

## Sexual cannibalism and its relation to male mating success in sagebrush crickets, *Cyphoderris strepitans* (Haglidae: Orthoptera)

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**Abstract.** Female sagebrush crickets, *Cyphoderris strepitans*, feed on the fleshy hind wings of males during copulation, and consume haemolymph flowing from the wounds they inflict. In a laboratory experiment, the mating success of males whose hind wings had been surgically removed (treated) was compared with that of males whose hind wings were left intact (untreated). Treated males called as much as untreated males and were mounted as quickly as untreated males. Some males were able to secure matings even though they had no hind wings. However, the possession of hind wings significantly increased a male's chances of successfully transferring a spermatophore once a female had mounted. Males without hind wings obtained significantly fewer matings, and appeared more vulnerable to injuries inflicted by females on other body parts.

In many arthropod species, males provide females with courtship food gifts prior to or during copulation (for examples see Thornhill & Alcock 1983; Zeh & Smith 1985). Prey items acquired by the male, secretions produced by specialized glands, or even male body parts can all function as nuptial gifts (Thornhill 1976; Zeh & Smith 1985; Quinn & Sakaluk 1986). In a variety of insect species, protein contained in food gifts is incorporated into eggs subsequently produced by the female (e.g. Friedel & Gillott 1977; Boggs & Gilbert 1979; Gwynne 1984) and positively affects female fitness (see review in Boggs 1990), while in other species, such an effect seems to be absent (Svärd & Wiklund 1988; Wedell & Arak 1989; Reinhold & Heller 1993).

In the orthopteran genus *Cyphoderris* mating occurs when a receptive female approaches a singing male. The female climbs onto the male's dorsum and begins chewing on his hind wings (Morris 1979; Dodson et al. 1983). Subsequently, the female consumes a portion of the wing material and any haemolymph flowing from the wounds she inflicts. While the female is mounted on the male, he transfers a spermatophore that remains attached to the female for up to several hours (Dodson et al. 1983). The male's soft and unusually fleshy hind

wings appear to be specifically modified for female wing feeding. However, it is unknown whether the condition of the male's hind wings actually influences the probability of successful spermatophore transfer. The aim of our study was to test the hypothesis that a male's modified hind wings increase the probability of successful spermatophore transfer and thereby enhance male mating success.

### NATURAL HISTORY OF SAGEBRUSH CRICKETS

*Cyphoderris strepitans* belongs to the Haglidae, an insect family considered the sister group of the modern Gryllidae. *Cyphoderris strepitans* occurs exclusively in the mountainous regions of Colorado and Wyoming and inhabits primarily sagebrush meadows (Morris & Gwynne 1978). Adults become active in May, soon after snow melt. Males begin singing in sage bushes around dusk and continue to call until about midnight. Stridulatory sounds, as in all Ensifera, are produced when males rhythmically rub their modified fore wings (tegmina) against one another. Both sexes are flightless, and females approach singing males by walking towards them.

For successful mating, the female has to mount the male and remain mounted until a spermatophore has been transferred (Dodson et al. 1983). Females may prevent spermatophore transfer by

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dismounting before the male has extruded the spermatophore. Completed matings, however, are terminated by the male pulling away from the female (Dodson et al. 1983). Afterwards, the male may resume singing to attract more females (Dodson et al. 1983). The breeding season continues until mid or late June. By this time, most males have had at least one mating opportunity and lost part or all of their hind wings through female wing-feeding behaviour (Morris et al. 1989; Sakaluk & Snedden 1990; personal observation).

## METHODS

We collected male and female *C. strepitans* between 4 June and 20 June 1991 from two sites in Grand Teton National Park: Deadman's Bar and Pacific Creek. Only virgin males whose hind wings were intact, i.e. had not been chewed on by females, were used in the study. In the laboratory, experimental animals were kept in plastic vials and fed fresh pieces of apple or carrot until they were used in the experiment. The laboratory room in which the insects were kept was illuminated by outside light entering through a window, such that the animals were exposed to the ambient photoperiod although at somewhat reduced light intensities.

