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

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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.

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 (Khazraïe & 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, *Gastrerosteus 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, *Libanasidus vittatus*: Bateman & Toms, 2013; house cricket, *Acheta domesticus*: 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. domesticus*: 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