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A lover, not a fighter: mating causes male crickets to lose fights

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Abstract Both resource-holding potential (RHP) and experience in aggressive contests are known to affect future aggressive behaviour. However, few studies have examined the effects of mating experience on agonistic behaviour, despite the fact that dominant males usually acquire more matings. We investigated the effect of mating experience on male aggressive behaviour including the relationship between RHP and fighting success in the fall field cricket, *Gryllus pennsylvanicus*. We formed pairs of size- and age-matched males that varied in RHP (relative weapon size) and conducted two experiments. In the first, we varied male mating experience by allowing one male in a pair to either be (a) 'mated': court, be mounted and copulate with a virgin female or (b) 'experienced': court, be mounted, but prevented from copulating. The second experiment varied postcopulatory experience where the male was allowed ('contact') or prevented from ('no-contact') continued contact with his recent mate. Following treatment, experimental males engaged in an aggressive contest with the naïve size- and age-matched male. In our first experiment, we found that mated and experienced males were equally likely to escalate contests to combat with a naïve opponent, but mated males were less likely than experienced males to win. There was no effect of mating on the relationship between RHP and fighting success. In our second experiment, we found no effect of maintaining contact with the female on the tendency to escalate or the probability of winning. As in the first experiment, males with relatively larger heads again won more fights and this relationship was unaffected by male experience. These results suggest that mating is itself detrimental to male success in aggressive contests, but that this effect is not sufficient to eliminate the effect of RHP on fighting success.

Keywords Aggression · Sexual selection · Resource-holding potential · Social experience · Weaponry · Field cricket

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Introduction

Aggressive competition among males is a major mechanism of sexual selection (Darwin 1871; Andersson 1994). Contests between males are often decided in favour of the male with the greater resource-holding potential (RHP), or the sum of phenotypic traits that affect his ability to win fights (Parker 1974). Additionally, the outcome of contests themselves often have carryover effects on subsequent contests such that prior winners are more likely to win again and losers are more likely to lose (Hsu et al. 2006). In most territorial species, the ultimate payoff to winning males is increased mating success (e.g. Le Boeuf and Peterson 1969; reviewed in Andersson (1994); Kelly (2008a)). Therefore, the experience of mating itself may affect both the subsequent aggressive behaviour of the mated male and the relationship between RHP and male fighting success.

Mating experience with females could affect male aggressive behaviour in a number of ways. First, fighting is costly in terms of energy used and wounds sustained (Darwin 1871; Maynard Smith and Price 1973; Huntingford and Turner 1987) so aggressive behaviour should be sensitive to the balance of costs and benefits (Kemp 2006). Once a male has mated, he may be less willing to engage in costly fighting since he has "more to lose" (i.e. increased expectation of future matings) than a male who has yet to pass on his genes (Kemp 2006). This type of effect may be the inverse of "desperado" effects, where males who are at a severe disadvantage are predicted to fight harder because they have nothing to lose (Grafen 1987). These effects should tend to weaken the relationship between RHP and fighting success if there is a negative feedback between mating and the probability of winning subsequent fights. Alternatively, males placing a greater value on a contested resource (e.g., food, territory, mates, etc.) are predicted to fight harder and be more likely to win (Enquist and Leimar 1987). Therefore, mating might increase a male's willingness to engage in costly fighting if he perceives the value of his territory to have increased, perhaps because he has attracted a female and now has an opportunity to mate repeatedly with her. Another possible effect of mating has to do with the energetic cost of mating itself, which is sometimes high for males, particularly in species where males provide females with material benefits during mating (e.g. Simmons 1988; Wagner et al. 2001; reviewed in Vahed 1998). Thus, a proximate effect of mating might be to reduce the energetic reserves that a male has to devote to fighting. Given these potentially divergent effects of mating experience on male success in subsequent contests and the relationship between these effects and RHP, there is a clear need for empirical work on this subject.

