

VIRGIN-MALE MATING ADVANTAGE IN SAGEBRUSH CRICKETS: DIFFERENTIAL MALE COMPETITIVENESS OR NON-INDEPENDENT FEMALE MATE CHOICE?

by

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Summary

Female sagebrush crickets (*Cyphoderris strepitans*) feed on males' fleshy hind wings during copulation and ingest haemolymph oozing from the wounds they inflict. The wounds are not fatal and usually only a portion of the hind wings are eaten at any one mating, so that mated males are not precluded from mating again. However, based on their relative abundance in the population, virgin males have a higher mating success than non-virgin males. One explanation for this virgin-male mating advantage is that non-virgin males, having been depleted of their energy reserves through the wing-feeding behaviour of their mates, are unable to sustain the same level of acoustic signalling they produce prior to copulation. Previous assays of male signalling behaviour have provided some support to this hypothesis. However, an alternative explanation is that females actively seek out virgin males as mates because of the greater material resources they offer. If the acoustic structure of males' signals were systematically altered by the loss of hind-wing material underlying the sound-producing tegmina, females could potentially discriminate against mated males through reduced phonotaxis to their calls. We tested this hypothesis by experimentally removing one hind wing from virgin males, thereby simulating the non-virgin condition without the attendant costs of copulation. We

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compared the mating success of these 'asymmetrical' males with that of sham-operated virgin males when competing under natural conditions. In a companion laboratory study, we used time-lapse video recording to examine the possibility that female preferences are exerted only after pair formation has occurred. There was no significant difference in male mating success across treatments in either study. We conclude, therefore, that the virgin-male mating advantage does not stem from an acoustically mediated, non-independent female mating preference, but rather, from the differential competitiveness of males.

Introduction

Non-independent mate choice occurs when the probability that a female selects a particular male as a mate is influenced by whether other females have selected that male (Pruett-Jones, 1992). The previous choice of a male as a mating partner may either increase or decrease his attractiveness to other females. Although there is considerable evidence for the former (*e.g.* mate copying: Knapp & Sargent, 1989; Gibson *et al.*, 1991; Dugatkin, 1992), there is little direct evidence that previous selection as a mate lowers a male's future mating success. Non-independent mate choice can affect the variance in male mating success, and thereby greatly influence the opportunity for sexual selection (Wade & Pruett-Jones, 1990).

The sagebrush cricket, *Cyphoderris strepitans*, is one of only five extant species belonging to an obscure orthopteran family, the Haglidae, and occurs exclusively in mountainous areas of the western United States, where it is found primarily in high-altitude sagebrush meadow habitat (Morris & Gwynne, 1978). Adults become sexually active in late spring, shortly after the snow melts, and remain active for the next 4-6 weeks. The acoustic signals produced by males function to attract females (Snedden & Irazuzta, 1994), and appear to be the principal means of pair formation (Snedden & Sakaluk, 1992; Sakaluk *et al.*, 1995b). Copulation 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 consumes the ends of the male's fleshy hind wings and haemolymph leaking from the wounds she inflicts (Dodson *et al.*, 1983; Eggert & Sakaluk, 1994; Sakaluk *et al.*, 1995a). The scalloped ends of the hind wings are left discoloured as a result of the female's feeding, and as the wounds dry, they become quite hardened. Males that succeed in obtaining additional matings lose successively more of their hind-wing material, such that by the end of the

breeding season, males still alive often are left completely without hind wings.

Sagebrush crickets appears to be especially well suited to an empirical examination of non-independent mate choice. A previous study involving the mark-recapture of a large number of males showed that once a male had mated, his probability of obtaining an additional copulation was reduced relative to that of a virgin male securing his first mating (Morris *et al.*, 1989). This 'virgin-male mating advantage' has since been replicated in field studies designed to measure lifetime male mating success over two consecutive breeding seasons (Snedden, 1995, 1996). One explanation for the virgin-male mating advantage is that non-virgin males, having lost a substantial portion of their energy reserves through sexual cannibalism by females and the transfer of a large spermatophore, may be unable to sustain the costly acoustical signalling activity required to attract additional females. In support of this 'differential male competitiveness' hypothesis, electronic assays of male signalling behaviour have shown that virgin male *C. strepitans* call for significantly longer durations than recently mated males (Sakaluk *et al.*, 1987; Sakaluk & Snedden, 1990).

