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Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests

Abstract Females are generally assumed to prefer larger, more dominant males. However, a growing number of studies that control for male-male competition have shown no correlation between dominance and attractiveness. Aggressive males can interfere with female mate preference either by physically coercing females into mating or by driving submissive males away and restricting mate choice. The most common method of assessing female mate choice is by using simultaneous two-choice tests. These control for male-male interactions, but usually interfere with physical and chemical cues involved in mate selection or alter male behaviour. They are therefore unsuitable for many study species, especially insects. Another method is the no-choice test that measures a female's latency to mating when placed with a single male as an indication of male attractiveness. No-choice tests control for male-male aggression while allowing full contact between pairs (they allow actual mating to be directly observed rather than to occur based on a correlated behaviour). So far, however, no study has confirmed that males that entice females to mate sooner actually enjoy increased longer-term mating success. As such, the accuracy of no-choice tests as a method of examining mate choice remains untested. Here, we used no-choice tests on the black field cricket, *Teleogryllus commodus*, to show that (1) females did not prefer males that won fights ("dominant" males), and (2) latency to mating predicts actual mating success. We have clearly demon-strated the usefulness of no-choice tests and, considering the advantages of this method, they should be more often considered for a wider variety of taxa.

Introduction

In most taxa, larger males are more likely to win fights (e.g. birds: Hagelin 2002; lizards: Lopez et al. 2002; spiders: Kotiaho et al. 1997). It is generally assumed that stronger, more dominant males are better quality mates (Berglund et al. 1996). One possible direct benefit of mating with these males is that they are more likely to protect the female during and after mating. Another benefit is that they may provide access to superior resources (e.g. better quality territories in birds). In addition, there is a potential genetic benefit if traits that increase success during male-male competition are heritable (Cordero and Eberhard 2003).

Although there is a mating bias favouring larger males in a variety of animal taxa, including many insects (reviews in Choe and Crespi 1997), the assumption that females prefer larger, presumably more dominant, males has been challenged (Qvarnström and Forsgren 1998). A small but growing number of new studies report no correlation between male fighting ability and attractiveness (frogs: Morrison et al. 2001; lizards: Lopez et al. 2002; birds: Andersson et al. 2002; fish: Wong 2004; insects: Moore and Moore 1999; Moore et al. 2001). This could occur because dominant males impose direct costs on females making them less attractive as mates. For example, they may provide less parental care (Forsgren 1997; Wong 2004), increase the risk of female injury while mating (Lebouef and Mesnick 1991), be more likely to transmit diseases (Freeland 1981) or be sperm depleted (Pitnick and Markow 1994; Preston et al. 2001). There may also be genetic costs if, for example, male size

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or dominance is negatively genetically correlated with female fitness, leading to the production of lower quality daughters (Chippindale et al. 2001). It is also possible that females do not prefer dominant males because dominance has no effect on female or offspring fitness, or because there are other traits, uncorrelated with fighting ability, that are better predictors of a male's effect on female fitness. Ultimately, the relative magnitude of any direct effects on female lifetime fecundity and indirect effects on net offspring fitness will determine whether females should prefer to mate with dominant males (Fedorka and Mousseau 2004).

The most common way to determine whether females prefer certain males is through simultaneous choice tests. Ideally these choice tests should exclude male-male interactions, otherwise the results are uninterpretable because increased mating success (or a surrogate thereof) for some males may be due to male-male competition circumventing female choice. This is true even in species where females appear to 'control' mating. For example, in house crickets, *Acheta domesticus*, a female must mount the male and remain stationary if spermatophore transfer is to occur successfully. When a female was placed with two male crickets that had been interacting for 10 min, the winner of the agonistic encounter was more likely to mate (Nelson and Nolen 1997). However, when a female was placed with each male separately the mean mating success (measured as whether or not a spermatophore was successfully transferred) of winners and losers did not differ. This study also illustrates that dominant males may not enjoy higher mating success when male-male competition is removed. Several other studies have reported similar findings (Radesater and Halldorsdottir 1993; Nilsson and Nilsson 2000).