For the experiment, we simultaneously placed two male-female pairs in a transparent plastic container (15 × 7 × 3 cm) divided in half to create two adjacent observation chambers. Small holes in the lid of the container prevented a build-up of excessive heat inside the chambers, and a small piece of branch was offered as a singing perch in each chamber. One of the experimental pairs included an intact virgin male that had been handled but not treated, while the other pair included a virgin male whose hind wings had been clipped at the base. We removed the hind wings of treated males the morning before the pairings were established; severing the hind wings at their point of insertion resulted in little or no bleeding. We initiated trials between 1800 and 1900 hours local time. Two red light sources (25-W bulbs) facilitated recording during the dark period of the trial. We recorded singing and mating behaviour occurring in the observation chambers over 12 h using a Panasonic time-lapse video-recorder. Analysis focused on the following variables.

(1) The amount of time the male spent singing during the period from 1900 to 0100 hours.

(2) Female response time as measured from the onset of male singing in a chamber to the time at which the female first mounted the male.

(3) The total number of spermatophores the male transferred during the trial.

(4) The number of female mounts that occurred before the first successful mating.

(5) The duration of female mounts, measured as the time the female spent on the male's back in a parallel position, regardless of feeding activity or genitalic coupling.

Data were analysed using the procedures of the Statistical Analysis System for personal computers (SAS Institute 1988). To compare the number of mounts and the total mounting time that males of both treatments required for spermatophore transfer, we employed a survival or failure time analysis. This kind of analysis was required because some of the data were 'right-censored' (i.e. in some cases, observation was terminated before spermatophore transfer had occurred). A simple comparison of the number of mounts observed prior to the first spermatophore transfer would be problematic because there were several pairs for which spermatophore transfer did not occur during the trial. In these pairs, the observed number of mounts would be an underestimate of the number of mounts required for spermatophore transfer. Survival analyses (procedures LIFEREG and LIFETEST in SAS) produce a chi-squared statistic for the comparison of the two samples and take right-censoring of data into account (Muenchow 1986; Pyke & Thompson 1986).

## RESULTS

### Male Calling Activity and Female Response

All males exhibited some calling activity during the course of a trial. There was no difference in the time untreated and treated males spent singing (measured as the number of 5-min intervals in which any singing occurred: Table I). The removal of the males' hind wings also had no significant effect on the time to the onset of singing, i.e. the time elapsed after the start of observation until the male started to call (Table I). Both results indicate that surgical removal of the hind wings did not impair male singing ability.

We also found no evidence for female discrimination against experimental males prior to mounting. In all trials ( $N=28$ ), females responded on

**Table I.** Mean ( $\pm$ SE) male calling activity and female response time in pairs involving untreated (possessing hind wings) and treated males (lacking hind wings) and results of statistical comparisons between treatments (paired *t*-tests)

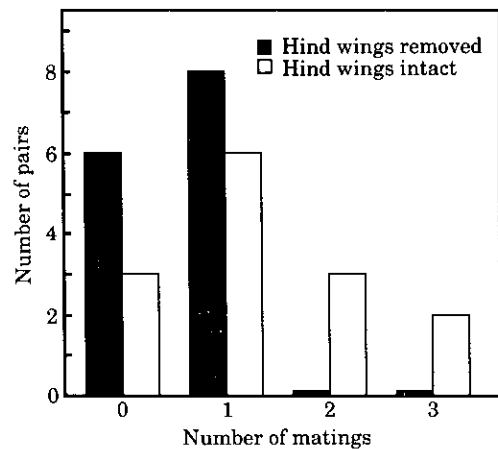
	Untreated males ( <i>N</i> = 14)	Treated males ( <i>N</i> = 14)	<i>t</i>	<i>P</i>
Number of 5-min intervals spent calling	60.6 $\pm$ 2.3	57.6 $\pm$ 3.7	-0.72	0.48
Interval between pair establishment and first calling	22.2 $\pm$ 8.9 min	13.3 $\pm$ 2.9 min	-0.983	0.34
Time from start of calling to first mount	95.5 $\pm$ 24.1 min	75.8 $\pm$ 17.9 min	-0.712	0.49

average to singing males of both treatments by mounting within the first 2 h of male singing, although there was considerable variation between individual pairs within each treatment (Table I). These results show that our experimental manipulation of males did not impair their calling activity, nor did it affect the females' readiness to initiate matings by mounting males.

