

## Virgin Male Mating Advantage in a Primitive Acoustic Insect (Orthoptera: Haglidae).

Glenn K. Morris,<sup>1</sup> Darryl T. Gwynne,<sup>1</sup> Dita E. Klimas,<sup>1</sup> and Scott K. Sakaluk<sup>2</sup>

Accepted 31 July 1987; revised 15 September 1987

---

*Male reproductive behavior in the relict flightless haglid, Cyphoderris strepitans, entails the generation of sound signals and the provision of nuptial gifts to mates. These food gifts take two forms: (1) a gelatinous mass (spermatophylax) augmenting the spermatophore and (2) fleshy metathoracic wings adapted to be eaten. The female consumes a portion of the male's underwings during courtship and copulation and the spermatophylax afterward. The incidence of wing-feeding wounds can be used to monitor the mating success of field-caught males. If, when a male mates, he compromises his ability to provide subsequent nutritive gifts, females would benefit by mating with virgin rather than nonvirgin males. To test this, mating success of virgin and nonvirgin males was compared in a field population. Virgins were found to obtain more matings than explained by their numbers relative to nonvirgins in the population. We conclude that, having mated, a male is at a disadvantage, relative to his virgin competitors, in securing further matings.*

---

**KEY WORDS:** Orthoptera; Haglidae; *Cyphoderris*; acoustic; mate choice; mating success; nuptial feeding; spermatophylax.

### INTRODUCTION

*Cyphoderris strepitans* Morris & Gwynne is a flightless orthopteran insect found in sagebrush meadows and pine woodland in the mountains of Wyoming and Colorado. Its breeding season extends from late May into June and commences shortly after the melt of the winter snow. At dusk males climb from the litter

<sup>1</sup>Department of Zoology and Erindale College, University of Toronto, Mississauga, Ontario, L5L 1C6, Canada.

<sup>2</sup>Department of Biological Sciences, Illinois State University, Normal, Illinois 61761.

up onto the sagebrush or the lower trunks of trees and begin to stridulate, using abbreviated forewings (Fig. 1). Their call is a sustained trill with a high-Q (sinusoidal) audio carrier frequency near 13 kHz (Morris and Gwynne, 1978).

Females and males form pairs and mating occurs either on the sage or on the ground. In other acoustic Ensifera the role of male calls in pair formation is demonstrated by the positive phonotaxis of conspecific females to a speaker broadcasting male song (see references cited by Morris and Fullard, 1983). Surprisingly, bioassay experiments of this sort have failed to discover a phonotactic response in *C. strepitans*; unmated females, released near the center of a circular arena 1 m in diameter and exposed to broadcasts of recorded conspecific song, made their first crossings of the arena periphery without reference to the location of the sound source (Morris, unpublished data).

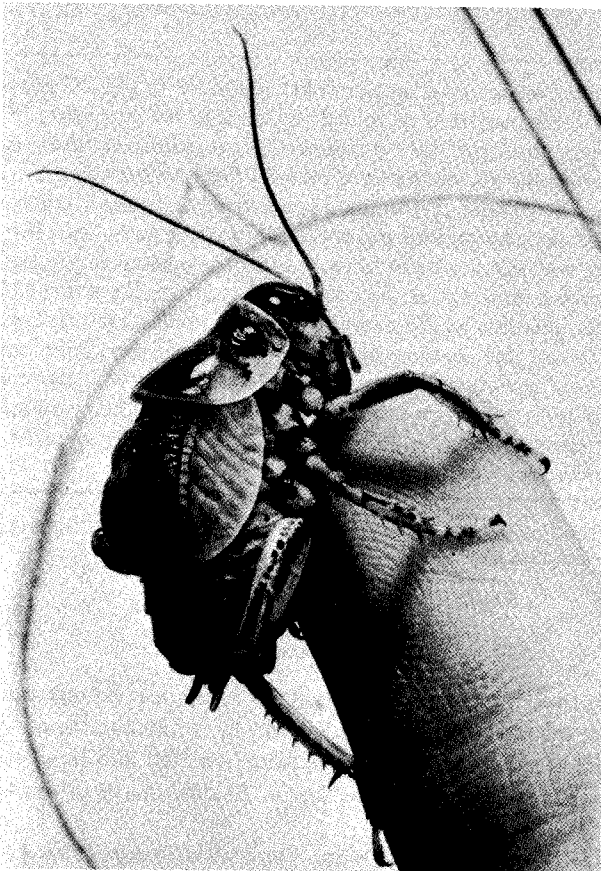


Fig. 1. Mature male of *C. strepitans*.