To control male-male competition, males are usually tethered or placed behind glass or mesh. This approach can also be problematic, for at least three reasons. First, female preferences for specific male traits can differ when the sexes are allowed full or restricted interactions (Candolin 1999; Nilsson and Nilsson 2000). Second, in many species males behave abnormally when tethered and a lack of close physical contact between the sexes denies females access to essential mate choice cues. It is particularly difficult to suitably control male-male competition in insects as they are either difficult to tether and/ or do not behave normally when tethered (black field cricket, *Teleogryllus commodus*, personal observation). Insects are also unsuitable for mate choice trials where males are placed behind glass, as some species have pheromones that may play an important role in mate choice (e.g. cuticular contact pheromones in the field cricket, *Gryllus bimaculatus* (Tregenza and Wedell 1997). Third, even in species that are amenable to simultaneous choice tests, the index of female preference in choice trials only indirectly measures actual mate choice. A relationship between, for example, visual orientation (Clark and Biesiadecki 2002) or time spent near a male and actual mating success is usually assumed. In a few cases this assumption is tested and supported (Clayton 1990),

but in others it is not (Gabor 1999). A major dilemma, however, is that to measure actual mating success individuals must interact. This makes it difficult to test this assumption without reintroducing the problematic effects of male-male competition on male mating success.

A second way to measure male attractiveness that resolves these three problems, while still excluding male-male competition, is to conduct no-choice tests (Pilastro et al. 2002). These tests usually measure a female's latency to mating when placed with a single male. Measuring attractiveness as mating latency has the benefit of allowing females to base their choice on all the physical and chemical cues males offer. It also has the advantage that female preference can be determined from an actual mating. No-choice tests measuring mating latency are most often used in fruitfly studies (Hegde and Krishna 1997; Koref-Santibanez 2001; Gowaty et al. 2002; Yenisetti and Hegde 2003), but they have also been employed in studies of birds (White et al. 2002), lizards (Tokarz 2002), fish (Houde and Torio 1992; Blanchfield and Ridgway 1997) and invertebrates (Peters and Michiels 1996; Parri et al. 1998; Bukowksi et al. 2001; Jones and Quinnell 2002). The main assumption of such tests is that a female's preference function includes a threshold value which males must exceed in order to mate. If female thresholds for a fixed trait such a coloration or the size of an ornament drop over time then more attractive males will exceed the threshold sooner (Backwell and Passmore 1996). Alternatively, or in addition, female thresholds could be based on the rate of courtship so that males with greater display rates will more rapidly exceed the threshold.

Although latency to mating is a useful way to calculate male attractiveness, to our knowledge no study has confirmed that males with a shorter latency to mating in no-choice trials actually enjoy increased longer-term mating success. For example, even if dominant males take longer to induce a female to mate in no-choice trials, if trials were conducted over a longer period would they be able to coerce females into mating as often as other males? It is not inevitable that males that induce females to mate sooner in no-choice trials will have higher mating success when paired with a female for a prolonged period. For example, there may be a phenotypic trade-off in males between the ability to induce females to mate and a male's subsequent recovery period before he can resume courtship; or there may be no correlation between a male's ability to induce a female to mate and the likelihood that she will then remate with him. Also, given possible variation in mating preferences among females (Jennions and Petrie 1997), the repeatability of latency to mating should be calculated. It is only meaningful to discuss the general attractiveness of a male if there is some consistency in the response he elicits in different females.

The black field cricket, *Teleogryllus commodus*, is ideal for studies of male fighting ability ('dominance') and female mate choice as their fighting and mating behaviours are easily quantified in the laboratory (Evans

1983, 1988). Females appear to control mate choice because the female must mount the male to accept his spermatophore. Importantly, females repeatedly mate with the same male and studies on the closely related sister species, *T. oceanicus*, indicates that there is no last male sperm precedence (Simmons et al. 2003). Consequently, the more spermatophores a female accepts from a given male, the greater is his probable share of paternity. The number of spermatophores a female accepts from a male is therefore a useful measure of his potential reproductive success.