Field crickets (Orthoptera: Gryllidae: Gryllinae) have long been known to show extreme aggression (Darwin 1871, Alexander 1961) and fight to defend territories from which they call and attract females (Loher and Dambach 1989). Males with greater RHP (e.g. body size: Simmons 1986; Hack 1997a; Shackleton et al. 2005; and weaponry: Judge and Bonanno 2008) win more fights, and have higher mating success (Simmons 1986; Rantala and Kortet 2004; Kortet and Hedrick 2005) than males with lesser RHP. Past fighting experience is also important in determining future contest outcomes, with winning and losing males likely to continue to win and lose, respectively (Simmons 1986; Khazraïe and Campan 1999; Hofmann and Stevenson 2000). Additionally, there are several lines of evidence to suggest that male-male aggression in field crickets is sensitive to male experience with females. Male *Gryllus bimaculatus* become more aggressive in the presence of females (Simmons 1986; Tachon et al. 1999). In *G. pennsylvanicus*, male-male aggression has been shown to be influenced by the operational sex ratio (Souroukis and Cade 1993), suggesting that aggression is motivated by the relative availability of females. Furthermore, as far back as the Sung Dynasty (A.D. 960–1278, Suga 2006), those involved in the sport of Chinese cricket fighting have often presented males with a female prior to competition since it is believed that mating increases male aggressiveness (Hsu 1928-1929; Arlington 1929; Suga 2006). Thus, field crickets are an ideal study system with which to investigate the possible effects of mating experience on aggression and contest ability, as well as selection on male RHP traits.

Scientific work on the effects of mating on aggression in field crickets has arrived at conflicting conclusions. Male dominance hierarchies in *G. pennsylvanicus* were reversed when the subordinate male was allowed to copulate (Alexander 1961, see also Killian and Allen 2008 for a similar effect in *Acheta domesticus*). However, the effect of mating on aggressive behaviour is unclear because dominant males (greater RHP) were not mated in these studies. In contrast, Brown et al. (2006, 2007) found that male *A. domesticus* paired with a female on four consecutive nights were less aggressive and won fewer fights than solitary males. None of these studies controlled for the effects of experiencing females independently of the effects of mating itself.

We examine the effect of mating on male aggressive behaviour in the fall field cricket, *G. pennsylvanicus*, a species in which RHP is determined partly by weaponry (enlarged head and mouthparts, Judge and Bonanno 2008). In our first experiment, we paired size- and age-matched males that varied in relative weapon size, and then randomly assigned one of each pair to receive an experimental treatment and the other to remain naïve. Our treatment had two levels, a virgin female was allowed to either (1) mount and copulate with the experimental male or (2) only mount the experimental male. We measured (a) the intensity of male contests, (b) the proportion won by the experimental male, and (c) the relationship between RHP and fighting success. Because there are sound theoretical arguments to predict both an increase and a decrease in male aggressive behaviour (see above), and the fact that previous work is contradictory, we refrain from making any directional predictions about the effect of mating on male aggression.

In our second experiment, we examine the effect of the presence of a male's recent mate on his aggressive behaviour. As above, males were paired according to size and age and one of each pair was randomly assigned to an experimental treatment while the other remained naïve. All experimental males were permitted to mate with a virgin female, and were either allowed or prevented from continued contact with her during the aggressive contests. Female *G. pennsylvanicus* will remate with a male as soon as he has formed a new spermatophore (KAJ, personal observation), suggesting that there are substantial benefits to males who guard their mates. We therefore predict that males in the contact treatment will be more likely to escalate to grappling than males in the no contact treatment, but given that the naïve stimulus male may be more aggressive in the presence of a female, we cannot predict which male will be more likely to win.