Males of many katydids (Orthoptera: Tettigoniidae) contribute to matings by accompanying their sperm with a large spermatophylax (Boldyrev, 1915; Gwynne, 1983). This gelatinous mass, appended distal to the paired sperm ampullae, is later eaten by katydid females and is known to increase female fitness (Gwynne, 1984). While *C. strepitans* is not a katydid, it is classified within the same superfamily as the Tettigoniidae (Kevan, 1977). A mating female of *C. strepitans* likewise receives (putative) nutritive benefits from her mate in the form of a spermatophylax; but in addition, while mounted atop the abdomen of the male (Fig. 2), she directs her head beneath his tegmina and feeds upon his metathoracic wings. These are fleshy (Fig. 3) and appear to be specially modified to this end (Morris and Gwynne, 1978; Morris, 1979; Dodson *et al.*, 1983). Feeding before coupling is quite variable in duration ( $\bar{X}$  = 6.5 min,  $N$  = 10), continues through a rather brief copulation interval ( $\bar{X}$  = 3.25 min,  $N$  = 8), and is ended by male withdrawal (Dodson *et al.*, 1983).

Variation in the ability of males to transfer nutritional benefits to their partners may create a basis for mate choice by females (Thornhill and Alcock, 1983, p. 380): on average, virgin males should be more able than nonvirgins to provide a maximally large and nutritious food gift. Such variation occurs in

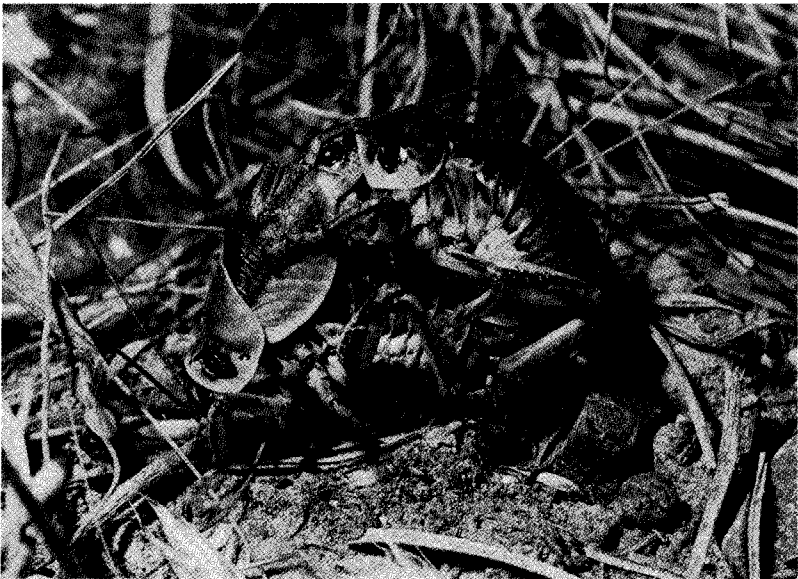


Fig. 2. A mating pair of *C. strepitans* copulating on the ground in a sagebrush meadow, just after dark. The male's body is arched and his gin trap (Morris 1979) grips the venter of the female's abdomen. She is feeding upon his underwings; the spermatophore has not yet appeared.



Fig. 3. A restrained male with his forewings displaced and revealing intact metathoracic wings. The label indicates that this specimen, designated 24, was caught on June 9.

the katydid *Requena verticalis* Walker, where the glands that produce the spermatophylax are significantly smaller in mated than in unmated males for up to 5 days after mating (Davies, 1984). Females that avoid males whose capacity to donate resources has been compromised by a recent mating should enjoy a selective advantage. This avoidance need not involve active discrimination by females; it might result passively (Parker, 1983) by a mechanism such as reduced male calling after mating. But whether active or passive, we would expect matings to virgin males to occur out of proportion to virgin male abundance (relative to nonvirgins) in the singing population. We set out to test this prediction in the case of *C. strepitans*.

