

The effect of male-male fight observation on female choice
and offspring quality in *Gryllus assimilis*

by

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Abstract

Theory suggests that behaviours previously thought only to play a role in intrasexual selection can also be co-opted to serve as honest indicators of male quality. In *Gryllus assimilis*, males fight more aggressively in front of a female audience; their elevated aggression may serve as a mate attraction signal. I investigated how observing a fight influenced various measures of reproductive success. I had two treatments: (1) females observed a fight between two males or (2) females observed two non-interacting males. I then assessed female mate preference using dichotomous and no-choice tests. After mating, I allowed females to lay eggs and raised a subset of their offspring to adulthood. Females were more likely to mount dominant males, regardless of whether they had watched the fight, but dominant males did not have increased fecundity, viability, or offspring size. Audience effects in this species may not have evolved due to eavesdropping.

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GENERAL INTRODUCTION

Linking Inter- and Intra- Sexual Selection

Elaborate traits, such as the bright coloration of peacock feathers, baffled Darwin (Darwin, 1860). These traits make the bearer more conspicuous to predators thus reducing their chance of survival. However, the prevalence of these traits can be explained by their reproductive benefit, or sexual selection. Sexual selection is the process by which the prevalence of certain traits in a population increases due to the reproductive benefit they incur. These traits can act by increasing the bearer's ability to attract mates (intersexual selection) or by increasing the bearer's ability to win fights with same-sex conspecifics over resources or mates (intrasexual selection) (Darwin, 1871). In the past, intrasexual and intersexual selection were seen as separate, often opposing, forces shaping secondary sexual traits and behaviours (Qvarnström & Forsgren, 1998). More recent research and theory suggests that there may be a more complex and tight link between the evolution of intra- and intersexual traits (Wong & Candolin, 2005). Berglund et al., (1996) suggest that males evolve traits used in male-male competition (i.e. armaments), and in turn females can use these traits as indicators of honest genetic quality (i.e. ornaments). This duality was first explored in morphological and physiological traits such as the epaulettes of red-shouldered widow-birds, *Euplectes axillaris*, horns of mountain sheep, *Ovis canadensis*, eye span in the stalk-eyed fly, *Cyrtodiopsis whitei*, etc. (see Wong & Candolin, 2005 and Berglund et al., 1996 for a review). This duality can also be applied to behavioural traits such as aggression.

Aggression can be a secondary sexual trait; females of many species, including humans (Giebel et al., 2013), have been found to prefer aggressive mates (Archer, 2009; Trivers, 1976).

Studies have also shown that traits correlated with increased aggression, such as burrow ownership in crickets (*Teleogryllus oceanicus*) (Thomas & Simmons, 2009) and territoriality in Jamaican Lizards (*Anolis garmani*) (Trivers, 1976), lead to increased reproductive success. Although aggression does not directly correlate with dominance, aggressive interactions can determine dominance and serve to enforce dominance hierarchies (Aquiloni et al., 2008; Khazraie & Campan, 1999). It is thus possible that female preference for more aggressive males occurs because it is linked with dominance, and dominant males often have higher reproductive success. For example, dominant male Atlantic salmon (*Salmo salar*) are more likely to gain access to and mate with fertile females (Järvi, 1990). Further, female elephant seals (*Mirounga angustirostris*) prefer to mate with dominant males who have just won a contest (Cox, 1981). In several species of songbirds, females incite male-male competition so that they can assess male dominance levels (Cox & Le Boeuf, 1977; Montgomerie & Thornhill, 1989). Female wild yak (*Bos mutus*) also incite fights between males and mate with more dominant individuals (Buzzard et al., 2014). Because males often fight, dominance hierarchies are often contested, and thus recent fight wins/loses tend to reflect current male fighting ability, a reflection of current male quality (Khazraie & Campan, 1999). As such, preference for more dominant males may be adaptive because it may confer some advantage to females.

Female Benefits to Preferring Dominant Males

Females' preference for dominant or aggressive males could be explained through the Handicap hypothesis, good genes hypothesis, or by direct benefits. Zahavi's handicap hypothesis

stipulates that for traits to be honest indicators of male quality, and thus for preference to be adaptive, the bearer of these traits must incur a cost (Zahavi, 1975). Intrasexual competition can be costly due to its energetic costs as well as possible injuries and death. Male fights in thrips (*Hoplothrips karnyi*) can often escalate and even lead to death if the males are similarly matched and fighting over females (Crespi, 1988). If, as stipulated by Zahavi's hypothesis, male fighting ability serves as an honest signal of male quality, it could also indicate good genes (Berglund et al., 1996). Thus mating with dominant males may offer indirect mating benefits to females in the form of good genes for offspring (Rantala & Kortet 2004). In bridge weaving spiders (*Lariniodes sclopetarius*) aggressive fathers have been found to sire more successful offspring (Kralj-Fiser et al., 2013). If dominance is an indicator of immunocompetence, as it is in *Gryllus bimaculatus*, mating with dominant males may ensure higher offspring quality because of the significant heritable component of immunocompetence (Rantala & Kortet, 2004). In several species, dominant fathers sire dominant sons (cockroach, *Nauphoeta cinerea*: Moore, 1990; deer mice, *Peromyscus maniculatus bairdi*: Dewsbury, 1990; bank voles, *Clethrionomys glareolus*: Horne & Ylönen, 1998; Japanese quail, *Coturnix japonica*: Nol et al., 1996)

Dominance could also lead to other non-genetic, direct benefits, given dominance is linked with the ability to obtain and defend resources (resource holding potential; Qvarnström & Forsgren, 1998). In species where males control resources females require for reproduction, dominant males can enjoy greater reproductive success than subordinate males (Simmons, 1986a). Increased aggression in males has also been found to be associated with increased parental care in the three-spine stickleback, *Gasterosteus aculeatus* (Candolin, 2000). In species

where dominance has clear physiological markers, such as when ornaments are armaments, females can determine social rank by assessing physiological traits (Berglund et al., 1996). However, when social rank has no clear physiological indicator (i.e. there are no armaments), females must instead observe interactions between males to determine dominance (Wong & Candolin, 2005).

Fighting and Mate Choice Occur in a Communication Network

Fights between males often occur in a social context with observers. In the past, aggressive calls and other visual cues that are exchanged during a fight were thought to be exchanged solely between the two participants of a fight (McGregor & Peake, 2000). However, recent studies have begun to view fights and the information they convey about male quality as occurring within a communication network (McGregor & Peake, 2000). Current research focuses on the other individuals that observe or listen to fights and how these individuals use the information gained while watching fights to base future behavioural decisions (i.e. to fight or not, to mate or not, etc.). For instance, female fighting fish (*Betta splendens*) that watched males fight preferred winners more than females that had not watched fights (Doutrelant & McGregor, 2000). Female wild yak (*Bos mutus*) mate preferentially with dominant males they have watched fight (Buzzard et al., 2014). Similarly, female crayfish (*Procambarus clarkii*) show an increased preference for fight winners (Aquiloni et al., 2008). In many bird species, song is an important component of aggressive interaction and increased song overlap in birds is a predictor of male dominance (Mennill & Ratcliffe, 2004). Kunc et al., (2006) analyzed the song of paired and unpaired

nightingales (*Luscinia megarhynchos*) and found that paired males had much more song overlap than unpaired birds, thus dominant males are more likely to obtain mates. Mennill et al., (2002) used song playback to experimentally manipulate male dominance hierarchies in black-capped chickadees (*Poecile atricapillus*) and found that when dominant males “lost” singing interactions, thus declining in the social hierarchy, their paternity decreased compare to males who had “won” or had no singing interaction. Thus females of many species use information they gain while eavesdropping on fights to make mating decisions, and they often prefer to mate with dominant males. This pattern is also apparent in sex-role reversed species, such as pipefish (*Syngnathus typhle*), where males prefer dominant females over attractive females (Berglund & Rosenqvist, 2001).

Female Preference for Less Aggressive and/or Subordinate Males

Despite the prevalence of preference for dominant males, life history traits play an important role in determining preference (Wong & Candolin, 2005; Kokko et al., 2003; Qvarnström & Forsgren, 1998). Female preference depends on the correlation between dominance or aggression and factors such as mate harm, courtship effort, resource holding potential, and heritable male quality (Wong & Candolin, 2005). Female three-spine sticklebacks (*Gasterosteus aculeatus*), for example, mate with less aggressive males despite showing equal initial interest in both aggressive and less aggressive males because aggressive males often break off courtship to attack other males, thus resulting in reduced courtship effort (Ward & FitzGerald, 1987). Mating with dominant males can sometimes be costly for females. Female

Japanese quail (*Coturnix japonica*) prefer to mate with dominant males (Ophir & Galef, 2004), unless they have seen the dominant male win a fight. Dominant males that have just won a fight tend to cause mate harm, and as such, females often choose to mate with subordinate males, possibly to reduce the possibility of mating injury at the cost of mating with a lower quality male (Ophir & Galef, 2003). Female Mexican live bearing fish (*Poecilia mexicana*) prefer to mate with non-dominant males for the same reason (Bierbach et al., 2013). In addition to mate harm, dominant males are also more likely to be sperm depleted (*Drosophila melanogaster*: Pitnick & Markow, 1994) and be vectors of disease and hosts of parasites (reviewed in Folstad & Karter, 1992; *Pan troglodytes schweinfurthii*: Muehlenbein & Watts, 2010). Further, dominant males do not always produce higher quality offspring (male brown trout, *Salmo trutta*: Jacob et al., 2007) and dominant males can also make poor or mediocre fathers (sand goby, *Pomatoschistus minutus*: Forsgren, 1997). Therefore, mate preference for dominant males depends on the species' life history.

Field Crickets

My research tested how aggression and dominance influence female mate choice and subsequent egg laying, offspring survival, and offspring condition, using Jamaican field crickets as a model organism. I focussed my study on field crickets because *Gryllinae* generally have a complex mating system that incorporates male-male aggression and acoustic mate attraction signalling (Alexander, 1961). Males compete with other males for access to territories and then use these territories to acoustically signal to attract potential mates. Males signal by raising their

forewings and rubbing them together. Each closing stroke produces a pulse of sound, and males concatenate these pulses into chirps. Females use male acoustic signalling to assess male quality (Bertram & Rook, 2012) to inform their mate preference. Because females must mount males for mating to occur, males cannot force copulations and thus mounting serves as an indicator of female choice.

Females have been found to prefer dominant males in many field cricket species, however some of the data are contradictory. Kortet & Hedrick (2005) found that field cricket, *Gryllus integer*, females prefer the scent of dominant over subordinate males when given the choice. In the African king cricket, *Libanasidus vittatus*, females tend to mate with dominant males when placed in an arena with six males that have previously established their dominance hierarchy (Bateman & Toms, 2013). Similar results were found when a female was placed with two male *Acheta domesticus* (Nelson & Nolen, 1997). Thus it seems that female crickets tend to prefer dominant males. However, the methods used to determine female preference may have skewed the results. When several males are placed with a female, the dominant males can suppress the courtship of subordinate males. Since females need to be courted to mate (Alexander, 1961), females would only mate with dominant males even if they may have an intrinsic preference for subordinate males. When male-male competition does not occur simultaneously with mate choice, such as in no-choice trials when a female is placed with a single male, female black field crickets, *Teleogryllus commodus* did not show decreased mating latency with dominant males, indicative of a lack of a preference for dominant males (Shackleton et al., 2005).

Male aggression also varies depending on the audience (Fitzsimmons & Bertram, 2013). A recent study of audience effects in the spring field cricket *Gryllus veletis* revealed that when males fought in front of a female audience, males were often more aggressive compared to when no audience was present (Fitzsimmons & Bertram, 2013). Similarly, in the Jamaican field cricket, *Gryllus assimilis*, males were found to fight more aggressively in front of a female audience than when there was no audience present (Montroy et al. submitted). Is there an adaptive reason for the increase in male aggression when females are watching? If females prefer dominant males as they do in many species (Alexander, 1961; Kortet & Hedrick, 2005; Simmons, 1986b; Simmons et al., 2013), perhaps more aggressive fights signal to females the males' dominance. How might preference for dominant males be adaptive for female crickets? In *Gryllus bimaculatus*, more aggressive and dominant males show evidence of increased immunocompetence (Rantala & Kortet, 2004). In addition, Thomas & Simmons (2009) have shown that dominant male *Teleogryllus oceanicus* have higher fertilization success. Further, dominant male *Gryllus bimaculatus* appear to be better able to control female oviposition rate, resulting in increased egg laying compared to females mated to subordinate males (Bretman et al., 2006). As such dominance may be an indicator of good genes or higher mate quality in many cricket species.

I tested for the effects of aggression and dominance on female mate choice (Chapter 1). In order to assess whether females use information from fights to inform later mating decisions, I had two separate trial types: Observer and Non-Observer females. In Observer trials, I fought males in front of a two female audience. These females subsequently chose between the males

they had seen fight. I then mated each female to either the fight winner or loser. In Non Observer trials, I fought males in front of a two female audience but, instead of evaluating the preference of the two females who had watched the fight, I evaluated the preference of two other females, who had watched two non-interacting males.

In Chapter 1, I tested whether eavesdropping on a fight between males influences female preference using simultaneous presentation trials (dichotomous choice trials) and no-choice trials. I also quantified the differences in female choice between winners and losers, and whether or not observing a fight influences preference. I hypothesized that fight winners would be preferred as mates and thus would have shorter mating latency regardless of whether or not females have watched the fight if females are able to detect male status through chemical signals (Kortet & Hedrick, 2005). Because males increase aggression when fighting in front of females (Fitzsimmons & Bertram, 2013), and there has been evidence that in some species females prefer more aggressive mates (Alexander, 1961; Kortet & Hedrick, 2005; Simmons, 1986b; Simmons et al., 2013), watching males win fights could impact female willingness to mate. This is either because they could gather more information on males or because watching fights increases female willingness to mate. If females exhibit an intrinsic preference for winning males, I predicted both Observer and Non-Observer females would prefer winning males. If, however, females had to eavesdrop on a fight to determine male dominance, then I predicted I would only see a preference for winners in Observer trials. Overall, I predicted that females would mate fastest with males they had watched win fights and slowest with fight losers and that females

who had not watched fights would mate with winners faster than losers but that their mating speeds would be intermediate to the Observer female pairs.

While mating latency and mounting provide indirect measures of mating success (Bateman, 1998; Simmons, 1988), measures of direct reproductive success such as number of eggs laid, hatchability, juvenile to adult moulting success and offspring size may better represent male fitness. Not only do these factors reflect male genetic quality, they are also affected by cryptic female choice and male sperm viability, which are measures of reproductive success that cannot be assessed by looking only at pre-copulatory measures. Previous research on the effect of dominance on post-copulatory measures has shown that male dominance is positively correlated to male sperm quality in *Teleogryllus oceanicus* (Thomas & Simmons, 2009) and their mate's egg laying rate in *Gryllus bimaculatus* (Bretman et al., 2006). In addition, research has found that females mated to preferred males gain direct benefits (increased fertility: Wagner & Harper, 2003; increased lifespan: Wagner et al., 2001). In order to better understand the effect of dominance on reproductive success, I also assessed various measures of post-copulatory reproductive success in *G. assimilis* in my second chapter. In Chapter 2, I tested whether mating with winners or losers of fights influenced the number of eggs laid by focal females, egg viability, and offspring size. Because of the possible correlation between aggression and good genes, I predicted that winners would have more offspring and that these offspring would be larger and have higher viability. If female preference leads to increased investment in offspring, I expect to see larger offspring when females are mated to winners that they had observed fighting versus losers or males whose fights they did not observe.

CHAPTER 1 - The effect of male dominance on female mate choice in a cricket (*Gryllus assimilis*)

1.1 - INTRODUCTION

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 attract mates (intersexual selection) or increase the bearer's ability to win fights with same-sex conspecifics over resources or mates (intrasexual selection). Research and theory in the past quarter century suggest a more complex relationship between the evolution of intra- and intersexual traits (Berglund, et al. 1996; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005). Size and development of traits used in intrasexual conflict determine male position within the social hierarchy (see Maynard Smith & Harper, 2003 for a review). Because male position within a hierarchy is often contested, male intrasexual traits should be honest indicators of male quality and dominance (Khazraie & Campan, 1999). Thus, females may be able to co-opt traits used in male-male competition in mate choice and as a result reinforce their inherent mating preferences (Berglund et al., 1996). Preference for dominant males has been seen in females of many species (in reptiles: Trivers, 1976; birds: Kunc et al., 2006; crayfish: Aquiloni et al., 2008; crickets, *Gryllus bimaculatus*: Simmons 1986a,b; and see Berglund et al., 1996 for a review).

Preference for more dominant males could lead to direct benefits for females, given that dominance is linked with the ability to obtain and defend resources (resource holding potential; Qvarnström & Forsgren, 1998). Dominance may also be a good indicator of

immunocompetence, since secondary sexual traits are often mediated by androgens, which in turn have an effect on immunocompetence (see Folstad & Karter, 1992 for a review). Males who can tolerate these immune costs are thought to be in better condition, and females can directly benefit from mating more dominant, immunocompetent males as it reduces their chances of infection or parasite transfer.

Preference for more dominant males could also lead to indirect benefits for females. Zahavi's handicap hypothesis stipulates that for traits to be honest indicators of male quality, and thus for mate preference based on these traits to be adaptive, the trait bearer must incur a cost (Zahavi, 1975). Intrasexual competition can be costly due to energetic costs as well as the possibility of injuries and death (house cricket, *Acheta domesticus*: Hack, 1997; thrips, *Hoplothrips karnyi*: Crespi, 1988). If male fighting ability serves as an honest signal of male quality, it could also indicate good genes for offspring (Berglund et al., 1996). The potential indirect benefits of mating with dominant males are further discussed in Chapter 2. Thus, there are many possible different, non-mutually exclusive, benefits to preferring more dominant males, resulting in intra- and inter-sexual selection being mutually reinforcing (Qvanstrom & Forsgren, 1998).

In some cases intra- and inter-sexual selection are not mutually reinforcing (see Qvanstrom & Forsgren 1998). Dominant males can cause mate harm (Japanese quail, *Coturnix japonica*: Ophir & Galef, 2003) and make mediocre or bad fathers (Pacific blue-eye fish, *Pseudomugil signifier*: Wong, 2004; sand goby, *Pomatoschistus minutus*: Forsgren, 1997). In addition, dominant males can be sperm depleted (*Drosophila melanogaster*: Pitnick & Markow,

1994) or be vectors of disease and hosts of parasites (reviewed in Folstad & Karter, 1992; *Pan troglodytes schweinfurthii*: Muehlenbein & Watts, 2010). Further, dominant males may not invest as much in mate attraction or courtship as subordinates (mate attraction: *Teleogryllus oceanicus*: Thomas & Simmons, 2009; courtship: threespine stickleback, *Gasterosteus aculeatus*: Ward & Fitzgerald, 1987). Thus, females sometimes find dominant males less attractive, resulting in intra- and inter-sexual selection working in opposition.

