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Loser in Fight but Winner in Love: How Does Inter-Male Competition Determine the Pattern and Outcome of Courtship in Cricket *Gryllus bimaculatus*?

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Animal females are generally assumed to prefer males that win fights. However, a growing number of studies in numerous animal taxa demonstrate no correlation between male fighting ability and their attractiveness, or even female preferences for fight losers. One of the methods to measure female preferences employs no-choice tests that evaluate a female's latency to mating when placed with a single male. Considering that courtship behavior generally contains multimodal signaling, we analyzed 19 behavioral elements demonstrated by both sexes of the cricket *Gryllus bimaculatus* during courtship. To estimate male dominance status, males were preliminarily tested in two rounds of fights. Females mounted males with different fighting ability equally often, but the latencies from the start of antennal contact to mount were shorter in fight losers than fight winners. During courtship, males with high fighting ability demonstrated one of the elements of agonistic display, rocking the body, more frequently, and for longer durations than males with low fighting ability. This element was negatively correlated with singing in fight winners but was positively correlated with singing a courtship song in fight losers. Rocking is thereby suggested to have multiple signaling functions in agonistic and courtship behavior. The song parameters were poorly related with male mating success. Fight winners, rather than fight losers, tended to produce a higher number of calling chirps, which could be explained by the inability of males with high fighting ability to quickly shift from aggression to courtship behavior. The results suggest that increased aggression in fight winners is likely to interfere with subsequent courtship.

Keywords: cricket, *Gryllus bimaculatus*, multimodal signaling, courtship song, dominance status, aggressiveness, female preference

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INTRODUCTION

It is generally thought that intrasexual selection (resulting from male-male competition) and intersexual selection (resulting from female choice) are mutually reinforcing processes (Qvarnstrom and Forsgren, 1998; Wong and Candolin, 2005). In the last quarter of a century, however, various studies have suggested a more intricate relationship between these two processes. Female preference for dominant males has been found in many species (Andersson, 1994; Berglund et al., 1996), in particular, in reptiles (Trivers, 1976), birds (Trail, 1985; Kunc et al., 2006), fishes (Far and Travis, 1986; Bisazza and Marin, 1991), crayfish (Aquiloni et al., 2008), flies (Alcock and Pyle, 1979; Borgia, 1981), and crickets (Simmons, 1986). Female preference for dominant males could have direct benefits if these males provide higher quality resources (Andersson, 1994) or better parental care (Hoelzer, 1989). Female preference for dominant males could also provide indirect benefits if these males sire offspring of superior genetic quality (birds: Norris, 1993; Petrie, 1994; Sheldon et al., 1997; crickets: Wedell and Tregenza, 1999; Bretman et al., 2006).

A growing number of studies, however, demonstrate no correlation between male fighting ability and their attractiveness (Qvarnstrom and Forsgren, 1998). This could occur because dominant males provide less parental care (Forsgren, 1997; Wong, 2004), harm their mates (Moore et al., 2001; Ophir and Galef Jr, 2003), have depleted sperm stores (Pitnick and Markow, 1994; Preston et al., 2001), or are more likely to transmit diseases (Folstad and Karter, 1992). Females could also ignore dominant males because these males might not invest as much in mate attraction or courtship as subordinate males. For example, it was shown in crickets *Teleogryllus oceanicus* that females even preferred subordinate males: rather than investing more in postcopulatory strategies, the subordinate males invested in an alternative precopulatory mating approach (Thomas and Simmons, 2009).

The most common way to investigate female preferences is conducted using simultaneous choice tests. If possible, these tests should exclude male-male interactions; otherwise it would be difficult to evaluate the relationship between intra- and intersexual selection. In crickets, such studies have been conducted using playback experiments (Rantala and Kortet, 2003) or offering filter papers with pheromones of males with different fighting ability (Kortet and Hedrick, 2005). Investigation of long-distance acoustic signals (calling song) could also allow choice tests without male-male interactions (Hedrick and Bunting, 2014).

In choice tests where a female was placed with two male crickets, the winner of the agonistic encounter was more likely to mate (Gryllus bimaculatus: Simmons, 1986; Acheta domesticus: Nelson and Nolen, 1997; Rantala and Kortet, 2004). It was shown that dominant males could prevent subordinate males from courting the females. Because females do not mate with non-courting males (Alexander, 1961), these experiments cannot measure the free choice of females. Moreover, males in the presence of a female were more likely to initiate fights and their fights were more aggressive than in the absence of a female (*G. bimaculatus*: Simmons, 1986; Tachon et al., 1999; *G. veletis*: Fitzsimmons and Bertram, 2013; *G. assimilis*: Montroy et al., 2016). If females prefer to mate with fight winners, thenincreased male aggression might be reinforced by intersexual selection.

A second way to measure female preferences is to conduct no-choice tests. These tests usually measure a female's latency to mating when placed with a single male. In no-choice tests conducted on various species of crickets, the results vary. In *A. domesticus* (Savage et al., 2005) and *G. assimilis* (Loranger and Bertram, 2016), males that win fights were shown to be more attractive to females. By contrast, Nelson and Nolen (1997) and Shackleton et al. (2005) showed that females did not prefer males that won fights in *A. domesticus* and *T. commodus*. In *T. oceanicus,* subordinate males upregulated the quantity of a number of cuticular compounds that increase male mating success; at the same time, they produced ejaculates of lower quality and sired fewer offspring than dominant males (Thomas and Simmons, 2009). Thus, the contact pheromones are not always an honest signal of males' quality, and females may not be able to detect this dishonesty.

