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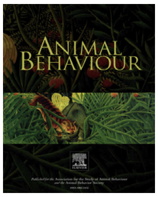

The effect of sire dominance and aggression on fitness measures in a field cricket (*Gryllus assimilis*)

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A R T I C L E I N F O

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Theory stipulates that females should prefer to mate with higher-quality mates to maximize their fitness. As such, traits that females prefer should be honest indicators of male quality. Dominant males are often higher quality, and mating with dominant males may confer indirect fitness benefits to females. Male Jamaican field crickets, *Gryllus assimilis*, fight more aggressively in front of a female audience than when there is no audience present. Males may increase their aggression because females prefer to mate with males who they have seen win a fight. To test this hypothesis we first allowed females to observe (treatment) or not observe (control) fights and then mated females to either fight winners or losers. We then assessed the following fitness measures: number of eggs oviposited, egg viability, offspring viability and offspring size at adulthood. Neither male fight victory status nor female observer/nonobserver status influenced any of the aforementioned female fitness measures; however, the aggressiveness level of the fight did. Females that mated with males that had participated in more aggressive fights produced offspring that were larger at adulthood. Given that females find larger males more attractive, and larger females oviposit more eggs, these larger offspring may experience greater reproductive success and as a result provide females with indirect fitness benefits.

Due to the high costs associated with selecting a mate and producing eggs, selection should favour traits that increase females' fitness while simultaneously minimizing their reproductive costs. Direct fitness benefits provide a simple explanation for why females have evolved mating preferences. Indirect fitness benefits (fitness benefits to offspring) may also explain female mating preference evolution (Fisher, 1930). The good genes hypothesis posits that elaborate sexual traits reflect their bearers' health and viability (Fisher, 1930; Hamilton & Zuk, 1982; Zahavi, 1975). Provided that both elaborate traits and female preferences are heritable, offspring should inherit their father's good genes for health and viability, and their mothers' good genes for preference, resulting in increased fitness. Females should therefore be selected to mate with males that enable them to produce high-quality offspring.

Females have been shown to gain indirect reproductive benefits by mating with better courters (wolf spider, *Pardosa milvina*: Hoefler, Carlascio, Persons, & Rypstra, 2009), better fathers (great tit, *Parus major*: Norris, 1993), more attractive males (e.g. males that females were more likely to mount) (house cricket, *Acheta domesticus*: Head, Hunt, Jennions, & Brooks, 2005) and brighter males (European kestrel, *Falco tinnunculus*: Palokangas et al., 1994; male blue grosbeaks, *Guiraca caerulea*: Keyser & Hill, 2000). However, despite the prevalence of empirical examples supporting the good genes hypothesis, a meta-analysis found only a small effect of elaborate traits on offspring fitness (Møller & Alatalo, 1999). Møller and Alatalo (1999) posited that this small effect size may be the result of only looking at how elaborate traits affect offspring survival in a laboratory, instead of other important life history traits.

The small effect size reported by Møller and Alatalo (1999) may also be due to the fact that elaborate traits can sometimes be dishonest indicators of quality, especially when elaborate traits are only used in mate attraction (Berglund, Bisazza, & Pilastro, 1996). Elaborate traits that are simultaneously used in both mate attraction and male–male competition should more honestly reflect quality because of the energetic and injury costs associated with competitive interactions, and because a male's position within the dominance hierarchy is repeatedly contested (Berglund et al., 1996). Thus, females may be selected to prefer dominant males as mates as their intrasexually selected traits may honestly reflect their quality, resulting in higher quality offspring.

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Females of many species prefer more dominant males (Atlantic salmon, *Salmo salar*: Järvi, 1990; elephant seals, *Mirounga angustirostris*: Cox, 1981; nightingales, *Luscinia megarhynchos*: Kunc, Amrhein, Naguib, 2006; field crickets, *Gryllus integer*: Kortet & Hedrick, 2005; humans, *Homo sapiens*: Giebel, Weierstall, Schauer, & Elbert, 2013). Female preference for dominant males may lead to direct reproductive benefits. For example, dominance is an honest indicator of male parental care quality in threespine sticklebacks, *Gasterosteus aculeatus* (Candolin, 2000). Dominance is also linked with the ability to obtain and defend resources, which females can access when mated to a dominant male (resource-holding potential; Qvarnström & Forsgren, 1998). Female preference for dominant males may also lead to indirect reproductive benefits. For example, dominant males may produce more dominant offspring (bank voles, *Clethrionomys glareolus*: Horne & Ylönen, 1998; common cockroach, *Nauphoeta cinerea*: Moore, 1990; Japanese quail, *Coturnix japonica*: Nol, Cheng, & Nichols, 1996; domestic dogs, *Canis familiaris*: Pérez-Guisado, Lopez-Rodríguez, & Muñoz-Serrano, 2006; deer mice, *Peromyscus maniculatus bairdi*: Dewsbury, 1990).

Given that it can be beneficial for females to mate with males that are more dominant, females may be selected to pay attention to competitive interactions between potential mates to aid in distinguishing fight winners from losers. Female black-capped chickadees, *Poecile atricapillus*, for example, base their mating decisions on their partner's dominance status, males who lost song playback interactions within earshot of their female partner suffered reduced paternity compared to those who won these aggressive interactions (Mennill, Ratcliffe, & Boag, 2002). Females sometimes even incite fights between males and then mate with the winners (wild yak, *Bos mutus*: Buzzard, Xu, & Li, 2014; elephant seals: Cox & Le Boeuf, 1977; several songbird species: Montgomerie & Thornhill, 1989).

