Male attractiveness covaries with fighting ability but not with prior fight outcome in house crickets

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In many species males that tend to win fights against other males are more attractive to females. There are three ways in which male fighting ability and attractiveness may be associated: (1) attractiveness and fighting ability are influenced by the same underlying traits (e.g., body size), (2) females prefer males that have directly observed winning fights, or (3) winning previous fights indirectly improves a male's chance of being preferred by females. The last possibility may arise as a consequence of the "loser effect"; in many species when a male loses a fight his probability of losing subsequent fights increases. There are, however, no studies testing whether such a "loser effect" also influences male attractiveness. Here we show that male attractiveness and fighting ability are positively correlated in the house cricket, *Acheta domesticus*. Our experiment was designed so that females could not directly observe the outcome of fights, thus eliminating possibility (2) above. We then tested between possibilities (1) and (3) by making use of the fact that in some cricket species the "loser effect" can be eliminated experimentally by 'shaking' a male and stimulating the motor program for flying. We showed that in *A. domesticus* 'shaking' does affect the outcome of subsequent fights. Males that had won two previous fights were less likely to win a fight after being 'shaken' than when subject to a control treatment. In contrast, males that had lost two previous fights were more likely to win a fight after being 'shaken' than when they were not shaken. There was, however, no effect of 'shaking' on male attractiveness. We conclude that the "loser effect" does not alter the tendency for large, dominant males to be attractive to females. Instead, it appears that there are traits correlated with both fighting ability and attractiveness. One such trait is body size. Fight winners were significantly larger than losers and attractiveness was positively correlated with male body size. *Key words: Acheta domesticus*, attractiveness, body size, fighting ability, "loser-effect." *[Behav Ecol]*

By choosing to mate with a male that is successful in fights against other males, females may ensure that they are mating with a male of superior quality (Berglund et al., 1996; Qvarnström and Forsgren, 1998). If fighting is costly and only high quality males can sustain the costs necessary to win, then the outcome of agonistic encounters may represent an honest signal of male quality (Grafen, 1990; Iwasa et al., 1991; Zahavi, 1975). Thus, male fighting ability per se or trait(s) signaling this ability should be important cues in female mate choice (Berglund et al., 1996; Qvarnström and Forsgren, 1998). Indeed, female preference for males that win fights has been demonstrated in numerous animal taxa (e.g., insects: Breed et al., 1980; reptiles: López et al., 2002; fish: Berglund and Rosenqvist, 2000; Bisazza and Marin, 1991; birds: Alatalo et al., 1991; Double and Cockburn, 2003; mammals: Cox and LeBoeuf, 1977; Horne and Ylönen, 1996), and females may even incite male competition to facilitate mate choice (Cox and LeBoeuf, 1977; Montgomerie and Thornhill, 1989). However, other empirical studies suggest that this relationship is not universal (Cremer and Greenfield, 1998; Forsgren, 1997; Gratson et al., 1991; Howard et al., 1997; Marchetti, 1998; Moore and Moore, 1999; Sorenson and Derrickson, 1994). Winning males frequently provide less parental care (Forsgren, 1997; Qvarnström, 1997; Sargent, 1985) and their mating interests are more likely to conflict with those of the

female (LeBoeuf and Mesnick, 1990; Moore and Moore, 1999; Moore et al., 2003). In such cases, males that win fights may actively be discriminated against as potential mates if they lower the net fitness of their partner (Qvarnström and Forsgren, 1998).

Empirical studies on species forming dominance hierarchies have provided much insight into how different components of sexual selection operate (e.g., Cremer and Greenfield, 1998; Howard et al., 1997; Moore and Moore, 1999). Intrinsic factors such as body size, size of weaponry, and signals of fighting ability are often important in establishing dominance hierarchies (reviewed by Huntingford and Turner, 1987), and in many species these traits are also the focus of mate choice (Berglund et al., 1996). However, extrinsic factors such as the value of the contested resource (Enquist and Leimar, 1987) and prior fight outcome (Elwood et al., 1998; Hofmann and Stevenson, 2000) are also important in determining the outcome of fights. As a result, dominance hierarchies are often unstable (Qvarnström and Forsgren, 1998) and the best fighter does not always hold the most dominant position in the hierarchy.