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 that shape secondary sexual traits and behaviours. It is therefore essential to test whether females prefer to mate with fight winners over losers. One caveat to consider in these tests is female ability to detect which males are most dominant. Since fights often occur within a social network, audience members can sometimes observe these fights (McGregor & Peake, 2000). Thus, unintended receivers (male or female) can use information that they glean from observing fights to inform later behaviour. Females can even incite fights between males (Elephant seals, *Mirounga angustirostris*: Cox & Le Boeuf, 1977; Wild yak, *Bos mutus*: Buzzard et al. , 2014; several bird species: Montgomerie & Thornhill, 1989). Females of many species prefer fight winners (fighting fish, *Betta splendens*: Doutrelant & McGregor, 2000; red swamp crayfish, *Procambarus clarkii*: Aquiloni et al., 2008; black-capped chickadees, *Poecile atricapilla*: Mennill et al., 2002). Since fights occur within a social network, and females can base mating decisions on fight observation, social networks can impact the evolution of communication signals, making the link between intra- and intersexual traits quite complex. To understand this

complexity, research on female preference should be conducted and interpreted within a social network framework and both intra- and intersexual selection should be tested for independently.

I examined how male dominance within a social network perspective influences female mate choice using Jamaican field crickets (*Gryllus assimilis*). *Gryllus assimilis* is an ideal species to use as fights between males are common since males fight for access to territories from which to signal to attract mates (Simmons, 1986b). Male-male fights follow a well-defined series of escalating behaviours and have clearly defined winners and losers (Adamo & Hoy, 1995; Bertram & Rook, 2012; Fitzsimmons & Bertram, 2013), allowing fight aggression levels to be quantified. Further, Jamaican field crickets mate and produce offspring readily in the laboratory environment, and their relatively short generation time lends well to cross-generational studies. Female crickets must also mount males for copulation to proceed (Alexander, 1961), ensuring they cannot be forced to mate, and mating latency has been shown to predict mating preference in related cricket species (Shackleton et al., 2005).

Montroy et al. (submitted) found that, when male *G. assimilis* fought in front of a female audience, males were more aggressive than when they had no audience. Similarly, Fitzsimmons & Bertram (2013) found that *G. veletis* males were more aggressive when fighting in front of a female audience than in front of a male audience or no audience. *Gryllus bimaculatus* also increases aggression in front of a female audience (Simmons, 1986b). This increased aggression bears a cost on males (Hack, 1997) and thus would have been unlikely to have evolved without a reproductive benefit. This potential benefit could be an increase in reproductive success if females prefer more dominant males. Therefore, I tested whether female eavesdropping on male

fighters influenced female mating decisions by fighting males in pairs, always in front of two female audience members.

To ascertain whether females had to watch a fight to be able to identify fight winners or losers, I set up two treatments, Observers and Non-Observers. Observer females watched a fight and were immediately mate-tested on the two males they watched fighting. Non-Observer females watched two non-interacting males and were then immediately mate-tested using two *other* males who had just fought in front of two other females, but had not been observed by the Non-Observer females. I included this latter treatment to determine if females could use non-visual cues (e.g., chemosensory cues) to detect male dominance without having observed the fights. In many species, there is a difference between the pheromones of dominant and subordinate males that females can sense (e.g. cockroaches, *Nauphoeta cinerea*: Moore et al. , 2001; bank voles, *Clethrionomys glareolus*: Kruczek, 1997; humans, *Homo sapiens*: Havlicek et al., 2005). Dominant and subordinate crickets may also exhibit chemosensory differences, as Kortet & Hedrick (2005) revealed that female *Gryllus integer* spent more time on paper filters where dominant males had stood relative to those on which subordinate males had stood even though the females had not interacted with either male or observed the males fight. In addition Thomas and Simmons (2009) found that subordinate *Teleogryllus oceanicus* males increase the number of cuticular hydrocarbons on their cuticle, possibly in an attempt to become more attractive to females. Therefore, females may be able to detect a difference between subordinate and dominant males that they can use to inform their mating preference. If females can discern whether males are dominant without watching fights, then both Observer and Non-Observer

females should prefer fight winners to losers. However, if females need to observe a fight to discern which male is more dominant, then only Observer females will prefer fight winners over losers.

There is some evidence to suggest that female crickets prefer dominant males. Simmons (1986b) placed six *Gryllus bimaculatus* males together in an arena with a female and burrows and found that females tended to prefer males that won more disputes, and thus more dominant males. Using the African king cricket, *Libanasisidus vittatus*, Bateman and Toms (2013) found that more aggressive males tended to have higher reproductive success when six males were placed with a single female. Nelson & Nolen (1997) found that when two male *Acheta domesticus* were allowed to establish dominance and a female was subsequently placed in the arena with them, the dominant male had higher mating success. Thus, in these cases, the males could interact with each other as well as the female, allowing the more dominant male to potentially interrupt the courtship of the subordinate male, which could affect female preference if intra- and intersexual selection work in opposing directions. Given a male cricket needs to court a female before the female will mount him (Alexander 1961), if the subordinate male is prevented from courting by the dominant male, he could not mate even if the female intrinsically preferred him. Thus investigations of female preference where males are prevented from interacting may serve as better indicators of female preference and may more accurately assess whether intra- and intersexual selection reinforce or disrupt one another. Intriguingly, in the aforementioned experiment, Nelson and Nolen (1997) found that, when a single male (either dominant or subordinate) and single female were placed together, female *A. domesticus* no

longer showed a preference for dominant males. In addition, when female *Teleogryllus oceanicus* are presented with one male and mating latency is used as an indicator of preference (no-choice tests), females do not prefer winners over losers (Shackleton et al., 2005). Thus it is possible that females only prefer dominant males because dominant males suppress the courtship of subordinate males because females need to be courted before they mount. However, Savage et al. (2004) found that female house crickets, *Acheta domesticus*, did prefer more dominant over subordinate males in no-choice tests, however these males had either lost or won several fights, thus making them “super” subordinate or dominant, respectively. Therefore, by placing a female in an arena with the two focal males, if intra- and intersexual selection work in opposite directions, competition between males may suppress the female’s inherent preference. This is why it is necessary to analyse female preference without male-male competition simultaneously occurring.

In my experiments I eliminated the possibility of courtship interference and assessed whether females intrinsically prefer winners over losers. I quantified female preference in two ways, (1) using a dichotomous choice test where each female (Observers and Non-Observers) could select between the fight winner and loser but where the fight winner and loser could not see each other, and (2) using a no-choice test where I placed each female (Observers and Non-Observers) at random with either the fight winner or the fight loser and quantified mounting latency. This dual approach allowed me to test the validity of no-choice tests while also assessing whether females preferred fight winners over losers. After I determined whether female audience members preferred male winners over losers and whether male dominance status affected female

mounting latency, I quantified whether the benefits of winning a fight included enhanced male mating success (reported in Chapter 2).

My study is one of the first to investigate the effect of eavesdropping on female choice. While a handful of studies have looked at the difference between naïve and experienced females when choosing between winners and losers (e.g., Judge, 2010; Ophir & Galef, 2004), these studies did not quantify the difference between these two female types in terms of mating latency, nor did they test how female preference is affected by eavesdropping on male fights. Thus my study investigated whether the cost of increased aggression in front of a female audience is alleviated by the benefit of increased reproductive success.

1.2 - METHODS

Cricket Rearing

The crickets I used in this experiment were lab-reared for 19-20 generations. The Bertram lab established the laboratory population of *Gryllus assimilis* using crickets caught in the field from September 15th to 24th, 2008 near Stengl Lost Pines Biological station of the University of Texas at Austin (latitude ~ 30° 17' N, longitude ~ 97° 46' W) in Bastrop County, Texas, United States. *Gryllus assimilis* were housed in communal plastic storage bins (64 x 40 x 42 cm) with 10 x 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% fiber, 7.4% ash), water, and cardboard (egg carton) shelter. Communal bins were kept in a greenhouse with 14:10 h light:dark illumination regime at a temperature of $\bar{X} \pm SD = 26 \pm 2$ °C. I checked bins of juveniles

every weekday for adults. I removed adults upon imaginal moult (i.e. day 0) and subsequently housed them in individual containers (520 ml) with a 4cm x 4cm mesh opening with *ad libitum* food, water, and one small piece of a cardboard egg carton for shelter.

On day 12 post-adult eclosion, I weight-matched males using one of two scales (Pinnacle Series model PI-314, Fisher Scientific, Ottawa, Ontario, Canada and Adventurer SL Analytical balance model AS64, OHAUS Corporation, Pine Brook, New Jersey, USA) to no more than 10% weight difference (*sensu* Jang et al. 2008), as weight has been shown to affect fight outcomes (Jang et al., 2008; Savage et al., 2004). I also size-matched females to no more than 10% weight difference (*sensu* Jang et al. 2008), as female weight has been shown to affect mate choice (Bateman et al., 2001; Savage et al., 2004). I painted male pronotum's with enamel nail polish to allow easy visual identification during trials one day before trials took place. Aggression and mate choice trials occurred 13-15 days post-adult eclosion. Males become sexually mature between 2 and 7 days post-adult eclosion (Sue Bertram, pers. com.) and since isolation increases aggression (Simmons, 1986b), fighting on day 13-15 assured that males were aggressive but still in their peak of mate attraction (Fitzsimmons & Bertram, 2011). Females were 13 to 15 days post-adult eclosion days to allow for maximum responsiveness to male acoustic signals (Pacheco et al., 2013). I conducted trials between February 25 and September 13, 2014 between 2pm-8pm as crickets were found to fight most often during this time (personal observation). All trials occurred under fluorescent light at a temperature of $\bar{X} \pm SD=25\pm 2$ °C.

Aggression Trials

I fought sixty-three male pairs, and each fight occurred in front of a two-female audience. I fought males once and females observed only one pair of males. Prior to the start of each fight, I placed two male and two female crickets in a Plexiglas arena (16 cm W x 32 cm L x 21 cm H) with four separate chambers (Figure 1.1A).

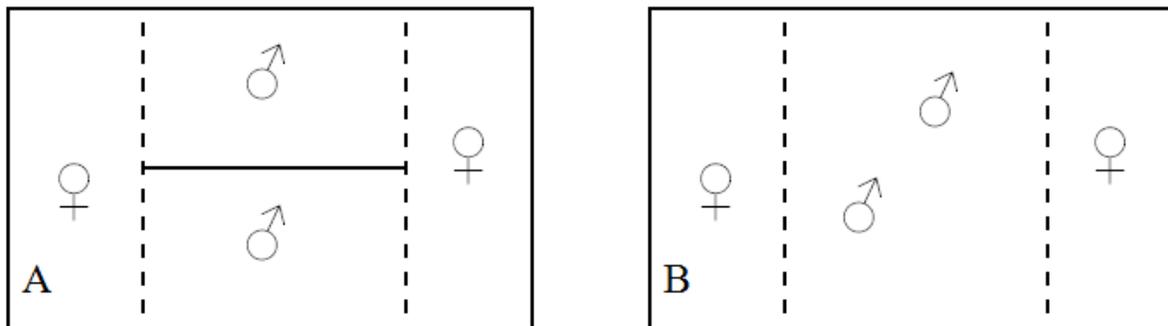


Figure 1.1: Fighting arena, view from above. Location of males and females is indicated by sex symbols, perforated Plexiglas is indicated by dashed line, non-perforated Plexiglas is indicated by a solid line. Figure 1.1A represents arena during acclimatization phase and 1.1B represent arena during aggression trials.

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 (Rantala & Kortet, 2004), while preventing inter- and intrasexual selection from being conflated. The Plexiglas sheet separating the two males was non-perforated to prevent chemical signals from being exchanged prior to the initiation of the fights. I covered the bottom of the arena with sand. I allowed the two male fighters and two female audience members to acclimatize to the arena for 5 minutes, after which time I removed the partition separating the two male fighters (Figure 1.1B). I then allowed the males to fight for 15 minutes in sight of the two female audience members. To reduce the

impact of chemical signals of previous fights with later trials I cleaned the arena's Plexiglas walls between trials with ethanol (95%), I raked the sand between each trial, and I changed the sand every 4 trials

My experiment consisted of two female treatments: Observers (N=31; Figure 1.2A) and Non-Observers (N=32; Figure 1.2B). The difference between these treatments was that in the Observer treatment the females *observed the fight* and then subsequently chose among the fight winner and loser. Conversely, in the Non-Observer treatment (N=32) the females *did not observe the fight* but then subsequently chose among the fight winner and loser. Note that (a) the males in the non-observer treatment were still fought in front of a female audience (non-focal females) to account for the effect of female audience on male aggression (Bertram et al., 2010; Montroy et al. submitted), and (b) the non-observer females observed two males that were not allowed to physically interact during the 5 min acclimation and 15 minute trial to control for the effect of familiarity with males on future mating decisions (Cheetham et al., 2008). These two female treatments are illustrated by the schematic diagram in Figure 1.2.

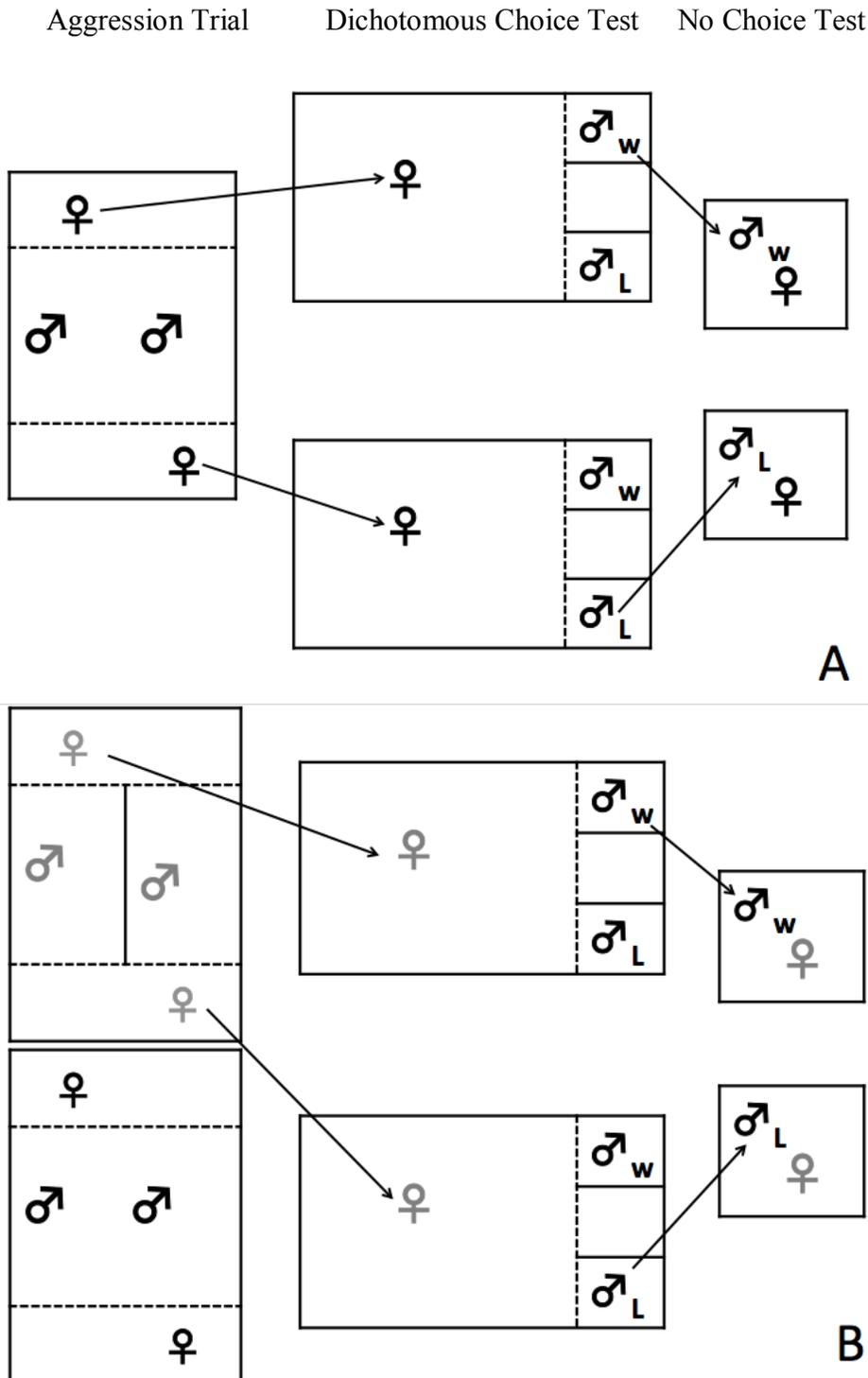


Figure 1.2: Observer (A) and Non-Observer (B) female treatment. Solid lines are opaque Plexiglas, dotted lines are transparent perforated Plexiglas.

Dichotomous Choice Test

Immediately after aggression trials were completed, I placed Observer and Non-Observer females in a dichotomous mate preference test arena (16 cm W x 24 cm L x 21 cm H) and their mating preferences for the fight winner and loser were quantified. I placed males in separate compartments divided by 2 opaque barriers and 5 cm of space in order to prevent males from seeing each other or interacting further (Figure 1.3). This prevented inter- and intrasexual selection from occurring simultaneously (Bluhm & Gowaty, 2004).

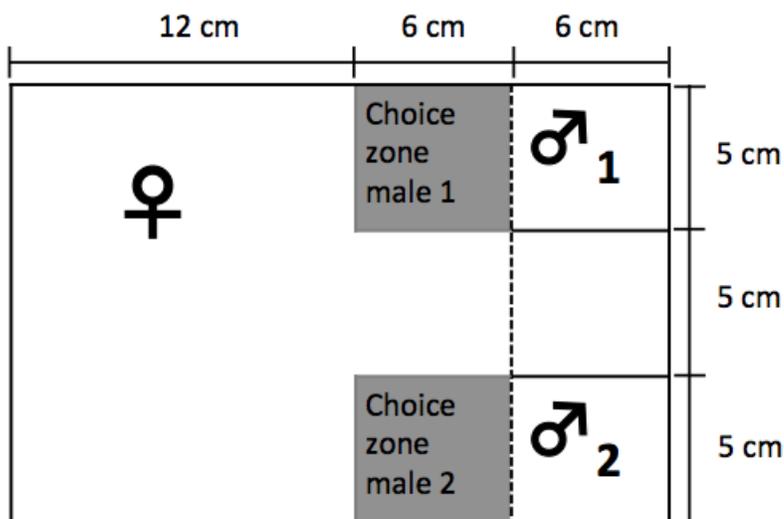


Figure 1.3: Female choice arena, as seen from above. Solid lines represent opaque Plexiglas, dashed lines represent transparent perforated Plexiglas. Choice zones are indicated in grey.

Observer females (N=62) chose between males they had seen fight while Non-Observer females (N=64) chose between males that had just fought but they had not seen fight. I placed one of the focal females (order assigned by random number generator in R) in the center of the female compartment under an opaque cup and allowed to acclimatize for 2.5 minutes. Then, I

removed the acclimatization cup and the female wandered freely for 7.5 minutes. I quantified the amount of time spent the female spent in each male's choice zone. To control for side bias, I then caught the female, swapped males from one side to the other, then placed the female under the acclimatization cup for 2.5 minutes and then repeated the dichotomous mate preference test. The Plexiglas separating the male and female compartments was transparent and perforated to allow for the transmission of visual, auditory, and chemosensory cues. The bottom of the arena was covered in sand, raked between trials and changed every 4 trials. Arena walls were wiped with 95% Ethanol between trials to reduce the effect of pheromones from earlier trials.