Materials and methods

Animal rearing

All experimental animals were third-generation offspring from adult fall field crickets, *G. pennsylvanicus*, collected from the grounds of the University of Toronto Mississauga, Mississauga, ON, Canada (43°32′50.51″N, 79°39′37.80″W). We reared all juvenile crickets in large communal plastic bins (48 cm long, 35 cm wide, 31 cm high) with layers of egg cartons for shelter, rabbit chow (Little Friends Rabbit Food, Martin Mills Inc.) for food, and cotton-plugged, water-filled vials for moisture. Food and water were changed weekly. We kept all crickets in an environmental chamber under the following conditions: 25°C, 70% relative humidity, and 12:12 h light:dark cycle.

General

Crickets were isolated at the late nymphal stage to maintain virginity and were kept in plastic deli containers (9 cm diameter, 8 cm high) with egg carton shelter, rabbit chow and a water vial. Adult males were matched for age (within 5 days post-adult moult) and mass (within 5%, measured 1 day prior to experiment) but weaponry (i.e. head and mouthpart size, a component of RHP, Judge and Bonanno 2008) varied. Paired males were identified using a small dot of nail polish on the pronotum (copper or blue, colour assigned randomly). One male was randomly assigned to receive the treatment (experimental male, EM) leaving the other as the naïve, stimulus male (SM). Following experimental treatment, aggressive contests were staged between experimental and stimulus males. Two researchers (MJF and KAJ) applied the treatments and two different researchers (JS and JJT), blind to the assignment of treatments, conducted the aggressive contests. Treatments and observations were conducted under red light to minimise visual disturbances for the animals. Males were a minimum age of 6 days post-adult moult (mean ± SEM= 15.8±0.9 days) and females were at least 10 days (14.6±0.5 days) to ensure sexual maturity.

Experiment 1: the effect of mating experience on aggression

We applied two treatment levels: ‘mated’ males were allowed to contact, court, be mounted, and then transfer a spermatophore to the female whereas ‘experienced’ males were prevented from mating by disrupting the spermatophore transfer with a blade of grass. Treatments were applied by placing each male in a clean deli container lined with a clean paper towel substrate. A female was then introduced to the experimental male following 2 min of acclimation. Stimulus males were also placed into a clean container and all actions were repeated except for the introduction of a female. We recorded latency to court for all trials. Males failing to court within 30 min were retested later that day. The female was removed and the males were transferred to a separate, but adjacent room to perform the aggression trials. Males were then transferred from their individual containers into an aggression arena. Transfer of crickets was conducted as gently as possible to minimise handling disturbance (i.e. Hofmann and Stevenson 2000). Aggression trials between experimental and stimulus males were performed 204±16 s following treatment application.

To further reduce potential handling/transfer disturbance, we conducted a second block of this experiment wherein the treatments were carried out within the aggression arenas. All other methods are identical to those above (block 1), except for the following features. Paired males were placed on either side of an opaque Plexiglas divider and the EM received treatment following acclimation. Following treatment application we placed a small opaque plastic box (AMAC brand: 3.02 cm length, 3.02 cm width, 6.67 cm height) over the female in a corner of the arena. This served to minimise disturbance and to avoid any interactions with the female during the aggression trials. Aggression trials between experimental and stimulus males were performed 249±29 s following treatment application.

Experiment 2: the effect of maintaining female contact on aggression

To further test the role of mating experience in subsequent male-male competition, we conducted an experiment in which we either allowed or prevented the male from maintaining contact with his mate during an aggressive encounter with a competitor (‘contact’ and ‘no-contact’ treatments, respectively). Experimental methods were identical to the mated treatment described above in block 2 of experiment 1 with the exception that (a) mated females were not contained within the opaque box in half of the trials and (b) an opaque box was also placed on the side of the stimulus male. Mated females never mated with the stimulus male during aggressive contests with the experimental male.