#### Male Mating Success

Untreated males transferred significantly more spermatophores on the average ( $\bar{X} \pm SE = 1.29 \pm 0.27$ ) than did treated males ( $0.57 \pm 0.14$ ) (Fig. 1: Wilcoxon two-sample test,  $z = 2.029$ ,  $P = 0.04$ ). Additionally, a greater proportion of untreated males transferred at least one spermatophore to the female (11 of 14 males) compared with treated males (8 of 14 males), but this difference was not statistically significant (*G*-test with Yates' correction for continuity,  $G = 0.655$ ,  $P = 0.42$ ).

We also measured the effects of hind-wing removal on male mating success by comparing treatments with respect to the number of mounts required for successful spermatophore transfer. This was done using a survival analysis, which takes into account instances in which spermatophore transfer did not occur during the course of an observation period and corrects for right-censoring of data (procedure LIFEREG in SAS). Treatments differed significantly in the number of mounts males required to transfer a spermatophore ( $\chi^2 = 8.805$ ,  $P = 0.003$ ). The mean ( $\pm$ SE) probability of spermatophore transfer for any one mount was  $0.25 \pm 0.14$  for untreated males and  $0.08 \pm 0.14$  for treated males. These means include data from several untreated males that transferred more than



**Figure 1.** Number of spermatophores transferred by untreated (possessing wings, *N* = 14) and treated male *C. strepitans* (lacking wings, *N* = 14) in a 12-h period.

one spermatophore to their respective mates. It could be argued that in the field, females do not usually remain near recent mating partners, and that our laboratory design artificially inflated opportunities for males to mate more than once with the same females. Therefore, we repeated the above analysis excluding mounts and spermatophore transfers that occurred after the first successful mating. Differences between treatments remained significant even when only the first of several matings was considered ( $\chi^2 = 6.058$ ,  $P = 0.014$ ). For treated males, the probability of spermatophore transfer for mounts preceding the first mating was as reported above, because double or triple matings did not occur in this treatment. Even for untreated males, however, the mean

( $\pm$ SE) probability of spermatophore transfer ( $0.24 \pm 0.19$ ) did not deviate much from the overall mean, partly because trials with more than one mating were rare and partly because males still retained considerable hind-wing material to feed females after initial matings.

Although untreated males required fewer female mounts for spermatophore transfer, there was no significant difference between treatments in the mean time required to complete spermatophore transfer (treated males:  $507 \pm 174$  s; untreated males:  $359 \pm 87$  s; procedure LIFETEST in SAS: log-rank test,  $\chi^2 = 1.898$ ,  $P = 0.17$ ).

There was also no significant difference between treatments in the length of successful (Wilcoxon two-sample test,  $N_1 = 10$ ,  $N_2 = 8$ ,  $z = -1.288$ ,  $P = 0.20$ ) or unsuccessful mounts (Wilcoxon two-sample test,  $N_1 = N_2 = 12$ ,  $z = 1.359$ ,  $P = 0.17$ ). In both treatments, however, mounts that resulted in spermatophore transfer were significantly longer in duration (Wilcoxon two-sample test,  $N_1 = 24$ ,  $N_2 = 18$ ,  $z = 4.640$ ,  $P = 0.0001$ ) than unsuccessful mounts (data pooled from both treatments, mean of successful mounts ( $\pm$ SE):  $261 \pm 41$  s; unsuccessful mounts:  $68 \pm 23$  s).

Dodson et al. (1983) observed unmanipulated male *C. strepitans* (both virgin and mated) and recorded the duration of mounts. In their study, copulation (coupling of genitalia and spermatophore transfer) occurred in seven out of eight pairs involving virgin males. In each case, the female mounted the male and fed on his wings. The copulation times they report ( $\bar{X} \pm$ SE =  $202 \pm 29$  s) cannot be compared with the durations of successful mounts we recorded, because Dodson et al. focused on the time during which the genitalia were coupled, while we measured the time the female was mounted on the male, with or without genitalic coupling.

Females did not always restrict their consumption of male body parts to the hind wings. One untreated male and four treated males experienced additional wounds during mounts; the untreated individual and one treated male had partially eaten tegmina, another treated male had incurred large puncture wounds in the first abdominal tergites, and two treated males had large abdominal puncture wounds as well as damaged tegmina. All these injuries were clearly inflicted by the female's mandibles during mounting. Three of the four treated males that were injured transferred a spermatophore during the course of the trial.