No-Choice Test

Immediately after the dichotomous choice tests, I paired females with either male fight winners (N=63) or male fight losers (N=63). I assigned pairs randomly using R as a random number generator. I placed mating pairs in a square Plexiglas arena with sand in the bottom (13 cm L x 13 cm W x 18 cm H). During acclimatization (5 minutes), males and females were separated by an opaque non-perforated barrier to prevent communication between individuals. I then removed the barrier and individuals were allowed to interact for 60 minutes. I measured courtship latency (time from the start of the trial to the start of juddering or courtship song) and mounting latency (time from the onset of courtship to first mounting).

After no-choice tests were complete, I placed male and female pairs in 500 ml containers with *ad libitum* food and water and one half of an egg carton shelter and where they could interact for 24 hours. This allowed for pairs that had not mated in the first 60 minutes to mate. I

removed males from the mating container after 24 hours and euthanized (frozen) them to allow for measurement of body size. Females laid eggs (used in a subsequent experiment for Chapter 2) for 4 weeks or until death, after which point they were also euthanized (by freezing).

I quantified body size by photographing the frozen cricket dorsally (Panasonic Lumix ZS40, Mississauga, Ontario, Canada) and then measuring the individual using ImageJ (version 1.48, National Institutes of Health, <http://imagej.nih.gov/ij/>). I quantified three body size measurements: 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).

Scoring Behaviours

I recorded all fights and mating behaviours were recorded from above (Canon Vixia HG10, Mississauga, Ontario, Canada) and later scored. I scored videos in real time using JWatcher (version 1.0, Blumstein et al., 2010, <http://www.jwatcher.ucla.edu/>). I scored all aggressive behaviour using a scale adapted from Stevenson & Rillich (2012) and Bertram & Rook (2012), which was in turn adapted from Adamo & Hoy (1995) (Figure 1.4 & Table 1.1).

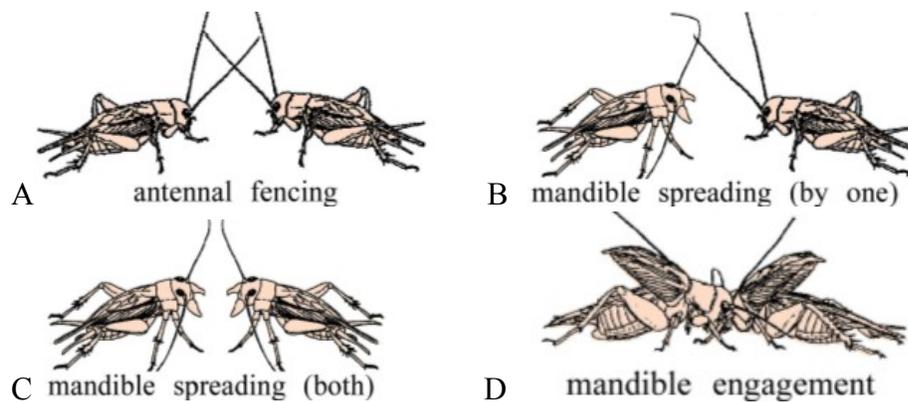


Figure 1.4: Representation of different cricket aggressive behaviours, adapted from Stevenson & Rillich (2012).

Table 1.1: Aggressive behaviour scoring adapted from Stevenson & Rillich (2012) and Bertram & Rook (2012), which was in turn adapted from Adamo & Hoy (1995)

Score	Behaviour	Description
0	No Aggressive behaviours	Male is not actively engaged in a fight (i.e. standing still or walking around the arena) or male is running away from the other male.
1	Antennal fencing	Male faces his opponent and rapidly flickers his antennae on the other male's body (Figure 1.2A). Can be unilateral (one male does it to the other) or bilateral (both males are doing the behaviour and directing it to each other).
2	Kicking	Male sharply extends his rear leg towards his opponent. It does not necessarily need to make contact with his opponent
3	Unilateral Mandible Flaring, Chasing, Aggressive Calling, or Biting	Male spreads his mandibles while facing his opponent (Figure 1.2B), male chases the other male around the arena, male produces an aggressive call (quieter than a long distance call and shriller), male bites any part of the other male's body. These behaviours are grouped in the same category as they often occur in quick succession or in concert (Adamo & Hoy, 1995).
4	Bilateral Mandible Flaring (Figure 1.2C), Chasing, Aggressive Calling, or Biting -	Both males are simultaneously performing the above mentioned behaviours either face to face or no more than a cricket length away
5	Mandible Engagement	Males lock mandibles and pull (Figure 1.2D)

In order to determine the aggressiveness of the trial, I multiplied the amount of time spent performing each behaviour by its score, thus yielding the maximum aggression score. I determined the identity of the winner and loser by careful analysis of the video. Winners often perform victory displays after a fight, which include body jerks (also known as judders or body rock displays) or body jerks coupled with aggressive signalling (Alexander, 1961; Fitzsimmons & Bertram, 2013; Jang et al., 2008). Since fight reversion can occur (Fitzsimmons & Bertram, 2013), losers had to flee at least twice before I determined which male won and which male lost. I also quantified the duration of victory displays but this measure was not included within the measure of aggression.

I measured the amount of time the females spent in each choice zone using JWatcher. Proximity to a male (or to speaker emitting male call) has been used as a measure of mate choice in many species of crickets (Black field cricket, *Teleogryllus commodus*: Shackleton et al., 2005; variable field cricket, *Gryllus lineaticeps*: Wagner & Reiser, 2000 and see Jennions & Petrie, 1997 for a review) and 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. I calculated proportion of time spent with a male, as the indicator of choice, using the following formula:

$$\begin{aligned} & \textit{proportion of time with focal male} \\ & = \frac{\textit{time spent with focal male}}{\textit{time spent with focal male} + \textit{time spent with other male}} \end{aligned}$$

Statistical Analysis

I analyzed data using JMP (version 12.0.0, SAS, Cary, NC, USA). I used one sample t-tests to assess whether females preferred winners over losers, assessing whether the proportion of time females spent in the winning male's choice zone relative to either choice zone was different from 0.5. I ran two t-tests, one for the Observers and one for the Non-Observers to ascertain whether watching a fight affected preference.

I used a nominal logistic regression to assess whether females mounted winners more than losers and whether male aggression affected female preference. Whether or not a male was mounted was the dependent variable. I included male status (winner or loser), female treatment (Observer or Non-Observer) and trial aggression as the main effects. I also included whether or not a male was preferred in the dichotomous trials as a main effect. I included an interaction between female treatment and male status and both male and female size to control for the effects of body morphology.

To analyze male preference, I used a general linear model using restricted maximum likelihood to examine how courting latency is influenced by dominance and morphological variation, with dominance status (winner or loser), female status (Observer or Non-Observer), their interaction, and whether or not a male was preferred as main effects. I log-transformed data to meet parametric assumptions. I included body size of both females and males in the model as covariates. I incorporated all body size measurements into a Principle Components analysis in JMP (version 12.0.0, SAS, Cary, NC, USA) to get an overall measure of body size for both males and females. The first principal component (PC1) was a good measure of overall female

size as it had an Eigenvalue greater than one (2.43), explained 81% of the variation, and all three measures were weighted virtually equally in the PC1. Similarly the first principal component (PC1) was a good measure of overall male size as it had an Eigenvalue greater than one (2.55), explained 85% of the variation, and all three measures were weighted virtually equally in the PC1. Maximum aggression score of the trial was included in the model to control for the effect of fight intensity. Because the behaviour of one cricket can influence that of the other cricket in the trial, I calculated the mean maximum aggression score for the trial and used these means in all analyses.

For the females that mounted their potential mates, I used a general linear model using restricted maximum likelihood to examine how courting to mating latency is influenced by dominance and morphological variation, with dominance status (winner or loser), female status (Observer or Non-Observer), their interaction, and whether or not a male was preferred as main effects. Body size of both females and males were included as covariates. Maximum aggression score of the trial was included in the model to control for the effect of fight intensity. Data was log transformed to fit parametric assumptions.

In order to assess whether fight escalation affects female preference, I ran a logistic regression. Whether or not the female mounted the male was the dependent variable and the average trial aggression was the independent variable. To tease apart whether watching a fight had an effect on female preference, Observer and no Observer female preference was analyzed separately. I corrected for multiple tests using Benjamini & Yekutieli (2001) false discovery rate (FDR_{B-Y}) method.

1.3 - RESULTS

Females did not spend a greater proportion of time with winners than losers in the dichotomous choice preference trials regardless of whether they had observed the fight (mean preference score: 0.494, DF=55, $p=0.517$) or not (mean preference score: 0.499, DF=57, $p=0.580$). Three females showed evidence of side bias (spent 80% or more of time in choice zone in either choice zone). When these females were removed from the analysis no change in significance occurred, therefore they were kept in the final model.

Females mounted males in 62 out of 126 no-choice trials (49%). Females were significantly more likely to mount the male if he was preferred in the dichotomous choice test (Table 2). Similarly, females were significantly more likely to mount the male if he was dominant. Females were also more likely to mount larger males (Table 2). Female treatment (Observers vs Non-Observers) and trial aggression were not significant (Table 2). There was no significant interaction between female treatment and male type, therefore the interaction term was removed from the final model.

Table 1.2: Nominal regression results analysing the effect of male status, aggression, and female treatment and preference on mounting likelihood; significant results bolded

Source	R ²	DF	X ²	P
Overall Model	0.119	6	18.600	0.005
Female Treatment		1	0.616	0.432
Male Status		1	4.873	0.027
Male PC1		1	5.877	0.015
Female PC1		1	0.782	0.377
Trial Aggression		1	2.453	0.117
Preferred or Non Preferred		1	5.427	0.020

Males initiated courtship sooner (lower latency to court) when paired with larger females (Table 1.3; Figure 1.5) and there was a non-significant trend of an interaction between male status and female type (Table 1.3; Figure 1.6). Males who won fights tended to court females that watched fights faster than females who did not. Conversely, males who lost fights tended to start courting those who did not watch fights before those who did. Male body size, female observation status, aggression intensity of the fight, and male dominance status did not influence male latency to court (Table 1.3). Mounting latency was not influenced by male dominance, female observation status, average aggression level of the fight, female and male body size, and female and male residual mass did not affect (Table 1.3). There was no significant interaction between male type and female type on mounting latency and the duration of the courtship to mounting interval (Table 1.3).

Table 1.3: GLM results analyzing the effect of male dominance status and female fight observation on measures of mating success; significant results bolded

Behaviour	Source	R²_{adj}	DF	Estimate	t	F	P
Log time to court	Overall Model	0.053	7,104			1.90	0.078
	Female type [Non-Observer]			0.023	0.27		0.786
	Male Status [Loss]			-0.001	-0.01		0.995
	Male Status [Loss] * Female type [Non-Observer]			-0.158	-1.89		0.061
	Male PC1			-0.034	-0.61		0.542
	Female PC1			-0.138	-2.48		0.015
	Average aggression			-0.001	-0.63		0.532
	Preference Type [Non-Preferred]			0.127	1.49		0.139
Interval between courtship and mounting	Overall Model	-0.068	7,48			0.499	0.830
	Female type [Non-Observer]			-0.244	-0.98		0.331
	Male Status [Loss]			-0.093	-0.39		0.702
	Male Status [Loss] * Female type [Non-Observer]			0.024	0.10		0.919
	Male PC1			-0.174	-1.09		0.279
	Female PC1			0.041	0.27		0.790
	Average aggression			-0.002	-0.65		0.517
	Preference Type [Non-Preferred]			0.068	0.27		0.792

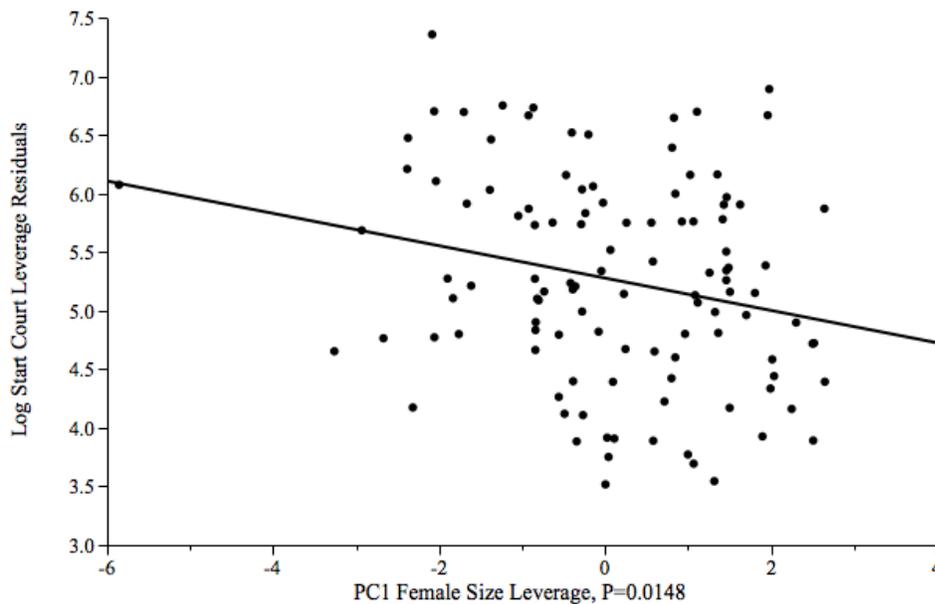


Figure 1.5: Leverage plot demonstrating the relationship between female size and male courtship latency. There is a significant negative interaction between female size and courtship latency (estimate=-0.138, p=0.015).

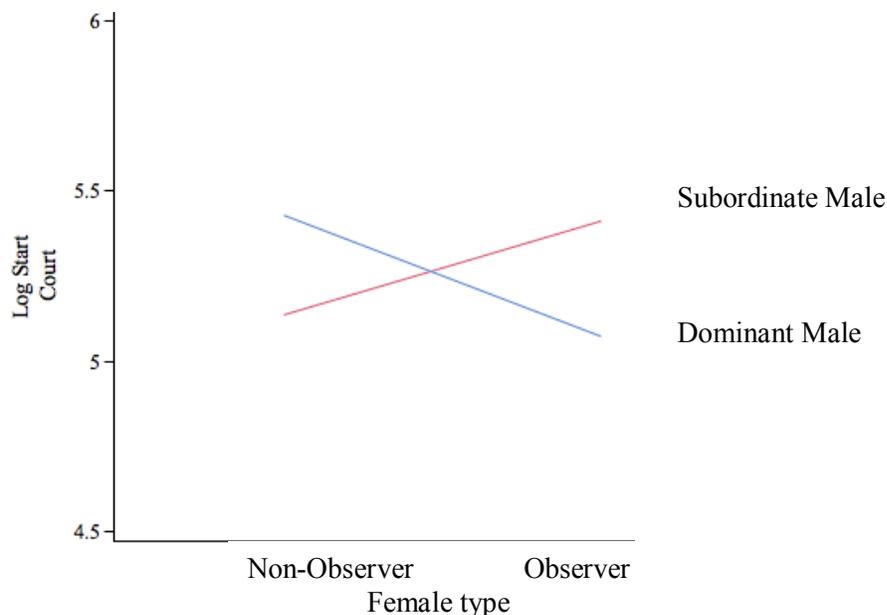


Figure 1.6: The interaction between sire's status and dam's type on the log courtship latency. Blue line represents the latency of winners and the red line represents the latency of losers. There is a non-significant interaction between sire's status and dam's type on log latency to start of courting (estimate=-0.158, p=0.061).

1.4 - DISCUSSION

The Link Between Intra- and Inter-Sexual Selection

My findings suggest that females are more likely to mount and attempt to mate with fight winners than they are with fight losers in no-choice mating trials. Montroy et al. (submitted) found that male *G. assimilis* fight more aggressively in front of a female audience. This increase in aggression is likely to come at an energetic cost to males, as Hack (1997) revealed that oxygen expenditure during fights is five times higher than resting oxygen consumption (in *Acheta domesticus*). For increased aggression to evolve when females are watching, the benefits to increased aggression must outweigh the costs. Given my no-choice mating trials reveal that females are more likely to mount and attempt to mate males of greater fighting ability, males are likely to experience increased fitness when they escalate their aggressive behavior and win fights. However, females did not prefer more aggressive males, since they did not preferably mount males who had been in more aggressive trials, whether they had watched the fights or not. Therefore, more dominant males gain reproductive success but ability to escalate fights does not inform female preference.

My finding that females are more likely to mate fight winners suggests that intersexual selection works in concert with intrasexual selection to increase male aggressive behaviour. Together this may partially explain the evolution of audience effects in male *G. assimilis*. Alternatively, males may be increasing their aggression for other reasons. In the wild, male crickets fight for access to territories and other resources (Alexander, 1961), and aggression and territory ownership has been linked in crickets (Jang et al., 2008). Resource value has been shown to affect fight intensity in many species (Enquist & Leimar, 1987). Access to a territory with females already present may lead to more reproductive opportunities and females

themselves prefer males with a burrow and territory (Simmons, 1986a). Therefore, males may perceive this territory to have a greater value and thus expend more energy to attain it, thus leading to an increase in aggression while fighting in front of a female audience. *Gryllus veletis* males also fight more intensely in front of a female audience, but not in front of a male audience (Fitzsimmons & Bertram, 2013). Having males in a territory does not make that a more valuable resource. Thus, the noted audience effect in *G. assimilis* (Montroy et al., submitted), might be occurring because of resource value in addition to reproductive benefits.

Effectiveness and Shortcomings of Dichotomous Choice Tests

My finding that female crickets prefer to mate with fight winners over losers is not that surprising, given females from many other species also show a mating preference for dominant males (wild yak, *Bos mutus*: Buzzard et al., 2014; elephant seal, *Mirounga angustirostris*; Cox & Le Boeuf, 1977; birds, *Luscinia megarhynchos*: Kunc et al., 2006; reptiles, *Anolis garmani* and *A. valencienni*: Trivers, 1976; crayfish, *Procambarus clarkii*: Aquiloni et al., 2008).

Interestingly, the picture is not as clear when investigating mate preference in the dichotomous choice tests, as females do not seem to prefer fight winners over losers when presented with both males simultaneously. This finding might suggest that dichotomous choice tests are not an accurate representation of female cricket mate choice. However, whether or not a female mounted a male was correlated with her preference during the dichotomous choice tests, and thus dichotomous choice preference appears to be an accurate predictor of mating preference. The experimental design of my dichotomous choice tests may not have allowed females to gather enough information about male winning status to influence her choice, since the perforated transparent Plexiglas may have limited the transmission of some visual and chemosensory cues.

Conversely, in the no-choice tests, females and males were able to freely interact and females may therefore have been better able to assess male quality and/or their cuticular hydrocarbon (CHC) profile.

