OPPORTUNISTIC COURTSHIP FEEDING IN SAGEBRUSH CRICKETS

◆

SCOTT K. SAKALUK ◆ PATRICIA J. BANGERT
LARS V. SWANSON ◆ ANNE-KATRIN EGGERT
ECOLOGY GROUP ◆ DEPARTMENT OF BIOLOGICAL SCIENCES
ILLINOIS STATE UNIVERSITY ◆ NORMAL

◆ INTRODUCTION

The sagebrush cricket, *Cyphoderris strepitans* is one of only five extant species belonging to an ancient insect lineage, the Haglidae, believed to be ancestral to modern-day crickets and katydids (Orthoptera: Ensifera) (Morris and Gwynne 1978, Vickery 1989). *C. strepitans* occurs exclusively in mountainous areas of Wyoming and Colorado, where it is found primarily in high-altitude sagebrush meadow habitat. Adults become sexually active in May, shortly after snow melt, and remain active for the next 4-6 weeks. Pair formation is mediated through acoustic signaling by males, which functions to attract sexually receptive females (Snedden and Sakaluk 1992). 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 feeds on the male's fleshy hindwings and bodily fluids leaking from the wounds she inflicts, behavior which constitutes a form of courtship feeding (Dodson et al. 1983, Sakaluk et al. 1987, Morris et al. 1989, Sakaluk and Snedden 1990). At the same time, the female is secured by the male's abdominal pinching organ, a device known as a "gin trap" (Morris 1979).

The gin trap of a male *C. strepitans* consists of two pairs of recurved spines, one pair directed anteriorily and the other posteriorly, located on the 10th and 8th tergites, respectively. The spines are brought together, pinching the female's abdomen, as the male's tergites are telescoped inward during his attempts to secure genitalic contact (Morris 1979). Although the gin trap clearly serves a reproductive role, its precise functional significance remains unknown; comparable reproductive structures are not known from any other family of the Orthoptera.

The objective of the proposed research was to test four hypotheses related to the functional significance of the gin trap:

1) The gin trap functions to permit males lacking adequate wing material to force-copulate females (see Thornhill 1980, 1984 for assessment of a similar hypothesis concerning the dorsal clamping organ of male scorpionflies). The "forced-copulation" hypothesis assumes that previously-mated males lack sufficient wing material to preoccupy females during copulation.

2) The gin trap functions to prevent females from opportunistically feeding on males. The "opportunistic-feeding" hypothesis assumes that wing feeding is energetically costly to males, resulting in selection on males to deter females from adopting an "eat-and-run" strategy. The occurrence of opportunistic feeding by females has been documented in a number of gift-giving insect species (Bell 1980, Freidberg 1981, Berg and Valley 1985, Sakaluk 1987), including *C. strepitans* (Dodson et al. 1983).

3) The gin trap functions to prevent males from being displaced by rival males during copulation.

124

The "copulation-disruption" hypothesis implies that the gin trap serves to reduce the risk of cuckoldry and the concomitant risk of sperm competition (Parker 1970, 1984).

4) The gin trap functions to ensure the correct alignment of male and female genitalia. The "genitalic-alignment" hypothesis implies that the gin trap is required for successful spermatophore transfer.

◆ METHODS

The study was conducted from May 15 - June 25, 1992 at the University of Wyoming-National Park Service Research Center in Grand Teton National Park. Virgin males (as evidenced by undamaged hindwings) and females of unknown mating status were collected at night at two study sites previously established within the park (Deadman's Bar and Pacific Creek) and at one additional site near the Bridger-Teton National Forest. 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 head lamp. Females, because they are mute, were found by systematically searching the sagebrush. Captured crickets were transported back to the research center and maintained according to standard procedures (Sakaluk et al. 1987, Sakaluk and Snedden 1990, Snedden and Sakaluk 1992). Males were assigned to one of four experimental treatments: 1) males whose hindwings and gin traps were left intact, 2) males whose hindwings were left intact but whose gin traps were disabled, 3) males whose hindwings were removed but whose gin traps were left intact, and 4) males whose hindwings were removed and whose gin traps were disabled. The hindwings of males were removed by severing them at their base. The gin traps of males were disabled by shearing off the anterior spines with microscissors, and covering the posterior spines with nail polish applied with an entomological pin.

Each night of the study, one male from each of the four treatments was paired with a female, and their mating activity monitored over a 12-hour period using time-lapse video photography. Experimental pairs were confined in a Plexiglas viewing chamber, divided into four equal compartments to prevent contact between crickets of different pairs. Upon review of video recordings, the following data were obtained for each male: 1) the duration of calling, 2) the total number of mounts by the female, 3) the duration of each mount, and 4) the number of mounts that resulted in successful transfer of the spermatophore. A total of 88 pairs, 22 pairs in each treatment, were observed in the course of the study.