Aggression trials

Arenas were Plexiglas boxes measuring 13 cm square by 18 cm high with sand substrate and a removable opaque divider across the diagonal. Arenas were wiped with 95% ethanol and the sand was thoroughly mixed between trials to reduce any residual pheromones. Winners are easily identified as they tremulate (shake their body), stridulate (sing), and often chase the loser (Alexander 1961; Hofmann and Schildberger 2001). We noted the maximum level of aggression (contest intensity) attained using a categorical scale of aggression (modified from Hofmann and Schildberger 2001) where: 0=mutual avoidance, 1=immediate dominance, 2=mutual antennation, 3=unilateral maxillae/mandible spreading, 4=bilateral maxillae/mandible spreading, and 5=grappling (including maxillae/mandible engagement). Crickets were returned to their original containers following contests. Specimens were maintained in the rearing chamber until death whereupon they were preserved in 70% ethanol for subsequent measurement of weaponry. Males have enlarged heads and mouthparts that serve as weapons during fights and so we measured maxillae span of preserved specimens (see Judge and Bonanno 2008 for details of measurement) as an index of RHP and included it in our analyses as a predictor of fight outcome.

Analyses

We tested for the effect of mating experience on contest escalation by using a logistic regression with treatment (mated or experienced), absolute relative weaponry (|EM–SM|), block and all interactions as independent variables, and with contest intensity as the categorical dependent variable. We tested for the effect of mating experience on the relationship between male weaponry and fighting success using a logistic regression with treatment (mated or experienced), relative weaponry (EM–SM), block and all interactions as independent variables, and with outcome (EM wins or loses) as the dependent variable. In both logistic models, we interpret a significant treatment× weaponry interaction as evidence that mating experience affected the relationship between RHP and contest behaviour. To test for the effect of maintaining female contact following mating on male aggressive contests, we conducted analyses identical to those described above except that (a) the treatment factor was female contact or no female contact and (b) there was no block factor in the analyses.

All statistical tests were two-tailed at the type I error rate of 5% and carried out using SPSS 10 for Windows (SPSS Inc.). Bootstrapped 95% confidence limits surrounding proportions of contests won by the experimental male were calculated using PopTools (Hood 2009).

Results

Table 1 gives the number of aggressive contests in each treatment for each experiment that escalated to a given contest intensity. All contests in which the males failed to engage in any aggressive behaviour (intensity=0) were removed from all subsequent analyses. In addition, because so few contests terminated at intensity levels less than grappling (Table 1), contest intensity was reduced to a binary variable (escalated to grappling: yes/no) for statistical analysis.

Experiment 1: the effect of mating experience on aggression

In the analysis of contest intensity, after removal of the nonsignificant three-way interaction, we found no significant interaction between treatment and absolute relative weaponry (Wald χ^2=1.143, p=0.285). The other two-way interactions were also nonsignificant (data not shown) and so all were removed from the final logistic model before evaluating the main effects. We found no effects of treatment, absolute difference in male weaponry or block on the probability that fights escalated to grappling (χ^2= 4.164, N=67, p=0.244, Nagelkerke R^2=0.083). In both experimental treatments, approximately 64% of contests escalated to grappling (Fig. 1a).

In testing for effects on contest outcome, again we found no significant interaction between treatment and relative

Table 1 Number of contests that reached a given contest intensity for experiments 1 and 2

	Experiment 1		Experiment 2	
Intensity	Mated	Experienced	Contact	No Contact
0	1	5	1	2
1	7	5	1	3
2	1	0	0	0
3	4	2	1	1
4	1	4	0	2
5	23	20	17	15
Total	37	36	20	23

Intensity codes are as follows: 0=mutual avoidance, 1=immediate dominance, 2=mutual antennation, 3=unilateral maxillae/mandible spreading, 4=bilateral maxillae/mandible spreading and 5=grappling

