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Male mate choice and female receptivity lead to reproductive interference

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Abstract Mating between species is common, but seldom adaptive. Mate preferences and receptivity to mating attempts may both contribute to such matings, also called reproductive interference. Here, we tested the hypothesis that both male mate preference for female body size and female receptivity contribute to reproductive interference between two secondarily sympatric insect species. In north-central Florida, the squash bug *Anasa tristis* co-occurs with a recently introduced, smaller congener, *Anasa andresii*. Male *A. andresii* are frequently found copulating with larger female *A. tristis* in the field. We found that male *A. andresii* prefer larger heterospecific females over conspecific females, that female *A. tristis* accept some mating attempts by heterospecific males, and that female *A. tristis* are more promiscuous with conspecifics than are female *A. andresii*. Our findings suggest that both male mate choice and female receptivity contribute to mating between these species.

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Introduction

Across-species mating is a surprisingly widespread phenomenon. It can sometimes be adaptive (Fitzpatrick and Shaffer 2007; Pfennig 2007); however, often it is not (reviewed in Gröning and Hochkirch 2008). When across-species mating results in fitness costs for one or both species involved, this is called reproductive interference. Reproductive interference can have important ecological and evolutionary consequences: it can impact population persistence (Hettyey and Pearman 2003; Liu et al. 2007; Hochkirch et al. 2007; Kishi et al. 2009; Tripet et al. 2011), habitat partitioning (Kuno 1992), species boundaries (Thum 2007), and the distributions of traits used in mate choice within populations (Alatalo et al. 1994; Konuma and Chiba 2007). The occurrence and costs of reproductive interference are affected by ecological factors such as relative abundance, sex ratio, and the spatial and temporal activity of each species (Singer 1990; Kuno 1992; Gröning et al. 2007; reviewed in Gröning and Hochkirch 2008; Noriyuki et al. 2012).

Why does reproductive interference occur? One possibility is that the same preferences that are adaptive in single-species contexts may increase the likelihood of across-species mating when two species come into proximity (Alatalo et al. 1994; Pfennig 1998). For example, in arthropods, the most common male preference is for large female body size (Bonduriansky 2001; Edward and Chapman 2011), a trait highly correlated with fecundity. However, males with a strong preference for large females may seek out matings with large heterospecifics when populations come into contact, leading to reproductive interference and a potential evolutionary trap (Pfennig 1998; Schlaepfer et al. 2002; D'Amore et al. 2009).

Here, we hypothesized that male preference for large female body size is contributing to reproductive interference in two closely related insect species (*Anasa tristis* and *Anasa*

andresii) that are secondarily sympatric in north-central Florida. Florida is part of the historic range of *A. tristis*, and *A. andresii* was first documented in the region ~40 years ago (Baranowski and Slater 1986). Today, individuals of both species can be observed in mixed-sex aggregations in the field (Hamel, Nease & Miller pers. obs.). Males and females of both species are promiscuous, and mating between these species occurs frequently (Fig. 1). Matings between species are typically observed in one direction: smaller male *A. andresii* copulate with larger female *A. tristis* (Hamel, Nease & Miller pers. obs.). We predicted that male *A. andresii* would direct more mating attempts (mountings) toward larger females. We also predicted that when male *A. andresii* encounter two females simultaneously, as occurs in the field, they should direct their first mounting and more overall mountings toward the larger female, irrespective of her species. Finally, we predicted that female *A. tristis* should reject most mountings by male *A. andresii*, because preliminary data suggest that matings between the two species do not produce viable offspring (Hamel, unpub.).

To test these predictions, we first assessed the effect of female body size on the number of mountings by male conspecifics in a single-pair, "no choice" design. We then used simultaneous choice assays to evaluate the effect of female body size on male *A. andresii* preference and mating effort. We examined whether the difference in female body size in the simultaneous choice tests predicted the difference in the number of mountings allocated to each female. We evaluated female receptivity in both the single-pair context and the simultaneous choice assays.