## MATERIALS AND METHODS

Wing feeding during copulation offers a way to monitor male mating success in the field: males reveal their mating history in the state of their metathoracic wings. Those with intact wings must be virgins, while males with wounded wings have mated at least once, receiving in the process a unique pattern of feeding damage. [These inferences must be qualified because wing wounding can also occur without successful mating (see Discussion).] Males mating for the first time usually retain two-thirds or more of the underwing mass and the ragged tissue left behind on the wing's distal extremity, initially wet with blood, dries over several hours into a distinctively shaped, crusted, and often blackened wound (Fig. 4). Sometimes the two wings congeal so as to adhere to each other. The further mating success of nonvirgin males can be established by making a photographic record of their unique wound pattern: changes in this pattern accompanied by additional substantial reduction in wing material can be interpreted as a mating in the interval between captures.

During June of 1982, by capture, release, and recapture, individually marked males were monitored for hindwing feeding damage. A field site was

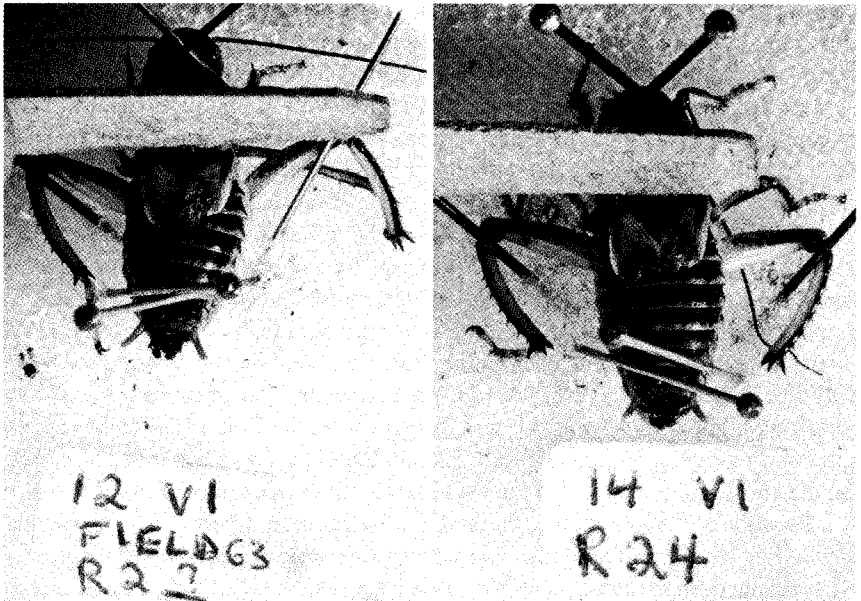


Fig. 4. Photo records of male 24, made after recaptures on the nights of June 12 and 14. Determination of identity was by recourse to pigmentation patterns in his June 9 photo (Fig. 3). Note the absence of change in the wounding pattern, indicating that this male had not mated in the interval between June 12 and June 14.

chosen in Grand Teton National Park beside the Snake River near Deadman's Bar (elevation, 2030 m). In a sagebrush meadow on a bench of the river's flood plain, a rectangular plot 500 m<sup>2</sup> was staked. On each of 4 collecting nights (the nights of June 9, 12, 14, and 17), beginning just after dark, the plot and a limited surrounding area were searched. Each singer in turn was localized by his call to a sage branch and then discovered with a flashlight and captured. Each collected male was placed into a numbered vial, and his perch marked with a flagged surveyor's stake. The vial number was labeled on the stake. Virtually all singers were located and removed from an area of approximately half a hectare, centered on, but greatly exceeding, the staked plot.

Because of the low temperatures involved, and because the insect is flightless and its hindlegs only weakly specialized for leaping, a male's capture, once sighted, is usually an easy matter. With air temperatures near freezing, especially after a soaking rain, many males perch near the ground and are then much harder to find. Singers are also sensitive to disturbance, more so at low densities, e.g., as singing activity gets under way. They typically become silent and motionless in response to nearby human movement and are very slow to renew song. Nevertheless, virtually all searches ended in capture.

