



## The effect of male dominance on female choice in a field cricket (*Gryllus assimilis*)



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### ARTICLE INFO

#### Article history:

Received 31 August 2015  
Initial acceptance 13 October 2015  
Final acceptance 22 December 2015  
Available online  
MS. number: A15-00750R

#### Keywords:

audience effect  
cricket  
dichotomous choice test  
female choice  
*Gryllus assimilis*  
intersexual selection  
intrasexual selection  
male–male aggression  
mate preference  
no-choice text

Theory suggests that behaviours previously thought only to influence intrasexual selection, such as aggression between males, can also be co-opted to serve in intersexual selection as honest indicators of male quality. Our previous research revealed an audience effect: male Jamaican field crickets, *Gryllus assimilis*, fight more aggressively in front of a female audience. One way for this to evolve is if females are more attracted to more aggressive males or fight winners. Given the potential interplay between intra- and intersexual selection, we investigated how observing a fight influences subsequent female mate choice and mating behaviour. We utilized two female treatments: Observers watched the two males fight, whereas Non-observers watched two noninteracting males. We then immediately tested Observer and Non-observer females for their mating preferences towards male fight participants using dichotomous and no-choice tests. Our approach enabled us to assess whether females preferred either dominant (winner) or subordinate (loser) males and whether females gathered information about males while watching them fight that informed their mating preferences. While females did not prefer fight winners over losers in dichotomous choice tests, in the no-choice tests, females were more likely to mount winners and mount males that they had preferred in the dichotomous choice tests. Intra- and intersexual competition appears to be mutually reinforcing in this species, but eavesdropping is unlikely to explain the evolution of audience effects.

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Intrasexual and intersexual selection have been traditionally seen as separate, often opposing, forces shaping secondary sexual traits and behaviours (Qvarnström & Forsgren, 1998). Traits were thought to either increase the bearer's ability to win fights with same-sex conspecifics over resources or mates (intrasexual selection) or increase the bearer's ability to attract mates (intersexual selection). Research and theory in the past quarter century suggests a more complex relationship between the evolution of intra- and intersexually selected traits (Berglund, Bisazza, & Pilastro, 1996; Hunt, Breuker, Sadowski, & Moore, 2009; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005). Size and development of traits used in intrasexual conflict determines male position within the social hierarchy (reviewed in Maynard Smith & Harper, 2003). Because male position within a hierarchy is often contested, male intrasexual traits should be honest indicators of male quality and dominance (Khazraie & Campan, 1999). Females may co-opt traits

used in intrasexual selection for use in mate choice and, as a result, may reinforce selection on these male traits (Berglund et al., 1996).

Female preference for dominant males occurs in many species (reptiles: Jamaican giant anole, *Anolis garmani*: Trivers, 1976; birds: nightingale, *Luscinia megarhynchos*: Kunc, Amrhein, & Naguib, 2006; crayfish: red swamp crayfish, *Procambarus clarkii*: Aquiloni, Buric, & Gherardi, 2008; crickets: Mediterranean field cricket, *Gryllus bimaculatus*: Simmons, 1986a, 1986b; reviewed in Berglund et al., 1996). Female preference for more dominant males could have direct benefits if male dominance is linked to the male's ability to obtain and defend resources used by females (resource defence hypothesis; Qvarnström & Forsgren, 1998). Female preference for more dominant males could also have indirect benefits ('good genes', offspring quality hypothesis; Berglund et al., 1996) if fighting ability serves as an honest signal of male quality. If female preference for dominant males has direct or indirect benefits, intra- and intersexual selection may be mutually reinforcing (Qvarnström & Forsgren, 1998).

Intra- and intersexual selection can also work in opposition (Qvarnström & Forsgren, 1998). Dominant males may harm their mates (Japanese quail, *Coturnix japonica*: Ophir & Galef, 2003) or provide reduced or mediocre parental care (Pacific blue-eye fish,

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*Pseudomugil signifier*: Wong, 2004; sand goby, *Pomatoschistus minutus*: Forsgren, 1997). In addition, dominant males can be sperm depleted (vinegar fruit fly, *Drosophila melanogaster*: Pitnick & Markow, 1994), be vectors of disease, or harbour parasites (reviewed in Folstad & Karter, 1992; eastern chimpanzee, *Pan troglodytes schweinfurthii*: Muehlenbein & Watts, 2010). Furthermore, dominant males may not invest as much in mate attraction or courtship as subordinate males (mate attraction: Australian cricket, *Teleogryllus oceanicus*: Thomas & Simmons, 2009; courtship: threespine stickleback, *Gasterosteus aculeatus*: Ward & FitzGerald, 1987). Thus, sometimes females prefer to mate with subordinate males, resulting in conflicting inter- and intrasexual selection influencing male dominance. Given the potential for intra- and intersexual selection to reinforce or conflict with each other, it is important to investigate the relationship between these two forces to understand how they shape secondary sexual traits (e.g. examine total sexual selection; Hunt et al., 2009).