Methods

Ecology of the interacting species

A. andresii and *A. tristis* are broadly-distributed pests of cucurbits that are commonly found feeding and mating on the same host plants in north-central Florida. While similar in appearance (Fig. 1), the species differ in behavior and habitat use (Hamel, unpub.). *Anasa tristis* tend to stay on or near the soil while they feed on plant stems, whereas *A. andresii* move frequently and are more often seen on the top sides of leaves and exposed surfaces. We most commonly (though not exclusively) have observed large, mixed-species mating aggregations in community gardens with a patchwork of cucurbit varieties. It may be that these species prefer different host varieties, but once they are in proximity, aggregation pheromones bring them into physical contact. Both species are heavily parasitized by a tachinid parasitoid that lays its eggs on the abdomens of its hosts (Mitchell 2000). We have not found evidence that copulation increases parasitism risk for either species (Hamel, Piñeros, Miller, unpub.).

Fig. 1 A copulating pair of *Anasa* spp.: male *A. andresii* (*left*) and female *A. tristis* (*right*). Photo by JA Hamel

Insect collection and rearing

We collected juveniles in their fifth, and final, instar of both *A. andresii* and *A. tristis* from five different sites in Alachua Co. and one site in Union Co., FL, May–August 2012. Collection sites included community gardens and organic farms.

We reared nymphs communally by species in mesh insect cages (BugDorm 2120 Insect Tents, MegaView Science Co., Ltd.), inside Florida Reach-In environmental chambers. Chambers were kept at 26.0±0.1 °C on a photoperiod of 16:8 (L:D). We provided nymphs with leaves and fruit from seasonally available host plants (*Cucurbita pepo* and *Cucurbita moschata*) and wet cotton dental wicks (Richmond Dental) in petri dishes. We refreshed water, leaves, and fruit daily, and collected leaves and fruit from local organic sources.

After the final molt to adulthood, individuals were immediately removed to ensure they remained unmated and were housed in individual 32-oz clear plastic containers with mesh lids. We provided each adult with cucurbit leaf, stem, fruit, and water, and refreshed these daily. We maintained all adult insects in a room at 29.5±1.2 °C on a photoperiod of 16:8 (L:D).

Experimental preparations

We categorized new adult females as "large" or "small" according to their pronotal widths, a measure highly correlated with overall body size in insects. We measured pronotal widths to the nearest 0.01 mm. Body size was normally distributed among female *A. tristis*. We therefore defined female *A. tristis* as large or small if they had pronotal widths of mean ±1/2 s.d., respectively. The body size distribution for female *A. andresii* varied as the season progressed. We therefore defined female *A. andresii* as small or large if their pronotal widths fell within the first or last quartiles of the body size distribution for the week in which they were collected. Female *A. tristis* were always larger than female *A. andresii*.

Behavioral trials occurred in the same room where the colony was maintained and were conducted May–

October 2012. To ensure adults were reproductively mature, individuals were tested between 3 and 6 weeks after their final molt. The day before the behavioral observation, each female was individually marked on the pronotum with a water-based paint pen. We placed each female with food and water in the plastic container in which she would be observed and allowed her to acclimate overnight. So that the observer's view of the insects was not obscured, we removed plant material from the container before introducing the male and starting the observation period.

Experimental design

We first documented male mounting behavior and female receptivity within species and without possible social interference by pairing (1) one male *A. andresii* with one female *A. andresii* ($n=14$) and (2) one male *A. tristis* with one female *A. tristis* ($n=16$).

Next, we examined male mounting behavior as a gauge of male preference and mating effort with regard to female body size and species. At the same time, we evaluated receptivity of female *A. andresii* and *A. tristis* to mating attempts (mountings) by male *A. andresii*. We introduced each male *A. andresii* simultaneously to (1) two female *A. andresii* (AA treatment), (2) two female *A. tristis* (TT treatment), and (3) one female of each species (AT treatment). Each pairing combination contained one large and one small female; in the AT treatment, the female *A. tristis* was always larger. Each observation lasted for 2 h. We found that most males mounted females (attempted mating) in the first 20 min after introduction to a female (*A. tristis* 14 ± 10 min; *A. andresii* 19 ± 18 min).

For mating to occur, a male must first climb on top of a female and extend his aedeagus to establish contact with her genital plate (mounting behavior). Females must open their genital plates to copulate, and females frequently reject mating attempts by males (see "Results" below). Immediately after copulation begins, male and female pivot 180° to face away from each other. Here, we defined a male mating attempt, or a mounting, as simultaneous contact by all six of a male's legs with a female, and we defined copulations as beginning when genitalia attached and the male and female pivoted 180°. We assessed male mating preference by recording which female received a male's first mounting. We evaluated female receptivity by scoring whether or not females copulated in response to male mountings. For trials where copulation did not occur (42/61 trials), we recorded the total number of times a male mounted each female during our observation period as an index of total male mating effort.