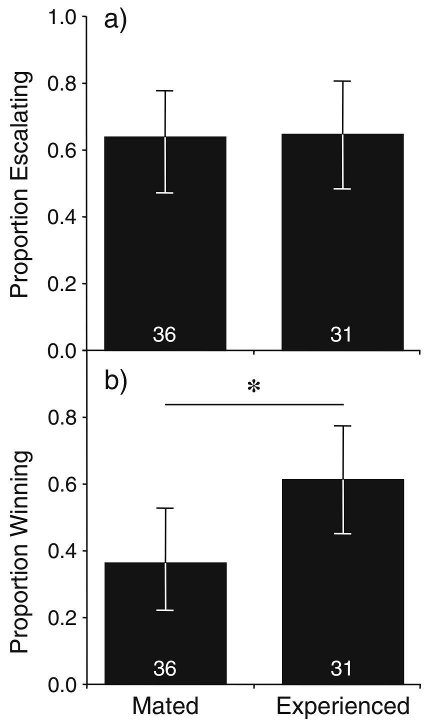

Fig. 1 The effect of mating experience on the proportion of aggressive contests that **a** escalated to grappling, and **b** were won by the experimental male. *Bars* represent bootstrapped 95% confidence intervals and sample sizes are indicated at the base of each column. An *asterisk* indicates a statistically significant difference

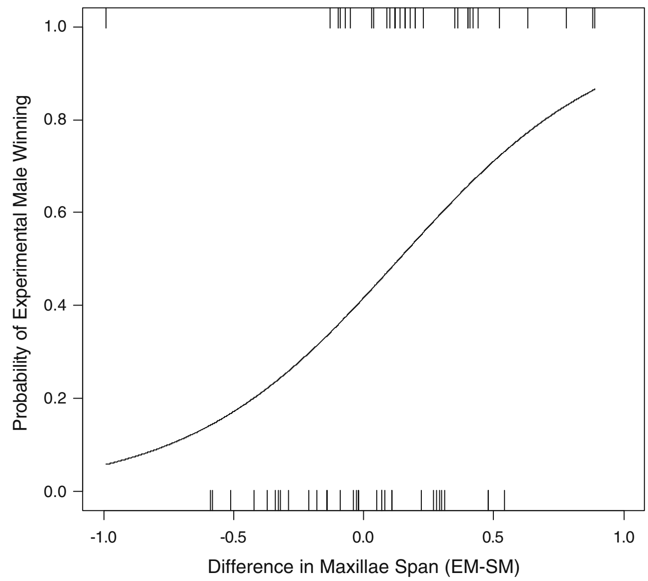

Fig. 2 The effect of relative weaponry on the probability that the experimental male (EM) would win an aggressive contest against a stimulus male (SM) when testing for an effect of mating experience. Relative weaponry is given by the difference in maxillae spans of the males in a pair (EM–SM)

weaponry (Wald χ^2=1.231, p=0.267; other three- and two-way interactions nonsignificant). The final logistic model (all interactions removed) was statistically significant (χ^2= 15.928, N=67, p=0.002, Nagelkerke R^2=0.272). Mated males were less likely to win contests with a naïve competitor than were experienced males (Wald χ^2=4.366, p=0.037, Fig. 1b). The likelihood of winning was significantly higher for males with larger weaponry relative to their competitor (Wald χ^2=7.085, p=0.008, Fig. 2). The effect of mating experience on contest outcome was less than the effect of RHP (log odds $\text{ratio}_{\text{experience}}$=−1.169± 0.559, log odds $\text{ratio}_{\text{RHP}}$=25.891±9.727,). We found no significant effect of block (Wald χ^2=1.734, p=0.188).

Experiment 2: the effect of maintaining female contact on aggression

There was no interaction between treatment and absolute difference in weaponry on the probability of contests escalating to grappling (Wald χ^2=0.042, p=0.838). After removing the interaction term, we failed to detect a statistically significant effect of maintaining contact with a female mate or absolute difference in male weaponry on the probability of contests escalating (χ^2=2.124, N=40, p= 0.346, Nagelkerke R^2=0.082; Fig. 3a).