An alternative hypothesis to account for the virgin-male mating advantage is that females discriminate against non-virgin males because these males, having lost about 10% of their body mass at copulation (Dodson *et al.*, 1983; Sakaluk & Snedden, 1990), have fewer material rewards to offer. If the acoustic structure of males' signals were systematically altered by the loss of hind-wing material underlying the sound-producing tegmina, then females could potentially discriminate against mated males through reduced phonotaxis to their calls (Morris *et al.*, 1989). Both theoretical and empirical work have shown that the air space between the wings and body of a stridulating cricket acts as an acoustic resonator that serves in both the filtering and amplification of the sound signal (Stephen & Hartley, 1995). Indeed, acoustic analyses of digitized calls of virgin, non-virgin, and experimentally de-winged male *C. strepitans*, indicate possible differences in the amplitude, and perhaps, spectral components of the signals (Snedden & Greenfield, 1995; M.G. Ritchie, pers. comm.). Hence, an acoustically mediated, female mating preference could contribute to the differential mating success of virgin and non-virgin males as much or more than any difference in signalling duration, but this possibility has not previously been tested.

One difficulty in distinguishing between the 'differential male competitiveness' and 'non-independent female mate choice' hypotheses as they apply to the virgin male mating advantage, is that non-virgin males may be disadvantaged in both contexts. In the present study, we circumvented this problem by altering the hind wings of virgin males in a way that mimicked the wing loss of non-virgin males, without the attendant costs of copulation. If loss of hind wing material systematically alters the structure of males' signals, and females rely on these differences to select virgin males, then the 'non-independent mate choice' hypothesis predicts that experimental removal of hind wing material from virgin males should lead to a reduction in their mating success relative to unmanipulated virgin males.

Methods

Mark-recapture study

A mark-recapture study was conducted from May 23 to June 18, 1997 in Grand Teton National Park, Wyoming. A rectangular study plot approximately 120 × 180 m was established in sagebrush meadow habitat adjacent to the Snake River at Deadman's Bar. During the early portion of the breeding season, we attempted to capture and mark all of the virgin males present in the study plot. Males were found at night by orienting to their calls and using head lamps to determine their exact location within a sagebrush bush. The mating status of males was determined by examining their hind wings for the wounds inflicted by females; only virgin males, as evidenced by intact wings, were used in experimental treatments. Each virgin male was placed in a collecting vial, numbered to correspond with a surveyor's flag placed at the capture location, and transported to University of Wyoming-National Park Service Research Station, approximately 30 km away, for processing.

Captured males were randomly assigned to either of two treatments in which the amount of hind-wing material retained by males was experimentally manipulated. In one treatment, we surgically removed one hind wing from the male by severing it at its point of insertion using fine dissecting scissors (asymmetrical males). This treatment was designed to mimic the loss of wing material that occurs at mating. Hind wing removal resulted in little bleeding owing to the rapid coagulation of haemolymph, in contrast to normal matings during which feeding by females promotes a steady flow of haemolymph. In a second treatment, small lesions were made in both hind wings of the male, but the hind wings were otherwise left intact (intact males). This operation controls for any detrimental effects of handling and/or haemolymph loss in males of the first treatment. Each male was marked individually with a numbered plastic tag secured to the pronotum with cyanoacrylic glue. Fluorescent paint was applied to the pronotum around the numbered tag, and to the femora of each individual. Portable ultraviolet lanterns, the illumination of which causes the paint to fluoresce, subsequently were used to facilitate cricket recapture. The following evening at sunset, marked males were returned to their respective points of capture. We marked and released a total of 106 males (53 non-virgin mimics, 53 sham-control) over the course of six nights (May 22-24, May 27, 28, June 2).

After experimental males were released, males were recaptured and examined for evidence of mating activity regularly over the course of the breeding season, usually every second night, weather permitting. The number of males recaptured on any given night varied from 1 to 44 ($N = 18$ nights). Mating was inferred by loss of hind wing material in both treatments. Wing wounds were classified as 'fresh' (visibly wet wounds with no discoloration indicating that the male had mated on the night of capture) or 'old' (dry, darkened wounds indicating that the male had mated on a night previous to the night of capture).

