

Acoustic signalling and its relation to male mating success in sagebrush crickets

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Abstract. Although the role of song in pair formation is well documented in crickets, there are a number of alternative mechanisms by which males are known to acquire mates, including silently searching for females, satellite mating behaviour, random encounters, and the use of alternative signalling modalities. None the less, the assumption that calling is vital to male mating success has never been directly challenged through experimental manipulation of the calling ability of males in a free-living population. The presumed relationship between calling and mating in sagebrush crickets, *Cyphoderris strepitans*, was tested by: (1) experimentally abolishing the calling ability of males in a natural population and (2) video recording nightly calling and mating activity in the laboratory. A lack of calling ability almost entirely extinguished male mating success in the field, suggesting that females rely almost entirely on male song for mate location. The importance of calling to male mating success was further evidenced by video studies: males successful at mating called for significantly longer durations and were more likely than unsuccessful males to be calling when copulations occurred. There was no difference in the mating success of virgin and non-virgin males in triadic interactions, thereby ruling out active mate choice as a proximate cause of the virgin-male mating advantage documented in a previous study. While a female preference of virgin males might be expected on the grounds that virgins have more to offer in the way of a courtship food gift, there was no evidence that females were less willing to mount or complete copulations with non-virgin males.

Crickets and katydids are best known for their conspicuous acoustic signalling behaviour, widely held to be the primary means by which mating pairs are formed (Alexander 1975; Cade 1979). Although the ability of calling males to attract sexually receptive females has been firmly established in numerous bioassays (Weber & Thorson 1989), there are none the less a number of alternative mechanisms by which males may obtain mates, including silently searching for females (Walker 1983; Hissmann 1990), satellite mating behaviour (Cade 1975, 1979), and the use of alternative signalling modalities such as pheromones (Sexton & Hess 1968; Otte & Cade 1976; Paul 1976) and substrate-transmitted vibrations (Morris 1980; Dambach 1989). Indeed, theoretical considerations and empirical work suggest that the use of silent mate-finding tactics may confer higher mating success than acoustic signalling under certain conditions, such as occur in high-density populations (French & Cade 1989) or populations sympatric with acoustically orienting parasitoids

(Cade 1981; Cade & Wyatt 1984) or predators (Sakaluk & Belwood 1984; Sakaluk 1990). None the less, the common assumption that calling is vital to male mating success has never been directly challenged through experimental manipulation of the calling ability of free-living males.

The sagebrush cricket, *Cyphoderris strepitans*, is a member of an ancient insect lineage, the Haglidae, a family believed to be ancestral to the ensiferan Orthoptera (crickets and katydids) and now nearly extinct (Morris & Gwynne 1978; Vickery 1989). *Cyphoderris strepitans* is known only from a few mountainous regions in Wyoming and Colorado, where it occurs primarily in high-altitude sagebrush (*Artemisia* spp.) meadows. In Grand Teton National Park, WY, adults become sexually active in early May, shortly after snowmelt, and remain active for the next 4–6 weeks. Each night of the breeding season, males emerge from the litter shortly after sunset, ascend sage bushes onto calling perches, and commence calling, which continues up until about midnight when males return to the

litter. Copulation occurs in the sagebrush or on the ground, and is initiated when a receptive female climbs onto the dorsum of a male, at which time he attempts to transfer a spermatophore. During copulation, the female feeds on the male's fleshy metathoracic wings and ingests any haemolymph oozing from the wounds she inflicts (Dodson et al. 1983). The wounds that result from wing feeding provide a convenient, permanent record of a male's mating status; through visual inspection of the metathoracic wings, it is possible to determine whether field-collected males are virgin or have experienced at least one mating opportunity prior to their capture (Dodson et al. 1983; Morris et al. 1989).