The four competing hypotheses concerning the function of the gin trap yield different predictions with respect to the outcome of the experiments. The forced-copulation hypothesis assumes the males with intact wings need not rely on the use of the gin trap to secure copulations, because these males can retain the cooperation of the female through courtship feeding. For such males, the hypothesis predicts that there should be no significant difference in the mating success of males whose gin traps have been left unaltered and those whose gin traps have been disabled. In contrast, males whose hindwings have been removed must rely on their gin traps to secure copulations; for these males, the hypothesis predicts that those with intact gin traps should experience a significantly higher mating success than males whose gin traps have been disabled.

In contrast to the forced-copulation hypothesis, the opportunistic-feeding hypothesis assumes that males are always at risk of the loss of resources to females who feed on their wings and dismount prior to the transfer of the spermatophore. Hence, the hypothesis predicts that males with intact gin traps should mate more frequently than males whose gin traps have been disabled, regardless of the condition of the hindwings.

The copulation-disruption hypothesis assumes that the gin trap confers an adaptive benefit only when copulating males are at risk of interference from neighboring males. Since experimental pairs were confined in the absence of rivals, the hypothesis predicts no difference in the mating success of males with or without intact gin traps, regardless of wing condition.

According to the genitalic-alignment hypothesis, the gin trap is required for the proper alignment of male and female genitalia during copulation. The hypothesis predicts that males lacking a functional gin trap should rarely, if ever, successfully transfer a spermatophore to the female, regardless of wing condition.

♦ RESULTS

CALLING ACTIVITY OF TREATED VS. UNMANIPULATED MALES

All but one experimental male exhibited at least some calling activity during the course of a trial. The amount of calling, measured as the number of 5-minute periods in which males called, was not significantly affected by either wing or gin trap treatment, nor was there any significant interaction of the two main effects (ANOVA, $F=0.31$, $p>0.05$). Based on the 5-minute sampling protocol, males called on average over a cumulative period of 268.5 minutes during the course of a trial ($n=88$, s.e. $=10.0$).

MALE MATING OPPORTUNITIES AND MATING SUCCESS

For a complete mating, the female must first mount the male and remain mounted long enough for the male to transfer the spermatophore. In the following analysis, only mounts that occurred before the first successful spermatophore transfer were considered, because it is unlikely that females in the field re-mount males, or even remain in their near vicinity after receiving a spermatophore. Males were mounted by females 6.6 times on average ($n=88$, s.e. $=0.9$). An ANOVA revealed no significant differences across treatments in the number of mounts ($=$mating opportunities), but the resulting F-value was only marginally short of statistical significance (ANOVA, $F=2.70$, $p=0.051$). Additional replicates would be useful here to increase the power of the statistical test and help clarify if there is indeed no effect of treatment on the number of mating opportunities secured by males.

In a total of 13 pairs, the female did not mount the male even once during the course of a trial. The frequency of pairs in which the female never mounted the male was not affected by gin trap treatment. In pairs involving males with intact hindwings ($n=44$), there were only three such pairs without mounts, one of which involved a male with an unmanipulated gin trap, and the others involving males whose gin traps had been disabled; this difference was not significant (G-test, $G=0.364$, $p>0.05$). For males whose hindwings had been removed, seven without a functional gin trap ($n=22$) and three with a functional gin trap ($n=22$) were not mounted at all; this difference also was not significant (G-test, $G=2.117$, $p>0.05$).

The proportion of pairs that successfully transferred at least one spermatophore was significantly affected by wing and gin trap treatment (Table 1, G-test: 15.784, $p<0.01$). Specifically, for males whose hindwings had been removed, those with functional gin traps experienced a significantly higher mating success than those whose gin traps had been disabled (G-test, $G=5.946$, $p<0.02$). However, for males whose hindwings had been left intact, there was no difference in the mating success of males with functional gin traps and those whose gin traps had been experimentally disabled (percentage of males transferring at least one spermatophore was the same, 36%, for both gin trap treatments). Another way of testing this effect is to compare the average number of matings males were able to obtain in each treatment. An ANOVA revealed significant differences across treatments in the number of spermatophores males transferred (ANOVA, $F=3.31$, $p<0.05$). Specifically, manipulation of the ability of males to feed females had a significant effect on the number of spermatophores transferred ($F=8.59$, $p<0.01$), whereas manipulation of the ability of males to secure females did not ($F=1.27$, $p>0.05$). There was no significant interaction between gin trap and wing treatments ($F=0.05$, $p<0.05$). The mean number of matings for males with hindwings was 0.41 (s.e. $=0.09$); for males without hindwings, the mean number of matings was 0.11 (s.e. $=0.05$).