Time-lapse video study

If female mating preferences were predicated on the amount of wing material males had to offer, such preferences could be exercised either in the context of long-distance mate attraction or through discrimination that takes place after pair formation. While the field study adequately addresses the former possibility, the rarity with which naturally occurring copulations are detected in the field precludes any assessment of female choice at mating as it occurs in the natural situation. Accordingly, we conducted a laboratory study in which we employed time-lapse video photography to record the mating behaviour of males whose hind wings were experimentally altered as in the field study. Virgin males and females of unknown mating status were collected at two sites within the park (Deadman's Bar and Pacific Creek) and at an additional site in Bridger-Teton National Forest. Captured crickets were transported back to the research center and maintained according to standard procedures (Snedden & Sakaluk, 1992; Eggert & Sakaluk, 1994). Males were assigned to either of the two experimental treatments, (1) asymmetrical males (non-virgin mimics) or (2) intact males (sham-control). Males were treated the morning after their capture and used in mating trials the second evening following their capture, thereby allowing them sufficient time to recover from their operations.

Each night of the study, one or two males from each of the two treatments were paired with females at about 1900 h, and their mating activity monitored over a 12-hour period using time-lapse video photography. Nighttime recording was facilitated by the illumination provided by a 25-W red light bulb. Experimental pairs were confined in a Plexiglas viewing chamber ($17 \times 12 \times 3.5$ cm), divided into four equal compartments to prevent contact between crickets of different pairs, each of which contained a short stick to serve as a calling perch. Upon review of video recordings, we determined: (1) the time spent calling by each male during the trial, measured as the number of 5-min intervals within which stridulation occurred (one-zero sampling; Altmann, 1974), (2) the number of times each male was mounted by the female, and (3) the number of matings (mounts resulting in successful transfer of the spermatophore). Matings were easily scored, as the spermatophore remains attached outside the female's body after copulation and is readily visible in video recordings. A total of 22 pairs, 11 in each treatment, were recorded. Experimental individuals were used in only one trial and released at their capture location the next night.

Data were analyzed using SYSTAT software for desktop computers (Wilkinson *et al.*, 1996) or in the case of failure-time analyses, the LIFETEST procedure of the Statistical Analysis System for personal computers (SAS Institute, 1988).

Results

Mark-recapture study

The majority of marked males were recaptured at least once (90/106), 79.2% of asymmetrical males (42/53) and 90.6% of intact males (48/53). The difference between treatments in the proportion of males recaptured was not statistically significant (Fisher exact test, $p = 0.17$), although it must be acknowledged that the power of the test to detect a difference of this magnitude is rather modest (power = 0.63, as determined by the procedure outlined by Zar (1996, p. 555-556). The proportion of males that mated was not significantly different across experimental treatments (Fisher exact test, $p = 0.82$); in fact, a slightly greater proportion of asymmetrical than intact males mated (Fig. 1). We employed failure time analysis to compare treatments with respect to the time taken by males to obtain copulations. Failure-time analysis accommodates censored data, observations in which an event such as mating may not have occurred by the end of the study, as was the case here. Omission of such data, as is frequently done in behavioural studies, may lead to a serious bias in comparisons across treatments (Fox, 1993). Failure-time analysis showed no significant difference between treatments in the time taken by males to obtain their initial copulations (Fig. 2; Log-Rank test, $X^2 = 0.38$, $p = 0.54$).

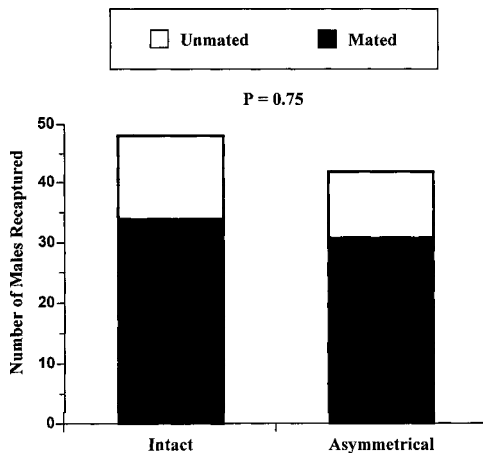


Fig. 1. Mating success of males with intact hind wings (sham control) and asymmetrical males (one hind wing was removed) observed in the field. There was no significant difference in mating success across treatments (Fisher exact test, $p = 0.82$).

