

REPRODUCTIVE BIOLOGY OF *CYPHODERRIS STREPITANS*:
COPULATORY BEHAVIOR AND THE EFFECT OF NUPTIAL FEEDING
ON MALE ACOUSTIC ACTIVITY

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Introduction

Cyphoderris strepitans is a relic species of the Haglidae, an ancient group abundant during the Triassic and thought to have given rise to the modern crickets and katydids. *C. strepitans* occurs in disjunct 'pockets' only in the mountains of Wyoming and Colorado and little is known of its role in the ecology of these sensitive areas.

Several features of this animals behavior are of interest to the evolutionary biologist. The mating period of *C. strepitans* occupies a very narrow time window of approximately 1 month and under ideal weather conditions most mating can take place within a period of several weeks. Males become acoustically active very early in the spring (early May) and are able to stridulate at temperatures below 0° C (Dodson et al 1983). In addition to providing females with a spermatophore at mating, males also provision females with a nuptial gift. This food gift takes the form of the male's fleshy matathorasic wings; females feed on the wing material, and resultant flow of hemolymph, while in copula. The mating behavior of *C. strepitans* has not previously been adequately described and thus it was the first objective of this study to quantify the specific behaviors of the copulatory sequence.

The environmental conditions under which males stridulate are extremely harsh and calling likely represents a physiologically costly endeavor. In a previous study (Sakaluk et al 1987) we hypothesized that non-virgin males, having invested in both a spermatophore and nuptial provisioning and thus lost a significant energy reserve, should be limited in their ability to sustain calling in a demanding environment. This should result in reduced attraction of females and consequently reduced remating success. The results of our 1986 study were inconclusive although significant differences between groups were noted (Sakaluk et al 1987). Our second objective was to retest this hypothesis using more sensitive techniques.

Methods

Adult male and female *C. strepitans* were collected, at night, from a primarily sage (*Artemisia tridentata*) meadow on the flood plain of the Snake River at Dead Man's Bar, Grand Teton National Park, during late May and early June 1988. Male mating status was determined by the presence (non-virgin) or absence (virgin) of metathorasic wing damage indicative of female nuptial feeding activity. Animals were transported to the University of Wyoming-National Park Service Research Center, housed individually in plastic snap-cap vials and provided pieces of apple as a food and water source. Pair-wise observation was facilitated by the use of a time-lapse video tape recorder. Pairs were placed into a plastic observation chamber, under dim red light, at approximately 1900 hrs. and allowed to freely interact until the following morning (approx. 0700 hrs.) at which time the tape was reviewed and mating behavior summarized. The timing, and duration, of (1) nuptial feeding, (2) copulation, (3) spermatophore transfer, and (4) spermatophore attachment were recorded. Additionally, the latency interval between spermatophore transfer and when the female first fed upon the spermatophore, and the time required to fully consume it were recorded. Males that mated in the chamber were released after use at a site close to their spermathecal contents to confirm sperm transfer. Additional mating observations were taken by S.K.S. at Illinois State University.

Males were collected as above. Only virgin males and males that showed evidence of having mated the night of collection (see Sakaluk et al 1987) were used in the calling activity experiment. Individuals were housed separately in plastic vials at ambient temperature. Food was not provided. Male calling activity was monitored the night following their capture. Males were placed individually into plastic acoustic chambers containing soil and sage, and fitted with an electret microphone. Microphones were connected to a custom microprocessor (Kidder and Sakaluk unpubl. man.) tuned to male carrier frequency (13KHz). The sensitivity of the microprocessor was adjusted such that there was no interference between channels (ie. microphones could not 'hear' calling activity in adjacent chambers). The temporal pattern of calling, and total calling duration were recorded for each individual and output to an Apple 2+ computer. Calling activity was monitored from approximately 1800 through 0800 hrs. This sampling period extended well beyond the actual range of calling activity. Males were released close to their point of capture the night following monitoring.

Results

A total of 25 male-female dyads were observed. The mating behaviors quantified are presented in Table 1. Successful copulation (transfer of spermatophore) occurred in 13 pairs. Of the 12 pairs in which copulation did not occur, female feeding on the male's underwings was observed in three pairs. No physical interaction was observed in the remaining pairs although males called actively in all cases. Two of the

Table 1. Summary of the copulatory sequence behaviors observed for 16 pairs of *Cyphoderris strepitans*. Means (\pm SD) are presented at the bottom of each column.