The progressive removal of males must severely affect mating activity on the four collection nights. The intervening nights (June 10, 11, 13, 15, and 16) were allowed to permit ample opportunity for undisturbed sexual behavior. The weather for all 9 nights of the study was conducive to singing and mating. With two exceptions, temperatures remained above 3°C as midnight approached. Exceptions were the night of June 17, when the temperature at midnight reached 1°C, and the night of June 12, which remained unusually warm (9°C at 11:30 PM).

Collecting incorporated the interval of the greatest singing activity (9:45–11:30 PM); it continued for about 2 h except for the night of June 14, when it lasted 3 h. Collection ceased when the designated collecting area was judged empty of singers, a criterion yielding total numbers that varied by only 13%. There were three searchers each night except that of June 17, when there were only two. The overall average search time expended per male on the first two collecting nights was 4.9 and 4.4 min, respectively. On June 14, with the insects apparently affected by a heavy rain early in the day, it was 6.8 min per insect. On the coldest night (June 17) the mean search time was only 3.5 min per male.

Brought to the laboratory, the males were processed between 2:00 AM and dawn. For each wounded male, his pattern of metathoracic wing damage was photographed; in many cases photographs were also made of virgin males. Each male was marked uniquely with dots of colored enamel paint. The males were then returned to the field site and released into the ground litter below the appropriate flagged stake. All males were returned by 2 h after dawn.

Although remarkably quiescent under most handling (e.g., when placed in

a plastic bag for weighing they remain motionless), *Cyphoderris* struggle vigorously when their tegmina are lifted to view possible underwing damage. And the tegmina must not be left with the wide lateral fields trapped in a fold against the body, since this leads after some hours to a blister-like accumulation of hemolymph. We used a restraining technique that avoided these problems as we photographed the wings. Each insect was secured against a small foam block with insect pins (Figs. 3 and 4). Two pins were crossed above the thorax, tightly against the lateral indentations of the pronotum. A pin pushed the anterior face of each partially extended metathoracic leg against the plane of the block and two pins were crossed overtop the abdomen. A cardboard probe was then used to lift and deflect the tegmina laterad. Released from this restraint, the insect resumed its normal alert stance immediately and showed no ill effects.

A number of recaptured insects had lost some or all of their paint markings, but because of the individually distinctive body pigmentation, especially that on the inner face of the hind femur, we were able in all these cases to establish an individual's identity by reference to pigmentation patterns in his earlier photos. Figure 4 illustrates this process: when first taken the night of June 9 this specimen was a virgin and was photographed with the designation *Red 24*; he was recaptured June 12 but had lost his red painted marking. Matching of pigmentation pattern with his June 9 photo (Fig. 3) established his identity. This male also illustrates assessment of subsequent mating opportunity in wounded males: a comparison of the June 12 and June 14 photos (Fig. 4) reveals that the same unique pattern of chewed metathoracic wing has been maintained.

## RESULTS

Changes in wing state of the collected males are summarized in Fig. 5. On the night of June 9 we captured, marked, and released a total of 74 males: 41 were intact-winged and 33 had wounded wings. The fresh wounds of 9 of these 33 indicated that they had mated that same night.

On June 12 we collected 82 males; 50 of these were recaptures of males marked on June 9. Twenty-one of these 50 males had intact wings and so are considered not to have mated in the interval; 29 had wounded wings. Of the 29 with wounded wings, 18 were revealed by the photographs to have possessed wounded wings on June 9 and to have maintained the same wound pattern; 11 insects had a changed wing state. Of these 11 altered insects, 9 were virgin when collected 3 nights earlier, while 2 had been nonvirgin and now had further wing wounding. Not a single male, marked or unmarked, was found with a fresh wing wound on the night of June 12. Marks were now placed on the 32 males captured for the first time on June 12, bringing the total number of individually marked males to 106.