Here, we investigated whether females prefer larger males that win fights as mates, using mating speed as a measure of male attractiveness. We then tested whether mating speed successfully predicts the actual rate of spermatophore transfer over a 3-day period when a male is assigned a single, randomly selected female. We selected males at the extremes of the distributions of attractiveness and fighting ability respectively to investigate the phenotypic relationship between these composite traits.

Methods

Experimental animals

We collected approximately 120 gravid female *Teleogryllus commodus* from field sites in Canberra, Australia, in February-March 2002. Females were individually housed and provided with a Petri dish of moist sand for oviposition. The F_1 generation nymphs were reared in six large communal tanks (34×55×29 cm), and provided with commercially available cat food (KitKat Krunch) and water ad libitum. Nymphs were sexed before maturation and transferred to single-sex rearing tanks. Approximately 200 adults were then used to produce each subsequent generation. For the current experiments, we used adults from the F_3 and F_4 generations. Late instar nymphs housed in single-sex tanks were isolated within 24 h of their adult moult. They were then housed with similar aged individuals of the same sex in 3l containers, and provided with food and water ad libitum until tested.

Estimating male fighting ability

There is a stereotypical sequence of events when male field crickets fight (Evans 1983; Hack 1997; Hofmann and Stevenson 2000; Nosil 2002). Initially, males make antennal contact and if neither male retreats they display their spread mandibles while producing an aggressive call. If the contest escalates, males interlock mandibles and wrestle until one eventually retreats. After defeat, the losing male typically avoids further aggressive encounters with the winning (Hofmann and Stevenson 2000). This results in one male repeatedly retreating when approached by the other, allowing the outcome of contests to be readily determined.

Individual males were ranked for fighting ability in blocks of eight randomly selected males. In total we tested 45 blocks of males (*n*=360 males). In each block, the maximum age difference was 0.38±0.15 days (range=0–3). All males were weighed on a Sartorius balance (±0.1 mg) and their pronotum marked with paint for individual identification. To estimate the relative fighting ability of males in each set we ran hierarchical competitions involving a series of dyadic contests.

Males were tested in three rounds of fights. In the first round, pairs of males were randomly assigned and placed in individual 5×5×5 cm plastic containers. The winner was determined by noting which male successfully initiated three acts of aggression towards his rival that caused him to retreat. This generated four males that won (W) and four that lost (L) their first round contest. The four winners were then randomly paired with each other. Likewise, the four losers were also randomly paired with each other. Second round fights were therefore between males with the same recent fight history. The third round similarly consisted of pairing males that had the same fight history (i.e. WW, WL, LW or LL). This technique is similar to that used by (Savage et al. in press) to assign male rank for fighting ability status in the field cricket.

The advantage of this process is that every male always competed against another male with the same outcome in his previous fights. This controls for any potential effects that the outcome of earlier fights might have on the current fight. In field crickets, success in previous fights increases the likelihood of victory in subsequent contests independently of the effect of intrinsic fighting ability (Khazraie and Campan 1999; Hofmann and Stevenson 2000; Savage et al. 2005). More importantly, this hierarchical procedure maximises the likelihood that the top and bottom ranked males differ in fighting ability because the top male won fights against previous winners and the bottom male lost fights against previous losers. The eight males were then ranked from 1 to 4 (strongest to weakest) for fighting ability based on the number of encounters they won (3, 2, 1 or 0).