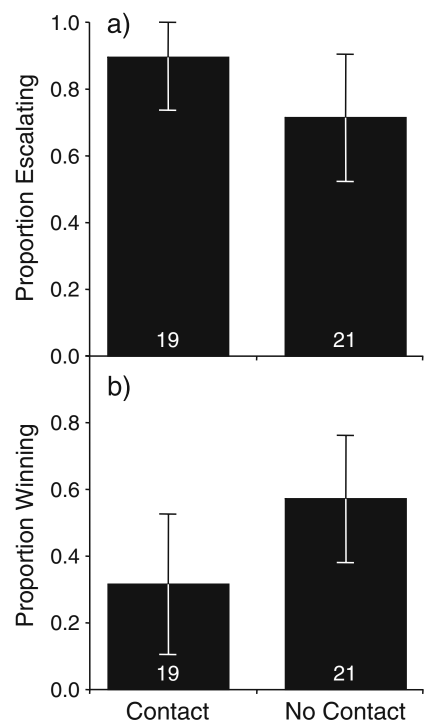

Fig. 3 The effect of maintaining contact with a mate on the proportion of aggressive contests that **a** escalated to grappling and **b** were won by the experimental male. *Bars* represent bootstrapped 95% confidence intervals and sample sizes are indicated at the base of each column

We found no significant interaction between treatment and relative weaponry on contest outcome (Wald χ^2=1.132, p= 0.287). The final reduced logistic model, relating treatment and male weaponry with contest outcome, was statistically significant (χ^2=10.611, N=40, p=0.005, Nagelkerke R^2= 0.312). Maintaining female contact during aggressive encounters did not significantly affect the probability of winning a fight (Wald χ^2=3.192, p=0.074, Fig. 3b). As in experiment 1, the likelihood of winning was significantly higher for males with larger weaponry relative to their competitor (Wald χ^2=5.995, p=0.014, Fig. 4) and the effect of RHP was stronger than the effect of maintaining female contact (log odds ratio$_{RHP}$=40.761±16.648, log odds ratio$_{experience}$=−1.374±0.769).

Discussion

Prior experience in aggressive contests is known to affect subsequent aggressive behaviour (reviewed in Hsu et al. 2006; examples in field crickets: Simmons 1986; Khazraïe and Campan 1999; Hofmann and Stevenson 2000). However, few studies have examined the effects of mating experience on agonistic behaviour, despite the fact that the result for males of winning a contest is thought to be increased mating success and/or control over resources used by females for reproduction. We investigated the effect of mating experience on male aggressive behaviour (tendency to escalate contests, fighting success, and the influence of RHP on winning) in the fall field cricket, *G. pennsylvanicus*. In two experiments, we manipulated male mating history and male postcopulatory experience with females, while allowing RHP (male weaponry) to vary freely between contestants. In our first experiment, we found that although mating had no effect on the proportion of contests that escalated to combat, males that courted and were mounted by a female (experienced) were more likely to win fights with a naïve opponent than were males that had courted, been mounted, but also transferred a spermatophore (mated). Males with greater RHP (enlarged heads and mouthparts) were more likely to win contests and this relationship was unaffected by mating experience. In our second experiment, we examined mating experience further by either preventing or allowing males to maintain contact with their mates. We detected no effect of our treatment on the tendency to escalate, the probability of winning, or the relationship between RHP and fighting success, which was positive.