Many cricket species display a repertoire that includes three structurally distinct signals, termed the calling (a long-range signal), courtship (a close-range signal) and aggression (produced during encounters with other males) songs (Alexander, 1961). In *G. bimaculatus,* the intensity of calling songs and the repetition rate of chirps and pulses was positively correlated with male size, and larger males gained more matings (Simmons, 1986, 1988). In the field, however, pulse rate was negatively related to male size, while the duration of pulses was positively related to size (Simmons and Zuk, 1992). In *G. integer*, the percentage of time spent singing calling songs was either negatively correlated with aggressiveness (for males caught in the field) or unrelated to aggressiveness (for males raised in the lab) (Hedrick and Bunting, 2014). The parameters of the courtship song have been more poorly investigated in relation to the cricket dominance status. No effect of body size on the dominant frequency of the courtship song was found in *G. bimaculatus* (Miyashita et al., 2016). At the same time, higher rates and durations of ticks (the parameters preferred by females) were positively correlated with high immunocompetence, which may indicate that females might benefit by increasing the parasite resistance of their offspring (Rantala and Kortet, 2003).

In no-choice tests, two parameters of female preferences are usually measured: the percentage of females that mated males and the latency to mating. In the current study, we videotaped male-female interactions and measured many different behavioral elements demonstrated by both sexes in no-choice tests. We hypothesized that males that won fights would behave more aggressively toward females than males that lost fights, and this could be a part of reason decrease mating success of fight winners. Taking into account multisensory courtship signals, we tried to evaluate which sensory modalities, chemical or acoustic, could be a better indicator of the male dominance status. We also analyzed different song parameters to determine whether the songs of dominant and subordinate males differed from each other.

MATERIALS AND METHODS

Crickets

Experimental animals came from a laboratory stock obtained from the Moscow Zoo culture. This culture was originally obtained in 1985–1990 from the cricket farms and pet food stores in Germany and Great Britain. Since this period, the Moscow Zoo culture has been constantly maintained at more than 1,000 individuals. The size of the laboratory stock varied from 30 to 200 individuals at different times; however, this stock was refreshed from the Zoo culture one–two times per year to reduce the potential effects of inbreeding. The crickets were reared in plastic containers (57 × 39 × 42 cm) at 22–27°C under a 12-h:12-h light/dark cycle. Food (dried amphipods and oatflakes) and water were provided *ad libitum*. The crickets were separated into individual containers (12 × 12 × 7 cm) not later than 24 h after the imaginal molt. Thus, individuals were physically but not acoustically isolated. All behavioral experiments were conducted on virgin individuals of one to 2 weeks old under dim red lights in a temperature controlled room (25°C).

Estimating the Male Social Rank

Individual males were ranked for fighting ability by methods similar to those of Shackleton et al. (2005), Savage et al. (2005), and Thomas and Simmons (2009). We tested males in blocks, with four randomly selected males in each block. The age difference of males within each block varied from 0 to 3 days. For discrimination between opponents during contests, males within each block were marked individually on the pronotum with correction permanent markers.

Males were tested in two rounds of fights (**Data Sheet 2**). In the first round, pairs of males were randomly assigned and placed in individual open-top plastic container (15 × 15 × 15 cm). Dominance status was usually established within the first few minutes, when a loser (male with low fighting ability) started to avoid all further aggressive encounters with a winner (male with high fighting ability). This generated two males that won and two males that lost their first round of contests. In the second round, the previous winners were paired (**Video Clip 1**) and the previous losers were paired (**Video Clip 2**). Only those males that lost ($n = 27$) or won ($n = 29$) both contests were used in subsequent experiments with females. The advantage of this method was that every male always competed against another male with the same recent fight history, since the success in previous fights has been shown to increase the likelihood of victory in subsequent fights in crickets (Khazraïe and Campan, 1999; Hofmann and Stevenson, 2000; Savage et al., 2005). By using this method, we also increased the difference between the males with different fighting ability. In all contests, males were left together for a period of 5–7 min. The floor of the arena was covered with a paper towel, which was replaced after each trial to remove any olfactory cues that might be left by the crickets.

Courtship Test Procedure

After the second round of fights (with an interval varied in the range of 1–7 min), we placed a randomly drawn female with the male, one female—with the double winner, and another—with the double loser. The experiments were performed in a cylindrical open-top arena (15 × 15 × 15 cm), in which the floor was covered with a paper towel, and the walls were formed by a metallic grid. We evaluated female preferences based on the readiness of the female to mount the male. During courtship, the male turns away from the female and presents his abdomen, while continuously stridulating. The female reacts by approaching from behind. The male spreads his hind wings and flattens his abdomen, allowing the female to mount him (**Video Clip 3**). Mounting of the male by the female is a prerequisite for copulation (Alexander, 1961; Adamo and Hoy, 1994). A male was introduced into the arena, and after about 1 min we introduced a female. Each trial lasted for up to 7 min. All trials were video recorded (Sony DCR-TRV 355E), and the video signals were transferred to a PC for analysis of courtship. In male–female interactions, each specimen was used only once.