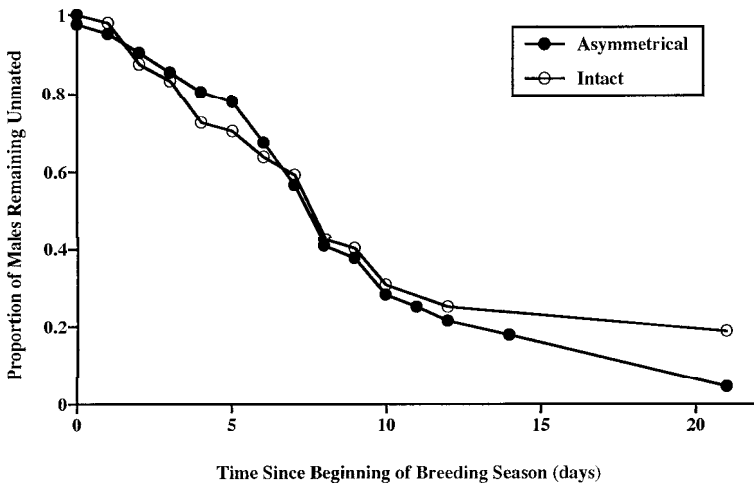


Fig. 2. Survival distribution function of the time to mating for asymmetrical and intact males observed in the field. The proportion of males remaining unmated is shown as a decreasing function of time. There was no significant difference in mating trajectories across treatments ($X^2 = 0.38$, $p = 0.54$).

TABLE 1. Median calling time and mating success of asymmetrical (one hind wing removed) and intact males (sham control) observed in the laboratory

	Asymmetrical ($N = 11$)	Intact ($N = 11$)	p
Time to first mounting	139 min (59-563)	106 min (38-468)	0.49
Time to first mating	167 min (63-720 ^a)	466 min (42-720 ^a)	0.34
No. mounts prior to mating	1 ^b (1-8)	3 ^b (1-6)	0.40
No. matings	1 (0-2)	1 (0-2)	1.00
Total calling time	275 min ^c (115-515)	380 min ^c (205-460)	0.61
Prop. of time spent calling before mating	0.50 ^b (0.32-0.97)	0.74 ^b (0.25-1.00)	0.49

Ranges are shown in parentheses. Probabilities are based on Mann-Whitney U -tests.

^a Did not mate.

^b Does not include 3 males that did not mate.

^c Based on one-zero sampling at 5-min intervals.

Time-lapse video study

Male mating success was the same in both treatments (Table 1), with 8/11 males mating in each instance (73%). Four males mated twice in the same

evening, two intact and two asymmetrical males. There were no significant differences between the two treatments in the time at which males were first mounted (Mann Whitney U -test, $U = 71$, $p = 0.49$), first mated ($U = 23$, $p = 0.35$), total calling time ($U = 41$, $p = 0.61$), or the proportion of time that males spent calling prior to mating ($U = 25.5$, $p = 0.49$).

Discussion

There was no significant difference in the mating success of asymmetrical males and intact males when competing under natural conditions. This result suggests that males lacking hind wing material are not compromised in their ability to attract females. We conclude, therefore, that the virgin-male mating advantage is not mediated by an acoustically-based female mating preference. In addition, there was no difference in the mating success of males of the two treatments when confined individually with females in the laboratory. These results corroborate the results of the field study, and suggest that even after pair formation, any alteration in males' acoustic signals stemming from the loss of hind wing material does not diminish male attractiveness. This in turn suggests that the virgin-male mating advantage documented in previous studies (Morris *et al.*, 1989; Snedden, 1995, 1996), can be attributed primarily to a reduction in the attraction of females to non-virgin males unable to sustain the same level of calling as occurs prior to copulation (Sakaluk *et al.*, 1987; Sakaluk & Snedden, 1990).

It could be argued that the removal of one hind wing does not accurately mimic the loss of hind wing material that occurs during normal mating and so does not result in the alteration of song parameters that might permit female discrimination. However, mated males bearing one intact hind wing and with the other almost entirely consumed, have been observed in natural populations, albeit rarely (pers. obs.). Moreover, the loss of material from one or both hind wings at a single copulation typically is far less than the amount of material lost through the removal of an entire hind wing (Morris *et al.*, 1989; pers. obs.); hence, our experimental manipulation actually exaggerates the amount of material normally lost through wing feeding, which should, if anything, lead to even greater distortion of sound signals. The extent to which wing feeding actually alters acoustic properties of males' songs appears to be moot, however, because females apparently do not act

on any variation in song quality induced by the loss of wing material, even if they have the ability to perceive such differences. Any such differences would need to be fairly large to be discernible to females, whose ears are poorly tuned to the carrier frequency of the species song (Mason, 1991) and whose auditory acuity is limited to a range of several meters (Snedden, 1995).

