's yeast and egg albumin mix on day one. Pupae were sexed according to morphological differences in their external genitalia (Vargas 1968) and segregated by species and sex in small containers (30 per container) for emergence. If a mistake during sexing was detected after emergence, the container was discarded. All adult mosquitoes were provided continuous access to 10% sugar solution and were 3–4 d old when used in experiments.

Mate Choice in the Presence of Heterospecifics. For each test, 25 males were aspirated into a cage containing 50 conspecific and 50 heterospecific females. They were left to cohabit for 24 h before the females were removed, dissected, and scored for the presence of sperm in their spermathecae. The sex ratio used in this experiment was chosen based on preliminary test results showing this ratio to be low enough for differences in conspecific mating to be detected, but still high enough for heterospecific mating to occur. Three repeats were carried out for *Ae. aegypti* and *Ae. albopictus* males from allopatric and sympatric populations with conspecific females of the same colony and heterospecific females from either sympatric or allopatric lines. Control treatments comprised 25 males caged with 100 conspecific females.

Effect of Exposure Time on Interspecific Mating. To establish a baseline of mating frequency in nonchoice trials, 100 *Ae. albopictus* males (ESL) and 100 *Ae. aegypti* females (KW) were aspirated into cages and left to cohabit for either 24 h, 1 wk, 2 wk, or 3 wk (three cages per treatment) before the females were removed, dissected, and scored for the presence of sperm in their spermathecae.

Statistical Analysis. The proportions of females inseminated were arcsine transformed, which gave normally distributed residuals when analyzed. Data were analyzed with a nominal logistic model in JMP (version 8; http://www.jmpdiscovery.com, accessed 27 January 2015) for effects of the independent variables population origin (sympatric vs allopatric) of males and females on the dependent variable likelihood of cross-mating. Variation among groups was analyzed by ANOVA and post hoc means comparisons.

Results

Mate Choice in the Presence of Heterospecifics. *Insemination of Conspecific Females. Ae. aegypti* (males). The results showed that the origin of the *Ae. aegypti* males ($F = 8.93$, df = 1, $P = 0.01$), but not that of the heterospecific females ($F = 0.49$, df = 1, $P = 0.50$; or the interaction term ($F = 0.16$, df = 1, $P = 0.70$)) influenced the percentage of conspecific *Ae. aegypti* females inseminated, suggesting adaptation in male mating behavior (Fig. 1A1).

Compared with purely conspecific crosses (no heterospecific females; sympatric population: 99.0% ± SE 0.7, allopatric population: 99.25% ± SE 0.48), *Ae. aegypti* males from populations sympatric with *Ae. albopictus* in the field inseminated a similar proportion of conspecifics (98.73% ± SE 0.78; $F = 0.13$, df = 1, $P = 0.73$) in the presence of heterospecific females,