Cuticular hydrocarbon (CHC) profiles appear to play an important role in cricket mate choice. Kortet and Hedrick (2005) found that in *G. integer* females might use CHC profiles in order to identify fighting ability in male crickets and seem to prefer the profiles of winning males. Further, Thomas and Simmons (2009) also found that male CHC profiles were affected by dominance in *Teleogryllus oceanicus*; subordinate males up regulated CHC in order to increase mate attraction. Thus female *G. assimilis* may be better able to assess male CHC profiles during the no-choice mating tests than in the dichotomous choice tests. Future dichotomous choice tests should allow for a greater degree of chemosensory transmission between male and females while still preventing males from exhibiting courtship interference.

Despite these limitations, dichotomous choice trials are still used widely in the female/male choice literature. Similar to my findings, female preference in dichotomous choice tests have been shown to be correlated with measures of mating preference in many species. For instance, dichotomous choice preference is correlated with increased receptivity in the northern swordtail, *Xiphophorus nigrensis* (Cummings & Mollaghan, 2006), increased mating success (as long as competition between males was weak) in Japanese medaka, *Oryzias latipes* (Howard et al., 1998) and mating decisions in the sand goby, *Pomatoschistus minutus* (Lehtonen & Lindström, 2008). Thus preference in dichotomous choice tests is an indicator of mating preference in several species.

Dichotomous assays of female preference in crickets have historically measured female preference for long distance mate attraction signalling. Males signal acoustically to attract

females from a distance, and then switch to close-range courtship song to entice females to mate. Two speakers at opposite ends of an arena are usually used to broadcast male acoustic signals and female phonotaxis is used to indicate preference (e.g. Hedrick, 1986; Pacheco & Bertram, 2014; Wagner & Reiser, 2000). Researchers have found a preference for many signalling traits that usually correlate with higher energy signalling (calling bout length in a field cricket, *Gryllus integer*: Hedrick, 1986; louder, higher effort signalers *G. assimilis*: Pacheco & Bertram, 2014; higher chirp rates in *G. lineaticeps*: Wagner & Reiser, 2000). Thus female preference is in part affected by male long distance mate attraction signalling, which I did not assess in this study.

Since males mostly only signalled acoustically during the fights and the mating trials (and then, only used aggressive signalling and not mate attraction signalling), females may not have been able to identify males during preference trials if females use acoustic signals to identify males. Male acoustic signals in fights may be correlated to those produced during courtship (as some long distance call parameters are correlated to courtship (Harrison et al., 2013)), allowing females that had watched fights to determine whether they were mating with the winner or loser. However, this may have only played a small role in male identification since, while female Observers did prefer male winners, it was only a trend.

Since my findings revealed that females are more likely to mount and attempt to mate with males they showed a preference for during the dichotomous choice tests, dichotomous tests may serve as a good indicator of mate preference. Mounting is a reliable indicator of mating success (Shackleton et al., 2005). I do not know by which set of criteria females chose the males they preferred, as male size and residual size did not affect female preference, however there are many other criteria that affect female choice that I could not evaluate in this study.

Mate preference in crickets is modulated by many different signals

Female mating preferences are modulated by multi-component sexual signals, thus the dichotomous choice tests may be dependent on other signals than fight outcome alone. For instance, Simmons et al. (2013) found that females show preference for both acoustic signalling traits as well as cuticular hydrocarbon profile and that this selection can be disruptive. In addition, crickets may choose mates based on how dissimilar their immune genes are in order to have offspring with heterozygous immune genes (immune gene hypothesis) (Trivers, 1972). Immune gene complementarity has been seen to be an important consideration in mate choice in many genera (as reviewed in mammals: Penn & Potts, 1999; in salmon, *Salmo salar*: Landry et al., 2001) and could be also important in *G. assimilis* as immunocompetence has been shown to play a role in mate choice in other cricket species (Rantala & Kortet, 2004). Male size and residual mass have been found to affect female choice (Bateman et al., 2001), however, this was not observed in this study. This may be due to the fact that males were size-matched in order to increase likelihood of fight occurrence (Jang et al., 2008). As males were less than 10% different in weight, females may not have been able to detect such a small weight difference, which might explain the lack of effect of size on mate preference.

Although I noted that females were more likely to mount winning males, I did not see an effect of male dominance on mating latency, unlike other studies (Shackleton et al., 2005). I may not have seen an effect of male dominance, female observation, and the size and weight of males and females because of the reduced size of our sample, as this analysis excluded half the females because they did not mount within the 60 minute window. While observing the trials until first mounting may have eliminated this problem, I question the relevance of such a practice. In the wild, crickets are free to roam and females control mating (Alexander, 1961). If females do not

mount males after they have been courted, females may leave the male and look for other mates, unlike in these trials where males and females were kept in small enclosures and females could not visit multiple males. Thus, while a longer observation period may have yielded more results, it may not have been representative of nature.

Males seemed to prefer larger females, as they started courting them more quickly than smaller females. Larger female crickets generally exhibit higher fecundity (Honek, 1993). Other studies in our lab have also found that larger *G. assimilis* females tend to lay more eggs (Bertram et al., in prep). Because of the energetic costs of courtship (Hack 1998), males may be investing more energy in courting females with greater fecundity. 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. in prep.; Simmons, 1986 a, b; Bateman, 1998; Bateman et al., 2001; Harrison et al., 2014) as well as mating preferences in other species (female tropical butterfly, *Brassolis sophorae*: Carvalho et al. 1998; male seed beetle, *Stator limbatus*: Fox et al., 1995; female Trinidadian guppies, *Poecilia reticulata*: Reynolds & Gross, 1992; female moose, *Alces alces*: Sand, 1996).

While mating latency and likelihood of mounting does serve as a measure of reproductive success (Bateman, 1998; Simmons, 1988) direct measures of reproductive success, such as number of eggs laid, hatchability, survival to adulthood and offspring adult size, may serve as better indicators of male reproductive success. These also incorporate the dual factors of cryptic female choice and male sperm viability which preference measures in this paper did not include. Researchers have found that male dominance affects male sperm quality in *Teleogryllus oceanicus* (Thomas & Simmons, 2009), and egg laying rate in *Gryllus bimaculatus* (Bretman et al., 2006). Females have also been found to benefit from mating with preferred males (increased

fertility: Wagner & Harper, 2003; increased lifespan: Wagner et al., 2001). In order to gain a more complete understanding of the effect of fight observation on fitness, my next chapter (Chapter 2) assesses how male dominance and information females gather while watching fights affects subsequent fecundity, egg hatching success, juvenile to adult moulting success, and offspring size.

Conclusions

While I found that females were more likely to mount male winners (and thus intra- and intersexual selection may reinforce one another in this species), watching males fight only had a small, non-significant effect on propensity to mount. Thus, while audience effects may play a role in the evolution of audience effects in this species, other benefits, such as burrow ownership in a territory with females, may also explain the evolution of this costly behaviour.

CHAPTER 2 – The effect of male dominance on various fitness measures in a field cricket (*Gryllus assimilis*)

2.1 - INTRODUCTION

Due to the high cost of egg production, selection will favour traits in females that increase fitness while minimizing the cost of reproduction (Eberhard & Cordero, 1995). As such, females should choose mates which produce the highest quality offspring or that give the most direct benefits at the lowest personal cost (as seen in *Gryllus integer*; Wagner et al., 2001). Females can gain reproductive benefits by mating with better courters (wolf spider, *Pardosa milvina*: Hoefler et al., 2009), better fathers (Great tit, *Parus major* (Norris, 1993), more attractive males (house cricket, *Acheta domesticus*: Head et al., 2005), and brighter males (European kestrel, *Falco tinnunculus*: Palokangas et al., 1994; male blue grosbeaks, *Guiraca caerulea*: Keyser & Hill, 2000). In a sex role-reversed species, more ornamented females are both more preferred by males and more fecund (pipefish, *Syngnathus typhle*: Berglund et al., 1997). Despite the prevalence of empirical examples supporting the good genes hypothesis in the literature, a meta-analysis of their effects found only a small effect of elaborate traits on offspring fitness (Moller & Alatalo, 1999). This may be due to the fact that traits used only in mate attraction can sometimes be a dishonest indicator of quality. However, when elaborate traits are simultaneously used in mate competition, they may remain more honest because of the potential costs imposed by injury and/or territory loss (Berglund et al., 1996). Thus, females may gain reproductive benefits by mating dominant males.

Since fights can be energetically expensive (Hack, 1997), the cost of maintaining a high position in the dominance hierarchy (winning several fights) might be too high for low quality males. As such, if male dominance is an honest indicator of male quality, female preference for

dominant males may be adaptive as it may lead to higher quality offspring (Zahavi, 1975). For instance, the sons of more aggressive male bridge spiders (*Larinioides sclopetarius*) have been shown to have higher fitness (Kralj-Fiser et al., 2013). In some ungulates, dominant females have been found to produce larger offspring (reviewed in Hewison & Gaillard, 1999). Dominant fathers are also more likely to father dominant sons in the cockroach *Nauphoeta cinerea* (Moore, 1990) and in deer mice, *Peromyscus maniculatus bairdi* (Dewsbury, 1990). Dominance has also been found to be an honest indicator of male parental care quality in three-spine stickleback, *Gasterosteus aculeatus* (Candolin, 2000). In addition, dominant males can control resources important for reproduction (resource holding potential, reviewed in Qvarnström & Forsgren, 1998) resulting in females that prefer more dominant males receiving direct benefits. Together, these aforementioned reasons may explain why females of many species prefer more dominant males as mates (Atlantic salmon, *Salmo salar*: Järvi, 1990; elephant seals, *Mirounga angustirostris*: Cox, 1981; nightingales, *Luscinia megarhynchos*: Kunc et al. 2004; field crickets, *Gryllus integer*: Kortet & Hedrick, 2005; possibly humans, *Homo sapiens*: Giebel et al., 2013).

Female preference for dominant males may lead to reproductive benefits. Dominance can be heritable (Horne & Ylönen, 1998; Moore, 1990; Nol et al., 1996; Pérez-Guisado et al., 2006) resulting in more dominant males often producing more dominant sons. This, in turn, can lead to increased fitness. However dominance is a trait determined by many factors, including environment, genes, and interactions of the two (Dewsbury, 1990), and thus it may be an oversimplification to assume that more dominant males often produce dominant sons.

Mating more dominant males has many other fitness effects than simply having dominant sons, and those effects are not always beneficial. In some species, dominant males can be mediocre or poor fathers (sand goby, *Pomatoschistus minutus*: Forsgren, 1997), or cause mate

harm (Japanese Quail, *Coturnix japonica*: Ophir & Galef, 2003). Further, dominant males do not always produce higher quality offspring (male brown trout, *Salmo trutta*: Jacob et al., 2007).

Thus it is always important to consider potential tradeoffs when evaluating the costs and benefits of reproduction (Wong & Candolin, 2005; Kokko et al., 2003; Qvarnström & Forsgren, 1998).

While females can control fitness by selectively mating with males (pre-copulatory mate choice), they can also exert post-copulatory mate choice. Females of certain invertebrate species have been shown to have some degree of control over egg fertilization due to their ability to store (mammals, birds, and reptiles: Birkhead & Møller, 1993; crickets, *Gryllus bimaculatus*: Simmons, 1987) and selectively use sperm (Eberhard, 1996). Since storing sperm decouples the act of mating and fertilisation, it allows females to have greater control over which sperm is used in fertilization. In species where females prefer dominant males, females mated to higher-ranking males may invest more in offspring production.

While females do have a large degree of control over reproduction, males can also influence female fecundity and offspring viability and quality in several ways. Bretman et al. (2006) revealed that *Gryllus bimaculatus* females mated to dominant males laid more eggs than females mated with non-dominant males. However, the experimental design did not allow them to differentiate between the possible causes of the result, such as increased male sperm quality, increased male ability to manipulate female fertility, or increased female post-copulatory preference for dominant males. Wagner & Harper (2003) showed that *Gryllus lineaticeps* females mated with preferred males lived longer and laid more eggs and that these eggs were more viable. Thus males may be producing seminal proteins that influence the female's life history. Studies have since shown that male crickets are able to produce such proteins (*Gryllus firmus* & *Gryllus pennsylvanicus*: Andrés et al., 2006). In tests of sperm competition, dominant

males of several species were found to have higher competitive success (bridge-weaving spider, *Larinioides sclopetarius*: Kralj-Fiser et al., 2013; Australian field cricket, *Teleogryllus oceanicus*: Thomas & Simmons, 2009) as well as bigger, more successful offspring (bridge-weaving spider, *Larinioides sclopetarius*: Kralj-Fiser et al., 2013). Therefore, dominant males of some species show increased post-copulatory control over female fertilization and greater sperm quality.

In order to assess the effects of mating with dominant males on offspring, I used crickets, more specifically *Gryllus assimilis*. Despite the extensive research on aggression in crickets, there have been few investigations on cricket audience effects and even fewer investigations on how eavesdropping influences female mate choice and its subsequent effects on offspring number and size. Work in the Bertram lab has shown that males fight more aggressively when in front of a female audience than in front of no audience. Male crickets have been observed to increase their levels of aggression when fighting in front of a female audience (the spring field cricket, *Gryllus veletis*: Fitzsimmons & Bertram, 2013; *Gryllus assimilis*: Montroy et al., submitted) (detailed further in chapter 1). Montroy et al. (submitted) found that, when male *G. assimilis* fought in front of a female audience, males were more aggressive than when they had no audience. Similarly, Fitzsimmons & Bertram (2013), found that *G. veletis* males were more aggressive when fighting in front of a female audience than in front of a male audience or no audience. *Gryllus bimaculatus* also increases aggression in front of a female audience (Simmons, 1986b). This increased aggression bears a cost on males (Hack, 1997) and thus would have been unlikely to have evolved without a reproductive benefit. In Chapter 1, I found that female *G. assimilis* prefer more dominant males in no-choice trials, as females were more likely to mount male winners than losers. Here I quantify offspring number and fitness of females mated to fight

winner and loser to assess the potential fitness benefits of winning a fight. I measured whether females would lay more eggs, whether the eggs exhibited higher hatching success, and whether the offspring were larger when females were mated to more dominant males. Since larger individuals have higher fitness in many species (female tropical butterfly, *Brassolis sophorae*: Carvalho et al. 1998; male seed beetle, *Stator limbatus*: Fox et al., 1995; female white-spotted charr, *Salvelinus leucomaenis*: Morita & Takashima, 1998; female Trinidadian guppies, *Poecilia reticulata*: Reynolds & Gross, 1992; female moose, *Alces alces*: Sand, 1996; field cricket, *Gryllus veletis*: Harrison et al., 2014), having larger offspring should lead to increased fitness.

To assess the effect of winning a fight on reproductive success, I fought males in front of two female audience members. After dominance had been established, I mated winners and losers to females that had either watched the fight (Observers) or females who had not watched the fight (Non-Observers). My experimental design allowed me to investigate whether females intrinsically prefer dominant males. If females preferentially allocate resources to offspring of dominant males, and if they can sense which males are dominant based on behavioural, morphological, and/or chemosensory cues, females should lay more eggs when mated with dominant males regardless of whether or not they watched the fights. However, if watching a fight informs female behaviour, then Observers and Non-Observers would show different preferences and reproductive investment, with Observers laying more eggs than Non-Observers when mated to dominant males.

If aggression is an indicator of good genes, or if dominant male sperm is of higher quality, male winners could also produce more viable eggs, higher juvenile to adult moulting success, and larger size adults. Since dominant male *G. bimaculatus* have been found to influence female egg laying (Bretman et al., 2006), increased egg-laying could also be due to increased dominant

male ability to manipulate female fecundity possibly through seminal proteins. If dominant males produce more seminal proteins that control female reproduction, then females mating with more dominant males may lay more eggs. Therefore, increased number, viability, and size of offspring could either be caused by increased female investment in offspring of dominant males, dominant males having better sperm, and/or dominant males being better able to manipulate female fecundity. While my experiment cannot tease apart these different possible causes, it can determine if females differentiate between fight winners and losers, whether winners and losers have different fitness, and whether observer status influences either result.

2.2 - METHODS

I used crickets from Chapter 1 in this experiment. As described in Chapter 1, I fought weight-matched male crickets in front of a two female audience and ascertained which male won and which male lost the fight. I then assessed female preference for winning or losing males using dichotomous choice trials. In half of the trials (Observer trials), females chose between males they had watched, and in the other half of the trials (Non-Observer trials) the females chose between males who had fought but whose fight they had not observed. I then randomly paired females with either the winner or loser, and assessed female preference using no-choice trials. My methods are described in detail in Chapter 1.

I allowed the male and female to mate freely and then gave females *ad libitum* food and water, an eggcup containing moistened sand as laying substrate, and half of an egg carton shelter. Females laid eggs for four weeks or until death; sand cups were replaced after 2 weeks. I gave eggs five weeks to hatch to ensure that all fertilized eggs had the opportunity to hatch, at which point the sand-filled eggcups were dried. Volunteers and I sifted sand to allow hatched and un-

hatched eggs to be counted. I kept offspring in family bins (W10 cm X L16.5 cm X H16.5 cm) with all siblings until 3rd/4th instar, at which point a random subset of 20 offspring were kept and raised to adulthood (the others were euthanized (frozen)). I placed offspring that were kept in a family bin (W10 cm X L16.5 cm X H16.5 cm) and gave them *ad libitum* food and water and large egg carton shelter. I checked bins thrice weekly to remove all adults. Adult offspring were euthanized (frozen) and their size quantified, using the same variables as previously described (Chapter 1). I assessed offspring size because larger males are preferred as mates when two randomly selected males are presented in dichotomous choice trials, and because larger females lay more eggs than smaller females (Bertram et al., in prep).

Statistical Analysis

I analyzed data using JMP (version 12.0.0, SAS, Cary, NC, USA). I incorporated all morphological measurements (head width, pronotum height, and pronotum width) into principle components analyses (PCA) to get an overall measure of body size, separate for females and males. Female PC1 (I included dams and F1 females in the PCA) had an Eigenvalue of 2.62 and explained 87.5% of the variation in pronotum width and height and eye distance. Male PC1 (I included sires and F1 males in the PCA) had an Eigenvalue of 2.72 and explained 90.6% of the variation in body size measures.

I used a general linear model using restricted maximum likelihood to examine how number of eggs laid, egg viability, and proportion of offspring that survive to adulthood were influenced by male dominance, female observer status, and morphological variation of parents. I transformed data to meet parametric assumptions. The model I constructed had sire status (winner or loser), dam type (Observer or Non Observer) and an interaction of the two as main

effects. The covariates I included were sire and dam body size (PC1), number of days females laid eggs, whether or not a female was mated to their preferred or non preferred mate, as well as male trial aggression. I did not include dam and sire weight or residual weight in the model due to multicollinearity with body size measures.

In order to assess the effect of dominance, observer status, and morphological variation on offspring size, I constructed two general linear models with restricted maximum likelihood with Offspring PC1 size as dependent variable, one model using only daughter size and the other only son size. In order to avoid problems of pseudo replication (as body size is heritable and same sex siblings should be similar sizes), I calculated the mean daughter and son size of each family and used those means as the dependant variables. The models I constructed had male status, female observation and an interaction of the two as main effects. The covariates I included were the body size of sires and dams, the mean trial aggression, and whether or not the female was mated to her preferred male.