Estimating male attractiveness

We ranked the attractiveness of individual males in each block based on the relative speed with which they induced females to mate with them (i.e. the latency to mating). Again, we tested males in blocks of eight and a total of 44 blocks of males (*n*=352 males) were examined. Of these, 35 were exactly the same blocks of males used in the fighting ability trials and the remaining 9 blocks were created from stock cultures. The males in these additional blocks were individually marked and weighed as described above. The mean maximum difference in male age per block was 0.61± 0.17 days (range=0–3).

The time it took a male to induce a female to mate was measured in four trials. In each trial all eight males were placed into individual 5×5×5 cm plastic containers. They were then simultaneously given one of eight randomly selected stock females. We then recorded the order in which the eight males were mounted ('latency to mating'). Pairs were immediately separated after the female mounted to prevent spermatophore transfer. Mounting is a very strong predictor of actual spermatophore transfer; females which mount a male allow copulation to take place within 2 h in 93% of cases (*n*=30 females, unpublished). Each trial lasted for up to 60 min, after which any females that had failed to mount the male were removed. Stock females were rotated among the males so that no male was assigned the same female more than once. Each set of males was tested with a unique group of females.

In each trial the order in which males were mounted was ranked from 1 to 8 (first to last). Males that had not been mounted after 60 min were given the average of the remaining ranks. In 259 of the 1,408 male-female pairings (18.4%), the female did not mount the male. Of the 352 males tested, 211 were mounted in every trial. We then calculated each male's average rank across the four trials. The final rank (1–8) of each male for latency to mating was then based on this value.

In addition, for 44 of the 45 blocks of males used in the fighting ability trials (previous section) we measured the attractiveness of males ranked top and bottom for fighting ability in each set (one block was not used because a male died). Both males in each block were tested with the same four females when assessing their relative ability to induce females to mate. In round one, two stock females were randomly assigned to the males. In the second round, the female assigned to the male ranked highest for fighting ability was switched with the female assigned to the male ranked lowest for fighting ability and vice versa. The same was done in rounds three and four. For example, if male A was paired with females 2, 5, 1 then 7, then male B would be paired with females 5, 2, 7 then 1.

By using the same four females to assess attractiveness, we more fully controlled for any variation among females in their willingness to mate when assessing the relationship between attractiveness and fighting ability.

The effects of attractiveness and fighting ability on mating success

To determine whether latency to mating was a meaningful index of male attractiveness we measured the actual mating success when paired with a randomly selected female of males ranked highest and lowest for attractiveness. We also tested whether our measure of male fighting ability correlated with actual mating rate. To ensure their virginity, test females were isolated within 24 h of adult moult. They were kept with similar aged females (±2 days) and provided with food and water ad libitum in 3-l containers. Females were weighed prior to mating (±0.1 mg). Females reach sexual maturity 10 days after adult moult, and were first placed with a focal male when they were 12–17 days old. Males from the same block were paired with females of similar age (±2 days).

For 32 blocks of males tested for latency to mating we selected the top and bottom ranked male. Likewise, for 30 blocks of males tested for fighting ability we selected the top and bottom ranked males. Each male was then housed with a single, randomly selected stock female for 8 h/day for 3 consecutive days. The same female was paired with a given male on all 3 days. We placed the pair in a darkened room and checked every 30 min whether the female had received a spermatophore. The mean attachment time of a spermatophore is 105 min, with 95% of spermatophore remaining attached for at least 60 min (Loher and Rence 1978). A male takes approximately 2 h after mating to regain sexual receptivity and resume courtship. Therefore, the maximum number of spermatophores transferred within 8 h is four. The number of successful matings each day was recorded and the total across the three days summed. Thereafter males were housed individually in 3-l containers with water and food ad libitum until death to record their adult lifespan.

Statistical analyses

All statistical analyses were conducted in S-Plus 6.4. Unless otherwise stated, summary statistics are presented as mean±SE. The power to detect a medium strength effect ($r=0.3$, $d=0.5$; Cohen 1988) at the $\alpha=0.05$ level (two-tailed) is reported for basic statistical tests that yielded non-significant results.