Preferring dominant males can also have detrimental effects, as dominant males can be mediocre or poor fathers (sand goby, *Pomatoschistus minutus*: Forsgren, 1997) and can cause their mates harm (Japanese quail: Ophir & Galef, 2003). Furthermore, dominant males do not always produce higher-quality offspring (male brown trout, *Salmo trutta*: Jacob et al., 2007). It is important to consider these potential trade-offs when evaluating the costs and benefits of reproduction, especially given that these trade-offs are often species specific (Kokko, Brooks, Jennions, & Morley, 2003; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005).

Here we used the Jamaican field cricket, *Gryllus assimilis,* to determine how mating with fight winners (dominant males) or losers (subordinate males) influenced females' subsequent fitness. To assess the potential female fitness benefits associated with mating with a fight winner versus a fight loser, we quantified the number of eggs females oviposited, egg-hatching success (egg viability), offspring success at achieving adulthood (offspring viability) and offspring size at adulthood. Offspring size at adulthood should be a strong indicator of future reproductive success because larger males are more preferred by females as mates (Bertram et al., 2016; Loranger & Bertram, 2016), and larger females oviposit more eggs (Bertram et al., 2016).

Females either watched the fight (observers) or did not watch the fight (nonobservers) prior to being mated to the fight winner (dominant male) or loser (subordinate male). We included a female observer treatment because male aggression level is influenced by who is watching; males fight more aggressively when a female audience is present than when no audience is present (Jamaican field cricket: Montroy, Loranger, & Bertram, 2016; spring field cricket, *Gryllus veletis*: Fitzsimmons & Bertram, 2013; field cricket, *Gryllus bimaculatus*: Simmons, 1986b). Audience effects occur when actors (male fighters) change their behaviour based on the presence of an audience (in this case, females; McGregor & Peake, 2000). Given that increased aggression bears energetic costs (Hack, 1997), this elevated aggression is unlikely to have evolved without a reproductive benefit. The presence of females in the territory may be enough of a reproductive benefit for males to elevate their aggression levels (resource-holding potential hypothesis; Qvarnström & Forsgren, 1998). However, our companion study also revealed that female *G. assimilis* prefer to mate with fight winners: we found that females were more likely to mount male winners than they were to mount losers in no-choice tests (Loranger & Bertram, 2016). If females preferentially allocate resources to the offspring of males that have won fights, females should oviposit more eggs when mated to fight winners. If females can determine which males have won fights based on nonvisual cues, female oviposition behaviour should not depend on observer status. However, if watching a fight informs female behaviour, then observers and nonobservers should show different reproductive investment, with observers ovipositing more eggs than nonobservers when mated to fight winners. Support for this last prediction would suggest an eavesdropping effect (McGregor & Peake, 2000).

Differences in offspring number, viability and/or size at adulthood could result from variation in dam investment in offspring (Smith & Fretwell, 1974), dominant sires having higher-quality sperm (Thomas & Simmons, 2009) and/or dominant sires being better able to manipulate dam fecundity via the production of seminal proteins (Bretman, Rodríguez-Muñoz, & Tregenza, 2006). While our experiment does not tease apart the underlying causes, it quantifies whether or not females that mate with fight winners have higher fitness, and whether observing the fight influences female fitness.

METHODS

Our study was conducted in accordance with the guidelines of the Canadian Council on Animal Care. We caught *G. assimilis* in Bastrop County, Texas, U.S.A. near Stengl Lost Pines Biological station of the University of Texas at Austin (~30°17′N, ~97°46′W) on 15–24 September 2008 (no field collecting permits were required). We imported *G. assimilis* into Canada (import permits were not required) and then reared them in communal plastic storage bins (64 × 40 × 42 cm) with 10 × 15 cm mesh openings and ad libitum food (powdered Harlan Teklad Inc. Rodent diet no. 8604M; 24.3% protein, 40.2% carbohydrate, 4.7% lipid, 16.4% fibre, 7.4% ash), water and cardboard (egg carton) shelter. We kept communal bins in a greenhouse with 14:10 h light:dark illumination regime at a mean ± SD temperature of 26 ± 2 °C; the greenhouse has plant pest containment level 1 certification (PPC1: PC-2014-053).

We used crickets that were reared in the laboratory for approximately 19–20 generations. To initiate our experiment, we checked bins of juveniles every weekday and removed individuals as soon as they underwent their imaginal moult. We housed these new adults in individual containers (520 ml) with a 4 × 4 cm metal mesh opening with ad libitum food, water and one small piece of a cardboard egg carton as shelter. When males reached 12 days postimaginal moult we weight-matched (to 10% weight difference) pairs and then painted their thorax with different colours of nail enamel to enable identification during fights. We fought pairs of males in front of a two-female audience (detailed in Loranger & Bertram, 2016) when males and females were 13–15 days postimaginal moult. Fights lasted 15 min. We quantified fight outcome by determining which male fled from the other male twice in a row (Fitzsimmons & Bertram, 2013); the fleeing male was identified as the fight loser (subordinate male) and the other male was identified as the fight winner (dominant male). Fight winners also usually produced victory displays (Alexander, 1961; Fitzsimmons & Bertram, 2013; Jang, Gerhardt, & Choe, 2008). We recorded fights