

ACOUSTIC BEHAVIOUR IN CYPHODERRIS STREPTANS

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Objectives

Cyphoderris strepitans, is a primitive orthopteran which survives only in the mountains of Wyoming and Colorado (Morris and Gwynne 1978). The males rub their forewings together to produce a calling song. This stridulation is presumed to function, as in other acoustic Orthoptera, in attracting conspecific females for mating and in maintaining a broadcast territory around each singer.

Because of the unusual mating habits of this species, which involve the female feeding upon and wounding the male's hind wings (Dodson 1984), a male's history can be determined by inspection. This has allowed assessment of male mating success in field populations. We have discovered that once a male of *C. strepitans* has mated, he becomes much less likely to experience a second mating (Morris 1982). The breeding population rapidly develops two classes of males, virgin and non-virgin, one of which is doing very much better than the other at mating. Since males provide females with a substantial nuptial food gift, a spermatophylax, in addition to the underwing material, and since mated males may be compromised in the quantity and quality of their subsequent gifts, selection should have favoured females that identify and pair preferentially with virgin males. The major objective of our current research is to discover the function of male calling song in virgin male mating success.

We can erect several hypotheses as to the role of the calling song in the differential mating success of virgin and once-mated males. The simplest possibility is that males sing substantially less after having mated (Hypothesis 1). Another mechanism could involve females exercising active choice (Hypothesis 2): since it is reasonable to expect that wounding of the underwings will affect the physical structure of the song generated by the overlying forewings, females could choose to associate with a preferred partner by responding only to physical features of the song diagnostic of virgins. It is also necessary to consider a song diagnostic of virgins. It is also necessary to consider a third hypothesis: that male interactions, for example, the aggressive displacement of rivals from sites favouring access to females, could be the basis of the observed differential male success, with females consorting passively.

Another and more general objective of our research is to discover major features in the mating system of *C. strepitans*. The exact location of the overwintering burrows of these insects remains a mystery, but one reasonable possibility is that the burrows are clumped together in particularly suitable soil habitat. If females mate on emergence, then males might maximize their mating opportunities by establishing singing territories as near as possible to burrow

aggregations. Under these conditions one would expect to observe that mating events are geographically clumped. Since Cyphoderris adults undergo little net displacement on a given night, finding a male with freshly wounded wings or a female with an attached spermatophore can be taken to reveal the site of a mating as effectively as actual interception of a copulating pair. In 1985 we attempted to locate and map the sites of field matings.

To summarize, we had three specific objectives in 1985: in a singing activity experiment we tested hypothesis 1: whether virgin mating success is correlated with greater singing activity by virgins. In a phonotactic study we attempted to test hypothesis by demonstrating a) that females are attracted to male calling song and b) that females so attracted will discriminate in favour of virgin over non-virgin song. In a field distribution study we mapped the geographical distribution of freshly-wounded, i.e. just mated, males.

Methods

Singing activity experiment

Beginning May 20, 1985, adult males of C. strepitans were collected from habitat near Deadman's Bar in Grand Teton National Park. (They were not taken from the study area, see below). These males were classified according to the state of their metathoracic wings: unwounded, freshly wounded, and with old wing wounds. Four individuals were selected in each category for a total of 12 insects; these were caged individually and their singing activity monitored over the succeeding four nights. Each of 12 electret microphones was connected to a custom built microprocessor unit (Cade and Wyatt 1984); this device transferred data to a teletype. The microprocessor censused each microphone for input at intervals of 4 s, summed all active intervals to determine total singing time, and caused the teletype to print singing activity in decimal hours every 15 mins. At the completion of four nights of monitoring, a new complement of insects was collected in the field.

Phonotactic experiment

Adult females were collected from habitat in the vicinity of Deadman's Bar (but not from the study area, see below) on several nights during the course of the reproductive season. These were maintained at the Center and ultimately transported to Toronto, Canada, where they were tested for phonotactic responsiveness in a series of playback trials. Two speakers were placed 120 cm apart, facing each other. Six petri dishes, each containing a female, were lined across the arena diameter equidistant from the speakers. The dish lids were removed and playback of male song begun from one of the speakers selected at random. Playback continued for 30 min or until all insects had walked from the petri dish to cross the arena circumference. The point of each individual's exit was noted as was latency to locomotion and the total time spent in walking.