Results

The relationship between male fighting ability, attractiveness and body weight

Are males that win fights more attractive?

We examined the relationship between male fighting ability, attractiveness and body weight in two ways. Firstly, we compared the rank scores from the 35 blocks of males ranked for both attractiveness (ranked 1–8) and fighting ability (ranked 1–4) by calculating Spearman's correlations for each male set. The correlation coefficients were normally distributed so we used a one-sample t-test to determine whether the mean differed from zero. There was no correlation between a male's rank for latency to mating and for fighting ability ($r_s=0.00\pm0.06$, $t_{34}=0.03$, $P=0.98$, $n=35$; power=81%). Secondly, we used the larger data set ($n=44$ male blocks) to compare the attractiveness of males that were ranked top and bottom for fighting
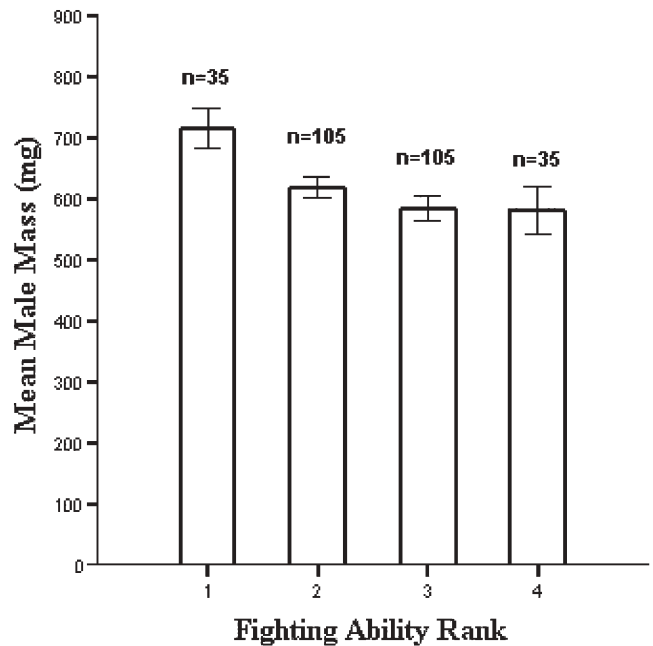

Fig. 1 Mean body mass of male black field crickets, *Teleogryllus commodus*, ranked 1–4 for fighting ability (1=highest ability, 4=lowest ability) ($n=35$, 105, 105, 35). *Error bars* show 95% confidence interval

ability in their male block using a binomial exact test. In 26 of the 44 pairs examined, the male ranked highest for fighting ability in the block was more attractive than the male ranked lowest for fighting ability when tested using the same four females. This result does not differ significantly from a probability of 0.5 (binomial exact test, $P=0.291$, $n=44$; power=52%) and therefore does not support a non-random association between male fighting ability and attractiveness.

How does body size relate to male attractiveness and fighting ability?

Male body weight varied significantly with male fighting ability ($F_{3,242}=19.47$, $P<0.001$, $n=280$). Males ranked highest were significantly heavier than those ranked second ($t_{242}=5.37$, $P<0.001$), and those ranked second were significantly heavier that those ranked third ($t_{242}=2.77$, $P=0.006$) (Fig. 1). There was, however, no significant difference in mass between third and fourth ranked males ($t_{242}=0.14$, $P=0.89$; power=97%) (Fig. 1). Using only data from the first trial per set when males were completely randomly paired in contests, 73% of encounters were won by the heavier male (binomial test, $P<0.0001$, $n=213$).

In contrast, there was no significant correlation between a male's attractiveness ranking and body weight ($r_s=-0.00\pm0.01$, $t_{34}=0.05$, $P=0.96$, $n=35$; power=81%). This is consistent with the finding that females showed no significant mating preference for males ranked higher for fighting ability.

The effectiveness of no-choice tests
to predict male mating success

Is male attractiveness repeatable?