Male fights often occur within a social network, allowing females the opportunity to observe them (McGregor & Peake, 2000). Female observers (audience members) may be able to use information that they glean from the fights to inform their mating preferences. Females that watch fights prefer fight winners in many species (fighting fish, *Betta splendens*: Doutrelant & McGregor, 2000; red swamp crayfish, *P. clarkii*: Aquiloni et al., 2008; black-capped chickadees, *Poecile atricapillus*: Mennill, Ratcliffe, & Boag, 2002). This suggests that social networks also have the potential to shape secondary sexual traits.

We examined how male dominance within a social network influences female mate choice using Jamaican field crickets, *Gryllus assimilis*. *Gryllus assimilis* males fight to obtain access to a territory and then use acoustic signals to attract potential mates (Alexander, 1961). Montroy, Loranger, and Bertram (2015) revealed audience effects in this species: males in the presence of a female audience were significantly more likely to initiate fights and their fights were significantly more aggressive than in the presence of no audience. Studies on other field cricket species have also found that males increase aggression when fighting in front of a female audience (spring field cricket, *Gryllus veletis*: Fitzsimmons & Bertram, 2013; *G. bimaculatus*: Simmons, 1986a; Tachon, Murray, Gray, & Cade, 1999). For increased aggression to be adaptive, the benefits of winning the fight must outweigh the costs. The costs of increasing aggression include both elevated energetic costs (Hack, 1997) as well as elevated risk of injury. The benefits of winning a fight include resource acquisition: the male that wins the fight not only gains access to the calling territory, but also the females residing in that territory (resource defence hypothesis; black-capped chickadees: Ficken, Weise, & Popp, 1990; bay goby, *Lepidogobius lepidus*: Grossman, 1980; reviewed in Dabelsteen, 2005). Thus, for males, female presence alone may outweigh the elevated costs associated with escalating a fight. However, increased male aggression might be simultaneously reinforced by intersexual selection if females prefer to mate with fight winners and/or more aggressive males. Under this female preference hypothesis, females find dominant males (fight winners) or more aggressive males more attractive and are more likely to mate with them.

In crickets, there is mixed support for the hypothesis that females prefer dominant males. In the experiments where females preferred dominant males over subordinate males as mates, males and females were allowed to freely interact (African king cricket, *Libanasisidus vittatus*: Bateman & Toms, 2013; house cricket, *Acheta domestica*: Nelson & Nolen, 1997; *G. bimaculatus*: Simmons, 1986b). Because crickets were allowed to interact, dominant males could have prevented subordinate males from courting the females. Given that females will not mate with noncourting males (Alexander, 1961), the experiments may not have measured the free

choice of females. Intriguingly, in experiments where females were shown to not prefer dominant males, researchers placed a single male and female together in an arena and quantified female willingness to mate (*A. domestica*: Nelson & Nolen, 1997; *T. oceanicus*: Shackleton, Jennions, & Hunt, 2005; but see Savage, Hunt, Jennions, & Brooks, 2004). The conflicting findings obtained using these two research approaches highlights the importance of carefully assessing whether females prefer more dominant males.

We tested whether allowing a female to observe males fight influences her subsequent mating decisions without the possibility of courtship interference. Females may use one or many cues to determine male victory while observing a fight. They may assess how aggressive a male is relative to his opponent, as the winner of the contest is the male who has escalated the fight to the point where the loser retreats (Adamo & Hoy, 1995). They may also use male victory displays, as male crickets produce an acoustic signal and judder after winning a fight (Alexander, 1961; Fitzsimmons & Bertram, 2013; Jang, Gerhardt, & Choe, 2008). We quantified female mating preference in two ways: (1) using a dichotomous choice test where females could select between the fight winner and loser but where the fight winner and loser could not see or interact with each other, and (2) using a no-choice test where females were paired at random with either the fight winner or the fight loser and their mounting behaviour was observed. This dual approach assessed whether females preferred fight winners over losers while simultaneously allowing us to test the validity of the no-choice experimental approach (Shackleton et al., 2005).

We also tested whether female preference for the winner of a fight was influenced by whether the female had observed (Observers) or not observed (Non-observers) the fight. Observer females watched a fight between two males and then had their mating preferences assessed for the two males they had just watched fight. Non-observer females watched two noninteracting males and then had their mating preferences assessed for two other males who had just fought. We included the Non-observer treatment to determine whether females could use nonvisual chemosensory cues to detect male dominance (e.g. humans, *Homo sapiens*: Havlicek, Roberts, & Flegr, 2005; Texas field cricket, *Gryllus integer*: Kortet & Hedrick, 2005; bank vole, *Clethrionomys glareolus*: Kruczek, 1997; lobster cockroach, *Nauphoeta cinerea*: Moore, Gowaty, Wallin, & Moore, 2001). If females typically prefer to mate with fight winners, both Observer and Non-observer females should prefer fight winners to losers, provided that females can discern whether males are dominant without watching fights. However, if females need to observe a fight to discern which male is more dominant (eavesdropping), then only Observer females should prefer fight winners over losers. This study is one of the first to investigate the effect of eavesdropping on female choice with the goal of ascertaining whether the cost of increased aggression in front of a female audience is alleviated by the benefit of increased reproductive success.