2.3 - RESULTS

Females mated to dominant males did not lay more eggs (Table 2.1). Females mated to less aggressive males and females that had not watched fights laid more eggs (Table 2.1; Figure 2.1 & 2.2 respectively). Larger females and females that survived longer laid more eggs (Table 2.1; Figure 2.3 & 2.4 respectively). No factors had an effect on egg viability (Table 2.1). Dominant males did not have offspring with higher juvenile to adult moulting success (Table 2.1). However, the offspring of less aggressive males had higher juvenile to adult moulting success, but whether or not a female watched a fight did not affect her offspring's juvenile to

adult moulting success (Table 2.1). Smaller males had offspring with higher juvenile to adult moulting success (Table 2.1).

Table 2.1: GLM results analyzing the effect of male dominance on measures of fitness; significant results bolded.

Fitness measures	Source	R²_{adj}	DF	Estimate	t	F	P
Sqrt Number of eggs	Overall Model	0.158	8,172			5.235	<0.001
	Number of days laying			0.426	3.03		0.003
	Female type [Non-Observer]			1.580	2.86		0.005
	Male status [Loss]			-0.634	-1.18		0.238
	Male status [Loss] * Female type [Non-Observer]			-0.046	-0.08		0.933
	Average aggression			-0.015	-2.19		0.030
	Preference type [Non-Preferred]			0.007	0.01		0.990
	Dam PC1			1.903	3.68		<0.001
	Sire PC1			0.330	0.67		0.504
% eggs hatched	Overall Model	-0.030	8,172			0.340	0.949
	Number of days laying			-0.002	-0.53		0.596
	Female type [Non-Observer]			0.013	0.81		0.419
	Male status [Loss]			-0.002	-0.15		0.882
	Male status [Loss] * Female type [Non-Observer]			-0.004	-0.24		0.814
	Average aggression			-0.0002	-1.33		0.184
	Preference type [Non-Preferred]			-0.002	-0.16		0.872
	Dam PC1			-0.004	-0.29		0.771
	Sire PC1			0.006	0.44		0.658
Moulting success	Overall Model	0.100	8,172			3.50	<0.001
	Number of days laying			-0.002	-1.53		0.128
	Female type [Non-Observer]			0.005	1.13		0.261
	Male status [Loss]			-0.001	-0.36		0.720
	Male status [Loss] * Female type [Non-Observer]			-0.003	-0.72		0.472
	Average aggression			-1.47e-4	-2.89		0.004
	Preference type [Non-Preferred]			-0.006	-1.56		0.120
	Dam PC1			0.002	0.48		0.634
	Sire PC1			-0.015	-4.00		<0.001

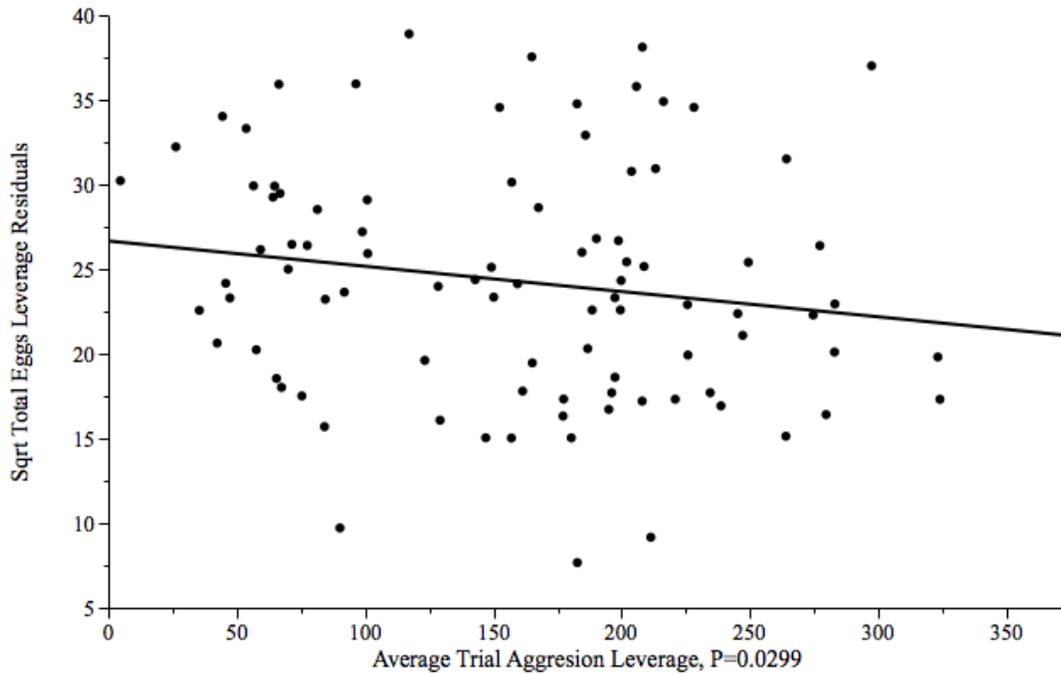


Figure 2.1: Leverage plot demonstrating the relationship between sire’s trial aggression and number of eggs laid. There is a significant negative relationship between sire’s aggression and log total eggs laid (estimate=-0.015, p=0.03).

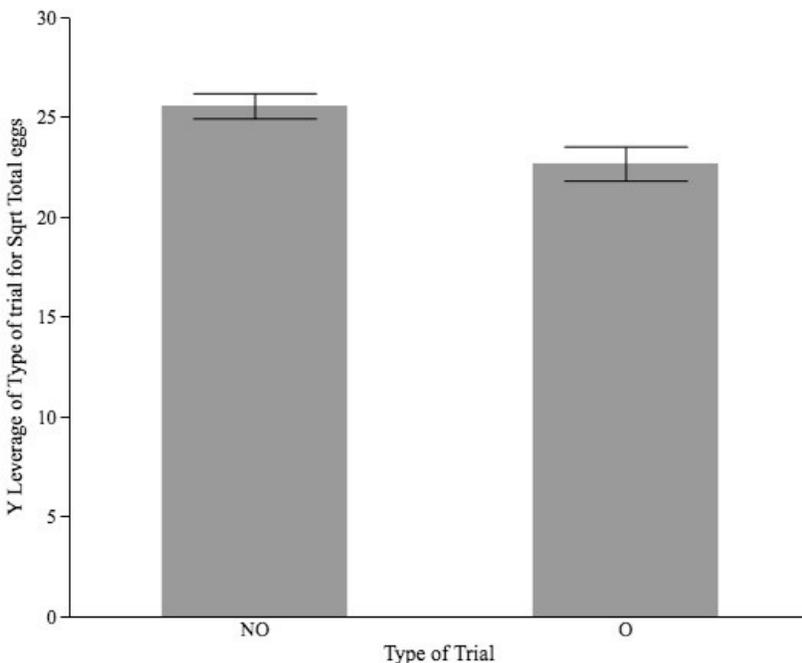


Figure 2.2: Leverage plot demonstrating the relationship between dam fight observation and number of eggs laid. Females that did not watch fights laid more eggs than those that did (estimate=1.58, p=0.005). Error bars represent one standard deviation from the mean.

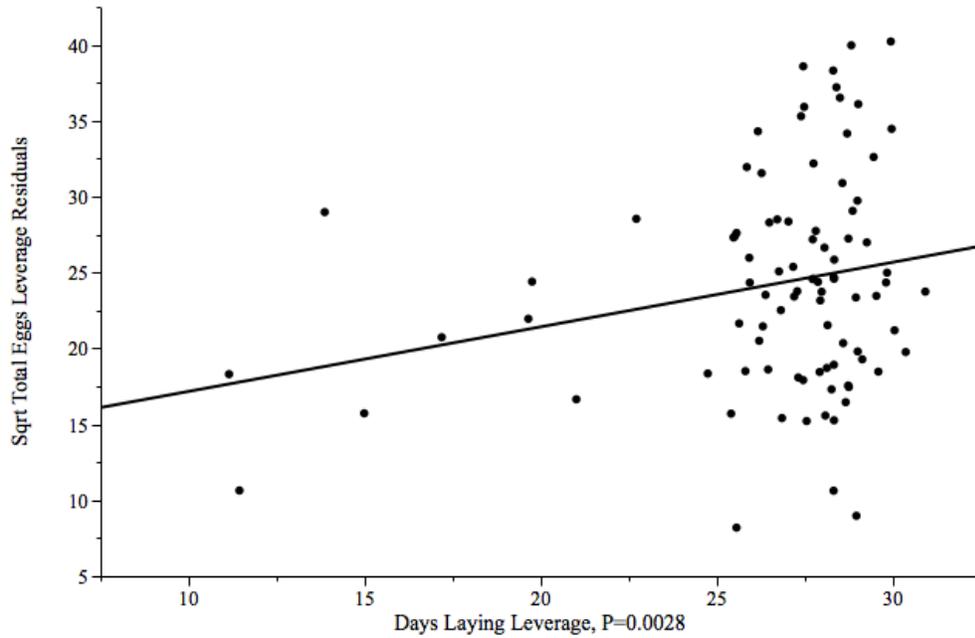


Figure 2.3: Leverage plot demonstrating the relationship between dam's size and number of eggs laid. There is a significant positive relationship between mother's size and log total eggs laid (estimate=1.903, p=0.0003).

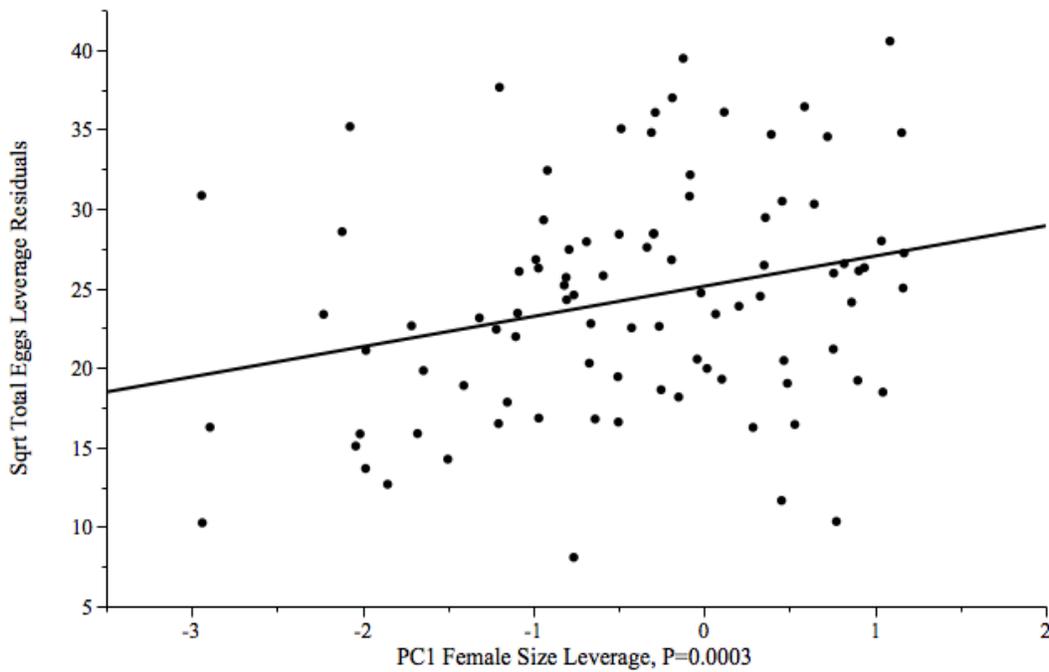


Figure 2.4: Leverage plot demonstrating the relationship between days spent laying and the square root number of eggs laid. Females that lived longer laid more eggs (estimate=0.426, p=0.003).

When analyzing the sizes of daughters and sons separately, there was no effect of dominance or female fight observation on offspring size (Table 2.2). Sons and daughters were larger when sires fought more aggressively (Table 2.2; Figure 2.5 & 2.6 respectively). No other variables had an effect on daughter or son size.

Table 2.2: GLM results analyzing the effect of male dominance on offspring size, daughters and sons analyzed separately; significant results bolded.

Source	R^2_{adj}	DF	Estimate	t	F	P
Overall Model (Daughters)	0.018	7,83			1.233	0.294
Female type [Non-Observer]			-0.078	-0.67		0.502
Male status [Loss]			0.139	1.23		0.224
Male status [Loss] * Female type [Non-Observer]			-0.163	-1.44		0.153
Average aggression			0.003	2.12		0.037
Preference type [Non-Preferred]			0.038	0.33		0.740
Dam PC1			-0.059	-0.54		0.589
Sire PC1			-0.016	-0.16		0.875
Overall Model (Sons)	0.022	7,82			1.281	0.270
Female type [Non-Observer]			-0.192	-1.53		0.130
Male status [Loss]			-0.021	-0.17		0.864
Male status [Loss] * Female type [Non-Observer]			-0.177	-1.45		0.150
Average aggression			0.003	2.17		0.033
Preference type [Non-Preferred]			0.006	0.05		0.961
Dam PC1			-0.126	-1.08		0.285
Sire PC1			0.077	0.69		0.492

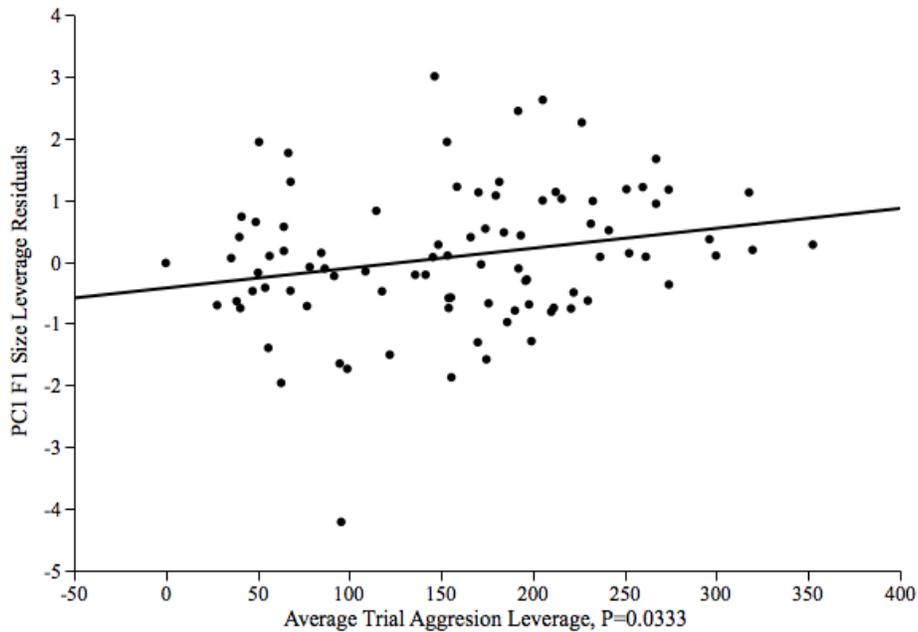


Figure 2.5: Leverage plot demonstrating the relationship between sire’s trial aggression and son’s size. There is a significant positive relationship between sire’s aggression and son’s size (estimate=0.003, p=0.03).

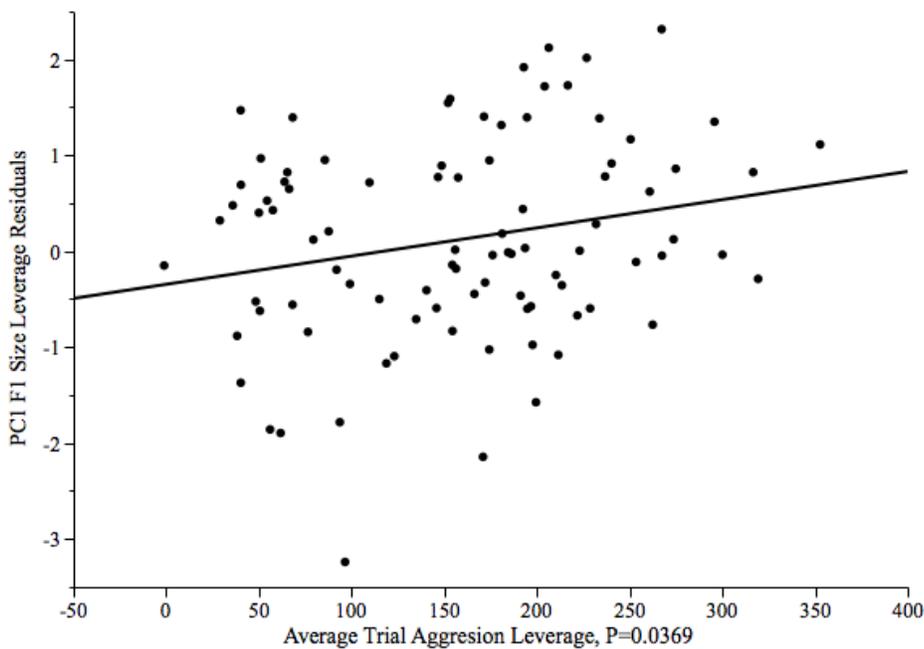


Figure 2.6: Leverage plot demonstrating the relationship between sire’s trial aggression and daughter’s size. There is a significant positive relationship between sire’s aggression and daughter’s size (estimate=0.003, p=0.04).

2.4 - DISCUSSION

While females are more likely to mount dominant males, females mated to dominant males did not lay more eggs and their eggs did not have higher viability, regardless of whether or not the females had watched the males fight. In addition, dominance did not seem to indicate good genes since dominant males did not sire larger offspring, nor did their offspring have higher juvenile to adult moulting success, regardless of whether their dams had watched the fights. Therefore, while females prefer to mount more dominant males there are no clear indirect benefits to this preference since they don't lay more eggs, the offspring are not more viable, and the offspring are not larger. Further, there are no apparent direct benefits to females preferring to mount more dominant males because *G. assimilis* does not have any parental care or nuptial gifts (Alexander, 1961). Further, *post hoc* tests revealed that mating with dominant males or preferred mates did not affect female longevity (dominant: t-test, DF=183, $t=-0.485$, $p=0.685$; preferred: t-test, DF=170, $t=-0.784$, $p=0.783$). Thus I found no direct or indirect benefit to mating with dominant males.

These findings, that more dominant males do not have more successful offspring, run counter to previous research; dominant males of many species have higher fitness (greater number of eggs laid in *Gryllus bimaculatus*: Bretman et al., 2006; more successful offspring in bridge weaving spiders, *Larinioides sclopetarius*: Kralj-Fiser et al., 2013; more dominant offspring in deer mice, *Peromyscus maniculatus*: Dewsbury, 1990; & see Qvarnström & Forsgren, 1998 for a review). But, more dominant males do not always have higher fitness (no effect on offspring size in brown trout, *Salmo trutta*: Jacob et al., 2007 or in Chinook salmon, *Oncorhynchus tshawytscha*: Pitcher & Neff, 2007). Therefore, my study seems to indicate that mating with dominant males does not give reproductive benefits to females.

There are many potential reasons why dominant males may not have had higher reproductive success than subordinate males in my experiment. It is possible that I did not see a benefit to mating with dominant males because of the methods I used to determine dominance. When dominance had an effect on offspring quality (*Gryllus bimaculatus*: Bretman et al., 2006), males that were used in that study had fought several times and had either won all their fights or lost all their fights. Thus, Bretman et al. (2006) utilized “super” dominant and subordinate males as their two treatments. Since males in my study were only tested in one fight, there may not have been enough of a difference in status between dominant and subordinate males to observe a statistically significant effect.