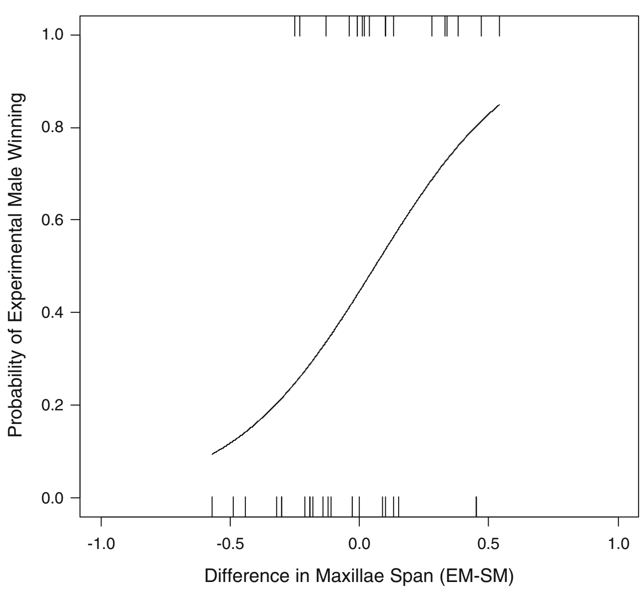

Fig. 4 The effect of relative weaponry on the probability that the experimental male (EM) would win an aggressive contest against a stimulus male (SM) when testing for an effect of maintaining contact with the female. Relative weaponry is given by the difference in maxillae spans of the males in a pair (EM–SM)

Male field crickets aggressively defend territories from which they call and attract females (Loher and Dambach 1989). Given that fighting is energetically costly (Hack 1997b), male aggressive behaviour should be sensitive to changes in residual reproductive value (Kemp 2006), resource value (Arnott and Elwood 2008) or energetic expenditure brought on by mating experience. In our study, recent mating experience reduced the mating male's probability of winning a subsequent agonistic interaction against a naïve opponent. This treatment difference could be due to several factors, including: (1) asymmetrical motivation to fight (decreased in mated males and/or increased in experienced males), or (2) decreased ability of mated males to fight due to the energetic cost of mating.

Changes in male motivation to fight might explain the greater probability of experienced males than mated males to win fights in a number of possible ways. First, female *G. pennsylvanicus* might become refractory following mating, causing the mated male's motivation to engage in costly fighting to decrease. However, *G. pennsylvanicus* females have been observed to mate repeatedly with the same male as soon as he is capable of transferring a spermatophore (KAJ, personal observation), indicating that there are substantial benefits to mate guarding. Second, experience with females is known to incite increased aggression in male field crickets (Simmons 1986; Tachon et al. 1999) and female cuticular hydrocarbons are attractive to males (Tregenza and Wedell 1997; Thomas and Simmons 2010). Although these results would explain increased motivation to fight in our experienced treatment, this explanation is contradicted by the fact that the naïve stimulus male in our contact treatment (who fought in the presence of a female) did not win a higher proportion of fights than in the no contact treatment. In addition, effects of our treatments on male motivation to fight seem less likely given that all treatments showed an elevated tendency to escalate to grappling and did not differ from one another. Future work into the effects of experience with females on male motivation to fight could make use of female cuticular hydrocarbons to vary male experience with both the quantity and quality of females.

Another possible explanation for the result that mated males were less likely to win than experienced males could be that mated males had less energy to devote to fighting. Aggressive contests between male grylline crickets are energetically costly (Hack 1997b). Spermatophore production is also costly: for example, male *G. pennsylvanicus* infected with a gut parasite take longer to replace a spermatophore than uninfected males (Zuk 1987) and male *G. lineaticeps* fed a lower quality diet took longer to produce a spermatophore (Wagner 2005). In other gryllines spermatophores are known to contain material benefits for females (Simmons 1988; Wagner et al. 2001) and these substances may contribute to spermatophore cost. When female grylline crickets dismount after copulation, the male starts to produce a new spermatophore (Loher and Rence 1978; Zuk 1987; KAJ personal observation). If he then encounters a rival male, a recently mated male may be at an energetic disadvantage because of the demands of both spermatophore production and physical combat. Our finding that mating decreased male fighting success is consistent with the widely held (e.g. Fischer 1997) but generally not well-supported (McGlone and Shrier 2000) belief that sex before competition is detrimental to contest performance.