## METHODS

### Cricket Rearing

Our study was conducted in accordance with the guidelines of the Canadian Council on Animal Care. No field-collecting permits were required. Furthermore, import permits were not required to bring *G. assimilis* into Canada. *Gryllus assimilis* are housed in a Plant Pest Containment (PPC) facility in accordance with PPC Level 1 Guidelines (PPC1: PC-2014-053).

*Gryllus assimilis* crickets used in our experiment had been reared in the laboratory for 19–20 generations. The original population was established near the Stengl Lost Pines Biological Station of the

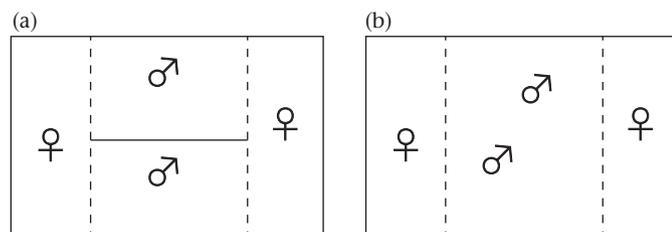
University of Texas at Austin (Bastrop County, TX, U.S.A.;  $\sim 30^{\circ}17'N$ ,  $\sim 97^{\circ}46'W$ ) during 15–24 September 2007. *Gryllus assimilis* recently expanded its range into Texas (Weissman, Walker, & Gray, 2009). While *G. assimilis* was thought to occur only in coastal areas, with a single voucher specimen in central Texas, our research team saw thousands of *G. assimilis* flying at lights around Smithville, Texas in 2007 and 2009. *Gryllus assimilis* individuals have morphological and mate attraction features that are distinct from those of other Texas crickets (morphological: Y-shaped ecdysial suture, narrow head, long wings, dense short brown hairs on the pronotum and lighter coloration; mate attraction: long interchirp interval, mean chirp rate = eight pulses/chirp, and pulse rate slows as a chirp progresses; Walker, 2011). Our team sent specimens and digitized mate attraction signals in August 2011 to D. B. Weissman, who confirmed our identification.

Laboratory-reared *G. assimilis* were housed in communal plastic storage bins ( $40 \times 64$  cm and 42 cm high) with  $10 \times 15$  cm mesh openings and ad libitum food (standard colony food: powdered Harlan Teklad Rodent diet no. 8604M; 24.3% protein, 40.2% carbohydrate, 4.7% lipid, 16.4% fibre, 7.4% ash), water and a cardboard egg carton shelter. Communal bins were kept in a greenhouse on a 14:10 h light:dark cycle at  $26 \pm 2^{\circ}C$ . Bins of juveniles were checked daily for adults. Adults used in our experiment were removed upon imaginal moult (i.e. day 0) and subsequently housed in individual containers (520 ml) with a  $4 \times 4$  cm mesh opening with ad libitum standard colony food, water and one small piece of a cardboard egg carton for shelter.

### Fights

On day 12 post imaginal moult, we weight-matched males (Adventurer SL Analytical balance model AS64, OHAUS Corporation, Pine Brook, NJ, U.S.A.) to no more than 10% weight difference (sensu Jang & Greenfield, 1998), as weight has been shown to affect fight outcome (Jang et al., 2008; Savage et al., 2004). We then painted each male's pronotum with a different coloured enamel nail polish to allow us to easily distinguish males during fights. On day 13–14 post imaginal moult, we fought 63 pairs of males; every fight was conducted in front of a two-female audience. The two female crickets were weight-matched to no more than 10% weight difference of each other (sensu Jang & Greenfield, 1998), as female weight can influence male mate choice (Bonduriansky, 2001). Males were fought only once and females observed only one pair of males. All males and females were 13–15 days post imaginal moult during the fight.