Virgin male sagebrush crickets obtain significantly more matings than non-virgin males, taking into account their relative abundance in the population (Morris et al. 1989). One explanation for the virgin-male mating advantage is that mated males are unable to sustain calling at pre-mating levels because of the energy lost at copulation. In support of this hypothesis, electronic assays of male signalling behaviour (Kidder & Sakaluk 1989) have shown that virgin males call for significantly longer durations than recently mated males (Sakaluk et al. 1987; Sakaluk & Snedden 1990). However, two observations render tenuous the presumed relationship between calling and male mating success: (1) virgin females tested for phonotaxis in a laboratory bioassay failed to exhibit any significant attraction to speakers broadcasting male song (Morris et al. 1989; however, one of us (W.A.S.) has recently obtained results that support a mate-attraction role to calling, see Discussion) and (2) time-lapse video studies have revealed that calling need not always precede successful mating (see below). Moreover, there are a number of plausible alternative mechanisms by which pair formation in sagebrush crickets could occur: (1) females can recognize airborne odours of males in laboratory tests, hence raising the possibility of pheromonally mediated mate attraction (unpublished data); (2) silent males are frequently found in bushes containing singing males (personal observation), thus raising the possibility of satellite mate-securing tactics; and (3) stridulating males almost invariably cause the foliage on which they are perched to quiver; although such substrate-transmitted vibrations may constitute little more than an incidental effect, it is also possible that they serve a mate-attraction function (Bell 1980a). Here we test

the presumed relationship between calling and male mating success by: (1) experimentally abolishing the calling ability of male *C. strepitans* in a naturally occurring population and (2) video recording nightly calling and mating activity of *C. strepitans* in the laboratory.

METHODS

Field Study

The field study was conducted from 17 May to 3 June, 1990, near the Snake River at Deadman's Bar in Grand Teton National Park, Wyoming, U.S.A. Four corners of a rectangular study plot (90 × 60 m) were staked out in relatively homogeneous, sagebrush-meadow habitat on a bench of the river's flood plain. During 4 nights of sampling early in the breeding season (17, 18, 21 and 22 May), we attempted to capture and mark all of the virgin males present in the study plot. Perching locations of males were found by orienting to the acoustic signals produced by individual males and then searching the sagebrush with the aid of a headlamp. Non-virgin males (as evidenced by wing wounding) were released at their point of capture immediately after their mating status had been ascertained. Each virgin male was placed in a numbered vial, corresponding to a numbered surveyor's flag placed at the capture location, and transported to a processing table located at the study site. Following experimental processing (see below), males were released at their capture sites, thereby preserving the original spatial distribution of males within the study plot.

Captured males were sequentially assigned, in order of their capture, to one of three experimental groups: (1) experimentally muted, (2) sham-operated, and (3) unmanipulated. Sequential assignment of males ensured that subsequent mating opportunities were equivalent across treatments and that locations of experimental males were drawn at random. Experimental males were rendered mute through surgical removal of the file on each forewing, structures essential to the production of sound. Removal of both files was required because males are capable of 'switch-wing' singing, in which one or the other file is employed during stridulation (Morris & Gwynne 1978). Sham-operated males also had a portion of each forewing removed, equal in area to that of the file (approximately 4 mm²), but distal to the sound-producing

structures. Unmanipulated males were physically handled, but their forewings were left intact. Males in each treatment were marked with a different colour fluorescent paint applied to the pronotum. We marked and released a total of 70 virgin males (24 mute, 23 sham and 23 unmanipulated).

Four days after the majority of the virgin male population had been marked, the study plot was systematically searched at night using portable UV lanterns. When illuminated by UV light, males' painted pronota glowed brightly and marked males were easily detected. The field was searched on 4 nights (26, 27, 28 May and 3 June), and recaptured males were examined for evidence of mating activity (wing wounding). Males recaptured as 'virgins' (males with intact wings) or 'non-virgins' (wounded males) were distinctively marked as such by marking either one (virgin) or both metathoracic femora (non-virgin) with nail polish, thereby ensuring that males were only counted once in the final determination of mating frequencies. Mating frequencies determined in this manner must be considered maximum estimates, since females are able to feed on males' wings opportunistically, dismounting males before spermatophore transfer has occurred (Dodson et al. 1983; present study). In contrast, we have never observed successful spermatophore transfer occur without wing feeding, such that males captured with intact wings undoubtedly were virgin.