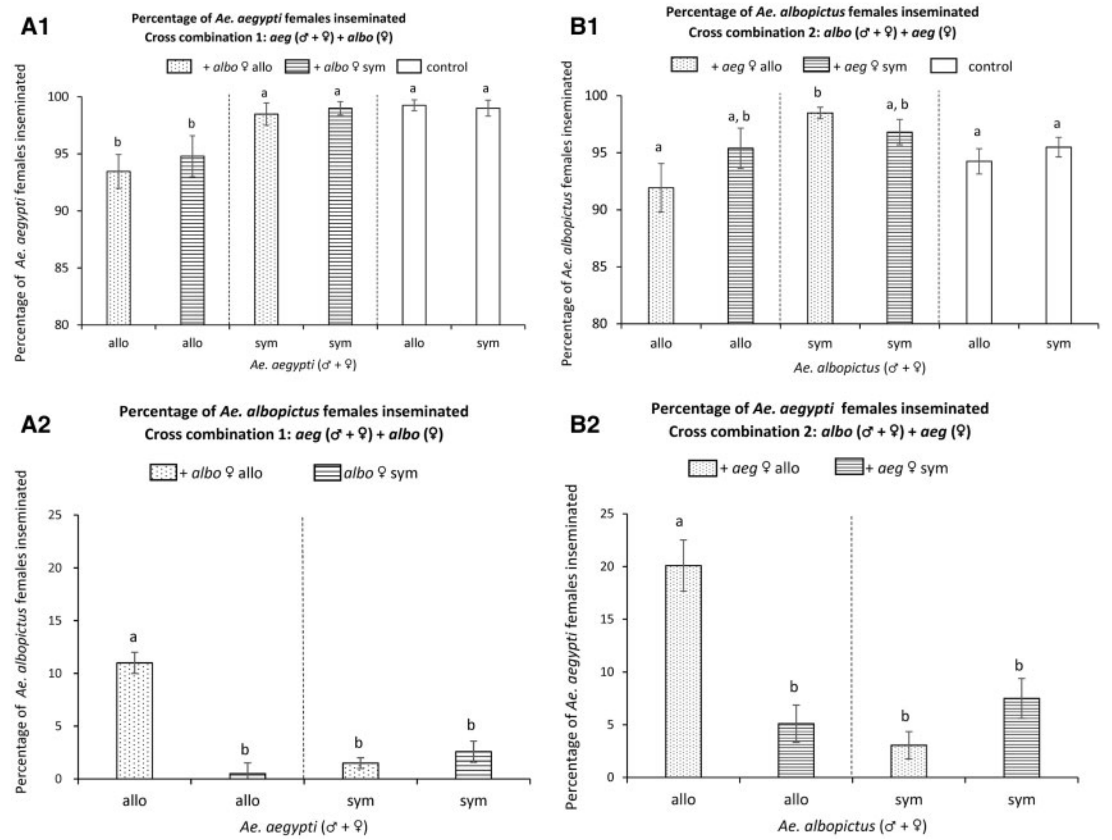

Fig. 1. Mate choice in the presence of heterospecifics. Each treatment within cross combinations was repeated three times. Abbreviations: *aeg*, *Ae. aegypti*; *albo*, *Ae. albopictus*; allo, allopatric; sym, sympatric. Origins: allopatric *Ae. aegypti*—Key West, sympatric *Ae. aegypti* and *Ae. albopictus*—Vero Beach, allopatric *Ae. albopictus*—East St. Louis. Error bars denote standard error. (A) Panels describe the results of the cross combination: *Ae. aegypti* males and females caged with *Ae. albopictus* females; (A1) showing the percentage of conspecific females inseminated, (A2) showing the percentage of heterospecific females inseminated. (B) Panels describe equivalent results for the cross combination: *Ae. albopictus* males and females caged with *Ae. aegypti* females. X-axes labels show the origin of conspecifics, while the fill patterns of bars show the origin of heterospecific females (see figure legend). In all panels, significant differences ($P < 0.05$) among arcsine-transformed proportions within species are denoted by different letters (post hoc means comparisons (Student-*t*) following ANOVA).

while males from populations that were allopatric to *Ae. albopictus* in the field inseminated significantly fewer conspecific females (94.13% ± SE 1.64; $F = 7.20$, df = 1, $P = 0.02$) in the presence of heterospecifics (Fig. 1A1).

Ae. albopictus (males). Neither the origin of *Ae. albopictus* males ($F = 4.54$, df = 1, $P = 0.06$), the origin of the heterospecific females ($F = 0.11$, df = 1, $P = 0.75$), nor their interaction ($F = 3.38$, df = 1, $P = 0.09$) significantly affected the percentage of conspecific females inseminated (Fig. 1B1).

Compared with purely conspecific crosses (sympatric population: 95.49% ± SE 0.86, allopatric population: 94.25% ± SE 1.11), *Ae. albopictus* males from populations sympatric with *Ae. aegypti* (93.66% ± SE 1.95; $F = 3.56$, df = 1, $P = 0.09$) as well as from populations allopatric to *Ae. aegypti* (97.65% ± SE 0.8) inseminated a similar percentage ($F = 3.74$, df = 1, $P = 0.09$) of conspecific females in the presence of heterospecifics (Fig. 1B1).