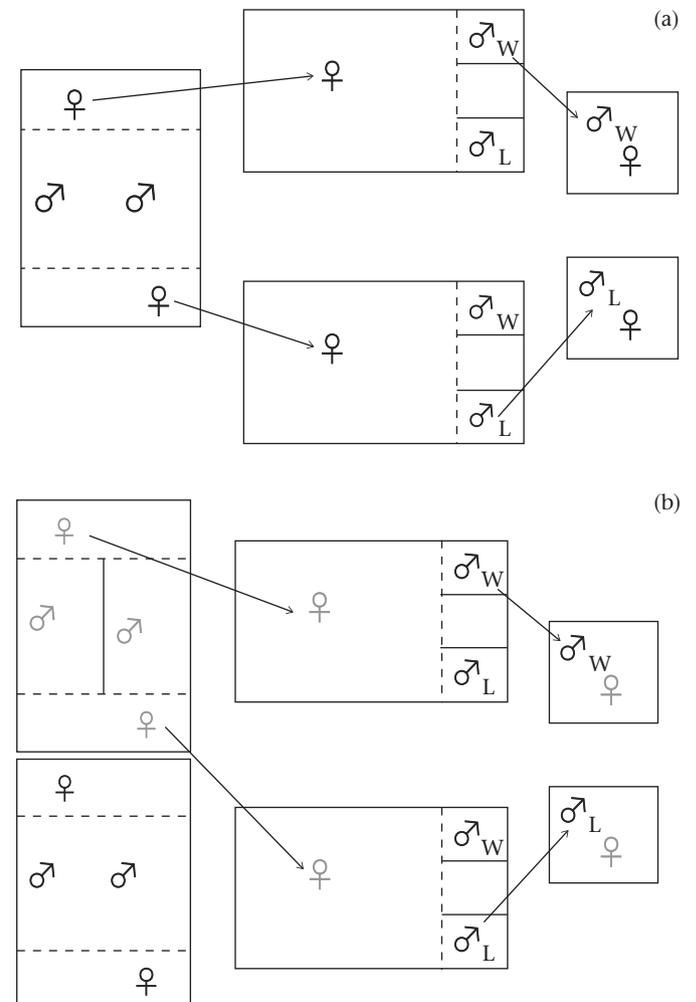
Prior to the start of each fight, we placed two male and two female crickets in a Plexiglas arena ( $16 \times 32$  cm and 21 cm high) with four separate chambers (Fig. 1a). Male and female chambers were separated by a perforated Plexiglas sheet to allow for transmission of chemical cues that may be important to cricket mating



**Figure 1.** Fighting arena, view from above. Location of males and females is indicated by sex symbols; perforated Plexiglas is indicated by a dashed line; nonperforated Plexiglas is indicated by a solid line. (a) Arena during acclimatization phase. (b) Arena during aggression trials.

(Rantala & Kortet, 2004), while preventing inter- and intrasexual selection from being conflated. The Plexiglas sheet separating the two males was nonperforated to prevent chemical signals from being exchanged prior to the fight. The bottom of the arena was covered in sand. After a 5 min acclimatization, we removed the Plexiglas partition between the two males (Fig. 1b) and recorded all male aggressive interactions for 15 min. We conducted all fights between 25 February and 13 September 2014 during 1400–2000 hours, under fluorescent lights, at  $25 \pm 0.5^{\circ}C$ . We cleaned the arena walls with 95% ethanol and raked the sand between each trial; we replaced the sand every four trials.

Our experiment consisted of two female treatments: Observers (Fig. 2a) and Non-observers (Fig. 2b). In the Observer treatment, the females observed a fight between two males and were then tested for mate preference between the fight winner and loser. In the Non-observer treatment, the females watched two (nonfocal) males that were not allowed to physically interact (during the 5 min acclimatization and the 15 min trial), and were then tested for mate preference between two other males who had just fought in front of two (nonfocal) female audience members. The Non-observer treatment controlled for the effect of familiarity with males on females' future mating decisions (Cheetham, Thom, Beynon, & Hurst, 2008) as well as for the effect of female audience on male aggression (Fitzsimmons & Bertram, 2013; Montroy et al., 2015).



**Figure 2.** Observer (a) and Non-observer (b) female treatments. Solid lines are opaque Plexiglas; dotted lines are transparent perforated Plexiglas.

### Mating Behaviour

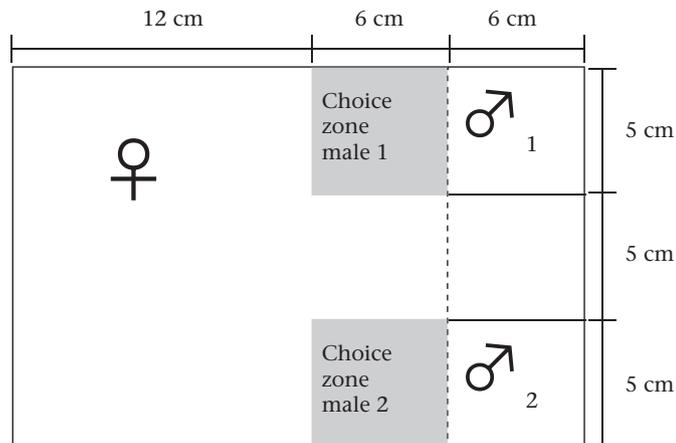
Immediately following the fights, we placed Observer and Non-observer females in a dichotomous mate preference test arena ( $16 \times 24$  cm and 21 cm high) and quantified their mating preferences for the fight winner and loser. We placed males in separate compartments divided by two opaque barriers to prevent males from seeing each other (Fig. 3; sensu Bluhm & Gowaty, 2004).