Table 1. Mating success of male *Cyphoderris strepitans*.

Wing treatment	Gin trap treatment	Spermatophore transferred?	
		yes	no
intact	intact	8(36%)	14
intact	removed	8(36%)	14
removed	intact	4(18%)	18
removed	removed	0(0%)	22

126

◆ CONCLUSIONS

The lack of a difference across treatments in the amount of calling exhibited by males indicates that our experimental manipulations did not have any detrimental effects on the males' ability to call. Additionally, there were no significant differences across treatments in the number of times females mounted males, suggesting that females did not discriminate against males of different treatments prior to mounting.

Three of the four functional hypotheses were effectively falsified by our results. The opportunistic-feeding hypothesis predicted that in both wing treatments, males with intact gin traps should mate more frequently than males without functional gin traps. This prediction was not upheld; there was no difference in the mating success of males with or without intact gin traps when males' hindwings had been left intact. The copulation-disruption hypothesis predicted no difference in the mating success across treatments; however, the higher mating success of males with intact gin traps in males without hindwings was not consistent with this hypothesis. Finally, the fact that in the treatments with intact hindwings, males without gin traps transferred no fewer spermatophores than males with gin traps, shows that the gin trap is not required for a proper alignment of male and female genitalia during copulation and thus falsifies the genitalic-alignment hypothesis.

The only hypothesis supported by our data was the forced-copulation hypothesis. The gin trap of male *Cyphoderris* apparently functions as a device for males with insufficient hindwing material to force copulation upon females unwilling to accept their spermatophores. The gin trap aids in extending the duration of a mount long enough for the male to successfully extrude the spermatophore and attach it to the female genitalia.

◆ ACKNOWLEDGEMENTS

◆ LITERATURE CITED

Bell, P. D. 1980. Opportunistic feeding by the female tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae). Can. Entomol. 112:432-432.

Berg, C. O., and K. Valley. 1985. Nuptial feeding in *Sepedon* spp. (Diptera: Sciomyzidae). Proc. Entomol. Soc. Wash. 87:622-633.

Dodson, G. N., G. K. Morris, and D. T. Gwynne. 1983. Mating behavior of the primitive orthopteran genus *Cyphoderris* (Haglidae). In: Orthopteran mating systems: sexual competition in a diverse group of insects (ed. by D. T. Gwynne & G. K. Morris), pp. 305-318. Boulder: Westview Press.

Freidberg, A. 1981. Mating behavior of *Schistopterum moebiusi* Becker (Diptera: Tephritidae). Israel J. Entomol. 15:89-95.

Morris, G. K. 1979. Mating systems, paternal investment and aggressive behavior of acoustic Orthoptera. Fla. Entomol. 62:9-17.

Morris, G. K., and D. T. Gwynne. 1978. Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. Psyche 85:147-167.

Morris, G. K., D. T. Gwynne, D. E. Klimas, and S. K. Sakaluk. 1989. Virgin male mating advantage in a primitive acoustic insect (Orthoptera: Haglidae). J. Insect Behav. 2:173-185.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525-567.

Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: Sperm competition and the evolution of animal mating systems (Ed. by R. L.

Smith), pp. 1-60. Orlando: Academic Press.

Sakaluk, S. K. 1987. Reproductive behavior of the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae): calling schedules, spatial distribution, and mating. Behaviour 100:202-225.

Sakaluk, S. K., G. K. Morris, and W. A. Snedden. 1987. Mating and its effect on acoustic signalling behavior in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): the cost of feeding females. Behav. Ecol. Sociobiol. 21:173-178.

Sakaluk, S. K., and W. A. Snedden. 1990. Nightly calling durations of male sagebrush crickets, *Cyphoderris strepitans*: size, mating and seasonal effects. Oikos 57:153-160.

Snedden, W. A., and S. K. Sakaluk. 1992. Acoustical signalling and its relation to male mating success in sagebrush crickets. Anim. Behav. 44:663-639.

Thornhill, R. 1980. Rape in *Panorpa* scorpionflies and a general rape hypothesis. Anim. Behav. 28:52-59.

Thornhill, R. 1984. Alternative hypotheses for traits believed to have evolved by sperm competition. In: Sperm competition and the evolution of animal mating systems (Ed. by R. L. Smith), pp. 151-178. Orlando: Academic Press.

Vickery, V. R. 1989. The biogeography of Canadian Grylloptera and Orthoptera. Can. Entomol. 121:389-424.