## DISCUSSION

While a number of earlier papers dealing with the biology and mating behaviour of *Cyphoderris* have described the female wing-feeding behaviour that occurs prior to spermatophore transfer (Morris 1979; Dodson et al. 1983; Sakaluk et al. 1987; Morris et al. 1989; Sakaluk & Snedden 1990; Snedden & Sakaluk 1992), the importance of this behaviour to male mating success has not been assessed experimentally prior to the present study. In our study, untreated virgin males were able to transfer a greater number of spermatophores in the course of the trial than the males whose hind wings had been surgically removed. The greater mating success of untreated males was not due to a greater singing activity of these males, nor was it due to females preferentially mounting males with intact hind wings. Males with intact hind wings were able to secure more matings than males without hind wings because of their greater success at actually transferring spermatophores once females had mounted them. Hence, treated males required a greater number of female mounts to successfully complete a mating. We conclude from this result that the male's hind wings currently function in facilitating spermatophore transfer. The fact that females tried to feed on male body parts while mounted on males supports this interpretation. In pairings involving untreated virgin males, the soft, protruding hind wings were readily available to mounted females, which apparently induce the female to extend the duration of a mount while ingesting a male's haemolymph. When the female stays mounted for a longer time, the male is more likely to succeed in attaching his genitalia to the female's, and to extrude and transfer the spermatophore before the female dismounts. Females were indeed mounted longer on males during actual matings than during mounts without spermatophore transfer.

The experimental situation in our study was artificial insofar as it confined the male and female together and thus increased the encounter rate between mating partners. It is not likely that in a field situation, a pair would remain this close to one another for a 12-h period. Therefore, the number of mounts and matings occurring in our trials must be regarded as overestimates of the number actually occurring in the field. However, the difference between treatments in the number of mounts preceding a successful spermatophore transfer is not

likely to be an artefact. In the laboratory, this differential probability of transferring a spermatophore led to a greater number of completed matings in pairs involving untreated males; in a field situation, it would probably have the same effect, although the number of matings for males on any given night would probably also be smaller than the numbers observed in our study.

The higher rate of spermatophore transfer in pairs involving winged males constitutes a mechanism by which females are able to preferentially mate with those males providing larger or more readily available nuptial food gifts. In addition to this form of female choice, mating preferences of female *C. strepitans* might also be exerted during other phases of sexual interactions: (1) during long-distance mate attraction, (2) after pair formation, but prior to mounting and (3) after copulation, through the premature removal of spermatophores. For example, assuming that the acoustic signals of males are systematically altered by the loss of hind-wing material underlying the sound-producing tegmina, females might discriminate against mated males through a reduced phonotaxis to the calls of such males (Morris et al. 1989). In the present study, we did not test for female preferences for the calls of different males. Females might also discriminate against non-virgin males through a lowered mounting rate after pair formation occurs; in this study, however, there was no evidence that females were less willing to mount wingless males. Finally, females might discriminate against non-virgin males by removing the spermatophores of these males earlier than those of virgin males. If females were not satiated after matings with males that provided them with only a small amount of haemolymph or hind-wing material, they might be more likely to remove the spermatophore sooner, leading to a reduction in the number of sperm transferred. The premature removal of spermatophores of males providing inadequate food gifts previously has been documented in another ensiferan, *Grylodes sigillatus* (Orthoptera: Gryllidae), a species whose food gift comes in the form of a gelatinous spermatophylax (Sakaluk 1984, 1985). However, no data are available to assess the validity of this hypothesis for *C. strepitans*.

Several males in our study were severely injured during trials. Under normal circumstances, such injuries would probably reduce a male's future mating opportunities: tegminal injuries probably compromise male singing ability, and abdominal

injuries may very likely result in the death of the injured individual within a day or two of the mating. All the males that incurred abdominal injuries in our study ( $N=3$ ) died the day after the trial. Despite these drastic consequences, it appears that males tolerated the injuries inflicted by females to obtain a mating. In matings involving untreated individuals, males pull away from their mates within seconds of transferring a spermatophore (Dodson et al. 1983; personal observation); consequently, a male should also be able to terminate copulation when the female begins to inflict serious injury. If males actually allow females to injure them severely to obtain a single mating, this single mating must be critical to the male's fitness. W. A. Snedden (personal communication) found that 88% of males in a field enclosure mated once or not at all during the course of the breeding season. Hence, it is conceivable that males actually tolerate these injuries in exchange for a mating.