Observer females ( $N = 62$ ) chose between males they had seen fight whereas Non-observer females ( $N = 64$ ) chose between males they had not seen fight. We placed one of the focal females (order assigned by random number generator in R) in the centre of the female compartment under an opaque cup for a 2.5 min acclimatization period. We then removed the cup and quantified the amount of time the female spent in each male's choice zone. Each female's movements were scored for 7.5 min. To control for side bias, we then recaptured the female, swapped the males from one side to the other, replaced the female under the acclimatization cup, and then repeated the dichotomous choice test as described above. The Plexiglas separating the male and female compartments was transparent and perforated to allow for the transmission of visual, auditory and chemosensory cues. Although no males produced long-distance mate attraction signals during the dichotomous choice tests, one male produced courtship signals; while we included this male in all statistical analyses, our findings did not change if this male was excluded. The bottom of the dichotomous choice arena was covered in sand, raked between trials and changed after every four trials. Arena walls were wiped with 95% Ethanol between trials to reduce the effect of pheromones from earlier trials.

Immediately after all four dichotomous choice tests (two females  $\times$  two repetitions/ female) were complete, we paired each female with either a fight winner ( $N = 63$ ) or a loser ( $N = 63$ ). We assigned mating pairs at random using R's random number generator. We placed mating pairs in a square Plexiglas arena with sand in the bottom ( $13 \times 13$  cm and 18 cm high). During acclimatization (5 min), each male and female pair were separated by an opaque nonperforated barrier to reduce the chance of communication between individuals. We then removed the barrier and observed male and female interactions in these no-choice tests.

### Body Size

We photographed each male and female cricket dorsally (Panasonic Lumix ZS40, Mississauga, ON, Canada) and then used



**Figure 3.** Female choice arena, as seen from above. Solid lines represent opaque Plexiglas; dashed lines represent transparent perforated Plexiglas. Choice zones are indicated in grey.

ImageJ, v.1.48 (Rasband, 2015) to measure head width (maximum distance between the eyes), pronotum height (maximum distance down the length of the pronotum) and pronotum width (maximum distance transversally across the pronotum). Crickets were euthanized (frozen) before photographing.

### Scoring Behaviours

We recorded all fights and mating behaviours from above (Canon Vixia HG10, Mississauga, ON, Canada). We scored videos in real time using JWatcher, v.1.0 (Blumstein, Daniel, & Evans, 2000). For each fight, we recorded the winner and the loser. Fight winners and losers could be easily determined because winners often performed victory displays after a fight, which included body jerks (also known as juddering or body rock displays) or body jerks coupled with aggressive signalling (Alexander, 1961; Fitzsimmons & Bertram, 2013; Jang et al., 2008). Since fight reversions can occur (Fitzsimmons & Bertram, 2013), we only determined male dominance status after the loser had fled twice.

Females may use multiple cues to assess male dominance status, including the male's production of victory displays, whether he chases his opponent away, his fighting vigour, and whether he initiates the fight. While the focus of our study was on dominance status and not aggression, aggression level (male fighting vigour) could be important. We therefore also quantified each male's individual aggression level (detailed in Supplementary Table S1). Fight winners had significantly higher aggression intensity scores than fight losers (pairwise  $t$  test:  $t_{63} = 12.98$ ,  $P < 0.0001$ ), resulting in the potential for collinearity between dominance status and individual aggression intensity score.

For the dichotomous mate preference tests, we quantified the amount of time that females spent in each choice zone. Proximity to a male (or to speaker broadcasting a male call) has been used as a measure of choice in many cricket species (black field cricket, *Teloeoryllus commodus*: Shackleton et al., 2005; variable field cricket, *Gryllus lineaticeps*: Wagner & Reiser, 2000; reviewed in Jennions & Petrie, 1997). Since females need to mount males in order for mating to occur, displacement towards males needs to occur for mating to take place and thus may be a good indicator of choice. We calculated the proportion of time that female spent with the winner by dividing the amount of time each female spent with the winner by the amount of time she spent with either the winner or loser (i.e. the time spent in a choice zone). To calculate the overall preference score, we averaged the proportion of time that females spent with the winner in the first and second dichotomous choice tests. In case female preference weakened with time, we also calculated the proportion of time that females spent with the winner in the first trial only and compared our findings using both scenarios (the first trial only versus both trials). This alternative approach did not change our conclusions.

For the no-choice tests, we quantified courtship latency, either from the start of the trial to the start of juddering (cricket plants his feet and rocks his body back and forth), or from the start of courtship song, and mounting latency, from the onset of courtship to the first mounting, for up to 60 min.

### Statistical Analysis

We analysed all data using JMP, v.12.0.0 (SAS Institute, Cary, NC, U.S.A.). We used  $t$  tests to assess whether females preferred winners over losers in the dichotomous choice tests, and to assess whether the proportion of time that females spent in the winning male's choice zone, relative to either choice zone, differed from 0.5. To ascertain whether watching a fight affected preference, we ran two  $t$  tests, one for the Observers and one for the Non-observers.