On June 14 we captured 79 males, 52 of which were marked. Of these

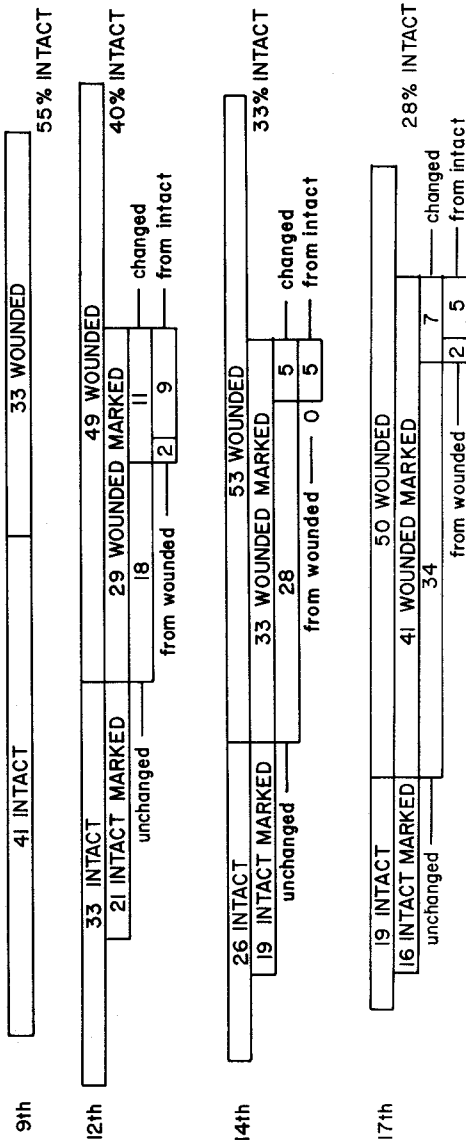


Fig. 5. A summary of the results of the marked male recovery study. Horizontal bars are scaled to the numbers of males collected in the various labeled categories. See text for further explanation.



latter, 19 had intact wings and 33 had wounded wings. For 28 of these 33 there was no change in wing state from the previous capture; 5 marked insects had changed, and all 5 from a previously unwounded condition. Three of these changed males were same-night matings (freshly wounded) taken previously on June 12; two exhibited old wounds and had not been seen since June 9. On the night of June 14 we added another 27 males to the marked population for a total of 133.

On June 17 we collected 69 males, 57 of which were marked. Of these, 16 had intact wings and 41 had wounded wings. Of the 41 wounded-wing males, 34 exhibited no change in their wings from the previous examination. Seven insects had changed: five of these were formerly taken as virgins, and two as wounded. Only one of these changed insects had a fresh wound on June 17, an individual observed as virgin on the night of June 12.

We tested the null hypothesis that virgin and nonvirgin males mate in proportion to their numbers in the population: that subsequent woundings detected in the monitored population occurred in accordance with the relative abundance of the two classes, intact and wounded (Table I). For the 23 detected (marked male) woundings, the expected distribution of cumulative wounding frequencies to virgins over the three intervals between census nights was compared to that actually observed. In calculating this expected wounding frequency the estimate of class proportions for each interval was derived from the immediately preceding census night and includes first-time captures. This comparison leads to a rejection of the null hypothesis ( $P \ll 0.001$ , Kolmogorov-Smirnov).

Since both absolute and relative numbers of virgin males fall throughout the study, it is reasonable to argue that our theoretical frequencies are based on a consistent overestimate of the proportion of intact-winged males. The proportion of marked virgins actually present in a given interval should always have been less than that used in our calculations. Since the observed frequency of virgin pairings reaches significance even with this overestimate, we have

**Table I.** Comparison of Theoretical ( $F_i$ ) and Observed ( $f_i$ ) Mating Frequencies of Intact *C. strepitans* Males (Kolmogorov-Smirnov Goodness of Fit,  $D = 8.64/19 = 0.45474$ ;  $P \ll 0.001$ )

	June 10, 11	June 13	June 15, 16	<i>N</i>
Proportion intact	0.55	0.40	0.33	
Obs. matings	11	5	7	
$F_i$	6.05	2.00	2.31	
$f_i$	9	5	5	19
Cum. $F_i$	6.05	8.05	10.36	
Cum. $f_i$	9	14	19	
$ d_i $	2.95	5.95	8.64	

increased confidence in rejecting the null hypothesis. We conclude that intact males experienced wounding at a greater rate than predicted by their numbers in the population.