Time-lapse Video Study

To determine how calling influences male mating success after contact with females has been established, a companion study involving time-lapse video recordings of triadic mating interactions was conducted over two breeding seasons (1989 and 1990). Male and female *C. strepitans* were captured at a site near, but disjunct from the field study plot. Because females are mute, they were found largely through chance encounters. Crickets were transported to the University of Wyoming-National Park Service Research Center, approximately 30 km from the field site, where they were housed in plastic vials provisioned every other day with a slice of apple.

Triadic mating interactions were staged in a Plexiglas arena (13.8 × 11.2 × 4.5 cm) containing a dead twig as a calling perch; the narrow aspect of the arena was dictated by the depth of field needed to adequately resolve spermatophore transfer.

Interactions were recorded using a time-lapse video-recorder (Panasonic AG-6050) and a camera equipped with a macro lens (Panasonic WV-3250/8AF). Each triad consisted of a virgin male, a non-virgin male and a female of unknown mating status. The confinement of three individuals in a small space undoubtedly introduced an element of artificiality, since neither males nor females were free to escape interactions; however, successful copulation generally requires voluntary mounting of the male by the female, so that this design enabled some degree of female choice even under unusually confining circumstances. Additionally, the close proximity of rival males, though not typical of normal male spacing, is occasionally observed in the field (personal observation).

Each night of the study, a single triad was established at approximately 2000 hours at which time recording commenced. All crickets were weighed prior to introduction into the arena. The video-recorder was set to the 12-h recording option; on this time mode, a single frame was recorded every 0.1 s. In total, we videotaped 43 triadic interactions (20 in 1989 and 23 in 1990) of which 30 resulted in matings (15 matings each in 1989 and 1990). When a mating occurred, the participants involved in the interaction were never used again, thereby avoiding pseudo-replication of data.

Upon review of videotape recordings of mating interactions, we recorded: (1) the number of mating opportunities for each male (as indicated by wing feeding behaviour of the female and/or clamping of the female's abdomen by the male's abdominal pinching organ; see Morris 1979); (2) the frequency and duration of copulations; and (3) the time spent calling by each male (measured as the total number of minutes in which a male called at least once). Unlike many other cricket species (Alexander 1962), male *C. strepitans* produce only one song type, thereby simplifying the measurement of calling times.

RESULTS

Field Study

Thirty-seven marked males (54%) were recaptured at least once, and recapture frequencies were homogeneous across treatments ($\chi^2 = 0.09$, $P > 0.05$). Of the sham-operated and unmanipulated males that were recaptured, all but one mated (24 of 25), whereas only two of 13 muted males

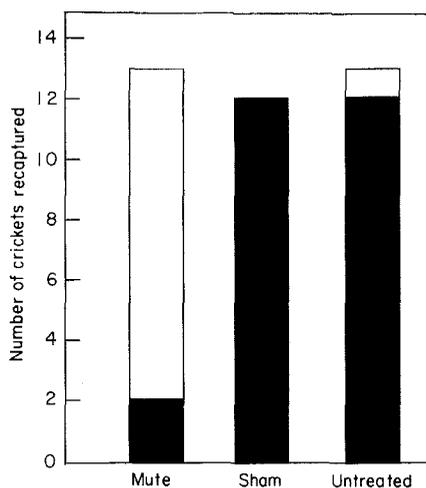


Figure 1. Mating success of experimentally muted male *C. strepitans* compared to sham-operated and untreated control males. □: virgin; ■: mated.

mated over the re-sampling interval (Fig. 1). Contingency table analysis revealed that these differences were highly significant ($\chi^2 = 25.89$, $P < 0.001$). Pairwise comparisons of treatments (Zar 1984) showed that the mating frequency of muted males was significantly lower than that of sham-control ($\chi^2 = 18.13$, $P < 0.001$) and unmanipulated males ($\chi^2 = 15.48$, $P < 0.001$), whereas there was no difference in the mating frequency of sham-control and unmanipulated males ($\chi^2 = 0.96$, $P > 0.05$).

The above analysis incorporates those instances in which the mating status of a male changed over successive recaptures. To provide a more conservative test of the null hypothesis, the data were re-analysed using first-time recaptures only. Of those marked males recaptured for the first time, one of 13 muted males, 10 of 12 sham-control males, and nine of 13 unmanipulated males had mated. As in the previous analysis, differences in male mating frequency across treatments were statistically significant ($\chi^2 = 16.50$, $P < 0.001$), and the results of pairwise comparisons remained unchanged.