Courtship behavior was analyzed with the BORIS program (Friard and Gamba, 2016). According to this program, the behavior type can be defined as a "state event" and a "point event" (having and not having duration, correspondingly). Overall, we distinguished 15 state and 4 point events in both male and female behavior (**Table 1**). All specific elements during male—female interactions were documented as previously described by Adamo and Hoy (1994). We measured the latency from the test start to the onset of the element (for all events), and the duration of the element (for state events only). We also calculated the latencies from the first antennal contact to male rocking, singing, female following and mount (**Data Sheet 1**).

Simultaneously with video recording, we conducted song recordings. A microphone (type 4191, 1/2 inch; Bruel & Kjær, Nærum, Denmark) was placed at a height of 8–10 cm from the top of the arena. The output of a conditioning amplifier (Bruel and Kjær 2690) was digitized (100 kHz sampling rate) using a custom-made A/D–D/A interface. The temporal parameters and power spectra of the songs were analyzed with COOLEDIT (Syntrillium, Seattle, WA). During courtship tests, males sometimes produced not only a typical courtship song, but also some elements of calling or rivalry (=aggressive) songs (**Figure 1**). A courtship song of *G. bimaculatus* was easy to distinguish from the other two types of the songs: the calling and rivalry songs consisted of chirps containing several pulses; the dominant carrier frequency was ca. 4.5–5.0 kHz (first harmonic). The more variable courtship song was composed of large-amplitude pulses (=ticks) separated by a number of smaller pulses; the energy of ticks was concentrated around 4–5 and 11–16 kHz. The duration of ticks comprised about half of the chirp pulse duration (Rheinlaender et al., 1976; Libersat et al., 1994; Shestakov and Vedenina, 2015). We measured 9 song characters: the ratio of the chirp to tick number, the number of pulses per chirp, the duration and period of the chirp pulses, the dominant frequency of chirps, the duration and period of ticks, the relative amplitude of the courtship pulses and ticks, and the dominant frequency of ticks (**Data Sheet 3**).

RESULTS

The Occurrence of Courtship Elements

Most of the specific elements recorded during male–female interactions occurred in more than 50% of trials (**Figure 2**). Among them, however, only the antennal contact was demonstrated by both sexes in almost all trials. There were no significant differences between males with different fighting ability in the occurrence of any behavioral elements (Fisher's Exact Test, two-tailed; $p > 0.05$), except for rocking ($p = 0.04$): fight winners rocked the body (**Video Clip 4**) more often than fight losers (in 83 vs. 56% of trials). Fight winners also followed females more often (in 69 vs. 44% of trials) and demonstrated pauses less often (in 69 vs. 89% of trials) than fight losers. These differences were, however, not significant ($p = 0.1$). The elements that usually preceded the mounting response (singing, turn, pushing back) occurred in 58–74% of experiments. Females mounted winners and losers almost equally often (in 59 and 67% of trials, respectively; $p = 0.59$).

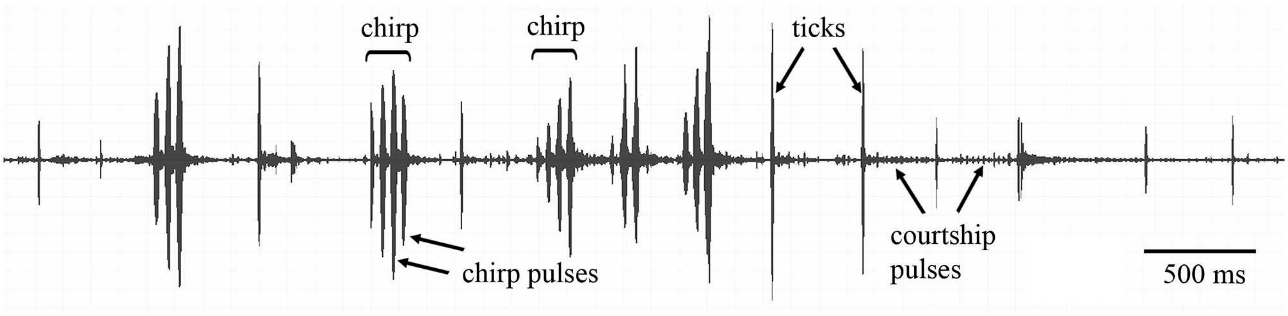

FIGURE 1 | Oscillogram of a song produced during male—female interactions in *Gryllus bimaculatus*. During courtship, the males could produce not only the elements of courtship song (ticks and courtship pulses), but also the elements of calling song (chirps and chirp pulses).