Data analysis

Male-female conspecific pairs

We first examined male mounting and female receptivity in single-species pairs. We examined the influence of female body size on the occurrence of male mounting (yes or no) using separate logistic regressions for each species. We next examined the influence of female body size on the total number of male mounts using generalized linear models (GLMs) fitted to the Poisson error distribution. Female receptivity could only be scored for those pairs where males mounted. We used Fisher's exact test to assess whether female receptivity differed between species.

Simultaneous choice tests

We used the exact binomial test to ask whether *A. andresii* males mounted larger females first, our gauge of male preference. We then used Fisher's exact test to look more closely at the case where males encountered a conspecific and heterospecific, and predicted that males would be more likely to mount heterospecific females first.

In trials where males mounted but copulation did not occur, we fitted a generalized linear mixed model (GLMM, R function glmer in library lme4) to the Poisson error distribution with a logit link function to estimate the fixed effects of female body size (larger/smaller) and pairing combination (AA, AT, or TT) on the number of male mountings. Because we were counting the number of mountings directed at each of two females in each trial, we included trial as a random effect. To examine whether the magnitude of the body size difference between females predicted the difference in number of mounts directed toward each female, we fitted a GLM to the Poisson error distribution, with difference in number of male mountings as the response and difference in body size between the two females and treatment as fixed effects.

We used logistic regression to assess whether female receptivity toward a male *A. andresii* varied according to female species. This model included female species and treatment as fixed effects. All statistical analysis was carried out using RStudio statistical software, v. 0.97.551.

Results

Male-female conspecific pairs

Most males of both species mounted females (9/14 male *A. andresii*; 14/17 male *A. tristis*). In this specific situation (single male-single female conspecific pairs), we did not find evidence that female body size influenced whether a male mounted a female (logistic regression: *A. andresii*, $n=14$ pairs,

$\chi^2=0.003$, $P=0.960$; *A. tristis*, $n=17$ pairs, $\chi^2=0.250$, $P=0.610$). Likewise, in this context, we did not find evidence that the total number of mountings was influenced by female body size (Poisson regression: *A. andresii*, $n=12$ pairs, $\beta=0.255$, SE=0.651, $z=0.392$, $P=0.695$; *A. tristis*, $n=7$ pairs, $\beta=-0.115$, SE=2.490, $z=-0.046$, $P=0.963$). Female receptivity differed by species: more female *A. tristis* than female *A. andresii* responded to a conspecific male mounting by mating with that conspecific (*A. tristis*: 10/14 versus *A. andresii*: 2/9, Fisher's exact test: $P=0.036$).

Simultaneous choice tests

Here, each male *A. andresii* was offered two females: two female *A. andresii* (AA), two female *A. tristis* (TT), or one female *A. andresii* and one female *A. tristis* (AT). The female receiving a male's first mounting was considered the preferred female. Male *A. andresii* overall preferred larger females (33/42 first mountings, $P<0.001$, exact binomial test, Fig. 2). When a male *A. andresii* was paired with two female *A. andresii*, he chose the larger conspecific in all eight cases (100 %). When a male *A. andresii* was paired with two female *A. tristis*, he chose the larger heterospecific in 10 out of 11 cases (91 %). The pattern was still present, albeit less pronounced and not statistically significant, when males were provided with one female *A. tristis* and one female *A. andresii* (AT). In this case, male *A. andresii* chose the larger female (who was also a heterospecific in all cases) in 15 out of 23 cases (65 %; $P>0.10$, exact binomial test). Some male *A. andresii* did not mount females during our 2-h observation period; there was not an obvious difference across the pairing combinations in the proportion of males that did not mount (AA 3 males of 11 total, AT 4/27, TT 1/12). We excluded these trials from further analysis.

We next scored the number of male mounts as a gauge of male effort in the trials that did not result in matings. We found a pattern that largely reflected the pattern based on first mounts (Figs. 2 and 3). Larger females received more than twice as many mounts from males on average (GLMM: likelihood ratio test (LRT)=13.484, $P<0.001$), and pairing combination had no significant effect on the number of male mounts a female received (GLMM: likelihood ratio test (LRT)=3.157, $P<0.206$). The number of male mountings was not influenced by the magnitude of the size difference between females in a trial (GLM: likelihood ratio test (LRT)=0.271, $P=0.603$; Fig. 4). The only males that directed a greater number of mountings toward smaller (i.e., conspecific females) were a small number of those that were provided with both con- and heterospecific females (the AT group; Fig. 4).