If latency to mating in a no-choice trial is an effective means to assess male attractiveness, it must be repeatable across different females. To measure its repeatability we calculated Kendall's coefficient of concordance (W) from the four ranks per male for each of 44 sets of males. We used a randomisation test to compare the mean W to the distribution created by randomly generating 999 sets of ranks from 4 trials for 8 males and then calculating W. We also noted how many of the individual male sets had coefficients that were in the top 5% of generated W values (i.e. $P<0.05$).

Our measure of male latency to mating was highly repeatable across four different females and therefore provides an effective measure of male attractiveness. The mean Kendall's W was 0.50 ± 0.02 (randomisation test, $P=0.029$, $n=44$). In 26 of the 44 sets of males the coefficient was significantly larger than expected by chance (randomisation test, $P<0.05$, $n=44$).

Do attractive males and males that win fights have greater mating success?

The number of copulations attained by males of high fighting ability and attractive males over the 3-day observation period had a Poisson distribution. We therefore analysed this variable in a generalised linear mixed model (GLMM) with a Poisson error distribution. Analyses were run using the *Mass* library of Venables and Ripley (2002) and the function *glmmPQL*. Model parameters were estimated using a maximum likelihood approach. 'Block' was included in the model as a random term. The initial maximal model included the terms female mass, male mass and male rank and all interactions between these terms. Model simplification proceeded by removing non-significant terms, starting with the higher-order interactions. The significance of terms was assessed by deletion tests, with deletion made with the current model at the level in question (see Crawley 2002, p. 454). We used the log-likelihood ratio (LLR) test to determine whether the inclusion of the term significantly increased the fit of the model to the data. Main effects which figured in significant interactions were retained. Finally, once the minimal adequate model was identified, the P-values associated with each term were determined by deletion tests. We also checked whether terms that had earlier been excluded from the model could explain additional variation by adding them to the minimal adequate model. For interaction terms, the significance level for retention in the final model was set at $\alpha=0.01$ level, for main effects it was set at $\alpha=0.05$ (Wilson and Hardy 2002).

In 25 of 32 male sets, the most attractive male (i.e. the shortest latency to mating) obtained more matings over the 3 day observation period than did the least attractive
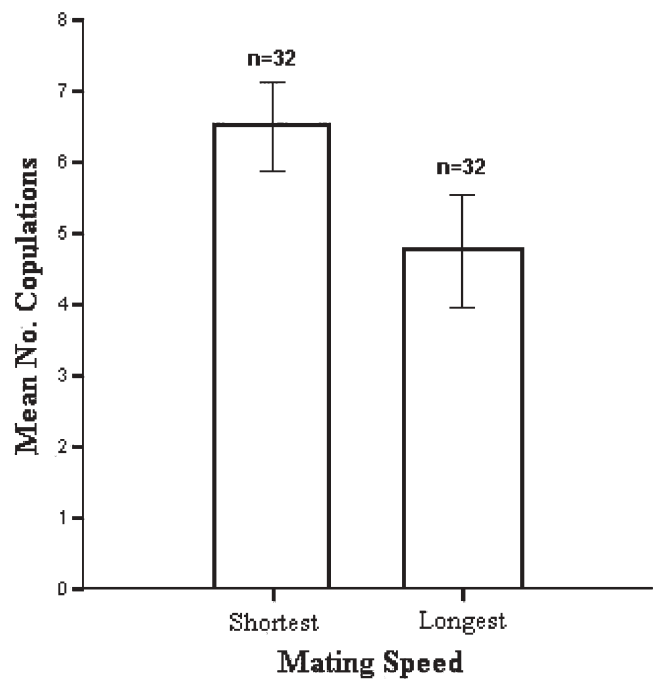

Fig. 2 Mean number of copulations by males ranked highest and lowest for attractiveness based on their latency to being mounted by females ("mating speed"). *Error bars* show 95% confidence interval

male (6.5 ± 0.30 versus 4.75 ± 0.39 matings, respectively)(Fig. 2). The only term that has a significant effect on the number of matings was male latency to mating. Males with a shorter latency to mating mated a significantly greater number of times than those with a longer latency to mating (LLR: $\chi^2_1=7.75$, $P=0.0054$). There was no effect of male mass (LLR=0.45, $P=0.50$), female mass (LLR=0.76, $P=0.38$) or any interactions.