Field distribution study

At the Deadman's Bar site, a rectangular area of about 1.2 hectares was marked

by stakes and searched systematically on each night of the peak breeding season (May 22 - May 28). Searching began about 2200 hr, 30 min after normal singing activity was underway. The locations of adult females and of males with freshly wounded wings were marked with dated surveyor flags. On the final night (May 28), a more comprehensive census was completed: the locations of adult virgin males, adult non-virgin males with old wounds and of nymphs were flagged in addition to those of the adult females and newly wounded adult males.

Results

Singing activity experiment

The incidence of stridulation in the three classes of males is presented in Table 1. These data were transformed by long ($X + 1$) and subjected to a one-way analysis of variance. Bartlett's test (2 df) substantiated that the sample variances of the transformed data were suitably homogenous (Chi-square = 2.895; $0.1 < p < 0.25$). At the 5% level we were unable to reject the null hypothesis that the population means for the three classes of males (unwounded, recently wounded and past wounded) are identical. But the probability of an F value this high ($F = 2.75$) under the null hypothesis is only 7.5%.

Phonotactic experiment

Of the 37 females tested for phonotactic responsiveness to conspecific calling song, 21 (approximately 60%) had sperm in their spermatheca and had therefore mated prior to capture. The pattern of exits of these mated females from the arena is depicted in Figure 1; it does not differ significantly from that to be expected under a null hypothesis of no acoustic effect. Corrected for continuity, $df=1$, chi-square = 0.95, ($0.25 < p < 0.50$). The exit pattern of the remaining 16 unmated and therefore presumably sexually receptive females is presented in Figure 2. Once again the exits occur without regard to the location of the speaker. Chi-square = 0.38, $df=1$, ($0.5 < p < 0.75$). A substantially higher proportion of mated than unmated females failed to exit during these trials.

Field distribution study

Only a preliminary examination of these data has been carried out. Figure 3 is a map of the locations where males with freshly wounded wings were discovered during the 7 nights that incorporate peak breeding activity. There was no dramatic clumping of mating sites within the study area such as one might expect if emerging receptive females were confined to a limited region.

Conclusions

With regard to the singing activity experiment, we are very close to establishing a significant relationship between mating history and stridulation incidence. Such a result would be consistent with hypothesis 1. The phonotactic experiment allows us to conclude that females with stored sperm exhibit no

Table 1. Analysis of variance in singing activity between *C. strepitans* males grouped according to metathoracic wing status as unwounded, recently wounded and with old wounds.

Decimal hours of singing per 4 nights

| Unwounded | Fresh wounds | Old wounds | Source of Variation | df | SS | MS | F |
|-----------|--------------|------------|---------------------|----|-------|-------|-------|
| 1.48 | 3.41 | .03 | Total | 44 | 2.107 | | |
| .86 | .16 | .18 | Between male groups | 2 | 0.244 | 0.122 | 2.745 |
| .50 | .54 | 0.00 | Residual | 42 | 1.863 | 0.044 | |
| .28 | 0.00 | .74 | | | | | |
| .16 | 0.00 | .03 | | | | | |
| 3.03 | 0.00 | 1.61 | | | | | |
| .13 | 0.00 | .07 | | | | | |
| .21 | .44 | .44 | | | | | |
| 2.83 | 0.00 | .50 | | | | | |
| 3.65 | 0.00 | .05 | | | | | |
| .22 | 1.78 | 0.00 | | | | | |
| 0.00 | 1.89 | .13 | | | | | |
| 2.69 | .07 | 1.92 | | | | | |
| 0.00 | .07 | .03 | | | | | |
| .67 | .12 | - | | | | | |
| 3.26 | - | - | | | | | |