Five of 34 (15 %) female *A. tristis* copulated after receiving a mounting from an *A. andresii* male during our observations. In contrast, 14 of 27 (52 %) female *A. andresii* copulated with
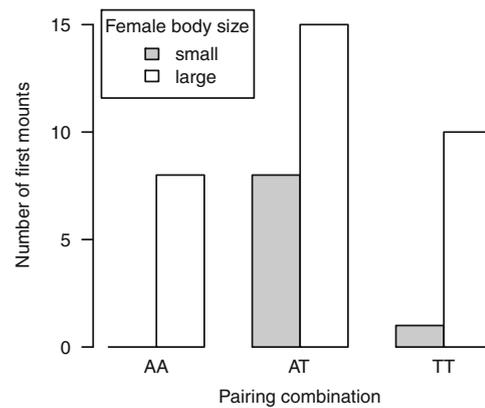

Fig. 2 In simultaneous choice tests, most male *A. andresii* attempted to mount the larger female first, across all pairing combinations. In the pairing combination (AT) where trials included one female of each species, the heterospecific female (*A. tristis*) was always larger

male *A. andresii* after a mounting, a statistically significant difference (logistic regression, LRT=8.671; $P=0.003$).

Discussion

Our results suggest that reproductive interference between *A. andresii* and *A. tristis* is at least partially driven by male mate preference. When male *A. andresii* were given a simultaneous choice between two females, males showed a consistent pattern of mounting larger females first and directing more total mounts toward these females. In the case when male *A. andresii* were provided one heterospecific and one conspecific female, this pattern was less pronounced, though the larger, heterospecific females still received more effort (Figs. 2 and 3). Male preference for large, fecund females is common across diverse taxa (Verrell 1985; Bonduriansky
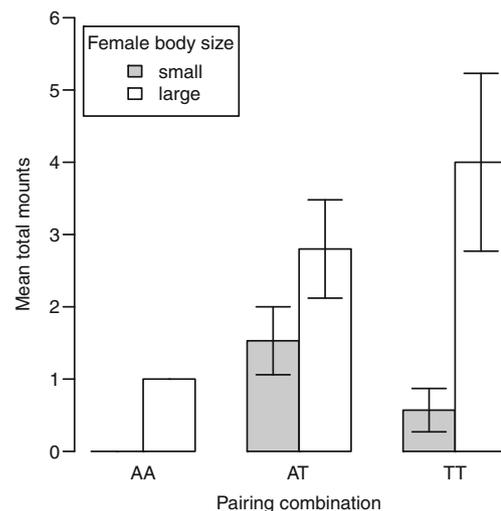
Fig. 3 In simultaneous choice tests, males performed more mountings on larger females. *Bars* show means for male mountings; *error bars* show SEs. Only trials where pairs did not copulate are included
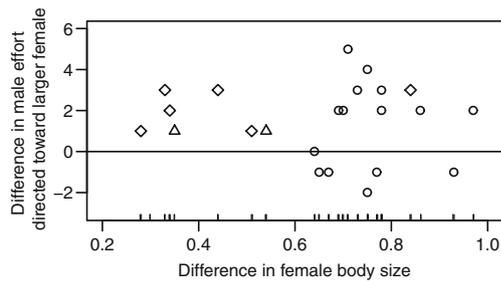
Fig. 4 In simultaneous choice tests, the difference in male effort directed toward the larger female was not influenced by the difference between female body sizes. Pairing combinations are shown as follows: *circles* AT, *triangles* AA, *squares* TT. *Points below the line at 0* represent males who directed more mountings toward smaller females. Only trials where pairs did not copulate are included

2001; Luddem et al. 2004; Dosen and Montgomerie 2004; Byrne and Rice 2006; Edward and Chapman 2012; Olsson 2013). Our findings add to a growing body of evidence that suggests this preference is an important driver of reproductive interference between species (reviewed in Gröning and Hochkirch 2008; D'Amore et al. 2009). Surprisingly, we found no evidence that the magnitude of the size difference between females influenced allocation of effort by male *A. andresii*. This finding contrasts with other recent work (Dosen and Montgomerie 2004; Edward and Chapman 2012) and may be because each male in our study was experiencing its first mating opportunity: male stringency in mate choice can increase after sperm resources are depleted (Byrne and Rice 2006).