In 17 of 30 sets the male with the higher rank for fighting ability obtained more matings (6.33 ± 0.42 versus 5.50 ± 0.37 matings). In three sets both males obtained the same number of matings. The final GLMM model only included the term 'female mass' (LLR: $\chi^2_1=6.18$, $P=0.0013$). Heavier females mated more often. There was no effect of male mass (LLR: $\chi^2_1=3.71$, $P=0.054$), or male rank for fighting ability (LLR: $\chi^2_1=0.88$, $P=0.35$).

Do males of higher fighting ability and attractive males live longer?

We compared the mean weight of males and their longevity between males ranked highest and lowest for fighting ability and attractiveness using paired t-tests. There were no significant differences in the body weight ($t_{31}=1.23$, $P=0.228$, $n=32$ pairs) or lifespan ($t_{29}=1.47$, $P=0.15$, $n=30$ pairs) of males ranked top and bottom for attractiveness (power: 76–78%). There was also no effect of male weight on lifespan (LLR: $\chi^2_1=0.06$, $P=0.80$). In contrast, there was a significant difference in the body weight ($t_{29}=6.62$, $P<0.001$), but not in the lifespan

($t_{29=}0.24$, $P=0.815$, $n=30$ pairs, power=76%) of males ranked top and bottom for fighting ability (power=76%). There was no effect of male mass on lifespan (LLR: $\chi^2_1=1.39$, $P=0.24$).

Discussion

The relationship between male attractiveness and fighting ability

It is often stated that males that win fights are preferred mates because they are of higher quality (Berglund et al. 1996). It is therefore generally assumed that females will prefer larger males, as they tend to win fights (Kotiaho et al. 1997; Hagelin 2002; Lopez et al. 2002). In the black field cricket, we found, as expected, that larger males won more fights. Females did not, however, mate sooner with males that won fights. In a second set of trials, we also showed that females do not prefer larger, heavier males as mates. This further supports our claim that female *T. commodus* do not prefer males of greater fighting ability. Although in many species the bulk of evidence still suggests that male dominance and attractiveness are positively correlated, our study adds to a growing number that do not find this relationship (e.g. Bonduriansky and Rowe 2003; Wong 2004). In crickets, there are no studies directly measuring the phenotypic correlation between behavioural measures of male attractiveness and dominance so it unclear how generalisable our findings are to other crickets. Even so, there are several studies showing that female crickets prefer larger males (Simmons 1986, 1988; Gray 1997; Bateman et al. 2002). Given that larger male crickets usually win fights (Tachon et al. 1999 and references therein), this suggests that, in these species at least, dominance and attractiveness are positively correlated. It is important to note that our measure of attractiveness is only based on short-range interactions during courtship. The correlation between male calling effort, which is the best predictor of attractiveness in the field (Hunt et al. 2004), and short-range attractiveness is presently unknown.

Our finding raises the important question of why do females not prefer to mate with males that win fights (i.e. more dominant males). Our measure of attractiveness is based on close-range interactions between the sexes. Male crickets attract females by loud and intense calling (Gerhard and Huber 2002). If larger, more aggressive males call with greater intensity or at higher rates they are more likely to attract females. Female choice may therefore favour larger males at this larger scale. There are, however, field reports that males courting a female are often challenged by another male (Evans 1983, pp. 275–276). Therefore, the lack of female discrimination against males that lose fights during close-range interactions could still have a substantial effect on male mating success in the field. At this short-range scale there does appear to be sexual conflict. In another study, we placed two males and a female together in a container and then observed which male was the first to successfully transfer a spermatophore. The larger of the two males was the first in 23 of 32 trials (paired *t*-test: $n=32$, $t=2.55$, $P=0.016$; hindleg length 10.50±0.71 versus 10.13±0.66 mm) (Jennions et al. in preparation). Given that in the present study females did not mated sooner or accepted more spermatophores from larger males, when combined these results suggests that male-male competition conflicts with unhindered female choice (see also Nelson and Nolan 1997).