Time-lapse Video Study

Preliminary analyses revealed that the year in which triads were video-recorded had no effect on any of the reproductive parameters measured. Consequently, data from 1989 and 1990 were pooled in subsequent analyses. Means are given \pm SE.

Table 1. Average pre-copulatory calling durations of male *C. strepitans* classified with respect to: (1) success at mating and (2) previous mating status

	N	Calling duration (min)		
		Mean	SE	Range
Success at mating				
Successful	30	170.4*	25.5	0–447
Unsuccessful	30	127.5	23.1	3–559
Previous mating status				
Virgin	30	165.8†	25.0	6–433
Non-Virgin	30	132.13	23.9	0–559

*Significantly different from unsuccessful males at $P < 0.05$.

†Not significantly different from non-virgin males.

In the 30 interactions leading to copulation, the male to first mate with the female was designated the 'successful' male while the other male was designated 'unsuccessful'. Since the behaviour of one male in a triad may be contingent on the behaviour of the other, behavioural attributes of successful and unsuccessful males were compared using paired-sample *t*-tests, except when differences were non-normally distributed in which case the Wilcoxon paired-sample test was used. Successful males experienced significantly more mating opportunities prior to copulation than did unsuccessful males (2.13 ± 0.39 versus 0.77 ± 0.30 , Wilcoxon paired-sample test, $P < 0.0005$). Initial copulations occurred, on average, 317.8 ± 33.8 min after the introduction of experimental individuals (range = 24–643 min) and lasted, on average, 272.3 ± 19.2 s (range = 120–595 s). In eight of the 30 interactions, two matings occurred during the recording interval; four of the second matings involved the successful male and four involved the unsuccessful male. There was no significant difference (paired *t*-test, $t = 0.11$, $P > 0.05$) in the mean mass of successful (776.2 ± 15.4 mg) and unsuccessful males (774.1 ± 20.0 mg).

Pre-copulatory calling durations of successful and unsuccessful males are shown in Table 1. The absolute difference in calling durations of successful and unsuccessful males covaried with the time at which the mating occurred ($r = 0.66$, $P < 0.0002$). This covariance was eliminated by transforming calling durations to their \log_{10} values ($r = 0.10$, $P > 0.05$), thereby allowing direct comparison of the calling times of successful and unsuccessful

males. The analysis revealed that successful males called for a relatively longer duration prior to copulation than did unsuccessful males (one-tailed paired t -test, $t=1.76$, $P<0.05$). Moreover, successful males were the last to call prior to copulation more often than expected on the basis of chance (16 of 20 interactions, $\chi^2_{\text{Yates}}=6.05$, $P<0.025$; in the remaining 10 interactions, both males were calling immediately prior to copulation). Calling did not always immediately precede a copulation. In four interactions, both males had ceased calling 2–47 min before copulation and on one occasion, the successful male did not call at all prior to mating, but was standing immediately adjacent to a calling rival at the time the female mounted him.

Sixteen of the 30 successful males mated as virgins, and 14 mated as non-virgins ($\chi^2_{\text{Yates}}=0.03$, $P>0.05$). Mean calling durations of virgin males were longer than those of non-virgins (Table I), but the difference in log-transformed calling times was not significant (one-tailed, paired t -test, $t=1.65$, $P=0.055$). There was no significant difference in the number of mating opportunities experienced by virgin and non-virgins prior to copulation (1.67 ± 0.40 versus 1.23 ± 0.33 , $P>0.05$).

DISCUSSION

The results of our field experiment demonstrate that acoustic signalling is vital to the mating success of free-living male *C. strepitans*. The most parsimonious explanation for this result is that females depend primarily on male song for mate location, such that males unable to sing mate only as a consequence of fortuitous encounters. The results of phonotaxis experiments, however, provide only equivocal support to this hypothesis. Morris et al. (1989) obtained no evidence of female phonotaxis in a laboratory bioassay, despite the fact that females were virgin and should have been amply motivated to respond to male song. In contrast, Snedden (unpublished data) recently obtained evidence of a significant phonotactic response of females tested in an outdoor enclosure. These apparently conflicting results suggest that female responsiveness may be facultative or at least temporally variable. Alternatively, efforts to demonstrate female phonotaxis in the laboratory may have failed because elicitation of a female response requires a period of auditory stimulation that exceeds the half-hour playback interval employed in the laboratory bioassay.