n=16 mean = 1.25 n=15 mean = 0.57 n=14 mean = 0.41

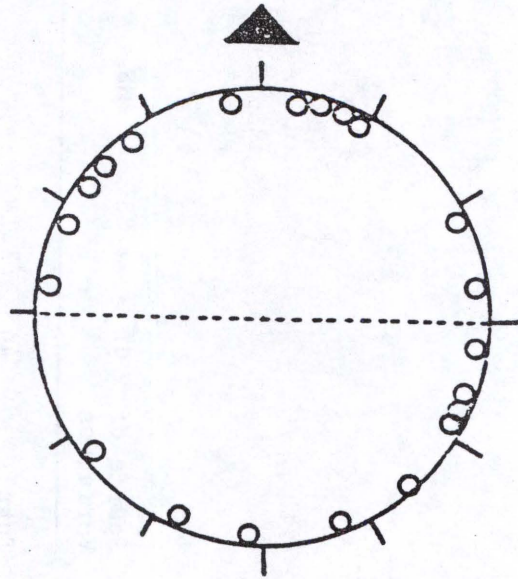


Figure 1. Exit distribution of mated *C. strepitans* females.

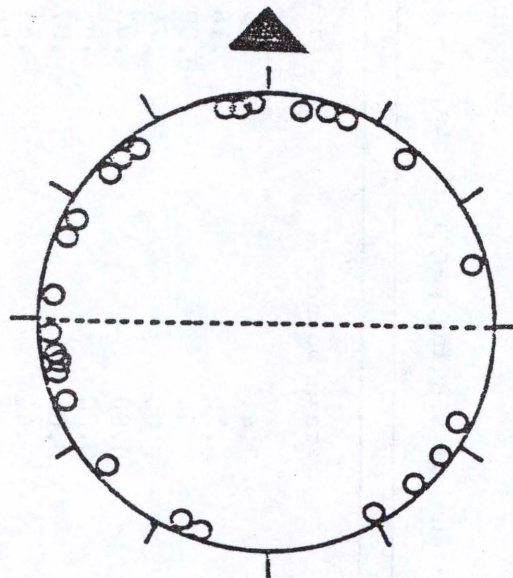


Figure 2. Exit distribution of unmated *C. strepitans* females.



Figure 3. Spatial distribution of freshly-wounded *C. strepitans* males May 22-May 28, 1985. Each location was mapped by measuring its angle from N and S respectively with a theodolite; the distance NS is 30 m.

attraction to the calling song of a conspecific male. This is consistent with the behaviour of some other acoustic Orthoptera, e.g. *Orchelimum gladiator* (Morris et al. 1975): once mated, the female's phonotactic response is extinguished. However the lack of phonotactic response by unmated *C. strepitans* females is puzzling. Even with a protracted 30 min presentation of calling song, 16 mature females which lacked sperm showed no tendency to approach the song of a calling male. This unexpected result is not in accordance with the behaviour of other acoustic Orthoptera. Given this outcome it was of course not possible to compare female preference for virgin over non-virgin song and to address hypothesis 2. The observed distribution of matings obtained in the field distribution study does not appear consistent with the hypothesis that females emerge and mate from clumped overwintering burrows.

Literature Cited

- Cade, W. H. and Wyatt, D. R. 1984. Factors affecting calling behaviour in field crickets, *Teleogryllus* and *Gryllus* (age, weight, density, and parasites). *Behaviour* 88:61-75.
- Dodson, G., Morris, G. K. and Gwynne, D. T. 1983. Mating behavior of the primitive orthopteran genus *Cyphoderris* (Haglidae). In D. T. Gwynne and G. K. Morris eds. *Orthopteran Mating Systems*. Westview Press, Boulder, CO.
- Morris, G. K., Kerr, G. E. and Gwynne, D. T. 1975. Ontogeny of phonotaxis in *Orchelimum gladiator* (Orthoptera: Tettigoniidae: Conocephalinae). *Can. J. Zool.* 53:1127-1130.
- Morris, G. K. and Gwynne, D. T. 1978. Geographical distribution and biological observations of *Cyphoderis* (Orthoptera: Haglidae) with a description of a new species. *Psych* 85:147-167.
- Morris, G. K. 1982. Differential pairing and mating in the primitive insect *Cyphoderis strepitans* (Orthoptera: Haglidae). Univ. of WY Nat'l. Park Serv. Res. Center Sixth Ann. Rept.