It is currently unclear why female *T. commodus* do not prefer males that win fights. In other species it has been suggested that there are direct costs to mating with dominant males. For example, they may be sperm depleted (Pitnick and Markow 1994; Preston et al. 2001) or more likely to damage the female during copulation. There may also be a negative effect of male dominance or body size on female lifetime fecundity. In *Drosophila melanogaster*, for example, females mated to larger males die sooner and lay fewer eggs (Pitnick and Garçia-Gonzalez 2002; Friberg and Arnqvist 2003; but for a counter-example in crickets, see Simmons 1987). In *T. commodus*, females that mate with males of greater fighting ability do not show reduced longevity. They do, however, suffer reduced lifetime fecundity (Shackleton et al. in preparation). Unless this direct cost is compensated for by genetic benefits accruing to their offspring (Fedorka and Mousseau 2004), females that mate with dominant males will suffer reduced fitness.

Latency to mating as an index of male attractiveness

Our conclusion that male *T. commodus* that win fights are not more attractive assumes that latency to mating in no-choice trials is a meaningful index of male attractiveness. Although many studies have used mating speed to measure male attractiveness (Moore and Moore 1999), our study is among the first to test how it is related to subsequent mating success (for a similar study, see Simmons 1988). A positive relationship is not inevitable because the ability to induce a virgin female to mate sooner may be negatively correlated with other factors that influence the ability of a male to transfer multiple spermatophores to a female. For example, some males may be 'sexually incompetent' and fail to attach spermatophores once mounted by a female (e.g. Simmons 1988). We therefore directly tested whether males with a shorter latency to mating during no-choice trials enjoyed increased mating success when isolated with a single, randomly chosen female. In 25 of 29 pairs of males that differed in the number of matings they obtained, the male with the shorter mating latency gained significantly more copulations. This would only be expected if females tend to agree on the relative attractiveness of males. This appeared to be the case as mating speed was highly repeatable in the four no-choice trials. This further supports the use of mating speed as a measure of attractiveness in *T. commodus*. Similarly, in *Gryllus bimaculatus*, smaller

males have to court for significantly longer before a female will mount them, and smaller males also have significantly lower long-term mating success when given access to multiple females (Simmons 1988). Although the test containers were small, the mean number of spermatophores transferred per female was almost the same as the number transferred per female in another study of a mixed-sex population placed in a large, semi-natural enclosure for 27 h (4.5 spermatophores; Evans 1983). This suggests that the mating rate was not inflated because females were harassed into mating.

Based on latency to mating, in *T. commodus* male fighting ability does not affect male attractiveness to females during short-range courtship interactions. Our results further suggest that males that win fights are unable to coerce females into copulating sooner or more often than males that lose fights despite their heightened aggressiveness and greater body size. In only 17 of 30 cases did the male ranked highest for fighting ability mate more often than the male ranked lowest. In addition, there was no correlation between the number of spermatophores transferred and male body size. Since fighting ability and body size are strongly correlated, this strengthens our conclusion that aggressive males cannot force females to copulate with them.

In *T. commodus*, latency to mating predicts the number of spermatophores that a male will transfer to a female. Because females mate multiply, increased sperm transfer is likely to translate into a greater share of paternity (Simmons 2001). Latency to mating therefore appears to be a useful index of male reproductive success in *T. commodus*. Studies of other species are needed, however, to see whether this is generally the case.

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