In the wild, cricket females mate multiply (*G. bimaculatus*: Bretman & Tregenza, 2005), and thus sperm competition may play a role in fitness of wild populations. Sperm competition may affect fitness if dominant males have higher sperm competitive success, as they do in many other species (cooperatively breeding fish, *Neolamprologus pulcher*: Fitzpatrick et al., 2006; Damaraland mole-rats, *Cryptomys damarensis*: Maswanganye et al., 1999; Australian field cricket, *Teleogryllus oceanicus*: Thomas & Simmons, 2009). However, this is not always the case (domestic fowl, *Gallus gallus domesticus*: Froman et al., 2002 & Pizzari et al., 2007; Artic char, *Salvelinus alpinus*: Rudolfsen et al., 2006). In my study, I provided no opportunity for sperm competition to take place since females were virgins prior to mating and I only allowed each female to mate once, either to the winner or loser. As such, I was unable to quantify any differences in sperm competitive ability with my experimental design. However, I did measure egg viability, which is tied to sperm viability as sperm need to be viable for the egg to hatch (Australian field cricket, *Teleogryllus oceanicus*: García-González & Simmons, 2005). I found no

difference between the egg viability of winners and losers. Given a direct test of sperm competitive ability would be informative, future studies should incorporate sperm competition in their analyses of reproductive success.

Intriguingly, I found that males that had more aggressive fights subsequently produced larger offspring. To my knowledge no other studies have shown that more aggressive fathers, in species with no parental care, have larger offspring. Other studies which have looked at the relationship between offspring size and parental aggression have not found a correlation between the two (dark-eyed junco, *Junco hyemalis*: Cain & Ketterson, 2013; bridge weaving spiders, *Larinioides sclopetarius*: Kralj-Fiser et al., 2013). Typically, in species with brood care, more aggressive fathers make poor fathers, which has negative effects on offspring (Azorean rock-pool blenny, *Parablennius parvicornis*: Ros et al., 2004; collared flycatchers, *Ficedula albicollis*: Qvarnström, 1997; western bluebirds, *Sialia mexicana*: Duckworth, 2006). However, this is not always the case (monogamous California mouse, *Peromyscus californicus*: Trainor & Marler, 2001; three-spine stickleback, *Gasterosteus aculeatus*: Candolin, 2000). In *G. assmilis* there is no parental care (Alexander, 1961), therefore it is unlikely that any behaviour correlated with aggression in the parents would affect offspring development. Instead aggression may be correlated to genes that confer fitness. Aggression itself has been shown to be heritable in several species (Horne & Ylönen, 1998; Kralj-Fišer & Schneider, 2012; A. J. Moore, 1990; Nol et al., 1996; Pérez-Guisado et al., 2006). No studies to my knowledge have investigated the heritability of dominance or aggression in crickets. However because of the morphological aspects of dominance (Brown et al., 2006; Judge & Bonanno, 2008) and since morphological traits are usual heritable, dominance may also be heritable in crickets.

It is important to note that females mated to more aggressive males laid fewer eggs and their offspring had lower juvenile to adult moulting success, resulting in family bins of more aggressive fathers being less populated than those of less aggressive males. It is thus possible that the positive relationship between aggression and offspring size results from differences in juvenile population density and not sire quality. Since population density affects offspring size (marbled salamanders, *Ambystoma opacum*: Scott, 1994; Red deer, *Cervus elapus*: Albon et al., 1987; mosquito, *Aedes aegypti*: Agnew et al., 2002), the offspring of aggressive sires may be larger simply because they were less crowded. In fact in a *post hoc* test, I found an inverse relationship between number of eggs hatched and offspring size ($R^2_{adj}=0.15$, Slope=-0.001, F=35.48, DF=1,194, $p<0.001$), revealing density predicts offspring size.

Given females mated to less aggressive males produce offspring that have higher juvenile to adult moulting success, less aggressive males may be of higher quality. Females may sense this, as they preferentially invest in egg production (by laying more eggs) when mated to less aggressive males. Since offspring size may simply be due to density dependent factors, it may be better to raise offspring in more density-controlled environments, or in isolation, to better understand parental effects without confounding factors. I attempted to control for density by splitting the bins and only keeping 20 juveniles, however, splitting the bins earlier may have been more effective.

Caution should be exercised before drawing conclusions about the effect of male aggression on fitness. Male aggression is dependent on both males fighting, as the fight will only escalate if the both males are willing to be aggressive. Thus, while an individual's aggression is dependent upon his energy reserves (Hack, 1997), personality (Kortet & Hedrick, 2007), and a

host of other factors, it is also dependent on his partner's behaviour, resulting in males having very different aggression scores dependent on their partners. As such, male aggression is not an individual property but a property of the group. This means that I expected to see a lot of noise in the data when I utilized aggression in my correlations. While sire aggression and offspring size were correlated, the models explained less than 3% of the variation. However, the fact that I saw a trend at all is surprising and suggests that the effect may have been even more pronounced had I been able to systematically quantify male aggression independent of his partner's behaviour.

I found that larger females laid more eggs, which is expected since heavier female invertebrates for the most part tend to have higher fecundity (reviewed in Honek, 1993; and seen in crickets, *G. assimilis*: Bertram & Rook, 2012; *G. integer*: Hedrick & Kortet, 2012; & *G. veletis*: Harrison et al., 2014). Surprisingly, I found that females that did not observe fights laid more eggs than those that did. A *post hoc* analysis of the effect of female type on number of eggs laid (using the leverage and residuals from the general linear model) shows that female type explains 4% of the variation in fecundity, thus while it may not be the driving force in the evolution of reproductive investment, it still seems to have a biologically relevant effect on fitness. Perhaps females that did not watch fights laid more eggs because they were unsure of a male's quality and invested more to ensure that some offspring survived to reproduce. Gowaty et al. (2007) theorized that females should invest more in egg production with males of lower quality in order to assure fitness. Perhaps females also invest more when unsure of a male's quality. However, females have been shown to prefer winners without watching a fight (Chap 1, *Gryllus integer*: Kortet & Hedrick, 2005) suggesting that subordinate and dominant males appear to differ in a way that females can detect. Perhaps watching fights causes a change in female egg laying behaviour.

Fighting causes changes in the neurochemistry of fighters in many different species (rats, *Rattus norvegicus*: van Erp & Miczek, 2000; crayfish, *Orconectes rusticus*: Huber, 2005; *G. bimaculatus*: Stevenson & Rillich, 2015; and reviewed in fish: Winberg & Nilsson, 1993). Since watching fights has been found to affect behaviour of audiences (Valone, 2007), and because of the link between behaviour and brain chemistry, watching fights may affect audience neurochemistry which may have a cascade of effects on females. Future research into this neurochemical link may prove valuable.

Offspring size is often heritable (pied flycatcher, *Ficedula hypoleuca*: Alatalo & Lundberg, 1986; *Drosophila buzzatii*: Prout & Barker, 1989; Trinidadian guppy, *Poecilia reticulata*: Reynolds & Gross, 1992; field cricket, *Gryllus bimaculatus*: Simmons, 1987a; Great tit, *Parus major*: van Noordwijk et al., 1988). However, I found that offspring size and parental size were not correlated. This is possibly due to the effect of dam size on egg laying, larger females laid more eggs, thus confounding density with mother's size. The multiple factors that unexpectedly affected offspring size may preclude me from making any definite claims about the treatment's effect on offspring body size.

Gryllus assimilis males fight more intensely in front of a female audience (Montroy et al. submitted). Since fighting is energetically costly (Hack, 1997), males should not evolve this costly response to female presence unless it confers some reproductive benefit. My study shows that females lay more eggs when mated to males they did not watch fight. Therefore the benefit of escalated fight aggression may not be increased reproductive success. In addition, I found no evidence of increased fitness in dominant males, relative to subordinate males, I did find that females mated with more aggressive males produced larger offspring, but laid less eggs and had

offspring with decreased survival. Thus aggression may reflect male genetic quality in the Jamaican field cricket, or this could be driven by juvenile density. However, this does not explain why females prefer to mount dominant males, since for preference to evolve it needs to confer some benefit. It is possible that preferring dominant males leads to benefits not studied in my experiment. Studies allowing females to mate with both dominant and subordinate males to investigate whether cryptic female choice and sperm competition play a role in fitness may allow researchers the ability to investigate fine scale measures of preference. Future investigations should investigate how aggression is correlated with good genes in a density-controlled environment. In addition, since dominant males have higher mating success, if dominance is heritable in *G. assimilis*, then dominant males may have higher fitness through their dominant offspring. Future studies should assess the heritability of dominance in this species. I assume that there are no direct benefits to mating with dominant males in this species, however, females have been found to gain reproductive benefits and longer lifespans when mated to preferred males (Wagner & Harper, 2003). Although I did not study the effect of mating on female lifespan, I gave females 4 weeks to lay, which is longer than females tend to live in nature (approximately 3 weeks (Rodríguez-Muñoz et al., 2010)). In addition, while males do not provide parental care, males will sacrifice themselves for a mate if a predator approaches by letting the female stand in his burrow while standing guard outside of it (Rodríguez-Muñoz et al., 2011). Thus it is possible that females gain direct benefits from mating with preferred or dominant males. This may explain the evolution of female preference.

GENERAL DISCUSSION

Audience Effects

Because animal population densities in the wild are usually high, communication between individuals can often be perceived by more than its intended receiver, resulting in most animals living within a communication network (McGregor & Peake, 2000). As such, behaviour and communication can be influenced by audiences and can in turn affect behavioural decisions by audience members.

One commonly studied behaviour affected by audiences is aggression. Audience effects, which occur when males increase or decrease their aggressive behaviour when fighting in front of an audience (Matos & Schlupp, 2005), have been noted to occur in many species (domestic canaries, *Serinus canaria*: Ung et al., 2011; fighting fish, *Betta splendens*: Doutrelant et al., 2001; field cricket, *Gryllus bimaculatus*: Tachon et al., 1999). Audiences can also eavesdrop on fights and use information gathered to inform future decisions, as seen in many taxa (Wild yak, *Bos mutus*: Buzzard et al., 2014; Japanese quail, *Coturnix japonica*: Ophir & Galef, 2003; black-capped chickadee, *Poecile atricapilla*: Mennill et al., 2002). Eavesdropping occurs when individuals observing an interaction between two actors (in this case two males fighting) gather information from their observations which informs later behavioural decisions.

Male crickets fight more aggressively when in front of a female audience than when they have no audience (*Gryllus bimaculatus*: Simmons, 1986; *Gryllus assimilis*: Montroy et al. submitted) or a male audience (*Gryllus veletis*: Fitzsimmons & Bertram, 2013). Because fighting is energetically costly (Hack, 1997), elevated aggressive behaviour is not likely to have evolved unless the benefits outweigh the cost. Because females often prefer to mate with dominant males

(Jamaican lizards, *Anolis garmani* and *A. valencienn*: Trivers, 1976; nightingales, *Luscinia megarhynchos*: Kunc et al., 2006; red swamp crayfish, *Procambarus clarkii*: Aquiloni et al., 2008; crickets, *Gryllus bimaculatus*: Simmons 1986a,b; and see Berglund et al., 1996 for a review), and females sometimes incite males to fight in order to mate with the winners (Elephant seals, *Mirounga angustirostris*: Cox & Le Boeuf, 1977; Wild yak, *Bos mutus*: Buzzard et al. , 2014; a review of several bird species: Montgomerie & Thornhill, 1989), I explored whether males elevate their aggressive behaviour when females are watching because winning a fight leads to increased likelihood that a female will prefer that male (Chapter 1) and invest more in his offspring (Chapter 2).

Aggression and dominance, while often equated by researchers, are not the same thing (Francis, 1988). While it is true that in dyadic fights the more dominant male is usually more aggressive, aggression also increases when opponents are more closely matched phenotypically (common house cricket, *Acheta domesticus*: Brown et al., 2006). Therefore, I investigated how both dominance and aggression in fights influenced subsequent female mate preference (Chapter 1) and subsequent offspring success (Chapter 2).

While female *G. assimilis* did not mount more aggressive males in no-choice mating trials, females were more likely to mount dominant males (fight winners). There was no effect of female status (whether they were fight Observers or Non-Observers), suggesting that females can tell the difference between dominant and subordinate males without eavesdropping on the fight. Kortet & Hedrick (2005) revealed that female *Gryllus integer* prefer to associate with filter paper containing the chemical cues of dominant males over subordinate ones. Thus, there may be a pheromone difference between winners and losers, either based on the profile of cuticular hydrocarbons

(*Nauphoeta cinerea*: Moore et al., 1997) or their quantity (in *Teleogryllus oceanicus*: Thomas & Simmons, 2009). Other researchers have found that chemical cues can indeed differ between males based on their dominance, and may be used by females as well as males to assess dominance or mate quality (Iberian rock lizards, *Lacerta monticola*: Martin & Lopez, 2007; *Nauphoeta cinerea*: Moore et al., 2001; and reviewed in Johansson & Jones, 2007). It is possible that the time scale of the experiment was not appropriate. Stevenson & Rillich (2015) found that chemicals (amines) build up in a cricket for an hour after a fight. If females are not visually eavesdropping on a fight but chemically getting information, then females may need be housed with the fighting males for 1 hour instead of for 15 minutes. However, I'm unsure of the biological significance of housing the crickets together for that long. In nature, we presume that after a male loses a fight, he flees from the winner. As such, two prospective mates are not likely to keep fighting and interacting for 1 hour and in the wild females will not experience such a long period of interaction and observation. Audience effects are unlikely to have evolved this way. However, perhaps direct contact between males and females before and after fights may have allowed a direct comparison of amine build-up and allowed for quicker determination of winner and loser. Because watching fights did not inform mate choice, it is unlikely that males are gaining a reproductive benefit from female eavesdropping in this species.

Mating success is only one component of fitness and since most females exert post-copulatory choice (Eberhard, 1996), it is important to consider fecundity, viability and offspring size when evaluating the fitness effects of mating with dominant or more aggressive males. I found that dominant males did not have higher fitness in any of the offspring measures studied. Instead, aggression rather than dominance was a better predictor of offspring size. Females mated to less

aggressive males laid more eggs and produced offspring that were more likely to survive to adulthood. On the other hand, females mated to more aggressive males had larger offspring. There may be a trade off between offspring number and size, such that females mated to less aggressive males lay more offspring in the ‘hope’ that some of her smaller offspring (which tend to have lower reproductive success) reproduce (Gowaty et al., 2007; Olofsson et al. 2009). Since less aggressive males have smaller offspring, and smaller individuals have lower fitness in many species (female tropical butterfly, *Brassolis sophorae*: Carvalho et al. 1998; male seed beetle, *Stator limbatus*: Fox et al., 1995; female white-spotted charr, *Salvelinus leucomaenis*: Morita & Takashima, 1998; female Trinidadian guppies, *Poecilia reticulata*: Reynolds & Gross, 1992; female moose, *Alces alces*: Sand, 1996; field cricket, *Gryllus veletis*: Harrison et al., 2014), females may be laying more eggs in an attempt to compensate for the reduced fitness of her offspring. While offspring of less aggressive males are smaller, they are more likely to survive to adulthood, suggesting that males with reduced aggression may not actually be of lower quality but that there may be other factors influencing offspring size.

The offspring of more aggressive male offspring may be larger because of reduced juvenile density. Females mated to less aggressive males laid more eggs, and had offspring with higher survivability and thus there were likely more offspring in the family bins of less aggressive males. Since juvenile density affects adult size in many species (marbled salamanders, *Ambystoma opacum*: Scott, 1994; Red deer, *Cervus elapus*: Albon et al., 1987; mosquito, *Aedes aegypti*: Agnew et al., 2002) the offspring of more aggressive males may have been larger because they were less crowded. My *post hoc* tests show that number of eggs hatched explains 15% of the variation in offspring size. Because of the multiple confounding factors affecting offspring size, it

is difficult to draw any conclusions using size as a measure of offspring fitness. Future studies on offspring size should control even more closely for rearing density to provide a more accurate picture of the effect of paternal aggression and dominance on offspring size.

Overall, I found that females prefer to mount more dominant males, regardless of whether they watched a fight or not. However, females did not lay more eggs with more dominant males, nor did their eggs have higher viability or produce larger offspring. Due to the cost of searching for a mate (Jennions & Petrie, 1997), females are not likely to evolve a preference unless it confers a reproductive benefit. So, why would females prefer to mount more dominant males if his preference does not lead to fitness benefits? The high density as juveniles may have masked effects of dominance on offspring size. It is also possible that my measures of fitness did not measure the traits affected by sire dominance. Other studies have found that more dominant males have higher sperm competitive success (cooperatively breeding fish, *Neolamprologus pulcher*: Fitzpatrick et al., 2006; Damaraland mole-rats, *Cryptomys damarensis*: Maswanganye et al., 1999; Australian field cricket, *Teleogryllus oceanicus*: Thomas & Simmons, 2009), are better at manipulating female fecundity (*Gryllus bimaculatus*: Bretman et al., 2006), and produce more dominant offspring (*Nauphoeta cinerea*: Moore, 1990). I did not measure any of these traits in my already robust study. Since dominance is correlated with traits such as body size (house cricket, *Acheta domesticus*: Brown et al., 2006; copperheads, *Agkistrodon contortrix*: Schuett, 1997; brown anoles, *Anolis sagrei*: Tokarz, 1985) and weapon size (*G. pennsylvanicus*: Judge & Bonanno, 2008; dung beetle, *Euoniticellus intermedius*: Lailvaux et al., 2005; black Dall's sheep, *Ovis dalli stonei*, and bighorn sheep, *Ovis canadensis canadensis*: Geist, 1966), and since body size (pied flycatcher, *Ficedula hypoleuca*: Alatato & Lundberg, 1986; *Drosophila buzzatii*: Prout

& Barker, 1989; Trinidadian guppy, *Poecilia reticulata*: Reynolds & Gross, 1992; field cricket, *Gryllus bimaculatus*: Simmons, 1987a; Great tit, *Parus major*: van Noordwijk et al., 1988) and morphological traits (red deer antler, *Cervus elaphus*: Kruuk et al., 2002; dorsal fin size and number in the sailfin molly, *Poecilia latipinna*, and the shortfin molly, *Poecilia mexicana*: Ptacek, 2009; aedeagus length in dung beetle, *Onthophagus taurus*: House & Simmons, 2012) are heritable, it is possible that dominant sires have dominant sons (and possibly also daughters). Therefore, a future study on the repeatability and heritability of dominance may yield interesting results and might explain why females prefer more dominant males in no-choice mating trials.

Returning to the social network perspective, does female preference for more dominant males explain the evolution of audience effects? While females do prefer fight winners over losers, females do not need to watch a fight to know which male is dominant. Thus it does not appear that females are gathering information from eavesdropping on fights to determine male dominance. However, there is a difference in the egg laying behaviour of females that did and did not watch fights; females that did not watch fights lay more eggs. Therefore, males are not gaining reproductive benefits from fighting in front of a female audience, in fact this may actually decrease their fitness. So why did audience effects evolve?