The mating success of experimentally muted males would be further reduced if the acoustic signalling of males functioned not only to attract females, but also as a territorial signal to other males mediating inter-male aggression. Hence, the decline in mating success of muted males could have come as much from an inability to acoustically dissuade intruding rivals as an inability to attract females. For this to be a plausible alternative, however, males would have to show evidence of territorial behaviour, defending an area from which other males were actively excluded. In contrast to this prediction, we have frequently observed more than one male (usually two) calling from within the same sagebrush and occasionally, side-by-side at the base of the same bush (personal observation). Moreover, male *C. strepitans* do not appear to exhibit any of the aggressive behaviour patterns typical of territorial Orthoptera (Morris 1971; Cade 1979); in approximately 1000 h of video recording, we have never observed any overt aggression between males, nor has such behaviour ever been observed in the field. Males do, however, appear to hear and react acoustically to the signals of other males: silent males can easily be induced to call through playback of conspecific song, at least in the laboratory (personal observation). It is possible, therefore, that males use calling song to actively avoid rivals and thus maintain non-overlapping, but undefended broadcast areas (Bailey & Thiele 1983).

The importance of signalling ability to male mating success is further demonstrated by the results of time-lapse video studies; males successful at mating called for significantly longer durations and were more likely than unsuccessful males to be calling when copulations were initiated. None the less, several matings occurred when neither male was calling in the recording chamber. This suggests that although acoustic signalling may influence a female's decision to mate even after physical contact with a potential mate has been established, calling is not a prerequisite for successful mating.

Perhaps surprisingly, there was no difference in the mating success of virgin and non-virgin males in triadic interactions. This appears to rule out 'active' mate choice (sensu Parker 1982) as a proximate cause of the virgin-male mating advantage observed in a previous study (Morris et al. 1989). While a female preference of virgin males might be expected on the grounds that virgins have more wing material to offer, there was no evidence that

females were less willing to mount or complete copulations with non-virgin males. Moreover, the ability of females to feed opportunistically on males without receiving any sperm (see also Bell 1980b; Sakaluk 1987), might negate any advantage to pre-copulatory mate choice. Instead, we suggest that the virgin-male mating advantage occurs primarily as a consequence of the greater ability of virgins to attract mates: nightly calling durations of virgin males are generally longer than those of non-virgins (Sakaluk et al. 1987; Sakaluk & Snedden 1990), such that virgins are more likely to be detected and located by sexually responsive females. In the present study, virgin males called more prior to copulations than did non-virgins, but the difference was not quite significant. It may be that the non-virgin males used in this study had sufficient time to replenish bodily resources lost at mating; previous studies (Sakaluk et al. 1987; Sakaluk & Snedden 1990) used 'freshly wounded' males that were captured shortly after mating.

The experimental alteration of male song or signalling ability is a powerful technique for assessing the influence of song on male mating success in natural situations, but one that has been rarely used (Searcy & Andersson 1986; Kroodsma & Byers 1991). Such experiments need not be restricted to examining the effects of the presence or absence of song, as was the case here. In crickets, for example, song structure of free-living males could be systematically altered through removal of individual teeth on the file, loading of tegminal song resonators or ablation of specific portions of the forewings (Bennet-Clark 1989). While far more sophisticated alterations in song content are possible using artificially generated acoustic models such as are commonly employed in standard laboratory bioassays (Weber & Thorson 1989), the evidence produced from such experiments can only establish correlations between specific song parameters and female responsiveness. A more complete understanding of the way in which sexual selection shapes the signalling behaviour of acoustic species requires that correlations established in the laboratory be augmented with evidence obtained through direct manipulation of male song in free-living animals (Searcy & Andersson 1986; Huber 1990; Wade & Kalisz 1990; Kroodsma & Byers 1991).

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