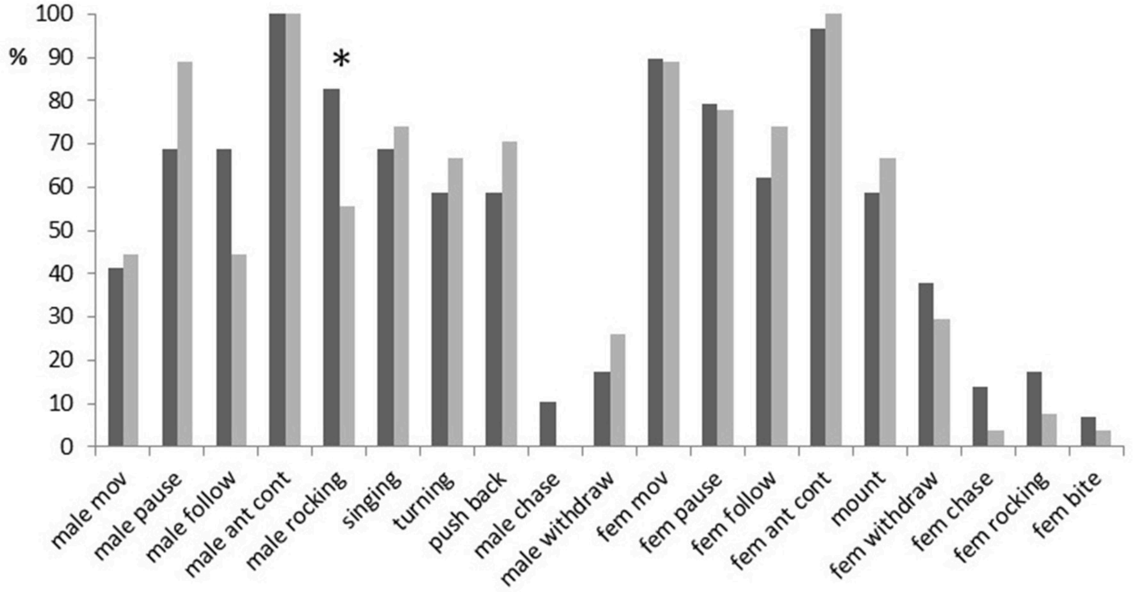

FIGURE 2 | A percentage of trials containing a given behavioral element in courtships of dominant males (black bars) and subordinate males (gray bars) in *Gryllus bimaculatus*. Abbreviations for behavioral elements are listed in **Table 1**. Asterisk indicate statistical significance of the differences between dominant and subordinate males (Fisher's Exact Test, two-tailed; *$p < 0.05$).

Some elements rarely occurred in male–female interactions. Males with high fighting ability moved away (withdrew) from any contacts with females in 17% of the trials, while males with low fighting ability exhibited this behavior in 26% of the trials. Crickets drove conspecifics out (chased) more often in experiments with fight winners (in 10–14% of cases) than in experiments with fight losers (in 0–4% of trials). Females rocked body and bit dominant males more often (in 17 and 7% of trials, respectively) than subordinate males (in 7 and 4%, respectively). None of these differences were statistically significant ($0.35 < p < 0.5$). We did not analyze latencies or duration of the elements that occurred in <30% of experiments because of the low sampling number.

The Latencies to Courtship Elements

Analysis of the latencies from the onset of experiment to the start of any element showed many differences between winners and losers. Despite these differences were not significant for all elements (after the correction for the false discovery rate; Benjamini and Hochberg, 1995), the consistent patterns can be found in these differences (**Figure 3**). For example, winning males started antennal contact (9 s) and rocking (12 s) earlier than losing males (19 and 32 s, respectively). By contrast, fight winners started to sing, follow females, turn and push back later than fight losers (of median values 53 vs. 31 s; 52 vs. 34 s; 61 vs. 42 s; 109 vs. 60 s, respectively). Females started to withdraw earlier from winning than losing males (32 vs. 62 s), and conversely, started to follow winners later than losers (61 vs.

TABLE 1 | Behavioral elements demonstrated by crickets *Gryllus bimaculatus* during male–female interactions.

Description of behavioral elements	Type of event	Abbreviations used for behavioral elements
Male actively moves for at least ½ body length	State	Male mov
Male remains immobile for at least 10 s	State	Male pause
Male follows female	State	Male follow
Male contacts female with at least one antenna	Point	Male ant cont
Male quickly rocks body back and forth	State	Male rocking
Male stridulates any song type	State	Singing
Male turns to present posterior to female	Point	Turning
Male pushes backwards while female mounts	State	Push back
Male drives female out (male aggression)	State	Male chase
Male moves away from contact with female	State	Male withdraw
Female actively moves for at least ½ body length	State	Fem mov
Female remains immobile for at least 10 s	State	Fem pause
Female follows male	State	Fem follow
Female contacts male with at least one antenna	Point	Fem ant cont
Female walks up onto male's abdomen	Point	Mount
Female moves away from contact with male	Point	Fem withdraw
Female drives male out (female aggression)	State	Fem chase
Female quickly rocks body back and forth	State	Fem rocking
Female pinches male with mandibles	Point	Fem bite

29 s). Females also mount dominant males later than subordinate ones (112 vs. 66 s).

Calculations of the latencies from the onset of antennal contact to the mounting response (**Figure 4**) revealed significant differences between the males with different fighting ability when conducting Mann–Whitney *U*-tests ($p < 0.03$), but not significant differences after the correction for the false discovery rate. The latencies from the onset of male antennal contact to mount were lower in losers (42 s) than winners (89 s). The same was found for the latencies from the onset of female antennal contact to mount (45 s in losers and 89 s in winners).