The evolutionary outcomes of reproductive interference are still poorly understood. Here, *A. andresii* and *A. tristis* are secondarily sympatric and may be caught in an evolutionary trap (Schlaepfer et al. 2002). In our study population, male *A. andresii* preference for large female body size may result in a preference for heterospecific females, though some males showed indication of preferring the small, conspecific females (Figs. 2 and 3). Long copulation durations and observations that females mate multiply suggest that such copulations may be costly for male *A. andresii*. If copulations with heterospecifics are more costly than those with low-quality conspecifics, selection may shift male preference from large to relatively small females, thereby leading to a reduction in heterospecific matings (*sensu* Pfennig 1998; Safi et al. 2006). We may be witnessing a point in this transition. Female spadefoot toads prefer calls by low-quality males in populations where heterospecific calls can be confused with those of high-quality conspecifics (Pfennig 2000).

When male *A. andresii* simultaneously encountered two females, they directed their first mountings toward the larger female and then persisted in directing more overall effort to the larger female. We did not find a similar pattern when males encountered a single female conspecific. In this context, female body size did not appear to influence the likelihood of a

male mounting or total number of male mountings. This single-pair design allowed us to evaluate female receptivity to conspecifics without social interference, but each male would have turned down a mating opportunity to show preference. In north-central Florida, mixed-sex aggregations of a single species or both species are common (Hamel & Miller, pers. obs.), suggesting that a simultaneous choice experimental design may be a good approximation of a common natural situation. However, individuals can and do encounter each other alone and in a variety of social contexts. Though we found contrasting results here, other insect studies have found that single-pair and simultaneous choice designs can yield similar patterns of choice and selection (Dougherty and Shuker 2014; Addesso et al. 2014; Gillespie et al. 2014).

We found that female *A. tristis* were more likely to accept copulation attempts from conspecifics than were female *A. andresii*. Why are female *A. tristis* relatively indiscriminate in their choice of mates? A surprising number of female insects go unmated or do not realize their potential fecundity (Rhainds 2010). Selection to ensure a sufficient number of matings may lead to maladaptive behaviors under certain conditions (*reviewed in* Burdfield-Steel and Shuker 2011). Female *A. tristis* mate multiple times and with multiple conspecific males, a behavior that may be adaptive when heterospecifics are not present. The heterospecific *A. andresii* has been present only ~40 years; thus, female *A. tristis* may not have had sufficient time and exposure to evolve strategies for consistently avoiding heterospecific matings. However, our results suggest that a modest barrier to heterospecific matings is present for *A. tristis* females. In response to a male *A. andresii* mounting, 52 % of female *A. andresii* mate while only 15 % of female *A. tristis* mate. In contrast, 71 % of female *A. tristis* mated with a male of their same species following a mounting. An obvious and necessary next step is to more rigorously assess the degree to which female *A. tristis* discriminate against male *A. andresii*, and whether female discrimination is reduced or increased when males of both species are present.

Future work should describe the fitness costs for individuals involved in reproductive interference, keeping in mind that costs are often asymmetrical between species (reviewed in Gröning and Hochkirch 2008). Key ecological parameters, such as habitat use, density, and timing of seasonal emergence may influence these costs so that they are not consistent over time and space (Singer 1990; Hettyey and Pearman 2003; Gröning et al. 2007). Sexual selection takes place in complex environments and is rarely a static process (*reviewed in* Miller and Svensson 2014). Thus, the evolution of barriers to reproductive interference may occur only at certain times and contexts.

In summary, our findings suggest that both male preference and female receptivity contribute to reproductive interference in a secondarily sympatric population. Our data from male-female conspecific pairs suggest a general difference in female

receptivity between our two focal species. Data from simultaneous choice tests show that male *A. andresii* prefer larger females, that this preference drives mating attempts toward female *A. tristis*, and that female *A. tristis* sometimes accept heterospecific mating attempts. Future work should test predictions about the influence of reproductive interference on the evolution of mate preferences and species recognition across historically allopatric, sympatric, and secondarily sympatric populations of reproductively interacting species.

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