We used a nominal logistic regression to assess whether females mounted winners more than losers and whether male aggression affected female preference in the no-choice tests. Whether or not a male was mounted was the dependent variable. We included male status (winner or loser), female treatment (Observer or Non-observer) and average trial aggression intensity score as the main effects. We included average trial aggression intensity score (details provided in [Supplementary Table S1](#)) to control for the effect of fight intensity. We used average trial aggression and not individual aggression because of a lack of independence: male–male aggression follows a stereotypic pattern of escalating behaviour, and males will only escalate if the other male also escalates ([Adamo & Hoy, 1995](#); [Alexander, 1961](#)). As such, the behaviour of the winner affects that of the loser and vice versa. Furthermore, individual aggression level is correlated with dominance status, resulting in collinearity. Since our primary aim was to explore whether females prefer dominant males over subordinate males (and not whether females prefer more aggressive males), we prioritized the dominance variable and used average trial aggression to control for the influence of overall aggressiveness on male physiology ([Stevenson & Rillich, 2015](#)). We also included whether or not a male was preferred in the dichotomous trials as a main effect. We included an interaction between female treatment and male status, and male size and status. The main effects of male and female size were used to control for the effects of body morphology. We tested for normality by assessing heteroscedasticity and the distribution of residuals. Assumptions of normality were not violated.

For the females that mounted their potential mates, we used a general linear model with restricted maximum likelihood to examine how mating latency (interval between time to court and time to mount) was influenced by dominance and morphological variation. We tested for normality by assessing heteroscedasticity and the distribution of residuals. We log transformed the data to fit parametric assumptions. We included male status (winner or loser), female treatment (Observer or Non-observer), their interaction, and whether or not a male was preferred as main effects in the model. We included female and male body size and the trial's average aggression intensity score as covariates. The first principal component was a good measure of overall size for both females and males (eigenvalue = 2.43 and 2.55, respectively), explaining 81% and 85% of the variation, and female and male body size and the trial's average aggression intensity score were weighted virtually equally in the first principal component. We also included an interaction of male size and male dominance in the model. Throughout, when interactions were nonsignificant, we reanalysed the models without the interaction terms, and we present the simpler models.

## RESULTS

Females did not prefer winners over losers in the dichotomous choice test ( $t$  test:  $t_{113} = -0.171$ ,  $P = 0.568$ ), regardless of whether they had observed the fight ( $t$  test:  $t_{55} = -0.202$ ,  $P = 0.580$ ) or not ( $t$  test:  $t_{57} = -0.041$ ,  $P = 0.517$ ). Using data only from the first replicate (in case female preferences weakened over time), instead of summing the time spent with males across both replicates, yielded the same qualitative results for all analyses described above ( $t$  test: overall:  $t_{113} = -0.075$ ,  $P = 0.530$ ; Observer females:  $t_{55} = 0.590$ ,  $P = 0.279$ ; Non-observer females:  $t_{57} = -0.682$ ,  $P = 0.751$ ). Following the dichotomous choice trials, females were randomly partnered with either their preferred or nonpreferred mate and observed for a period of 1 h. While only half of the females mounted males (62 out of 126) during this period, females were significantly more likely to mount the male if he was preferred (39/56 = 70%) than if he was not preferred in the dichotomous choice

test (17/56 = 30%; in six cases, the females did not show a preference for the winner or loser in the dichotomous choice test; [Table 1](#)). Similarly, females were significantly more likely to mount the male if he was dominant (had won the fight; 37/62 = 60%) than if he was subordinate (had lost the fight; 25/62 = 40%; [Table 1](#)). Females were also more likely to mount larger males, especially if the males were losers ([Table 1](#), [Fig. 4](#)). Female treatment (Observers versus Non-observers) and trial aggression were not significant ([Table 1](#)). Female latency to mount was not influenced by male dominance, female observation status, average aggression level of the fight or body size ([Table 2](#)).

## DISCUSSION

Male *G. assimilis* fight to obtain access to a territory used in acoustic mate attraction. Recently we revealed that male *G. assimilis* dynamically adjust their aggressive behaviour depending on social context; males are more likely to initiate and escalate fights in the presence of a female audience than when no audience is present ([Montroy et al., 2015](#)). Given that fight initiation and escalation involve elevated costs, dynamically adjusting aggressive behaviour may be an adaptation that provides reproductive benefits. Female presence alone might provide a valuable enough resource for the males (resource defence hypothesis). However, if females simultaneously prefer dominant or more aggressive males as mates (female preference hypothesis), fight winners may gain an added reproductive benefit. Evidence of audience effects in *G. assimilis* prompted us to examine how male dominance within a social network influences female mate choice.