One important determinant of the outcome of a fight is the previous fighting experience of the contestants. In many species a male's success in recent fights has a strong influence over his performance in a given fight (insects: Otronen, 1990; arachnids: Whitehouse, 1997; crustaceans: Daws et al., 2002; fish: Frey and Miller, 1972; Hsu and Wolf, 1999, 2001; reptiles: Schuett, 1997; birds: Drummond and Osorono, 1992). In field crickets (*Gryllus bimaculatus*), recently defeated males have a higher than expected probability of losing subsequent fights (Khazraïe and Campan, 1999). However, Hofmann and

Stevenson (2000) demonstrated that, by stimulating the motor program for flying, this "loser-effect" could be removed and fighting ability restored to a level comparable to socially naïve males.

Any link between male fighting ability and attractiveness to females may be due to three nonexclusive effects: (1) females prefer males that they have directly observed winning fights, (2) females prefer males with traits that are positively correlated with fighting ability, or (3) females prefer males on the basis of traits that are influenced by a male having recently won a fight. Here we exclude the first possibility and test the latter two possibilities in a manipulative experiment on the house cricket, Acheta domesticus.

A. domesticus has been an important species for studies of both male dominance (Hack, 1997a,b; Nelson and Nolen, 1997; Nosil, 2002) and female mate choice (Gray, 1997; Nelson and Nolen, 1997). As in many gryllid species (reviewed by Zuk and Simmons, 1997), larger males are more likely to win contests (Hack, 1997a; Nelson and Nolen, 1997; Nosil, 2002) and females prefer the calls of larger males that contain more pulses per chirp (Gray, 1997). However, additional components of resource holding potential (i.e., ability to monopolize a resource) and resource value (i.e., hunger levels) can override the effect of male size on the outcome of fights over food in A. domesticus (Nosil, 2002). Therefore, although there is indirect evidence suggesting that females find large males that are more likely to win fights more attractive than small males that are more likely to lose fights, a causal basis for this relationship has not yet been provided. In this study, we compared the attractiveness of males of high and low fighting ability. We also independently manipulated the influence of prior success in fights (by shaking males, see Hofmann and Stevenson, 2000) in a two-way factorial design to elucidate the links between male fighting ability, prior success in fights, and attractiveness.

MATERIALS AND METHODS

Experimental animals

Approximately 1500 Acheta domesticus were purchased from a commercial cricket breeder (Pisces Enterprises®) as final-instar nymphs. Nymphs were reared with constant access to food (Friskies Go-Cat®) and water in single sex culture tubs (4 × 80 L containers per sex) until eclosion. Female and male nymphs were separated as soon as they could be sexed. At eclosion, adults were maintained in single sex populations for a further 10 days prior to experiments to ensure they were sexually mature virgins.

Estimating male fighting ability and the effect of 'shaking'

Fights between male field crickets follow a stereotypical and escalated sequence of events (Hack, 1997a,b; Hofmann and Stevenson, 2000; Nosil, 2002). Unless one male immediately retreats, the contestants initially fence with their antennae and then display spread mandibles while producing an aggressive call. If the contest escalates, males interlock mandibles and wrestle until one male eventually retreats. After defeat, the subordinate male typically avoids all further aggressive encounters with the dominant male (Hofmann and Stevenson, 2000). This stereotypical sequence of events means that the outcome of contests can be clearly and accurately determined (Hack, 1997; Hofmann and Stevenson, 2000; Nosil, 2002).

To estimate the general fighting ability of individual males, we applied two levels of phenotypic selection on male dominance using a hierarchical competition based on a series of dyadic contests. We started with 160 randomly selected males. Males were randomly paired in individual plastic containers (5 × 5 × 5 cm). Each contest was observed until one male clearly gained dominance and the other was submissive. Males were then immediately separated to prevent injury to the subordinate male. This created 80 males that won their contest (W) and 80 males that lost (L). The 80 winners were then randomly paired with each other. Likewise, the 80 losers were also randomly paired with each other. This second round of contests produced 40 males that won both contests (WW) and 40 males that lost both contests (LL). The advantage of our selection process is that every male participated in two fights and males always competed against others with the same outcome in previous fights. This procedure controls for any potential effects that the number of fights and/or the outcome of previous fights may have on assessment of fighting ability (Hofmann and Stevenson, 2000; Khazraïe and Campan, 1999).

In crickets, success in previous fights has been shown to increase the likelihood of victory in subsequent contests (Hofmann and Stevenson, 2000; Khazraïe and Campan, 1999). However, in the field cricket Gryllus bimaculatus when males are shaken in clasped hands and thrown into the air to initiate a flight response, aggressiveness is restored to levels comparable to naïve males (Hofmann and Stevenson, 2000). We therefore imposed a second treatment of shaken (S) or not shaken (N) to males previously classified as having a high or low fighting ability (WW or LL) to test whether shaking had an effect on the outcome of a subsequent fight. Half the males in each fighting ability group were randomly allocated to either the shaken or non-shaken treatment ($n = 20$ males per treatment combination). Males in the shaken treatments were removed from their individual containers and shaken vigorously in clasped hands for 1 min to initiate the flight response. Hofmann and Stevenson (2000) have previously demonstrated that as little as 10 s is required to remove the "loser effect." Males in the non-shaken treatment were not handled and remained in their original containers until their final contest.

