



Female crickets are driven to fight by the male courting and calling songs

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Crickets have traditional sex roles, where males compete aggressively for access to selective polyandrous females. However, in a laboratory experiment, we found that normally nonaggressive female *Gryllus campestris* fought each other vigorously in the presence of a courting male, resulting in a dominant female that gained a greater probability of receiving the spermatophore. Female–female fights included the same series of characteristic actions known from male–male fights, which demonstrates that the females can perform the full repertoire of agonistic actions except for the production of the aggressive rival song. Since females remained nonaggressive towards each other in the vicinity of a muted male, but were induced to fight each other in the complete absence of a male by the auditory experience of the courtship song, this song is both sufficient and necessary to induce female competition for males. Calling song was as effective as courtship song at inducing female aggression, whereas rival song was least effective. We therefore speculate that the calling and courtship songs may signal a male's resource value. © 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

While in most species males compete aggressively for access to females, it is unusual for females to compete for males (Andersson 1994). Although females are known to interact aggressively during the breeding season or when they are highly receptive (red-winged blackbirds, *Agelaius phoeniceus*: Hurly & Robertson 1984; bonobos, *Pan paniscus*: Hohmann & Fruth 2003; red deer, *Cervus elaphus*: Bebié & McElligott 2006), it is mostly unclear whether they compete for food or territories (reviewed in Rosenqvist & Berglund 1992; Jennions & Petrie 1997) or mating opportunities (lion tamarins, *Leontopithecus rosalia*: French & Inglett 1989; green poison-dart frog, *Dendrobates auratus*: Summers 1989; cichlid fish, *Lamplogus ocellatus*: Walter & Trillmich 1994; capuchin monkey, *Cebus apella*: Linn et al. 1995). Most studies of female contests have focused on 'sex role-reversed' systems, where male parental investment is comparatively high (reviewed in Gwynne 1991; katydids, *Anigozanthos manglesii*: Gwynne & Simmons 1990; blenny, *Salaria pavo*: Almada et al. 1995; sand goby, *Pomatoschistus minutus*: Forsgren et al. 1996). More recent studies, however, have addressed the consequence of female aggression for reproductive success in animals with conventional sex roles (reviewed in Cunningham & Birkhead 1998; birds: Slagsvold & Lifjeld 1994;

European starling, *Sturnus vulgaris*: Sandell & Smith 1997; pipefish, *Syngnathus typhle*: Berglund & Rosenqvist 2001; prairie vole, *Microtus ochrogaster*: Bowler et al. 2002). Such investigations suggest that females should compete for males not only when the operational sex ratio is female biased or when males have similar parental investments, but also when winning secures mating opportunities with high-quality, high-ranking males (reviewed in Berglund et al. 1993; European lobster, *Homarus gammarus*: Debusse et al. 1999; chacma baboon, *Papio cynocephalus ursinus*: Palombit et al. 2001). Thus, female contests for males should be far more common than has been documented.

We evaluated female aggression in the cricket *Gryllus campestris*. These crickets have conventional sex roles whereby males produce the calling song to attract females (Zuk & Simmons 1997), which are choosy (Hedrick 1986; Bateman et al. 2001), and fight with other males to secure and guard them (Simmons 1986; Wynn & Vahed 2004). Females are mute but, like males, may occupy burrows and 'defend them against conspecifics' (Hissmann 1990). Females are not, however, known to compete aggressively for mates in the field (see also Rost & Honegger 1987; Ritz & Köhler 2007). Under laboratory conditions, female crickets, in contrast to males, rarely interact and usually avoid contact, but will compete aggressively for food when starved (Adamo & Hoy 1995; Nosil 2002). Even so, the agonistic behavioural repertoire of females seems more limited than males: Adamo & Hoy (1995) did not observe mandible spreading, mandible interlocking or grappling in

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a detailed videotape analysis of *Gryllus bimaculatus*. Although animal contest structure need not always be the same in the two genders (see e.g. Draud et al. 2004 on cichlids *Herichthys cyanoguttatum*), the observation that drugs, such as the opiate antagonist naloxone, dramatically increase the incidence of mandible spreading in *G. bimaculatus* females (Dyakonova et al. 2002) indicates that there may be natural circumstances where female crickets show the same agonistic traits as males. Since the aggressive motivation of an animal can be elevated by the presence of a valuable resource (Enquist & Leimar 1987), such as food in crickets, we speculated that female crickets may also be induced to compete aggressively by the presence of a male, a potential mate and provider of a nutritious spermatophore (Simmons 1988a, b). We therefore compared interactions between weight-matched adult females in an arena in the absence and presence of a mature adult male, noting in particular the frequency of mandible spreading and physical fighting. Since male crickets may signal their quality by singing (e.g. Wagner & Reiser 2000), we also evaluated female aggressiveness in the presence of a muted male and with playback recordings of the three male songs: the calling song, which attracts females by evoking phonotaxis, the courtship song, which guides the female and triggers mounting, and the aggressive rival song, which is produced when the male confronts, and defeats, a conspecific male (Huber 1962).