In *C. strepitans*, a male that can provide hind-wing material and haemolymph clearly increases his chances of obtaining a mating with a female that has mounted him. In this respect, the male's investment can be regarded as mating effort sensu Trivers (1972). No data are available on the effect of nuptial feeding on the female's reproductive success. Although we do not know how the specific modification of male hind wings evolved, the preference of females for males providing wing material and haemolymph clearly contributes to the maintenance of this trait.

Consumption of body parts such as the hind wings of *Cyphoderris*, or the glandular tibial spurs of some nemobiine crickets (Orthoptera: Gryllidae; Mays 1971; Bidochka & Snedden 1985), has been classified as sexual cannibalism (Thornhill & Alcock 1983). However, Simmons & Parker (1989) have suggested a different classification of nuptial offerings, distinguishing four types of gifts: prey gifts, seminal gifts (sperm and accessory gland products), somatic gifts (part of the male's body is eaten, not normally causing the male's death), and suicide gifts (true sexual cannibalism). True sexual cannibalism is known to occur in many arachnid families (e.g. Araneidae: Elgar & Nash 1988); the issue of whether sexual cannibalism in mantids is an artefact caused by confinement, disturbance, female unreceptivity or undernourishment has long been contentious (Roeder 1935, 1963; Kyriacou 1987; Liske & Davis 1987; Birkhead et al. 1988; see also Prete & Wolfe 1992). A recent field study of

mantid mating behaviour, however, has demonstrated unequivocally that sexual cannibalism is not an artefact of studies using captive animals (Lawrence 1992).

Somatic gifts differ from suicide gifts in their less drastic effect on male survival. After his first mating, a male *Cyphoderris* is likely to be alive and to have at least some hind-wing material to offer to another female (Sakaluk et al. 1987; Morris et al. 1989). Gift-giving thus compromises, but does not preclude future matings for the male. A male *Mantis*, in contrast, foregoes any potential future reproduction when his entire body is consumed as a food gift. This may account for differences in a male's readiness to provide a nuptial gift: male *Cyphoderris* apparently comply with female consumption of their hind wings until spermatophore transfer is complete, whereas accounts of mantid mating behaviour stress the 'cautious' behaviour of males minimizing the risk of being eaten by the female (Liske & Davis 1987; Birkhead et al. 1988; Lawrence 1992). A model developed by Buskirk et al. (1984) concludes that sexual cannibalism may even confer a reproductive benefit to males through the production of more or fitter offspring, especially if the number of matings males can expect during their lifetime is small; however, there appears to be little evidence for male complicity in true sexual cannibalism (Gould 1984).

It may appear surprising that any of the *C. strepitans* males without hind wings were able to secure any matings. Some males had other body parts consumed by the mounted female, but others provided no immediate benefit to the female. Females may remain mounted on males without hind wings long enough for them to transfer the spermatophore because the males force them to do so, using an abdominal structure known as a 'gin trap' (Morris & Gwynne 1978; Morris 1979). This organ consists of two pairs of recurved hooks, one pair directed forward on the 10th tergite, and the other directed backward on the eighth tergite. These hooks are used to prevent the female from pulling away from the male during copulation (Morris 1979), and presumably could be used to forcefully mate with females that do not receive a food gift. In the scorpionflies *Panorpa latipennis* and *P. vulgaris*, males also offer nuptial gifts to females prior to or during mating. In these species, males possess specialized organs ('notal organ', 'dorsal clamp') which can be used to force unwilling females to mate ('rape') or to extend consensual

matings, as demonstrated in experimental studies that manipulated the male's ability to provide a courtship food gift, as well as the functionality of the dorsal clamp (Thornhill 1980; Thornhill & Sauer 1991). In our study, males in both treatments were observed to thrust their abdomen upward in attempts to secure the mounted female's abdomen with the gin trap. However, we did not test whether or not this gin trap was necessary for successful matings in untreated or treated males. A study that manipulates both a male's hind wings and his gin trap independently is needed to elucidate the function of the gin trap.

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