## DISCUSSION

*Wing Wounds and Mating.* The accuracy of mating estimates based on wounds is placed into question by laboratory evidence that feeding and wounding can occur without mating (Dodson *et al.*, 1983): females may feed on a male's wings and then the pair separate without sperm transfer and wounds can result from feeding by other males rather than females. Accuracy will also be affected if a change in wing state, over a possible several days between captures, represents not one, but a succession of matings.

It is only reasonable to expect that not all field pairings are consummated and not all woundings represent matings. But 9 of the 12 reported lab woundings did accurately predict matings, so wing damage must at least represent "mating opportunities which have a very high probability of having culminated in a copulation" (Dodson *et al.*, 1983). At the least, our results here could be restated as follows: intact males secure more mating *opportunities* than predicted by the relative abundance of intact and wounded males in the population.

Under certain laboratory conditions, males will feed on the wings of other males (Dodson *et al.*, 1983). If this behavior occurs in the field, there is the possibility that some woundings observed in the present study represent neither matings nor mating opportunities and are, instead, the result of exploitation by other males. The scarcity of receptive females in field populations, together with the observation that wounding of over 50% of a wild population can occur in just 3 nights, led Dodson *et al.* to suggest that males might be selected for an indiscriminate response to potential mates and that appreciable wing-feeding by males was to be expected in nature.

But there are counterarguments to our earlier interpretation. Wing-feeding by males has never been observed between free-living individuals and it occurred in the laboratory only under conditions of abnormally high male densities, restricted movement, and sparse plant substrate. The existence of a severely limited mating time window that leads to appreciable wounding by male feeding is based in part (circularly) on the assumption that wounds do represent matings. Per diem wounding rates have now been observed in other seasons and at other localities (Morris, unpublished) and are lower than in the cited (1983) example. Woundings in field populations continue at an appreciable rate for several weeks after the appearance of the first wounded males, so that a failure to mate early need not be viewed as virtually a failure to reproduce. (In the present study first detection of a wounded individual at the site occurred June 2 and wounding was still taking place two weeks later.)

However, the most telling argument is theoretical: males that are fed upon by other males simultaneously benefit a competitor and compromise their future ability to invest nutritionally in a mate. Such doubly detrimental behavior should place a male at a strong selective disadvantage. In a system where nuptial gifts are so prominent, it is difficult to view male wing-feeding as a tolerable cost, and on balance we discount male wing-feeding as affecting our results.

Regarding the possibility that each wound detected in the field population represents multiple feedings by a succession of females, rather than a *single* pairing, we note that more than 75% of males went unwounded in each of the intervals between census nights. In the first interval there was 1 wounding for every 4.5 males; in the second interval only 1 male in 10 was wounded; in the last, there was 1 wounding for every 8 males.

This low wounding incidence may be interpreted in two ways: (1) that each wounding represents a single encounter in a population where receptive females are relatively rare or (2) that each detected wound represents multiple encounters in a population where females are abundant but where these females seek out as mates a minority of superior males.

For 18 of the 23 individuals whose changed wing state was documented, the time between successive captures was about 72 h. Given this short 3-day recapture interval for 80% of the changed males, and if *C. strepitans*, like *R. verticalis* (Davies, 1984), retains the glandular effects of a mating for up to 5 days thereafter, multiple encounters per detected wound are unlikely. Further, as we began our study, wounded males comprised 45% of the population, so that situation 2 requires the bulk of superior males to be already wounded. Intercepted wing changes over the ensuing study should occur primarily to wounded males, those whose past wounding demonstrates their superior attractiveness. Their intact-wing competitors have been passed over and should continue to go unmated. Our results do not support these predictions, since the great majority of detected changes occurred to previously intact rather than previously wounded males. We therefore consider it probable that each of our intercepted woundings represents contact with only one female.

*Mechanisms of Differential Mating.* Having established that virgin males enjoy a mating advantage, it is appropriate to ask by what mechanism. Reduced singing activity after mating might function as a passive mechanism of mate choice. Newly mated males may have to move to forage and restore depleted food and moisture reserves. Virgin mating advantage could stem from a temporary physical inability of just-mated males to sing. Studies carried out in 1986 (Sakaluk *et al.*, 1987) reveal that an individual's calling activity is indeed depressed after mating. For fresh-wound and old-wound males, compared with themselves, calling is significantly less on the first as compared to the second night of monitoring; virgin males maintain the same output over both nights.