We found few correlations between the latencies to different courtship elements in males that won fights. The latencies to male and female antennal contacts highly positively correlated (Spearman rank correlation; $r = 0.98$, $p = 0.0000$), and the latency to singing positively correlated with the latencies to pushing back ($r = 0.51$, $p = 0.035$) and female movement ($r = 0.62$, $p = 0.01$). Notably, we did not find any correlations for the latency to rocking in tests with dominant males. In males that lost fights, more correlations between the latencies to different courtship elements were been found. The latency to rocking positively correlated with latencies to singing and turning ($r = 0.86$–0.9, $p < 0.01$). The latency to singing also correlated with latencies to male antennal contact ($r = 0.62$, $p = 0.006$), turning ($r = 0.93$, $p = 0.0000$), pushing back ($r = 0.79$, $p = 0.0000$), following by female ($r = 0.66$, $p = 0.007$), and mount ($r = 0.79$, $p = 0.0000$). All these correlations were only calculated for successful courtships.

The Duration of Courtship Elements

We found the differences in duration of some courtship elements between males with different fighting ability (**Figure 5**), but none of these differences was significant after the correction for the false discovery rate. Fight winners demonstrated longer rocking (7% of all courtship duration), singing (23%) and following of females (8%) than fight losers (2, 14 and 4%, respectively). By contrast, fight winners moved less (5%) than fight losers (11%). Also, females withdrew longer from winning males (8%) than from losing males (4.6%).

We found almost no correlation between the durations of different elements for courtships of fight winners. In successful courtships, two elements only, durations of male rocking and singing, were negatively correlated (Spearman rank correlation; $r = -0.59$, $p = 0.045$). In courtships of fight losers, we found significant positive correlations between the durations of singing and following of females ($r = 0.7$, $p = 0.035$), singing and female movement durations ($r = 0.53$, $p = 0.043$), male movement and female following durations ($r = 0.9$, $p = 0.037$), male and female pause durations ($r = 0.82$, $p = 0.002$). Interestingly, we found a significant negative correlation between the durations of male rocking and mount ($r = -0.83$, $p = 0.01$).

The Songs Produced During Courtship Tests

Almost all males singing in our experiments mated: 17 of 20 singing males that won fights and 18 of 20 singing males that lost fights were successful in courtship. The number of chirps emitted by winners was twice as many as by losers; this difference, however, was not significant (**Table 2**, **Figure 1**). None of the chirp parameters differed between the songs of winners and losers. Ticks, the main element of the courtship song, appeared to differ significantly between the males in dominant frequency, which was higher in dominant than subordinate males. Other parameters of the courtship song were qualitatively but not significantly different between the males. Dominant males tended to produce longer ticks of a shorter period than subordinate males; low-amplitude pulses that alternated with ticks were more prominent in the songs of subordinate than dominant males.

DISCUSSION

Females Mate With Fight Losers Faster Than With Fight Winners

Our results demonstrated that females of *G. bimaculatus* mounted equally often fight winners and fight losers. The latencies from the start of the trial to mount also did not differ in males with different fighting ability. However, the latencies from the start of antennal contact to mount were shorter in males that lost fights. We suggest the latter characteristic to be

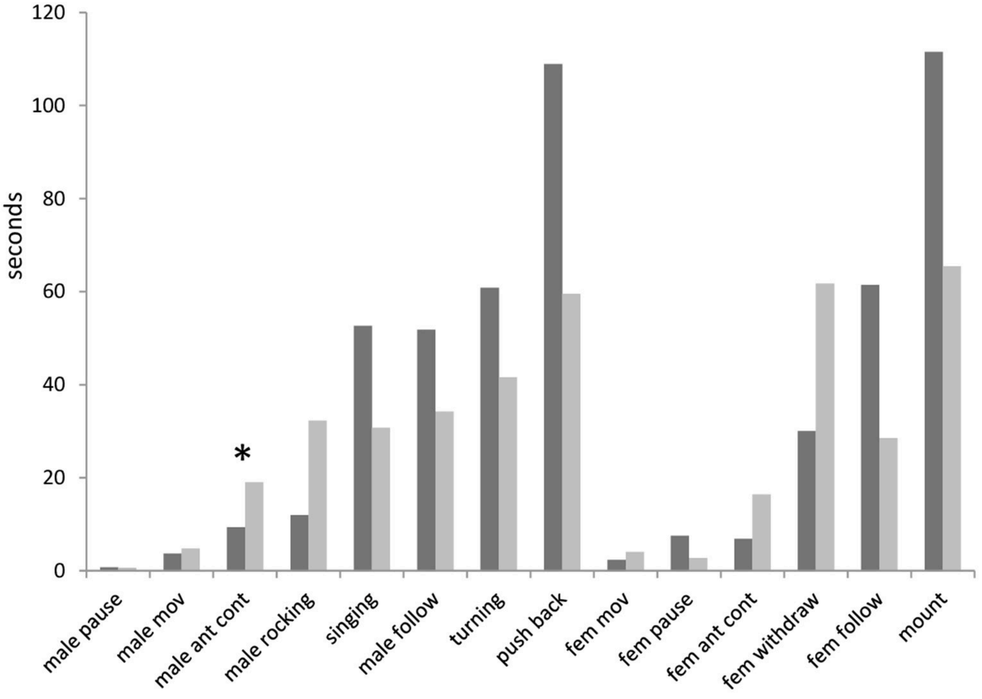

FIGURE 3 | Latencies from the onset of experiment to the start of behavioral elements in courtships of dominant males (black bars) and subordinate males (gray bars) in *Gryllus bimaculatus*. Experiments with successful courtships are only included ($n = 17$ for dominant males and $n = 18$ for subordinate males). Asterisk indicate statistical significance of the differences between dominant and subordinate males (Mann-Whitney *U* Test; $^*p < 0.05$).

the important one since the antennal sensory cues are crucial for mounting responses (Loher and Rence, 1978; Adamo and Hoy, 1994). Moreover, contact chemoreception, rather than mechanoreception was shown to be the key modality for mate recognition (Balakrishnan and Pollack, 1997; Tyler et al., 2015).