Insemination of Heterospecific Females. Ae. aegypti (males). The origin of *Ae. aegypti* males ($F = 27.87$, df = 1, $P < 0.001$), that of the heterospecific females ($F = 17.30$, df = 1, $P = 0.001$), as well the interaction term were significant ($F = 42.16$, df = 1, $P < 0.01$; (Fig. 1A2). These differences are driven largely by the high number of heterospecific females inseminated in the allopatric (*Ae. aegypti* males + conspecific females) × allopatric (*Ae. albopictus* females) combination (11% ± SE 1.00) compared with all other combinations (range: 0.51–2.59%; Fig. 1A2).

Ae. albopictus (males). The origin of *Ae. albopictus* males ($F = 7.85$, df = 1, $P = 0.02$), that of the heterospecific females ($F = 15.05$, df = 1, $P < 0.001$), as well the interaction term ($F = 26.42$, df = 1, $P < 0.01$) were significant (Fig. 1B2). Again, these differences are driven largely by the high number of heterospecific females inseminated in the allopatric (*Ae. albopictus* males + conspecific females) × allopatric (*Ae. aegypti*

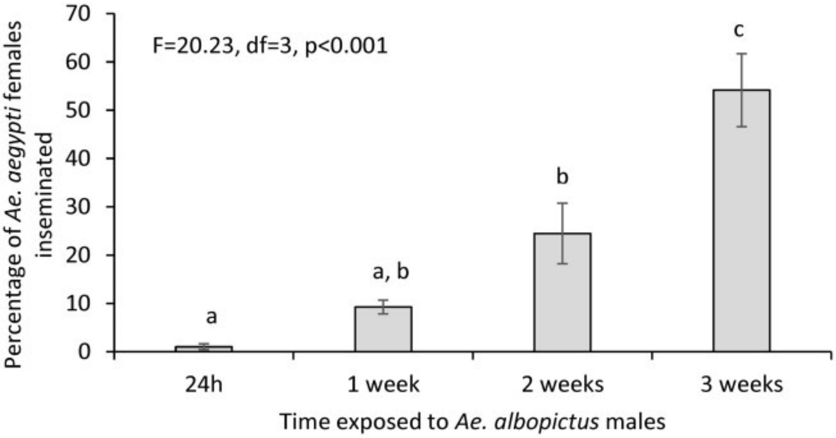

Fig. 2. Effect of exposure time on interspecific mating. Three repeats were carried out for each time point. Significant differences among arcsine-transformed proportions at measured time points are denoted by different letters (post-hoc means comparisons (Student-*t*) following ANOVA). Error bars denote standard error.

females) combination (20.09% ± SE 2.43) compared with all other combinations (range: 3.05–7.50%; Fig. 1B2).

Effect of Exposure Time on Interspecific Mating. Exposure time significantly affected interspecific insemination ($F = 20.23$, df $= 3$, $P < 0.001$), with insemination rates increasing from 1.04 (±SE 0.61)% after 24 h to 54.13 (±SE 7.56)% after 3 wk (Fig. 2).

Discussion

Despite extensive literature on *Ae. aegypti* and *Ae. albopictus*, owing largely to their status as important vectors of both dengue and chikungunya viruses (Vazeille et al. 2007, Kyle and Harris 2008, Pages et al. 2009, Paupy et al. 2010), comparatively little is known about their mate recognition systems, particularly with regard to male behavior (reviewed in Oliva et al 2014). Most studies cover female aspects of reproduction and date from the 1970s. However, more recent reports include the possible existence of an "aggregation pheromone" (produced by both males and females) that may modulate swarming behavior in *Ae. aegypti* (Cabrera and Jaffe 2007) and the discovery that male and female mosquitoes synchronize their flight tones (wing beat frequencies) before mating (Cator et al 2009). While it has been established that the flight tones of *Ae. aegypti* and *Ae. albopictus* females differ significantly (Brogdon 1994) and flight tone recognition seems to be involved in species recognition in anophelines (Pennetier et al 2010), it is still unclear whether this is the case in aedines (Roth 1948, Nijhout and Craig 1971). Nijhout and Craig (1971) instead suggest the involvement of a species-specific pheromone that enables recognition following contact, although subsequent investigators have been unable to confirm this.