Another possible mechanism is active mate choice: females may respond

directly to males, accepting or rejecting them on the basis of perceived wing state. Although this discrimination could occur as the female mounts the male and gains immediate access to his wings, wing state could also be manifest in his song, allowing female assessment at a distance. This is because of physical differences in sound parameters which must (theoretically) result from wounding of the underwings: their reduced mass and altered shape will affect the acoustic impedance presented by the air mass between the dorsum and the sound-radiating tegminal membranes (Morris *et al.*, 1975).

The obvious test of active mate choice by song is to expose females to simultaneous broadcast of virgin and wounded-male signals and observe, through their phonotaxis, if they prefer to approach the stridulation of virgins. But as alluded to in the Introduction, mature female *C. strepitans*, even those without sperm, and hence presumably reproductively receptive, fail to exhibit phonotaxis. If active mate choice contributes to the differential mating success we have discovered in this species, the current evidence suggests that it is not mediated by male acoustic signals.

### ACKNOWLEDGMENTS

This study was supported by a grant (Operating 4946) to G.K.M. from the Natural Sciences and Engineering Research Council of Canada; it was conducted at the University of Wyoming and National Park Service Research Center in Grand Teton National Park, U.S.A. We gratefully acknowledge the cooperation of Dr. Kenneth L. Diem, Center Director, and of Mr. Robert Wood and Mr. Rocky Craight of the Park Service. Others contributed to data collection: Edward J. Morris, Dr. Gary Dodson, Jill Dodson, and Godfrey Aedy.

### REFERENCES

- Boldyrev, B. T. (1915). Contributions à l'étude de la structure des spermatophores et des particularités de la copulation chez Locustodea et Gryllodea. *Horae Soc. Entomol. Rossicae* **41**: 1-245.
- Davies, P. (1984). *An Aspect of Mating Costs in Requena verticalis*, B.Sc. thesis, University of Western Australia, Perth.
- Dodson, G. N., Morris, G. K., and Gwynne, D. T. (1983). Mating behavior of the primitive orthopteran genus *Cyphoderris* Haglidae. In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview Press, Boulder, Colo., pp. 305-318.
- Gwynne, D. T. (1983). Male nutritional investment and the evolution of sexual differences in Tettigoniidae and other Orthoptera. In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview Press, Boulder, Colo., pp. 337-366.
- Gwynne, D. T. (1984). Courtship feeding increases female reproductive success in bushcrickets. *Nature* **307**: 361-363.
- Kevan, D. K. McE. (1977). Suprafamilial classification of "Orthopteroid" and related insects; A draft scheme for discussion and consideration. In Kevan, D. K. McE. (ed.), *The Higher Classification of the Orthopteroid Insects*, Lyman Entomological Museum Memoir 4, McGill University, Quebec, pp. 1-31.

- Morris, G. K. (1979). Mating systems, paternal investment and aggressive behavior of acoustic Orthoptera. *Fla. Entomol.* **62**: 9-17.
- Morris, G. K., and Fullard, J. H. (1983). Random noise and congeneric discrimination in *Conocephalus* (Orthoptera: Tettigoniidae). In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview Press, Boulder, Colo., pp. 73-96.
- Morris, G. K., and Gwynne, D. T. (1978). Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. *Psyche* **85**: 147-167.
- Morris, G. K., Aiken, R. B. and Kerr, G. E. (1975). Calling songs of *Neduba macneilli* and *N. sierranus* (Orthoptera: Tettigoniidae: Decticinae). *J. N.Y. Entomol. Soc.* **83**: 229-234.
- Parker, G. A. (1983). Mate quality and mating decisions. In Bateson, P. (ed.), *Mate Choice*, Cambridge University Press, Cambridge, pp. 141-164.
- Sakaluk, S. K., Morris, G. K. and Snedden, W. A. (1987). Mating and its effect on acoustic signalling behaviour in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): The cost of feeding females. *Behav. Ecol. Sociobiol.* **21**: 173-178.
- Thornhill, R., and Alcock, J. (1983). *The Evolution of Insect Mating Systems*, Harvard University Press, Cambridge, Mass.