Our results mainly support the data of Nelson and Nolen (1997) and Shackleton et al. (2005) obtained on *A. domesticus* and *T. commodus,* who found no difference between winners and losers in mating success in no-choice experiments. The shorter latencies to mating in fight losers demonstrated in our tests may also support the results on pheromone expression in *T. oceanicus* (Thomas and Simmons, 2009). Subordinate males of *T. oceanicus* upregulate the quantity of a number of cuticular hydrocarbons (CHC) that increase male mating success. Conversely, dominant males invest less in their pheromone signals but produce ejaculates of higher quality and sire more offspring than subordinate males. Similar results were shown in *Drosophila melanogaster*: females that became very attractive to males by allocating too many CHC resources produced fewer offspring or offspring of lower quality (Wicker and Jallon, 1995; Howard et al., 2003). In crickets, fighting success was shown to be more strongly linked to an increased investment in overall CHC profile rather than to specific CHC blends (Steiger et al., 2013). At the same time, mating success was tightly linked to both a lower investment in overall CHC expression and the higher relative abundance of specific CHC blends (Simmons et al., 2013; Steiger et al., 2015).

Can High Aggressiveness of Males Interfere With Their Motivation to Court?

Fight winners in our tests started to rock their body earlier and demonstrated more frequent and longer rocking than fight losers. The function of rocking, or juddering, is controversial. Rocking is usually suggested to be a component of agonistic display in crickets (Tachon et al., 1999; Bertram et al., 2010). The energetic expense of this display was shown to be of intermediate level, being, however, much higher than during aggressive stridulation (Hack, 1997). Male crickets also rock as a part of their courtship display (Adamo and Hoy, 1994; Vedenina and Pollack, 2012). In different species of arachnids, juddering was shown to signal male quality (Kotiaho, 2000), stimulate females to mate (Briceño and Bonilla, 2009), or serve multiple signaling functions (Gibson and Uetz, 2008). In our experiments, we found a negative correlation between rocking and singing durations in fight winners, but a positive correlation between rocking latency and latencies to singing and turning (that is usually performed by the male to singing the courtship song) in fight losers. We suggest that fight winners demonstrated rocking as a part of agonistic display, whereas fight losers rocked in the context of courtship display. Thus, rocking in *G. bimaculatus* can also be regarded as conveying multiple messages.

Fight winners had a tendency to start singing, follow females, turn and push back later than fight losers. Conceivably the high level of aggressiveness that was retained in winners prevented them from starting a “normal” courtship display. Because of the

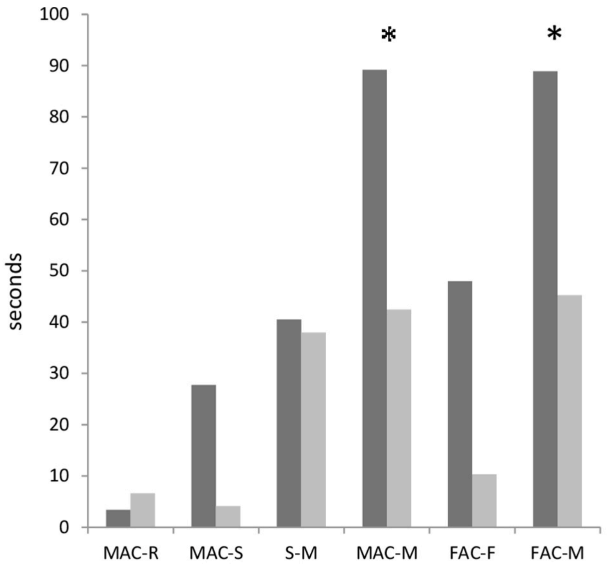

FIGURE 4 | Latencies (median values) from the onset of one to onset of another elements in courtships of dominant males (black bars) and subordinate males (gray bars) in *Gryllus bimaculatus*. Experiments with successful courtships are only included ($n = 17$ for dominant males and $n = 18$ for subordinate males). MAC-R: male antennal contact to rocking; MAC-S: male antennal contact to singing; S-M: singing to mount; FAC-F: female antennal contact to following; FAC-M: female antennal contact to mount. Asterisks indicates statistical significance of the differences between dominant and subordinate males (Mann–Whitney *U*-Test; $^*p < 0.05$).

methods used in our tests, the level of the winner aggressiveness was experimentally set too high. Winners used in the courtship tests won fights in two rounds. We allowed a male to compete against another male with the same recent fight history, since success in previous fights increases the likelihood of victory in subsequent fights in crickets (Khazraïe and Campan, 1999; Savage et al., 2005). In our tests, the second round of fight was usually much more severe than the first round of fight (**Video Clip 1**). To test whether the high level of aggressiveness could interfere with motivation to court, it would be worthwhile to increase the number of fight rounds and study the latencies to singing and other courtship elements after several rounds.