Our no-choice mating trials revealed that females are more likely to mount and attempt to mate with fight winners than with fight losers. Winning a fight therefore both provides the male access to a signalling territory and increases the male's attractiveness to potential mates. Given this support for the female preference hypothesis, intra- and intersexual selection appear to positively reinforce selection on male aggressive behaviour. Our findings align with many other studies showing that more dominant males are preferred by females as mates (wild yak, *Bos mutus*: [Buzzard, Xu, & Li, 2014](#); elephant seal, *Mirounga angustirostris*: [Cox & Le Boeuf, 1977](#); birds: *L. megarhynchos*: [Kunc et al., 2006](#); reptiles: *A. garmani* and Jamaican twig anole, *Anolis valencienni*: [Trivers, 1976](#); crayfish: *P. clarkii*: [Aquiloni et al., 2008](#); house crickets: *A. domesticus*: [Savage et al., 2004](#)). The probability of a female mounting a male was also influenced by male body size, with females preferentially mounting larger males. This finding aligns with previous studies on field cricket mating preferences ([Bertram et al., 2016](#); [Harrison, Raubenheimer, Simpson, Godin, & Bertram, 2014](#)).

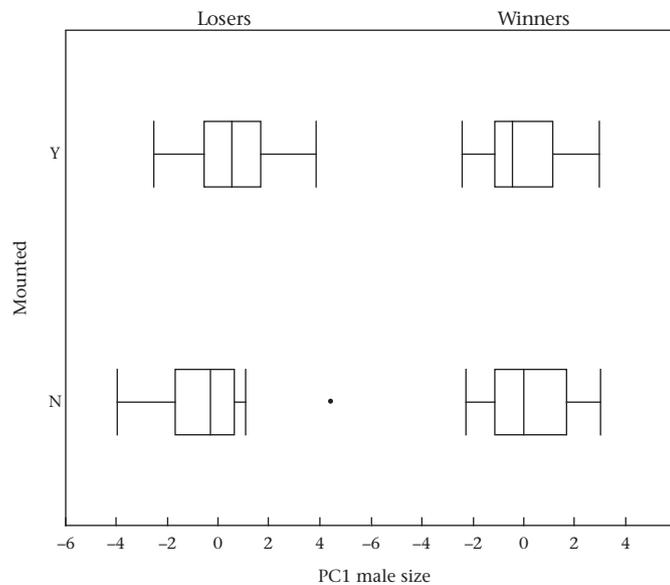
Even though female *G. assimilis* prefer fight winners, they do not appear to be gathering information solely on male dominance from watching the fights, given that Non-observers (blind to the fight)

**Table 1**

Nominal regression results analysing the effects of male status and aggression and female treatment and preference on mounting likelihood

Source	R <sup>2</sup>	df	χ <sup>2</sup>	P
<b>Overall model</b>	<b>0.152</b>	<b>7</b>	<b>24.049</b>	<b>0.001</b>
Female treatment		1	0.507	0.477
<b>Male status</b>		<b>1</b>	<b>5.032</b>	<b>0.025</b>
<b>Male size</b>		<b>1</b>	<b>5.613</b>	<b>0.018</b>
Female size		1	0.922	0.337
Trial aggression		1	2.12	0.145
<b>Preferred or nonpreferred</b>		<b>1</b>	<b>5.539</b>	<b>0.019</b>
<b>Male size * male status</b>		<b>1</b>	<b>4.160</b>	<b>0.041</b>

Significant results are shown in bold.



**Figure 4.** Mounting likelihood of males given status (winner or loser) and body size. The line within each box denotes the median, boxes denote interquartile ranges, and whiskers denote the highest and lowest values, excluding outliers. Dots denote outliers. Y: yes; N: no.

did not significantly differ from Observers (watched the fight) in their mating preferences. Females may use nonvisual chemosensory cues such as cuticular hydrocarbons (CHCs) to detect winners. This finding aligns with a handful of other studies suggesting that females can use nonvisual chemosensory cues to detect male dominance (e.g. field crickets, *G. integer*: Kortet & Hedrick, 2005; *T. oceanicus*: Thomas & Simmons, 2009; cockroaches, *N. cinerea*: Moore et al., 2001; bank voles, *C. glareolus*: Kruczek, 1997; humans: Havlicek et al., 2005). It is also possible that females use behavioural cues other than those examined here to detect male position within the dominance hierarchy. While there was no significant difference between the courtship latency of dominant and subordinate males (see Supplementary Table S2), some other behavioural differences may exist between these males. Future studies should investigate the behavioural cues of both types of males to assess whether females may be able to identify male dominance by behavioural cues as well as chemical cues. Our finding that females do not have to observe fights in order to identify winners suggests that audience effects in this system are not being driven by selection for females to eavesdrop.

A previous study by Savage et al. (2004) also found that females are more likely to prefer dominant males despite not having watched fights. Males in Savage et al.'s (2004) study varied considerably in body size, so females may have been able to use differences in body size to assess male dominance. We more closely size-matched males in our study, with the result that female preference was not significantly dependent on male size.