Though it is unclear which traits are subject to change, we here demonstrate that mate recognition systems can evolve in the presence of closely related species whose geographic distribution did not overlap until ranges expanded by means of human-aided invasions. If mating attempts directed at heterospecifics are costly in terms of reproductive success, either through direct or indirect measures, natural selection may increase divergence between sympatric taxa by selecting against these "misdirected" mating attempts. This process may result in reproductive character displacement (Howard 1993), where sympatric populations of closely related (interacting) species diverge in mate recognition to a greater extent than allopatric populations (Higgie and Blows 2008). Our recent work on satyrization in *Ae. aegypti* and *Ae. albopictus* (Bargielowski et al. 2013, Bargielowski and Lounibos 2014) has shown such reproductive character displacement in the mating behavior of females, with *Ae. aegypti* females from allopatric origins being more likely to engage in interspecific mating than females from sympatric origins. Here we document a similar behavioral shift in males. We note that the experimental design employed does not readily distinguish between a response in male behavior versus a response in conspecific female behavior. However, as discussed below we propose the biologically most probable interpretation is indeed that of male adaptation. *Ae. aegypti* males from sympatric populations mate significantly more conspecific females in the presence of heterospecific females than do males of allopatric origin. Males from sympatric populations may have developed a more specialized species recognition mechanism allowing them to better distinguish conspecific from heterospecific females. Their allopatric counterparts, lacking evolution of this trait, may thus waste time and energy courting and inseminating heterospecific females, instead of directing their attentions to conspecifics, in the process diminishing their reproductive potential. Our earlier work (Bargielowski et al. 2013, Bargielowski and Lounibos 2014) showed that the same does not apply for sympatric *Ae. albopictus* females, which actually mated interspecifically more frequently than their allopatric counterparts. Conversely, in this article, we saw that *Ae. albopictus* males showed a trend, though not statistically significant, similar to male *Ae. aegypti.* We speculate that this trend was not significant because of the unexpectedly low mating success of the control cages (compared with similar measures of *Ae. albopictus* interspecific mating rates observed in our laboratory) and suggest that this trend may indeed represent a biologically relevant phenomenon. Therefore, for *Ae. albopictus*, the two sexes demonstrate contrary responses to interactions with *Ae. aegypti*. One speculative explanation may be in the respective cost of misdirected mating for either sex. *Ae. albopictus* females may lose a small amount of time and energy engaging in interspecific mating, but ultimately are able to remate a conspecific male with no (documented) loss of reproductive potential, as females require only one compliment of sperm to fertilize a lifetime's supply of eggs. Males on the other hand, have been shown to have limited mating potential over the course of their lifetimes. Boyer et al. (2011) report that in laboratory trials, *Ae. albopictus* males mated on average 8.6 females over a 2-wk period (once it had been established that mating ceased following this time point). Thus, males lose time, energy and reproductive potential with each interspecific mating.

For both species combinations, the heterospecific insemination rates were highest in the (F/M) "allopatric" + (F) "allopatric" combinations. Given the fact that the lineages of both the females and males in these cross combinations had no histories of interspecific encounters, this result is not unexpected. However, the magnitude of the difference compared with all other cross combinations was large. Furthermore, the relatively high rates of heterospecific insemination observed in 24 h were surprising (up to 11% for *Ae. albopictus* females (Fig. 1A2) and 20.09% for *Ae. aegypti* females (Fig. 1B2) compared with only 1.04% for *Ae. aegypti* females in the nonchoice trial (Fig. 2)). The nonchoice trials ((F) *Ae. aegypti* (KW) × (M) *Ae. albopictus* (ESL)) showed that increasing cohabitation time significantly increased interspecific insemination rates. Though the proportion of males versus females differed in the choice versus nonchoice trials (1:4 vs 1:1), it appears that the presence of conspecifics increased heterospecific mating. It is conceivable that the presence of conspecifics elicited courting behavior and perhaps, partially due to their confinement in cages, these courting attempts were more frequently misdirected at heterospecifics than in nonchoice scenarios.

This study demonstrates that co-occurrences of these two invasive species lead to evolution and adaptation of reproductive behaviors to changing circumstances. Understanding the processes driving development of mate choice preferences or avoidance mechanisms may help predict future changes in the distribution and abundance of vector populations.

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