In the wild, males of *G. bimaculatus* tend to find shelters from which they call to attract receptive females (Alexander, 1961; Simmons, 1986). A calling song, however, attracts not only females but also other males; thus, several successive fights with different males could easily happen in nature. If increased aggressiveness would correlate with increasing latency to court females, as could be expected from our tests, this might be maladaptive. Females, however, were more likely to mate with shelter residents: shelters seemed to benefit males by providing protection since calling may attract both parasitoids and predators (Cade, 1975; Simmons, 1986; Robert et al., 1992; Wagner, 1996). Presumably, such a preference of shelter residents allowed a relaxation of selection pressure for a quick shift from aggression to courtship behavior in dominant males.

In contrast to the high level of winner aggressiveness, the level of the loser submissiveness was not set experimentally too low in our tests. The second round of fight was usually much less fierce than the first one (**Video Clip 2**). Thus, the level of readiness to court in losers was closer to that of inexperienced male than the level of such readiness in winners. We suggest that this is part of the reason why fight losers tended to demonstrate the shorter latencies to all main courtship elements. In natural habitats, subordinate males have to be capable of quickly shifting from encounters with another male to courting a female. Subordinate males are unlikely to have shelters which could additionally attract females, and selection pressure acting on male behavioral plasticity through female choice could be stronger in subordinate than dominant males.

A Poor Relationship Between Song Parameters and Male Mating Success

The duration of singing was higher in fight winners than in losers. At the same time, the latencies from the start of singing to mount did not differ significantly between the males with different fighting ability. There were no differences in song parameters between winners and losers except for the difference in dominant frequency of ticks. Ticks (high-amplitude pulses) were found to be a crucial component of a successful courtship song (Libersat et al., 1994). Ticks produced by dominant males were of the higher dominant frequency (11.7 kHz) than ticks generated by subordinate males (9.7 kHz). In playback experiments, however, synthesized songs with different carrier frequencies of ticks (varied from 5 to 17 kHz) were as attractive to females as courtship of muted males accompanied by playback of the recorded song (Shestakov and Vedenina, 2015). Thus, the difference in tick dominant frequency between winners and losers was unlikely to influence female preferences but it might reflect differences in body size of males. As it was shown in many animals, both vertebrates and invertebrates, smaller individuals tend to produce higher-frequency calls due to resonant cavities and muscular rate contractions scaling with body size (e.g., Bailey, 1970; Wallschager, 1980; Brown et al., 1996). The lower dominant frequency of ticks shown in fight losers could indicate that they were on average larger than the fight winners. This seems contrary to the results in several studies obtained earlier on different cricket species (Simmons, 1986; Savage et al., 2005; Shackleton et al., 2005), which demonstrated that larger males won more fights. Hofmann and Schildberger (2001), however, found that weight asymmetry was not a very reliable predictor of outcome, duration, or intensity of fights between two males of *G. bimaculatus*. We measured neither weight nor body length, but noticed that lighter males sometimes won fights even when the weight asymmetry was large.

Female crickets prefer courtship songs with a long duration of ticks (Rantala and Kortet, 2003). In our tests, tick duration tended to be higher in the songs of winners, which were definitely not preferred by females. Our results seem to match the data of our previous study, in which increasing the duration of ticks had a crucial effect on female response rate, decreasing female responsiveness (Shestakov and Vedenina, 2015).

The number of chirps emitted by winners was twice as many as that emitted by losers. Despite this difference was non-significant, we suggest that a tendency to produce a higher number of chirps by dominant males in the presence of a female could be also explained by their inability to quickly shift