To determine the effect of our experimental treatments on fight outcome we performed a final round of dyadic contests. Males in each of the four treatments were paired in an individual plastic container with a male haphazardly selected from the single sex cultures. Again, we determined the fighting ability of the focal male in each dyad using behavioral observations. To identify the focal male in each dyad, each randomly selected competitor was marked with a dot of white paint on the pronotum the evening prior to the trials. Male weight was measured as an index of overall body size, as pronotum width and body weight correlate strongly in this species ($F_{1,29} = 217.39$, $r^2 = .88$, $p = .0001$). All behavioral trials were conducted under red lighting to minimize observer disturbance.

The effects of fighting ability and prior success in fights on male attractiveness

To test whether males that win fights are more attractive to females than males that lose fights, and whether this attractiveness is influenced by the shaking treatment, we set up a further 320 males as outlined above to produce 40 males in each of our four treatment combinations (WW-S, WW-N, LL-S, and LL-N). We then measured male attractiveness by placing a randomly drawn virgin female with each male and scoring whether or not he was successfully mounted by her within a 30-min period. Each focal male was then tested with a second virgin female. Mounting by a female was scored as successful if the female remained motionless on top of the male for at least 30 s and the male started transferring

a spermatophore. In a pilot study, 46 of 50 mating attempts (92%) that reached this stage lead to the immediate and successful transfer of a spermatophore. Mounting was used in preference to mating as our measure of attractiveness because males require at least one hour to produce a new spermatophore and to regain sexual activity prior to mating. Therefore, our measure of attractiveness is based on a male's ability to convince a female to mate rather than on his ability to attract a female to him from long distances.

Because a male is required to court a female prior to mating (Evans, 1983; Loher and Rence, 1978), males not courting were excluded from analysis, as it was not clear that females were assessing the attractiveness of these males. We classified a male as attractive if he actively courted the female and was successfully mounted by at least one of the two females he was tested with. While males not courting could arguably be viewed as unattractive, our classification provides a more conservative estimate of male attractiveness.

RESULTS

Male fighting ability and prior success in fights

Fighting ability is largely determined by adult body size in *A. domesticus*. After two levels of phenotypic selection on male fighting ability, winning males were significantly heavier than losing males ($t = 13.66$, df = 150, $p = .0001$; WW males = 311.6 ± 6.1 mg, LL males = 206.2 ± 2.9 mg, mean $\pm$ SE).

To determine the effects of past fighting ability and the shaking treatment on the outcome of current contests, we performed a nominal logistic regression including the weight difference between the focal and random male competitor as a covariate and past fighting ability and shaking treatment as factors. Controlling for the difference in competitors' size, WW males were significantly more likely to win fights than were LL males ($\chi^2 = 8.71$, df = 1, $p = .0032$). There was no effect of shaking per se on a males ability to re-win fights ($\chi^2 = 0.12$, df = 1, $p = .727$); however, the interaction between past fighting ability and shaking had a significant effect on contest outcome ($\chi^2 = 15.17$, df = 1, $p = .0001$). Previously winning males were less likely to win after shaking, and the reverse was true for previously losing males. Across treatments, males were more likely to win fights when they were larger than their competitor ($\chi^2 = 16.25$, df = 1, $p = .0001$), but the magnitude of this size advantage differed among the four experimental treatments (Figure 1).

To examine the effect of size on fight outcome more closely, we performed separate nominal logistic regressions for each treatment using the weight difference between the focal male and his competitor as the independent variable and the focal male's competitive success as the dependent variable. Regardless of the effect of shaking, larger WW males had a clear advantage in fights (WW-S: $\chi^2 = 22.64$, df = 1, $p = .0001$; WW-N: $\chi^2 = 8.34$, df = 1, $p = .0001$; Figure 1). However, a WW male in the shaken treatment had an equal probability of re-winning when he was 2.01 mg heavier than his opponent, whereas a WW male in the non-shaken treatment was equally likely to win a contest even when he was 10.03 mg smaller than his opponent (Figure 1). In contrast, larger LL males were more likely to win a fight when they had been shaken, but were likely to lose irrespective of their size if they were not shaken (LL-S: $\chi^2 = 9.64$, df = 1, $p = .0019$; LL-N: $\chi^2 = 1.45$, df = 1, $p = .23$; Figure 1).