Our inability to find evidence of an acoustically mediated, female mating preference for males with intact wings can be attributed perhaps to constraints on females' auditory sensitivity, or alternatively, we may instead have been operating under a faulty premise concerning females' underlying motivation to mate. We assumed: (1) that virgin males have more material resources to offer females than do non-virgin males and (2) that females would benefit, therefore, by selectively orienting to virgin males. However, either assumption may be false. Sagebrush crickets continue to feed as adults, and even if non-virgin males are initially depleted at mating of haemolymph and the accessory-gland secretions used to construct spermatophores, presumably they can recoup these materials over time through continued foraging. Moreover, females retain the option of re-mating with another male should they not secure the necessary resources at any one mating. Indeed, Johnson *et al.* (1999) recently showed that when females are precluded from wing feeding during an initial copulation, they remate significantly sooner than females allowed to feed freely during their initial mating. This form of cryptic mating preference (Thornhill, 1983; Eberhard, 1996) may obviate any benefits to a pre-copulatory, acoustically mediated mating bias.

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Zusammenfassung

Weibchen der Art *Cyphoderris strepitans* (Orthoptera: Haglidae) fressen während der Paarung an den fleischigen Hinterflügeln ihrer Partner und nehmen Hämolymphe auf, die aus den so entstandenen Wunden austritt. Männchen, die bereits mit einem Weibchen kopuliert haben, sind nicht von weiteren Paarungen ausgeschlossen, da die erlittenen Verletzungen für Männchen nicht lebensbedrohend sind, und da die Männchen bei einer Paarung meist nur einen Teil ihrer Hinterflügel verlieren. Solche sexuell erfahrenen Männchen haben aber relativ zu ihrer Häufigkeit in der Population einen geringeren Paarungserfolg als jungfräuliche Männchen. Eine mögliche Erklärung für dieses Phänomen besteht darin, daß die Energiereserven von Männchen durch den bei der Paarung erlittenen Verlust von Hämolymphe erschöpft werden, so daß Männchen anschließend nicht mehr in der Lage sind, ihre Gesangsaktivität im selben Umfang aufrechtzuerhalten wie ihre jungfräulichen Konkurrenten. Die Ergebnisse früherer Untersuchungen zur Gesangsaktivität von Männchen stützen diese Hypothese. Eine andere mögliche Erklärung besteht aber darin, daß Weibchen aktiv nach jungfräulichen Männchen suchen, weil diese ihnen größere materielle Ressourcen bieten. Wenn der Verlust von Hinterflügelmaterial unter den lauterzeugenden Tegmina die akustische Struktur des Männchengesangs verändert, könnten Weibchen theoretisch gegen sexuell erfahrene Männchen diskriminieren, indem sie auf deren Rufe weniger stark phonotaktisch reagieren. Wir prüften diese Hypothese, indem wir jungfräulichen Männchen experimentell einen der Hinterflügel entfernten, um Männchen zu erzeugen, deren Gesang zwar dem sexuell erfahrener Männchen ähnelte, denen aber die Kosten einer tatsächlichen Kopulation erspart geblieben waren. Wir verglichen den Paarungserfolg solcher 'asymmetrischen' Männchen mit dem von scheinoperierten Männchen, mit denen sie unter natürlichen Bedingungen konkurrierten. Gleichzeitig untersuchten wir im Labor mit Hilfe von Zeitraffer-Videoaufnahmen, ob Weibchen eventuell erst nach der Partnerfindung eine Präferenz zeigen. In keiner der beiden Untersuchungen gab es signifikante Unterschiede im Paarungserfolg der Männchen. Daraus schließen wir, daß der Paarungsvorteil jungfräulicher Männchen nicht von einer akustisch

vermittelten Paarungspräferenz der Weibchen herrührt, sondern von der unterschiedlichen Gesangsaktivität der Männchen.