We found that the relationship between male weaponry and fighting success was strong and positive, but unaffected by male mating experience with females. This is in contrast to the effects of female social experience on mate choice in this same species. Female *G. pennsylvanicus* with social experience (including mating experience) were choosier and favoured males with larger weaponry (relatively wider heads) compared with virgin females with no social experience (Judge 2010). Recently, attention has been drawn to the ecological and social factors that influence the strength of sexual selection (reviewed in Cornwallis and Uller 2010). Our results, when compared with those of Judge (2010) suggest that sexual selection via male-male competition is stronger and more consistent than selection via female choice. Future work should investigate the effects of social experience on the relative strength of male-male competition and female choice under more natural conditions (i.e. Souroukis and Cade 1993) since social factors could have implications for the evolution of alternative male mating strategies (Cade 1979).

We were able to corroborate previous observations of the effect of head size on contests (Figs. 2 and 4; Judge and Bonanno 2008) which have roots in Chinese cricket fighting culture. However, our results failed to support another Chinese practice, that of mating male crickets prior to aggressive contests to increase vigour and fighting success (Suga 2006). Our divergent results may reflect our methodology or the interspecific variation in the adaptiveness of maintaining exclusive access to recent mates. It is not clear how quickly male crickets are mated prior to fights in China; however, it is unlikely to happen as immediately as in our experimental setup given the strict regulations surrounding the culture (Suga 2006, JJT and JS, personal observation). Given the prevalence of the long-standing belief that mating crickets increases male aggression, it is likely that the effect (if any) is a long term one, when the energetic costs of spermatophore formation are over. Additionally, cricket fights in China typically utilise the genus *Velarifictorus* (Hsu 1928-1929, Suga 2006), and many details of its reproductive biology (i.e. patterns of sperm precedence) have not been studied in detail.

Postcopulatory aggression can be directed by a male at his recent mate (Bussière et al. 2006, Kelly 2008b, Wynn and Vahed 2004) and this female-directed aggression is thought to be adaptive (reviewed in Zuk and Simmons 1997). However, inasmuch as rival males may interfere with his mate's sperm transfer or attempt to initiate courtship, a recently mated male should engage such rivals vigorously in an attempt to drive them away (Zuk and Simmons 1997). However, in our experiment, we failed to detect a significant difference in the intensity of contests that involved either mated or experienced males (Fig. 1a), or males that were prevented or allowed contact with their mates (Fig. 3a). In fact, mated males were less likely to win than experienced males (Fig. 1b). Collectively, these results suggest that, once mated, the costs of fighting outweigh the benefits of maintaining contact with, and defending, a recent mate.

It is possible that male *G. pennsylvanicus* aggressive behaviour is sensitive to experience with females, but that more than one mating or encounter with a female is required to have an effect on contest escalation and male fighting success. Work by Brown et al. (2007) found that *A. domesticus* males with nightly exposure to females (and thus likely multiple matings) had decreased fighting success when matched against males with no access to females. However, Alexander (1961) found that subordinate *G. pennsylvanicus* males could defeat previously dominant males if the former were allowed to copulate immediately prior to their fight. A similar result was recently found in *A. domesticus* (Killian and Allen 2008). The inconsistencies between our results and Alexander (1961) may lie in the social context in which the experiments were conducted. For example, whereas we applied our treatments to virgin males who then engaged in their first aggressive encounter, Alexander (1961) allowed males with previous adult fighting experience to mate and then fight. Thus, postcopulatory aggression may be sensitive to both male mating experience and success in previous fights, the latter of which has been found in conventional male-male agonistic interactions (Simmons 1986, Khazraïe and Campan 1999).

This study examined the effect of mating and post-copulatory experience in *G. pennsylvanicus.* We found that mating experience had no effect on the relationship between RHP and fighting outcome, and post-copulatory mate presence did not influence the contest between mated males and their naïve rivals. However, we demonstrated that the act of mating itself negatively affected a male's subsequent fighting ability. To our knowledge, this is the first experiment to control for the social experience that accompanies mating, and our novel findings highlight the need to evaluate all variables in mating experience.

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