The effects of fighting ability and prior success in fights on male attractiveness

A total of 33 out of 160 males (21%) failed to court females in the attractiveness trials. WW males were significantly more
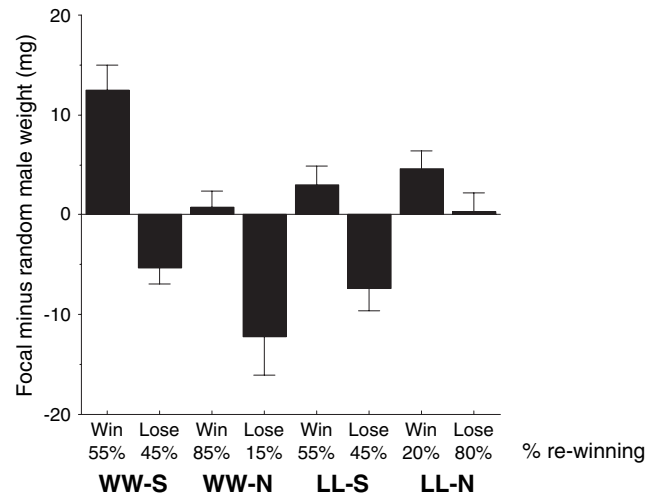

Figure 1
The size difference (mean $\pm$ SE) between a focal and stock male for focal males that either won or lost a test fight. Focal males were categorized into those that had either won or lost their previous two fights (WW or LL) and were then either shaken (S) or not shaken (N). The percentage of focal males in each of these four categories that won the test fight is also provided (see text for more details).

likely to court a female than were LL males ($\chi^2 = 6.29$, df = 1, $p = .0128$). Shaking did not significantly effect the likelihood that a male would court a female ($\chi^2 = 0.36$, df = 1, $p = .56$), nor was there a significant interaction between shaking and past fighting ability on a male's likelihood of courting ($\chi^2 = 0.39$, df = 1, $p = .55$). Furthermore, body size did not affect a male's likelihood of courting a female ($\chi^2 = 2.41$, df = 1, $p = .13$).

To determine the effects of shaking and past fighting ability on male attractiveness, we performed a two-factor nominal logistic regression including the weight of the focal male as a covariate in the analysis. Dominant WW males were significantly more attractive than subordinate LL males ($\chi^2 = 6.29$, df = 1, $p = .013$). Body size also had a significant positive effect on male attractiveness ($\chi^2 = 8.85$, df = 1, $p = .0029$). Shaking did not significantly affect a male's attractiveness ($\chi^2 = 0.42$, df = 1, $p = 0.43$), nor was there a significant interaction between shaking and fighting ability on attractiveness ($\chi^2 = 0.84$, df = 1, $p = .38$).

To further examine the relationship between male size and attractiveness we analyzed our data within treatments using nominal logistic regressions. As attractiveness is independent of male's prior success in fights, we pooled our data across these treatments in our analysis. For WW males, attractiveness was positively related to body size ($\chi^2 = 4.74$, df = 1, $p = .029$; Figure 2). In contrast, attractiveness was unrelated to body size for LL males ($\chi^2 = 1.34$, df = 1, $p = .25$; Figure 2).

DISCUSSION

Our results demonstrate that males that win fights are more attractive to female *Acheta domesticus*. Moreover, because females did not witness fights we can exclude the possibility that this is due to females directly observing male dominance. Therefore, our results suggest that females prefer males based on one or more traits associated with male fighting ability.

We found that the outcome of prior contests was important in determining the outcome of current fights, a result that is consistent with previous findings in the field cricket *Gryllus bimaculatus* (Hofmann and Stevenson, 2000; Khazraïe and
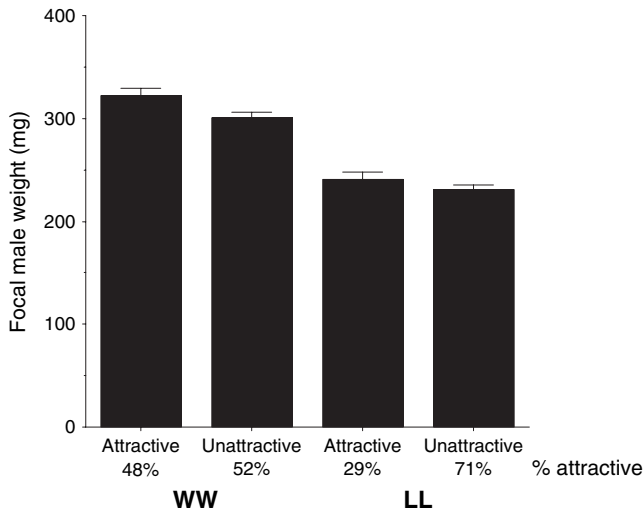
Figure 2
The body weight (mean ± SE) of males of high or low fighting ability (WW or LL), which were classified as attractive or unattractive (whether or not the male mated). The percentage of attractive and unattractive males in each of the two fighting ability categories is also provided (see text for more details).