Females may use male juddering to identify dominant males. Male fight winners judder as part of a victory display (Bertram, Rook, & Fitzsimmons, 2010); males also judder as part of their courtship display (Tachon et al., 1999). Juddering in the no-choice trials may allow females to identify dominant males. Juddering was never observed in the dichotomous choice trials, possibly contributing to why females did not show a mating preference in the dichotomous choice tests. While juddering in other species is a multimodal signal (e.g. brush-legged wolf spider, *Schizocosa ocreata*: Gibson & Uetz, 2008), it is unknown whether males show extensive variation in their juddering behaviour and whether females use these differences to identify suitors. Juddering may communicate information on male energy reserves (wolf spiders, *Hygrolycosa rubrofasciata*: Kotiaho, 2000), and thus perhaps quality, or juddering may stimulate females to mate (scorpion, *Centruroides margaritatus*: Briceño & Bonilla, 2009; web-building spider, *Stegodyphus lineatus*: Maklakov, Bilde, & Lubin, 2003). Future research should investigate the use of juddering as a courtship display as well as male variation in juddering behaviour, and whether females can use differences in juddering to identify dominant males.

#### *Effectiveness and Shortcomings of Dichotomous Choice Tests*

Whether or not a female mounted a male during the no-choice trials was significantly correlated with female preference during dichotomous choice tests. Given that mounting is a reliable indicator of mating success (Shackleton et al., 2005), no-choice trials appear to be a good indicator of overall female mating preferences.

Interestingly, however, females did not prefer fight winners over losers in dichotomous choice tests even though they showed a significant preference for them in no-choice tests. Dichotomous choice tests may not allow females to gather enough information about male dominance to influence their preference, possibly because the perforated transparent Plexiglas limited the transmission of CHCs. Female preference for winners over losers may have occurred in the no-choice tests because females were better able to assess male quality, as the female freely interacted with the male. Caution is warranted in the use of dichotomous choice tests; future dichotomous choice tests should allow for a greater degree of chemosensory transmission between males and females while still preventing males from showing courtship interference.

Although females were more likely to mount winning males, there was no effect of male dominance on mating latency, unlike other studies (Shackleton et al., 2005). This may be due to our small sample size given that half of the females were excluded from the analysis because they did not mount within the 60 min observation period. While observing the trials until first mounting may have eliminated this problem, it would not have been relevant to situations in the wild. In the wild, crickets are free to roam. Given that females control mating (Alexander, 1961), if they do not mount the male immediately after courtship, then they might be more likely to leave the area.

**Table 2**  
GLM results analysing the effect of male dominance status and female fight observation on mounting latency

Source	$R^2_{adj}$	df	Estimate	t	F	P
Overall model	-0.071	6, 48			0.612	0.719
Female treatment (Non-Observer)			-0.219	-0.87		0.388
Male status (Loser)			-0.077	-0.32		0.753
Male PC1			-0.195	-1.17		0.247
Female PC1			0.080	0.45		0.655
Average aggression			-0.002	-0.73		0.472
Preference (Nonpreferred)			0.069	0.27		0.790

Females preferred larger males, as they were more likely to mount them. Females may prefer to mount larger males because large males signal more attractively, producing louder signals and with lower carrier frequencies (Bertram et al., 2016; Pacheco & Bertram, 2014). Males also seem to prefer larger females, as males started courting larger females more quickly than smaller females (Supplementary Table S2).

While mating latency and probability of mounting provide measures of reproductive success (Bateman, 1998; Simmons, Thomas, Simmons, & Zuk, 2013), direct measures of reproductive success, such as number of eggs laid, hatchability, survival to adulthood and offspring adult size, would be preferable. These direct measures of reproductive success incorporate the dual factors of cryptic female choice and male sperm viability. Male dominance could affect male sperm quality (e.g. *T. oceanicus*; Thomas & Simmons, 2009) and egg-laying rate (e.g. *G. bimaculatus*; Bretman, Rodríguez-Muñoz, & Tregenza, 2006). Females may also benefit from mating with preferred males because of increased fertility (e.g. *G. lineaticeps*; Wagner & Harper, 2003) or increased life span (e.g. *G. lineaticeps*; Wagner, Kelley, Tucker, & Harper, 2001). To gain a more complete understanding of the effect of fight observation on fitness, future studies should assess how male dominance and the information that females gather while watching fights affect subsequent fecundity, egg-hatching success, juvenile-to-adult moulting success and offspring size. These studies are currently underway in our laboratory.

## Acknowledgments

We thank Sarah J. Harrison, Genevieve Ferguson and Amy Villarreal for their comments on a draft of this paper. This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (no. RGPIN 327856), the Canadian Foundation of Innovation, the Ontario Research Fund (Project no. 13207), the Animal Behavior Society and Carleton University.

## Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.01.020>.

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