METHODS

Experimental Animals

Male and female *G. campestris* were collected in their last nymphal stage from south-facing sloping grassland west of Leipzig city, Saxony, Germany, during April. The sexes were kept physically and acoustically separated in plastic containers (25 × 40 cm and 28 cm high), with at most 30 animals in each, at Leipzig University under standard conditions (22–24 °C, 40–60% relative humidity, 12:12 h light:dark regime, see Staudacher & Schildberger 1998). The experimental animals were returned to their natural habitat after the experiment. All experimental procedures are in accord with animal welfare regulations in Germany.

Evaluation of Aggression

We staged all interactions in an equilateral triangular arena fashioned from clear Perspex (each side 25 cm long and 7 cm high) and with a sand-covered floor. A centrally positioned, 'Y'-shaped door, constructed from three individually removable squares (65 × 65 mm) of grey opaque plastic, served to divide the arena into three corners of equal area. We placed pairs of previously isolated, weight-matched, adult females in separate corners, and, when required, a male in the third corner, and left the animals for 5 min to adapt to the new surroundings. The doors were then opened manually and interactions between the animals were noted and videotaped (Sony DCR-TRV 130 Digital8 Camcorder) for a continuous observation period of 5 min, using focal animal sampling and continuous event-sampling rules.

As a measure of female aggressiveness we noted the frequency of occurrence of the following key agonistic behaviours (see Stevenson et al. 2000), defined as the percentage of contests in which they occurred at least once. Nonaggressive: after initial antennal contact no further interaction occurred. Antennal fencing: after initial antennal contact the two females turned towards each other and lashed their antennae while maintaining a raised body posture. Mandible spreading: the two crickets faced each other and one or both broadly spread its mandibles. Physical fighting: the two females interlocked their mandibles, pushed and occasionally bit

the opponent. These aggressive behavioural acts are not mutually exclusive and can be reliably identified even by inexperienced observers. In our experiment the scores of two independent observers were in full agreement.

Experimental Groups

For all interactions, we used mature adults, taken 7–28 days after the final moult and transferred to individual glass jars at least 24 h before the interactions by which time influences of prior social contact on aggression are extinguished (Adamo & Hoy 1995; Hofmann & Stevenson 2000; Stevenson et al. 2005). Supporting this, a comparison of the aggressiveness of females that had no previous contact with a male with that of females that had had social contact with a male on the previous day revealed no significant differences in the frequency of occurrence of the evaluated elements of aggression (Fisher's exact test: $N = 47$, $P = 1.0$ for antennal fencing, 0.76 for mandible spreading, 0.72 for physical fighting). Data from these two female categories were thus pooled. In total we analysed the fighting behaviour of 282 adult female and 66 adult male crickets. In some cases a female was used in more than one interaction, but never on the same day, and never against a previous contestant, as a further precaution against influences of previous agonistic experience. The two contestants were always matched for weight (weight difference < 5%) and their interactions were recorded in the arena under the following experimental conditions.

(1) Control: females in the absence of males or the male song ($N = 36$ pairs).

(2) Male: females in the presence of a courting male ($N = 47$ pairs).

(3) Mute: females in the presence of a courting male that was prevented from producing the courtship song by sticking the forewings together with a water-soluble adhesive, which was later removed ($N = 36$ pairs).

(4) Mute + song: females in the presence of a muted courting male and a played-back recording of a male cricket's courtship song ($N = 27$ pairs). For the latter, long uninterrupted bouts of courtship songs were recorded from a randomly selected singing male with a high-fidelity microphone (ECM MS 907, Sony) on a tape recorder (WM-D6C, Sony) and replayed through a tweeter loudspeaker (Conrad Electronics, Wernberg, Germany) placed 15 cm from the arena (70–80 dB). The same methods were used to record and present the male's rival song and calling song (see below).

(5) Courtship song: females presented with the played-back recording of a male's courtship song, in the absence of a male ($N = 26$ pairs).

(6) Rival song: females presented with a played-back recording of a male's rival song, in the absence of a male ($N = 42$ pairs).

(7) Calling song: females presented with a played-back recording of a male's calling song, in the absence of a male ($N = 25$ pairs).

(8) White noise: as an acoustic control, this group of females ($N = 21$ pairs) were presented with cyclically repeated bursts of white noise (200 ms on, 800 ms off), generated electronically using standard software (peak 3.2, bias sound creative, Bias Inc., Petaluma, CA, U.S.A.).

(9) Male–male: for comparative purposes, we also evaluated the aggressive interactions of weight-matched adult male crickets ($N = 33$ pairs).

Statistics and Data Analysis

For statistical tests we used the software package Prism 5 (GraphPad Software Inc., San Diego, CA, U.S.A.). The Fisher's exact probability test was used to obtain the significance level of the

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