Campan, 1999). We found that males successful in contests were more likely to win in subsequent encounters and males losing in earlier contests were more likely to lose in future encounters. In contrast to the findings of Hofmann and Stevenson (2000), however, we found that shaking a male had opposing effects for males that previously won or lost fights. Although experimentally removing the "loser-effect" by shaking elevated the probability that losing males would be victorious in future contests (as shown by Hofmann and Stevenson, 2000), we found that the reverse was true for males that were successful in previous fights. Therefore, our results suggest that a male's recent fight experience, the memory of which is modified by shaking, is important in determining the outcome of future fights for males of both high and low fighting ability.

Our results allow us to exclude one potential pathway that may link male fighting ability to attractiveness in *A. domesticus*, namely the direct effects of losing or winning a fight on male behavior. Contrary to our findings for fighting ability, removing a male's memory of previous wins or losses by shaking did not influence his subsequent attractiveness to females. Similarly, Adamo and Hoy (1994) suggested that social effects were unlikely to be important to male courtship behavior (and thus attractiveness) in *G. bimaculatus* because males reared in social isolation did not differ in the timing or in the behavioral sequence of their courtship behaviors when compared to males reared with exposure to social interactions. Collectively, our findings suggest that male dominance, but not attractiveness, is largely determined by interactions with other males for its expression (i.e., it has a large social component) in *A. domesticus*. The ramifications of this, including the possibility of evolution via indirect genetic effects mediated through social interactions (Moore et al., 2002; Wolf et al., 1998), provide an intriguing avenue for further study.

Our results corroborate earlier findings that large males win in contests with other males (Hack, 1997a,b; Nelson and Nolen, 1997) and are preferred by females as mates (Gray, 1997; Nelson and Nolen, 1997). The preference shown by females for dominant males could not be explained entirely by a preference for larger males; dominant males were clearly more attractive, even when male size was statistically con-

trolled. Thus, females either base their mate choice on a trait (that we did not measure) that is positively correlated with both male dominance and size, or on size and another (unmeasured) trait that is correlated with dominance.

Male contests in *A. domesticus* begin with aggressive calling and may then escalate to fighting which is much more costly, both energetically (Hack, 1997b) and presumably in terms of injury and predation risk. Hack (1997a) has suggested that both male body size and willingness to invest in the costly stages of escalated fighting are important determinants of fight outcome. Males of high phenotypic quality (e.g., in good condition sensu Hunt et al., 2004; Rowe and Houle, 1996) may be better fighters with aggressive calling and willingness to escalate fights signaling their fighting ability. If so, it is likely that these traits will be correlated with other signals, including advertisement and courtship calls, used to attract females. So, females that choose dominant males may obtain mates of higher quality, as predicted by Berglund et al. (1996). In our study, however, females did not observe male fights, and a male's own assessment of his success in previous fights (which is presumably altered by shaking) had no effect on female choice. Thus, dominance is probably only a correlate of male attractiveness rather than a direct determinant thereof.

The relationships between fitness components are of prime importance to the eventual strength and direction of selection (Kokko et al., 2002). For example, in the cockroach (*Nauphoeta cinerea*) pheromone profiles that made males more attractive to females result in lower status within male dominance hierarchies (Moore and Moore, 1999). This may result in balancing selection on pheromone concentrations and compositions and maintaining additive genetic variation in these important fitness traits. Our results, however, indicate no such phenotypic trade-off in *A. domesticus*. Traits that confer male dominance in intra-sexual contests, which probably include body size, also confer attractiveness in inter-sexual mate choice. Moreover, there is evidence that large males are also fitter with respect to a number of other important fitness components (e.g., immunocompetence: Ryder and Siva-Jothy, 2000, 2001; sperm competitiveness: Gage and Barnard, 1996), and there is no evidence yet of any cost of large male body size. Whether or not larger males have a higher net fitness remains to be shown in *A. domesticus*. Future studies that obtain formal estimates of the selection gradients operating on male body size (and other correlated traits) will prove extremely valuable in explaining why male size does not appear to be constrained in this species.

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