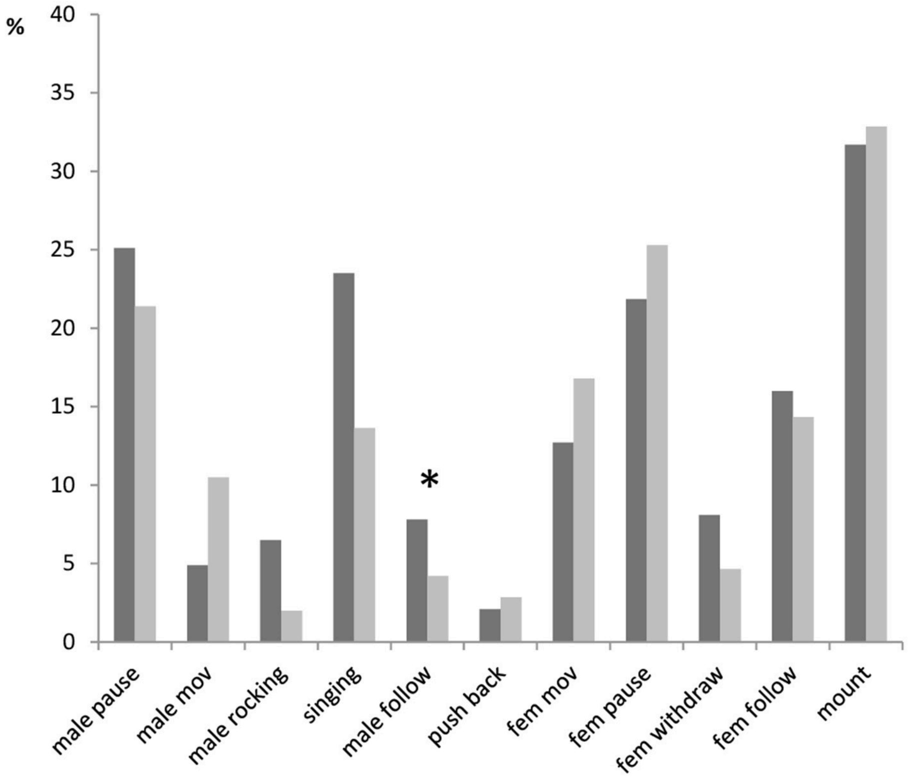

FIGURE 5 | Relative duration (median value) of behavioral elements in courtships of dominant males (black bars) and subordinate males (gray bars) in *Gryllus bimaculatus*. Experiments with successful courtships are only included ($n = 17$ for dominant males and $n = 18$ for subordinate males). Asterisk indicate statistical significance of the differences between dominant and subordinate males (Mann–Whitney *U*-Test; $^*p < 0.05$).

TABLE 2 | The values of the song parameters produced during male-female interactions in *Gryllus bimaculatus* by dominant and subordinate males, and statistics of comparisons between the two male groups.

Parameter	Dominant males	Subordinate males	*T*-test	Mann–Whitney *U*-Test
The number of chirps in relation to ticks, %	37.55 (1.28; 66.19)	15.24 (0; 43.33)	n/a	$U = 170$; $p = 0.14$
Chirp pulse duration, ms	21.99 ± 3.21	20.21 ± 4.02	$t = 1.27$, df = 25, $p = 0.22$	n/a
Chirp pulse period, ms	39.37 ± 5.23	38.36 ± 5.95	$t = 0.46$, df = 25, $p = 0.65$	n/a
Pulse number per chirp	3.59 ± 1.26	3.11 ± 0.54	$t = 1.15$, df = 25, $p = 0.26$	n/a
Chirp dominant frequency, kHz	4.914 ± 0.179	4.934 ± 0.284	$t = -0.23$, df = 25, $p = 0.82$	n/a
Tick duration, ms	11.60 ± 1.93	10.04 ± 3.22	$t = 1.78$, df = 36, $p = 0.08$	n/a
Tick period, ms	346.94 ± 89.27	424.13 ± 314.19	$t = -1.01$, df = 36, $p = 0.32$	n/a
Tick dominant frequency, kHz	11.691 ± 2.041	9.687 ± 2.944	$t = 2.41$, df = 36, $p = 0.02$	n/a
Courtship pulse to tick amplitude	0.057 ± 0.033	0.078 ± 0.073	$t = -1.12$, df = 36, $p = 0.27$	n/a

The median values and lower/upper quartiles are shown for the first parameter; the mean and standard deviation are presented for other parameters.

from aggression to courtship behavior. Because of the relatively low number of pulses per chirp (3-4), we suggest they belong basically to the calling but not to the rivalry song (Zhantiev and Dubrovin, 1974; Rheinlaender et al., 1976). In any case, singing of the calling or rivalry song nearby a female could signal to a female that the male is not ready to copulate. Fight winners thereby appeared to be less ready to mate than fight losers.

Perspectives

Our analysis showed that subordinate males demonstrated shorter latencies from antennal contact to mount as compared with dominant males. This result is not consistent with the traditional view that females should prefer males with increased fighting ability. Using the method of the two-round fights we enhanced the level of aggressiveness in fight winners, thus increasing the difference between winners and losers. As a result, during the male—female interactions, fight winners demonstrated one of the elements of agonistic display, i.e., rocking body, more frequently, and for longer durations than the fight losers, and this behavior seemed to interfere with subsequent courtship. Future research should investigate whether an increase of the fight round number would lead to slower latencies to singing or other courtship elements. It is also possible that the high level of aggressiveness might inhibit the immediate shift to courtship behavior; however, this inhibition may disappear with increasing the delay time from the last fight to courtship. It was shown in *G. bimaculatus* that the aggressive behavior of males was influenced by prior agonistic experience for 6 h and the effect disappeared entirely after 24 h (Khazraïe and Campan, 1999). The submissive behavior was also shown in subordinate males for at least 3 h (Stevenson and Rillich, 2016). Future studies that estimate the influence of aggressiveness on courtship success depending on the delay time after fight could provide insights into our understanding of the physiological mechanisms underlying such behavior.

ETHICS STATEMENT

All animal handling and behavior sampling methods followed the quidelines of the Institutional Animal Ethics Committee and complied with the laws of Russia.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

VV and LS were equally involved in design of the study, conducting the experiments and performing statistical analyses. VV wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00197/full#supplementary-material

Data Sheet 1 | Latencies and durations of courtship elements.

Data Sheet 2 | Experimental protocol of fights and courtships.

Data Sheet 3 | Courtship song measurements.

Video Clip 1 | Second round of fight between previous winners.

Video Clip 2 | Second round of fight between previous losers.

Video Clip 3 | Courtship and copulation.

Video Clip 4 | Rocking the body by fight winner.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor is currently organizing a Research Topic with one of the authors, VV, and confirms the absence of any other collaboration.

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