Resource Value

While it seems intuitive to investigate the evolution of audience effects by assessing the behavioural changes of audiences (i.e. are male audience members more likely to engage in antagonist interactions with males they have watched fight; are female audience members more likely to mate with winners), we may be neglecting to analyse another important perspective: that

of the fighting males themselves. Male field crickets in the wild fight over territories from which to call and attract females (Alexander, 1961), similar to lekking species. While females may lay eggs around the male's territory in mole crickets, (we do not know if this occurs in *G. assimilis* and more closely-related species) neither parent cares for offspring (Alexander, 1961). If fights between males in crickets are over territories, then the arenas in which males fight in the laboratory may be interpreted as a territory. If a male can sense a female's presence in the arena, this would indicate that the "territory" already has females in it. Since males signal acoustically to attract females (Alexander, 1961) and signalling comes at an energetic cost (Hack, 1998), having females near his territory means that he will not need to expend as much energy to attract females. As males have been found to fight more aggressively for access to more valuable resources (Enquist & Leimar, 1987), males may be fighting more when females are present because the territory they are fighting over is more valuable. This may explain why, when Fitzsimmons and Bertram (2013) fought males in front of a male audience, males did not fight more aggressively relative to when there was no audience; a single male's presence in a territory does not change its value.

Overall, my results suggest that there is no reproductive benefit to increased aggression. Perhaps males are fighting more aggressively simply because the territory they are fighting over is more valuable due to the presence of the female. Varying territory value by either increasing the number of females or varying female size may allow us to further examine this hypothesis. It is also possible that the number of females in the territory, since it indicates a much more drastic change in resource value, may more clearly influence male aggression. Future studies should investigate this aspect of audience effects.

Future Studies

While audience effects appear to be caused by male resource assessment, the fact that females preferably mount male winners without deriving any reproductive benefits indicates that there may be benefits to female choice that I did not assess. It is unlikely that female preference would evolve without being beneficial as it is a costly behaviour (Jennions & Petrie, 1997). Future studies should investigate other possible benefits of mating with dominant males, heritability of dominance may be a worthwhile topic to pursue due to its morphological components (Judge & Bonanno, 2008).

While I assume that there are no direct benefits to females of mating with dominant males, this may not be the case. Females can gain lifetime as well as reproductive benefits by mating with preferred males (Wagner & Harper, 2003) and may have reduced predation in the wild when mated to males with burrows (Rolando Rodríguez-Muñoz et al., 2011). Assessing how dominance affects these direct benefits to females may prove informative and help explain the evolution of female preference for dominant males.

Future studies should carefully control the effects of juvenile density. While I attempted to do this by reducing each family down to 20 individuals, I may have done this too late in juvenile development, and therefore not controlled the juvenile development environment carefully enough. Since *G. assimilis* females lay a large number of eggs (one female laid 1501 eggs over a 4 week period in my experiment), females could have been given only one or two weeks to lay eggs. This would reduce some of the crowding. In addition, if only 70 pinheads had been kept and raised to adulthood, that may have given a better estimate of survivability than juvenile to adult survival

and eliminate the problem of crowding. Then only 5 female and male offspring should have been measured, since the energy and time spent measuring 20 offspring to only obtain 2 measures of body size per family (one for the sons another for the daughters) could have been better spent obtaining other variables, such as son's long distance signalling data or measures of mandible size.

Conclusions

The increase in aggression when males fight in front of a female audience may not have evolved because it increases male reproductive success. Instead, males may fight more when females are watching because the females represent an increase in the quality of the male's potential territory. While females are more likely to mount dominant males over subordinate ones, watching a fight does not inform female choice and dominant males do not have larger offspring. In fact it seems that females invest more in reproduction when mated to less aggressive males and that these males may be of higher quality. Thus audience effects may occur because males are treating the fighting arena as a display territory and the presence of females increases the territory's value. Future research into audience effects should investigate the effect of territory value (by varying female number and weight) on male aggression to test this hypothesis.

References

- Adamo, S. A., & Hoy, R. R. (1995). Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. *Animal Behaviour*, *49*, 1491–1501. Retrieved from <http://www.sciencedirect.com/science/article/pii/0003347295900705>
- Agnew, P., Hide, M., Sidobre, C., & Michalakis, Y. (2002). A minimalist approach to the effects of density-dependent competition on insect life-history traits. *Ecological Entomology*, *27*(4), 396–402. <http://doi.org/10.1046/j.1365-2311.2002.00430.x>
- Alatato, R. V., & Lundberg, A. (1986). Heritability and selection on tarsus length in the piedflycatcher (*Ficedula hypoleuca*). *Evolution*, *40*(3), 574–583.
- Albon, S. D., Clutton-Brock, T. H., & Guinness, F. E. (1987). Early development and population dynamics in red deer . II . Density-independent effects and cohort variation. *Journal of Animal Ecology*, *56*(1), 69–81.
- Alexander, R. D. (1961). Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour*, *17*(2/3), 130–223. Retrieved from <http://www.jstor.org/stable/10.2307/4532972>
- Andersson, M. B. (1994). *Sexual selection*. Princeton, N.J.: Princeton University Press.
- Andrés, J. A., Maroja, L. S., Bogdanowicz, S. M., Swanson, W. J., & Harrison, R. G. (2006). Molecular evolution of seminal proteins in field crickets. *Molecular Biology and Evolution*, *23*(8), 1574–1584. <http://doi.org/10.1093/molbev/msl020>
- Aquiloni, L., Buric, M., & Gherardi, F. (2008). Crayfish females eavesdrop on fighting males before choosing the dominant mate. *Current Biology*, *18*(11), 462–463. <http://doi.org/10.1016/j.cub.2008.04.006>
- Archer, J. (2009). Does sexual selection explain human sex differences in aggression? *Behavioral and Brain Sciences*, *32*(3-4), 249–311. <http://doi.org/10.1017/S0140525X09990951>
- Bateman, P. W. (1998). Assortative mating by both sexes in the cricket *Platygyryllus pritnifortnis* (Orthoptera: Gryllidae; Gryllinae). *Transactions of the American Entomological Society (1890-)*.
- Bateman, P. W., Gilson, L. N., & Ferguson, J. W. H. (2001). Male size and sequential mate preference in the cricket *Gryllus bimaculatus*. *Animal Behaviour*, *61*(3), 631–637. <http://doi.org/10.1006/anbe.2000.1617>

- Bateman, P. W., & Toms, R. B. (2013). Mating, mate guarding and male-male relative strength assessment in an African king oricket (Orthoptera: Mimnermidae). *Transactions of the American Entomological Society (1890-)*, 124(1), 69–75.
- Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *The Annals of Statistics*, 29(4), 1165–1188. Retrieved from <http://www.jstor.org/stable/10.2307/2674075>
- Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385–399. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.1996.tb01442.x/abstract>
- Berglund, A., & Rosenqvist, G. (2001). Male pipefish prefer dominant over attractive females. *Behavioral Ecology*, 12(4), 402–406.
- Berglund, A., Rosenqvist, G., & Bernet, P. (1997). Ornamentation predicts reproductive success in female pipefish. *Behavioral Ecology and Sociobiology*, 40(3), 145–150. <http://doi.org/10.1007/s002650050327>
- Bertram, S. M., & Rook, V. (2012). Relationship between condition, aggression, signaling, courtship, and egg laying in the field cricket, *Gryllus assimilis*. *Ethology*, 118(4), 360–372. <http://doi.org/10.1111/j.1439-0310.2011.02019.x>
- Bertram, S. M., Rook, V. L. M., & Fitzsimmons, L. P. (2010). Strutting their stuff: victory displays in the spring field cricket, *Gryllus veletis*. *Behaviour*, 147(10), 1249–1266. <http://doi.org/10.1163/000579510X514535>
- Bierbach, D., Sassmannshausen, V., Streit, B., Arias-Rodriguez, L., & Plath, M. (2013). Females prefer males with superior fighting abilities but avoid sexually harassing winners when eavesdropping on male fights. *Behavioral Ecology and Sociobiology*, 67(4), 675–683. <http://doi.org/10.1007/s00265-013-1487-8>
- Birkhead, T. R., & Møller, A. P. (1993). Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds and mammals. *Biological Journal of the Linnean Society*, 50(4), 295–311. <http://doi.org/10.1111/j.1095-8312.1993.tb00933.x>
- Bluhm, C. K., & Gowaty, P. A. (2004). Social constraints on female mate preferences in mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Animal Behaviour*, 68(5), 977–983. <http://doi.org/10.1016/j.anbehav.2004.01.013>
- Bretman, A., Rodríguez-Muñoz, R., & Tregenza, T. (2006). Male dominance determines female egg laying rate in crickets. *Biology Letters*, 2(3), 409–411. <http://doi.org/10.1098/rsbl.2006.0493>

- Bretman, A., & Tregenza, T. (2005). Measuring polyandry in wild populations: a case study using promiscuous crickets. *Molecular Ecology*, *14*(7), 2169–2179. <http://doi.org/10.1111/j.1365-294X.2005.02556.x>
- Brown, W. D., Smith, A. T., Moskalik, B., & Gabriel, J. (2006). Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. *Animal Behaviour*, *72*(1), 225–233. <http://doi.org/10.1016/j.anbehav.2006.01.012>
- Buzzard, P. J., Xu, D., & Li, H. (2014). Sexual/aggressive behavior of wild yak (*Bos mutus* Prejevalsky 1883) during the rut: influence of female choice. *Chinese Science Bulletin*, *59*(22), 2756–2763. <http://doi.org/10.1007/s11434-014-0247-0>
- Cain, K. E., & Ketterson, E. D. (2013). Costs and benefits of competitive traits in females: aggression, maternal care and reproductive success. *PloS One*, *8*(10), e77816. <http://doi.org/10.1371/journal.pone.0077816>
- Candolin, U. (2000). Male-male competition ensures honest signaling of male parental ability in the three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, *49*(1), 57–61. <http://doi.org/10.1007/s002650000267>
- Carvalho, M. C., Queiroz, P. C. D., & Ruszczyk, A. (1998). Protandry and female size-fecundity variation in the tropical butterfly *Brassolis sophorae*. *Oecologia*, *116*(1/2), 98–102. <http://doi.org/10.1007/s004420050567>
- Cheetham, S. A., Thom, M. D., Beynon, R. J., & Hurst, J. L. (2008). The effect of familiarity on mate choice. In J. L. Hurst, R. J. Beynon, S. C. Roberts, & T. D. Wyatt (Eds.), *Chemical signals in vertebrates 11* (pp. 271–280). New York: Springer.
- Cox, C. R. (1981). Agonistic encounters among male elephant seals: frequency, context, and the role of female preference. *American Zoologist*, *21*, 197–209. Retrieved from <http://icb.oxfordjournals.org/content/21/1/197.short>
- Cox, C. R., & Le Boeuf, B. J. (1977). Female incitation of male competition: A mechanism in sexual selection. *The American Naturalist*, *111*(978), 317–335. Retrieved from <http://www.jstor.org/stable/10.2307/2460066>
- Crespi, B. J. (1988). Risks and benefits of lethal male fighting in the colonial polygynous thrips *Hoplothrips karnyi* (Insecta : Thysanoptera). *Behavioral Ecology and Sociobiology*, *22*(4), 293–301. Retrieved from <http://link.springer.com/article/10.1007/BF00299845>
- Cummings, M., & Mollaghan, D. (2006). Repeatability and consistency of female preference behaviours in a northern swordtail, *Xiphophorus nigrensis*. *Animal Behaviour*, *72*(1), 217–224. <http://doi.org/10.1016/j.anbehav.2006.01.009>

- Darwin, C. R. (1860). Letter 2743 - Darwin, C. R. to Gray, Asa [3 Apr 1860]. In *Darwin Correspondence Project*. Cambridge University. Retrieved from <http://www.darwinproject.ac.uk/darwinletters/calendar/entry-6033.html>
- Darwin, C. R. (1871). *The Descent of Man and Selection in Relation to Sex* (1st ed.). London: John Murray.
- Dewsbury, D. A. (1990). Fathers and sons: genetic factors and social dominance in deer mice, *Peromyscus maniculatus*. *Animal Behaviour*, 39(2), 284–289. [http://doi.org/10.1016/S0003-3472\(05\)80872-3](http://doi.org/10.1016/S0003-3472(05)80872-3)
- Doutrelant, C., & McGregor, P. K. (2000). Eavesdropping and mate choice in female fighting fish. *Behaviour*, 137(12), 1655–1669.
- Doutrelant, C., McGregor, P. K., & Oliveira, R. F. (2001). The effect of the sex of an audience on male-male displays of Siamese fighting fish (*Betta splendens*). *Behavioral Ecology*, 12(3), 283–286. <http://doi.org/10.1163/15685390260437344>
- Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, 17(6), 1011–1019. <http://doi.org/10.1093/beheco/arl035>
- Eberhard, W. G. (1996). *Female control: Sexual selection by cryptic female choice* (1st ed.). Princeton: Princeton University Press.
- Eberhard, W. G., & Cordero, C. (1995). Sexual selection by cryptic female choice on male seminal products - a new bridge between sexual selection and reproductive physiology. *Trends in Ecology & Evolution*, 10(12), 493–496. [http://doi.org/10.1016/S0169-5347\(00\)89205-8](http://doi.org/10.1016/S0169-5347(00)89205-8)
- Enquist, M., & Leimar, O. (1987). Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, 127(2), 187–205. [http://doi.org/10.1016/S0022-5193\(87\)80130-3](http://doi.org/10.1016/S0022-5193(87)80130-3)
- Fitzpatrick, J. L., Desjardins, J. K., Stiver, K. A., Montgomerie, R., & Balshine, S. (2006). Male reproductive suppression in the cooperatively breeding fish *Neolamprologus pulcher*. *Behavioral Ecology*, 17(1), 25–33. <http://doi.org/10.1093/beheco/ari090>
- Fitzsimmons, L., & Bertram, S. (2013). Playing to an audience: the social environment influences aggression and victory displays. *Biology Letters*, 9(4), 20130449. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/23843219>
- Fitzsimmons, L. P., & Bertram, S. M. (2011). The calling songs of male spring field crickets (*Gryllus veletis*) change as males age. *Behaviour*, 148(9), 1045–1065. <http://doi.org/10.1163/000579511X588812>

- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, 139(3), 603–622. Retrieved from <http://www.jstor.org/stable/10.2307/2462500>
- Forsgren, E. (1997). Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society B: Biological Sciences*, 264(1386), 1283–1286. Retrieved from <http://rspb.royalsocietypublishing.org/content/264/1386/1283.short>
- Fox, C. W., McLennan, L. A., & Mousseau, T. A. (1995). Male body size affects female lifetime reproductive success in a seed beetle. *Animal Behaviour*, 50(1), 281–284. <http://doi.org/10.1006/anbe.1995.0242>
- Francis, R. C. (1988). On the relationship between aggression and social dominance. *Ethology*, 78(3), 223–237. <http://doi.org/10.1111/j.1439-0310.1988.tb00233.x>
- Froman, D. P., Pizzari, T., Feltmann, A. J., Castillo-Juarez, H., & Birkhead, T. R. (2002). Sperm mobility: mechanisms of fertilizing efficiency, genetic variation and phenotypic relationship with male status in the domestic fowl, *Gallus gallus domesticus*. *Proceedings of the Royal Society B: Biological Sciences*, 269, 607–612. <http://doi.org/10.1098/rspb.2001.1925>
- García-González, F., & Simmons, L. W. (2005). Sperm viability matters in insect sperm competition. *Current Biology*, 15, 271–275. <http://doi.org/10.1016/j>
- Geist, V. (1966). The evolutionary significance of mountain sheep horns. *Evolution*, 20(4), 558–566. <http://doi.org/10.2307/2406590>
- Giebel, G., Weierstall, R., Schauer, M., & Elbert, T. (2013). Female attraction to appetitive-aggressive men is modulated by women's menstrual cycle and men's vulnerability to traumatic stress. *Evolutionary Psychology*, 11(1), 248–262. Retrieved from <http://kops.ub.uni-konstanz.de/handle/id-16/browse?authority=pop01516&type=author>
- Gowaty, P. A., Anderson, W. W., Bluhm, C. K., Drickamer, L. C., Kim, Y.-K., & Moore, A. J. (2007). The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. *Proceedings of the National Academy of Sciences of the United States of America*, 104(38), 15023–15027. <http://doi.org/10.1073/pnas.0706622104>
- Hack, M. A. (1997). The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behavioral Ecology*, 8(1), 28–36. <http://doi.org/10.1093/beheco/8.1.28>
- Hack, M. A. (1998). The energetics of male mating strategies in field crickets (Orthoptera: Gryllinae: Gryllidae). *Journal of Insect Behavior*, 11(6), 853–867. <http://doi.org/10.1023/a:1020864111073>

- Harrison, S. J., Raubenheimer, D., Simpson, S. J., Godin, J.-G. J., & Bertram, S. M. (2014). Towards a synthesis of frameworks in nutritional ecology: Interacting effects of protein, carbohydrate and phosphorus on field cricket fitness. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792), 20140539. <http://doi.org/10.1098/rspb.2014.0539>
- Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: effects of menstrual cycle and relationship status. *Biology Letters*, 1(3), 256–259. <http://doi.org/10.1098/rsbl.2005.0332>
- Head, M. L., Hunt, J., Jennions, M. D., & Brooks, R. (2005). The indirect benefits of mating with attractive males outweigh the direct costs. *PLoS Biology*, 3(2), 0289–0294. <http://doi.org/10.1371/journal.pbio.0030033>
- Hedrick, A. V. (1986). Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology*, 19(1), 73–77. <http://doi.org/10.1007/BF00303845>
- Hedrick, A. V., & Kortet, R. (2012). Effects of body size on selectivity for mating cues in different sensory modalities. *Biological Journal of the Linnean Society*, 105(1), 160–168. <http://doi.org/10.1111/j.1095-8312.2011.01786.x>
- Hewison, A. J. M., & Gaillard, J.-M. (1999). Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution*, 14(6), 229–234.
- Hoefler, C. D., Carlascio, A. L., Persons, M. H., & Rypstra, A. L. (2009). Male courtship repeatability and potential indirect genetic benefits in a wolf spider. *Animal Behaviour*, 78(1), 183–188. <http://doi.org/10.1016/j.anbehav.2009.04.012>
- Honek, A. (1993). Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, 66(3), 483–492.
- Horne, T. J., & Ylönen, H. (1998). Heritabilities of dominance-related traits in male bank voles (*Clethrionomys glareolus*). *Evolution*, 52(3), 894–899.
- House, C. M., & Simmons, L. W. (2012). The genetics of primary and secondary sexual character trade-offs in a horned beetle. *Journal of Evolutionary Biology*, 25(9), 1711–1717. <http://doi.org/10.1111/j.1420-9101.2012.02559.x>
- Howard, R. D., Martens, R. S., Innis, S. A., Drnevich, J. M., & Hale, J. (1998). Mate choice and mate competition influence male body size in Japanese medaka. *Animal Behaviour*, 55(5), 1151–1163. Retrieved from http://bilbo.bio.purdue.edu/~www_eco/faculty/howard/pdfs/medakaMS.pdf

- Huber, R. (2005). Amines and motivated behaviors: A simpler systems approach to complex behavioral phenomena. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 191(3), 231–239. <http://doi.org/10.1007/s00359-004-0585-5>
- Jacob, A., Nusslé, S., Britschgi, A., Evanno, G., Müller, R., & Wedekind, C. (2007). Male dominance linked to size and age, but not to “good genes” in brown trout (*Salmo trutta*). *BMC Evolutionary Biology*, 7, 207. <http://doi.org/10.1186/1471-2148-7-207>
- Jang, Y., Gerhardt, H. C., & Choe, J. C. (2008). A comparative study of aggressiveness in eastern North American field cricket species (genus: *Gryllus*). *Behavioral Ecology and Sociobiology*, 62(9), 1397–1407. <http://doi.org/10.1007/s00265-008-0568-6>
- Järvi, T. (1990). The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic salmon *Salmo salar*. *Ethology*, 84, 123–132. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0310.1990.tb00789.x/abstract>
- Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, 72(2), 283–327. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9155244>
- Johansson, B. G., & Jones, T. M. (2007). The role of chemical communication in mate choice. *Biological Reviews*, 82(2), 265–289. <http://doi.org/10.1111/j.1469-185X.2007.00009.x>
- Judge, K. A. (2010). Female social experience affects the shape of sexual selection on males. *Evolutionary Ecology Research*, 12(3), 389–402.
- Judge, K. A., & Bonanno, V. L. (2008). Male weaponry in a fighting cricket. *PloS One*, 3(12), e3980. <http://doi.org/10.1371/journal.pone.0003980>
- Keyser, A. J., & Hill, G. E. (2000). Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology*, 11(2), 202–209. <http://doi.org/10.1093/beheco/11.2.202>
- Khazraïe, K., & Campan, M. (1999). The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes*, 44(3), 341–348. [http://doi.org/10.1016/S0376-6357\(98\)00058-8](http://doi.org/10.1016/S0376-6357(98)00058-8)
- Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B: Biological Sciences*, 270, 653–664. <http://doi.org/10.1098/rspb.2002.2235>

- Kortet, R., & Hedrick, A. (2005). The scent of dominance: female field crickets use odour to predict the outcome of male competition. *Behavioral Ecology and Sociobiology*, *59*(1), 77–83. <http://doi.org/10.1007/s00265-005-0011-1>
- Kortet, R., & Hedrick, A. (2007). A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biological Journal of the Linnean Society*, *91*(3), 475–482. Retrieved from <http://dx.doi.org/10.1111/j.1095-8312.2007.00812.x>
- Kralj-Fišer, S., Sanguino Mostajo, G. A., Preik, O., Pekar, S., & Schneider, J. M. (2013). Assortative mating by aggressiveness type in orb weaving spiders. *Behavioral Ecology*, *24*(4), 824–831. <http://doi.org/10.1093/beheco/art030>
- Kralj-Fišer, S., & Schneider, J. M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behaviour*, *84*(1), 197–204. <http://doi.org/10.1016/j.anbehav.2012.04.032>
- Kruczek, M. (1997). Male rank and female choice in the bank vole, *Clethrionomys glareolus*. *Behavioural Processes*, *40*(2), 171–176. [http://doi.org/10.1016/S0376-6357\(97\)00785-7](http://doi.org/10.1016/S0376-6357(97)00785-7)
- Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., & Clutton-Brock, T. (2002). Antler size in red deer: heritability and selection but no evolution. *Evolution*, *56*(8), 1683–1695. <http://doi.org/10.1111/j.0014-3820.2002.tb01480.x>
- Kunc, H. P., Amrhein, V., & Naguib, M. (2006). Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. *Animal Behaviour*, *72*(1), 25–30. <http://doi.org/10.1016/j.anbehav.2005.08.014>
- Lailvaux, S. P., Hathway, J., Pomfret, J., & Knell, R. J. (2005). Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Functional Ecology*, *19*(4), 632–639. <http://doi.org/10.1111/j.1365-2435.2005.01024.x>
- Landry, C., Garant, D., Duchesne, P., & Bernatchez, L. (2001). “Good genes as heterozygosity”: the major histocompatibility complex and mate choice in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society B: Biological Sciences.*, *268*, 1279–1285. <http://doi.org/10.1098/rspb.2001.1659>
- Lehtonen, T. K., & Lindström, K. (2008). Repeatability of mating preferences in the sand goby. *Animal Behaviour*, *75*(1), 55–61. <http://doi.org/10.1016/j.anbehav.2007.04.011>
- Martin, J., & Lopez, P. (2007). Scent may signal fighting ability in male Iberian rock lizards. *Biology Letters*, *3*(2), 125–127. <http://doi.org/10.1098/rsbl.2006.0589>

- Maswanganye, K. A., Bennett, N. C., Brinders, J., & Cooney, R. (1999). Oligospermia and azoospermia in non-reproductive male Damaraland mole-rats *Cryptomys damarensis* (Rodentia: Bathyergidae). *Journal of Zoology*, 248(3), 411–418. <http://doi.org/10.1017/S0952836999007128>
- Matos, R. J., & Schlupp, I. (2005). Performing in front of an audience: signallers and the social environment. In P. K. McGregor (Ed.), *Animal Communication Networks* (1st ed., pp. 63–83). Cambridge: Cambridge University Press.
- Maynard Smith, J., & Harper, D. (2003). Signals during contests. In *Animal Signals* (pp. 90–111). New York: Oxford University Press.
- McGregor, P. K., & Peake, T. M. (2000). Communication networks: social environments for receiving and signalling behaviour. *Acta Ethologica*, 2(2), 71–81. <http://doi.org/10.1007/s102110000015>
- Mennill, D. J., & Ratcliffe, L. M. (2004). Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour*, 67(3), 441–450. <http://doi.org/10.1016/j.anbehav.2003.04.010>
- Mennill, D. J., Ratcliffe, L. M., & Boag, P. T. (2002). Female eavesdropping on male song contests in songbirds. *Science*, 296, 873. <http://doi.org/10.1126/science.296.5569.873>
- Moller, A. P., & Alatalo, R. V. (1999). Good-genes effects in sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, 266, 85–91. <http://doi.org/10.1098/rspb.1999.0607>
- Montgomerie, R., & Thornhill, R. (1989). Fertility advertisement in birds: a means of inciting male-male competition? *Ethology*, 81(3), 209–220. <http://doi.org/10.1111/j.1439-0310.1989.tb00767.x>
- Moore, A. J. (1990). The inheritance of social dominance, mating behaviour and attractiveness to mates in male *Nauphoeta cinerea*. *Animal Behaviour*, 39(2), 388–397. [http://doi.org/10.1016/S0003-3472\(05\)80886-3](http://doi.org/10.1016/S0003-3472(05)80886-3)
- Moore, A. J., Gowaty, P. A., Wallin, W. G., & Moore, P. J. (2001). Sexual conflict and the evolution of female mate choice and male social dominance. *Proceedings of the Royal Society B: Biological Sciences*, 268(1466), 517–523. <http://doi.org/10.1098/rspb.2000.1399>
- Moore, P. J., Reagan-Wallin, N. L., Haynes, K. F., & Moore, A. J. (1997). Odour conveys status on cockroaches. *Nature*, 389, 25. <http://doi.org/10.1038/37888>

- Morita, K., & Takashima, Y. (1998). Effect of female size on fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. *Journal of Fish Biology*, 53(5), 1140–1142. <http://doi.org/10.1111/j.1095-8649.1998.tb00471.x>
- Muehlenbein, M. P., & Watts, D. P. (2010). The costs of dominance: testosterone, cortisol and intestinal parasites in wild male chimpanzees. *BioPsychoSocial Medicine*, 4, 21. <http://doi.org/10.1186/1751-0759-4-21>
- Nelson, C. M., & Nolen, T. G. (1997). Courtship song, male agonistic encounters, and female mate choice in the house cricket, *Acheta domesticus* (Orthoptera: Gryllidae). *Journal of Insect Behavior*, 10(4), 557–570. <http://doi.org/10.1007/BF02765377>
- Nol, E., Cheng, K., & Nichols, C. (1996). Heritability and phenotypic correlations of behaviour and dominance rank of Japanese quail. *Animal Behaviour*, 52(4), 813–820. <http://doi.org/10.1006/anbe.1996.0226>
- Norris, K. (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature*, 362, 537–539. <http://doi.org/10.1038/362537a0>
- Olofsson, H., Ripa, J., & Jonzén, N. (2009). Bet-hedging as an evolutionary game: the trade-off between egg size and number. *Proceedings of the Royal Society B: Biological Sciences*, 276(1669), 2963–2969. <http://doi.org/10.1098/rspb.2009.0500>
- Ophir, A. G., & Galef, B. G. (2003). Female Japanese quail that “eavesdrop” on fighting males prefer losers to winners. *Animal Behaviour*, 66(2), 399–407. <http://doi.org/10.1006/anbe.2003.2230>
- Ophir, A. G., & Galef, B. G. (2004). Sexual experience can affect use of public information in mate choice. *Animal Behaviour*, 68(5), 1221–1227. <http://doi.org/10.1016/j.anbehav.2003.12.023>
- Pacheco, K., & Bertram, S. M. (2014). How male sound pressure level influences phonotaxis in virgin female Jamaican field crickets (*Gryllus assimilis*). *PeerJ*, 2, e437. <http://doi.org/10.7717/peerj.437>
- Pacheco, K., Dawson, J. W., Jutting, M., & Bertram, S. M. (2013). How age influences phonotaxis in virgin female Jamaican field crickets (*Gryllus assimilis*). *PeerJ*, 1, e130. <http://doi.org/10.7717/peerj.130>
- Palokangas, P., Korpimäki, E., Hakkarainen, H., Huhta, E., Tolonen, P., & Alatalo, R. V. (1994). Female kestrels gain reproductive success by choosing brightly ornamented males. *Animal Behaviour*. <http://doi.org/10.1006/anbe.1994.1058>

- Penn, D. J., & Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist*, *153*(2), 145–164. <http://doi.org/10.1086/303166>
- Pérez-Guisado, J., Lopez-Rodríguez, R., & Muñoz-Serrano, A. (2006). Heritability of dominant-aggressive behaviour in English Cocker Spaniels. *Applied Animal Behaviour Science*, *100*, 219–227. <http://doi.org/10.1016/j.applanim.2005.11.005>
- Pitcher, T. E., & Neff, B. D. (2007). Genetic quality and offspring performance in Chinook salmon: implications for supportive breeding. *Conservation Genetics*, *8*(3), 607–616. <http://doi.org/10.1007/s10592-006-9204-z>
- Pitnick, S., & Markow, T. A. (1994). Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila packera* and its relatives. *The American Naturalist*, *143*(5), 785–819. Retrieved from <http://www.jstor.org/stable/10.2307/2462877>
- Pizzari, T., Cornwallis, C. K., & Froman, D. P. (2007). Social competitiveness associated with rapid fluctuations in sperm quality in male fowl. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1611), 853–860. <http://doi.org/10.1098/rspb.2006.0080>
- Prout, T., & Barker, J. S. F. (1989). Ecological aspects of the heritability of body size in *Drosophila buzzatii*. *Genetics*, *123*(4), 803–813.
- Ptacek, M. B. (2002). Patterns of inheritance of mating signals in sailfin and shortfin mollies (Poeciliidae: Poecilia: Mollienesia). *Genetica*, *116*, 329–342. <http://doi.org/10.1111/j.1439-0310.2009.01683.x>
- Qvarnström, A., & Forsgren, E. (1998). Should females prefer dominant males? *Trends in Ecology & Evolution*, *13*(12), 498–501. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/21238407>
- Qvarnström, A. (1997). Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B: Biological Sciences*, *264*(1385), 1225–1231. <http://doi.org/10.1098/rspb.1997.0169>
- Rantala, M. J., & Kortet, R. (2004). Male dominance and immunocompetence in a field cricket. *Behavioral Ecology*, *15*(2), 187–191. <http://doi.org/10.1093/beheco/arg103>
- Reynolds, J. D., & Gross, M. R. (1992). Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proceedings of the Royal Society B: Biological Sciences*, *250*(1327), 57–62. <http://doi.org/10.1098/rspb.1992.0130>

- Rodríguez-Muñoz, R., Bretman, A., Slate, J., Walling, C. A., & Tregenza, T. (2010). Natural and sexual selection in a wild insect population. *Science*, 328(5983), 1269–1272. <http://doi.org/10.1126/science.1188102>
- Rodríguez-Muñoz, R., Bretman, A., & Tregenza, T. (2011). Guarding males protect females from predation in a wild insect. *Current Biology*, 21(20), 1716–1719. <http://doi.org/10.1016/j.cub.2011.08.053>
- Ros, A. F. H., Brintjes, R., Santos, R. S., Canario, A. V. M., & Oliveira, R. F. (2004). The role of androgens in the trade-off between territorial and parental behavior in the Azorean rock-pool blenny, *Parablennius parvicornis*. *Hormones and Behavior*, 46(4), 491–497. <http://doi.org/10.1016/j.yhbeh.2004.04.007>
- Rudolfson, G., Figenschou, L., Folstad, I., Tveiten, H., & Figenschou, M. (2006). Rapid adjustments of sperm characteristics in relation to social status. *Proceedings of the Royal Society B: Biological Sciences*, 273(1584), 325–332. <http://doi.org/10.1098/rspb.2005.3305>
- Sand, H. (1996). Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia*, 106(2), 212–220. <http://doi.org/10.1007/BF00328601>
- Savage, K. E., Hunt, J., Jennions, M. D., & Brooks, R. (2004). Male attractiveness covaries with fighting ability but not with prior fight outcome in house crickets. *Behavioral Ecology*, 16(1), 196–200. <http://doi.org/10.1093/beheco/arh143>
- Schuett, G. W. (1997). Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour*, 54(1), 213–224. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9268451>
- Scott, D. E. (1994). The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology*, 75(5), 1383–1396. <http://doi.org/10.2307/1937462>
- Shackleton, M. A., Jennions, M. D., & Hunt, J. (2005). Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behavioral Ecology and Sociobiology*, 58(1), 1–8. <http://doi.org/10.1007/s00265-004-0907-1>
- Simmons, L. W. (1986a). Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, 34(5), 1463–1470.
- Simmons, L. W. (1986b). Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, 34(2), 567–579. Retrieved from <http://www.sciencedirect.com/science/article/pii/S0003347286801269>

- Simmons, L. W. (1987a). Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). *Behavioral Ecology and Sociobiology*, 21(5), 313–321. <http://doi.org/10.1007/BF00299969>
- Simmons, L. W. (1987b). Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus*. *Behavioral Ecology and Sociobiology*, 21, 197–202. <http://doi.org/10.1007/BF00303211>
- Simmons, L. W. (1988). Male size, mating potential and lifetime reproductive success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, 36(2), 372–379. [http://doi.org/10.1016/S0003-3472\(88\)80008-3](http://doi.org/10.1016/S0003-3472(88)80008-3)
- Simmons, L. W., Thomas, M. L., Simmons, F. W., & Zuk, M. (2013). Female preferences for acoustic and olfactory signals during courtship: male crickets send multiple messages. *Behavioral Ecology*, 24(5), 1099–1107. <http://doi.org/10.1093/beheco/art036>
- Stevenson, P. A., & Rillich, J. (2012). The decision to fight or flee - insights into underlying mechanism in crickets. *Frontiers in Neuroscience*, 6(118), 1–12. <http://doi.org/10.3389/fnins.2012.00118>
- Stevenson, P. A., & Rillich, J. (2015). Adding up the odds—Nitric oxide signaling underlies the decision to flee and post-conflict depression of aggression. *Science Advances*, 1(2), e1500060.
- Tachon, G., Murray, A., Gray, D. A., & Cade, W. H. (1999). Agonistic displays and the benefits of fighting in the field cricket, *Gryllus bimaculatus*. *Journal of Insect Behaviour*, 12(4), 533–543.
- Thomas, M. L., & Simmons, L. W. (2009). Male dominance influences pheromone expression, ejaculate quality, and fertilization success in the Australian field cricket, *Teleogryllus oceanicus*. *Behavioral Ecology*, 20(5), 1118–1124. <http://doi.org/10.1093/beheco/arp105>
- Tokarz, R. R. (1985). Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Animal Behaviour*, 33(3), 746–753. [http://doi.org/10.1016/S0003-3472\(85\)80006-3](http://doi.org/10.1016/S0003-3472(85)80006-3)
- Trainor, B. C., & Marler, C. A. (2001). Testosterone, paternal behavior, and aggression in the monogamous California mouse (*Peromyscus californicus*). *Hormones and Behavior*, 40(1), 32–42. <http://doi.org/10.1006/hbeh.2001.1652>
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. G. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago: Aldine.

- Trivers, R. L. (1976). Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution*, 30(2), 253–269. Retrieved from <http://www.jstor.org/stable/10.2307/2407700>
- Ung, D., Amy, M., & Leboucher, G. (2011). Heaven it's my wife! male canaries conceal extra-pair courtships but increase aggressions when their mate watches. *PLoS ONE*, 6(8), e22686. <http://doi.org/10.1371/journal.pone.0022686>
- Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology*, 62(1), 1–14. <http://doi.org/10.1007/s00265-007-0439-6>
- Van Erp, A. M. M., & Miczek, K. A. (2000). Aggressive behavior, increased accumbal dopamine, and decreased cortical serotonin in rats. *The Journal of Neuroscience*, 20(24), 9320–9325. <http://doi.org/20/24/9320> [pii]
- Van Noordwijk, A. J., van Balent, J. H., & Scharloo, W. (1988). Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genetical Research*, 51(2), 149–162. Retrieved from <http://dx.doi.org/10.1017/S0016672300024162>
- Wagner, W. E., & Harper, C. J. (2003). Female life span and fertility are increased by the ejaculates of preferred males. *Evolution*, 57(9), 2054–2066. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/14575327>
- Wagner, W. E., Kelley, R. J., Tucker, K. R., & Harper, C. J. (2001). Females receive a life-span benefit from male ejaculates in a field cricket. *Evolution*, 55(5), 994–1001. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11430659>
- Wagner, W. E., & Reiser, M. G. (2000). The importance of calling song and courtship song in female mate choice in the variable field cricket. *Animal Behaviour*, 59(6), 1219–1226. <http://doi.org/10.1006/anbe.1999.1428>
- Ward, G., & FitzGerald, G. J. (1987). Male aggression and female mate choice in the threespine stickleback, *Gasterosteus aculeatus* L.*. *Journal of Fish Biology*, 30, 679–690. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8649.1987.tb05797.x/full>
- Winberg, S., & Nilsson, G. E. (1993). Roles of brain monoamine neurotransmitters in agonistic behaviour and stress reactions, with particular reference to fish. *Comparative Biochemistry and Physiology - C Pharmacology Toxicology and Endocrinology*, 106(3), 597–614. [http://doi.org/10.1016/0742-8413\(93\)90216-8](http://doi.org/10.1016/0742-8413(93)90216-8)
- Wong, B. B. M. (2004). Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Animal Behaviour*, 67(3), 583–590. <http://doi.org/10.1016/j.anbehav.2003.08.015>

Wong, B. B. M., & Candolin, U. (2005). How is female mate choice affected by male competition? *Biological Reviews of the Cambridge Philosophical Society*, 80(4), 559–571. <http://doi.org/10.1017/S1464793105006809>

Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology*, 53(1), 205–214. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/1195756>