Number of feeding bouts	Wing feeding duration (min.)	Duration of wing feeding during coupling (min.)	Coupling duration (min.)	Latency (min)*	Spermatophore feeding Fully consume (min.) ⁺
1	1.05				
7	5.97	3.72	1.12		
2 ^a	7.50	6.65	2.57	25.47	12.57
2 ^a	6.67	4.25	4.63	5.62	15.32
4 ^b	7.18	3.97	3.97	213.07	11.35
1 ^b	8.38	8.38	8.38		
2	8.58	8.27	5.92	192.42	13.30
2	9.45	7.75	7.08	130.02	
3	5.90	4.18	3.05	202.52	
2	8.30	2.78	2.42		
3	5.03	3.00	3.00	105.43	41.75
8	9.68	3.07	2.23	57.72	
5	667.18	3.02	2.07	64.57	35.33
33	20.85				
22	25.92	1.35	1.35	83.90	
6	23.30				
2	2.22	1.95	1.48	73.67	
5	2.88	1.17	0.77	272.18	
(6.1 \pm 8.3)	(45.9 \pm 155.2)	(4.2 \pm 2.4)	(3.3 \pm 2.3)	(118.9 \pm 83.4)	(21.6 \pm 13.3)

* latency period was defined as the time lapsed from complete transfer of the spermatophore until the female initiated consumption of the spermatophore.

+ time required for female to fully consume the spermatophore.

a - pair remated during observation period.

b - pair remated during observation period.

pairs mated twice in one night and males attempted a second copulation in several cases. Full consumption of the spermatophore was observed in 5 cases. In one of these cases the pair mated twice in one night. Male use of the gin trap (genital claspers used to secure the female) appeared to increase in frequency as the mating season progressed. Wing feeding duration was significantly correlated with coupling duration. Correlations between coupling duration and (1) time to initiation of spermatophore consumption and (2) time to fully consume the spermatophore were not significant.

Total nightly calling was transformed [$\log(\text{calling duration}+1)$] prior to analysis. Analysis revealed no significant difference between groups in total nightly calling duration (ANOVA, $P > 0.05$). Calling duration was not significantly different between groups when adjusted for the covariate effect of temperature (ANCOVA, $P > 0.05$) or seasonal effect (ANOVA, $P > 0.05$) or temperature + seasonal effect (ANOVA, $P > 0.05$). A reduction in nightly calling duration associated with season was noted for both groups. Calling data were thus divided into 'early' and 'late' blocks for subsequent analysis. The division point was determined as the date corresponding to an equal proportion of virgins and non-virgins in field collections predicted from the regression of percent virgins on standardized date (Fig 1). Calling data are in Table 2. This yielded an overall difference between the four groups (ANOVA, $P < 0.05$). Total calling by the "early virgin" group was greater than the "early non-virgin" group (Fisher PLSD, $P < 0.05$). Total calling did not differ between the non-virgin subgroups (Fisher PLSD, $P > 0.05$) or between the two late subgroups (Fisher PLSD, $P > 0.05$). Calling by the "early virgin group" was significantly greater than both the "late virgin" group (Fisher PLSD, $P < 0.05$) and "late non-virgin" group (Fisher PLSD, $P < 0.05$).

Conclusions

Mating observations indicate that females are able, at least occasionally, to feed on the male hindwings while avoiding mating. Females may supplement their protein intake with a 'free meal'; this could constitute an important protein source for females in a protein poor environment. Selection should act on males to prevent such theft, and the male gin trap has likely evolved to this end. The correlation between wing feeding duration during coupling and coupling duration suggests that males are allowing females to feed on their wings only as long as it takes to transfer the spermatophore. This suggestion is further supported by the observation that coupling is male terminated. Nuptial provisioning of females reduces male ability to sustain high levels of calling. This affect was most pronounced early in the mating season when environmental conditions were most harsh. The convergence of virgin and non-virgin calling duration late in the season, at a level below that of earlier males, suggests that these virgins are less vigorous. Some males are likely out-competed for access to females early in the season. As most mating takes place over a short period of time, there is a premium on sustained calling early in the season when

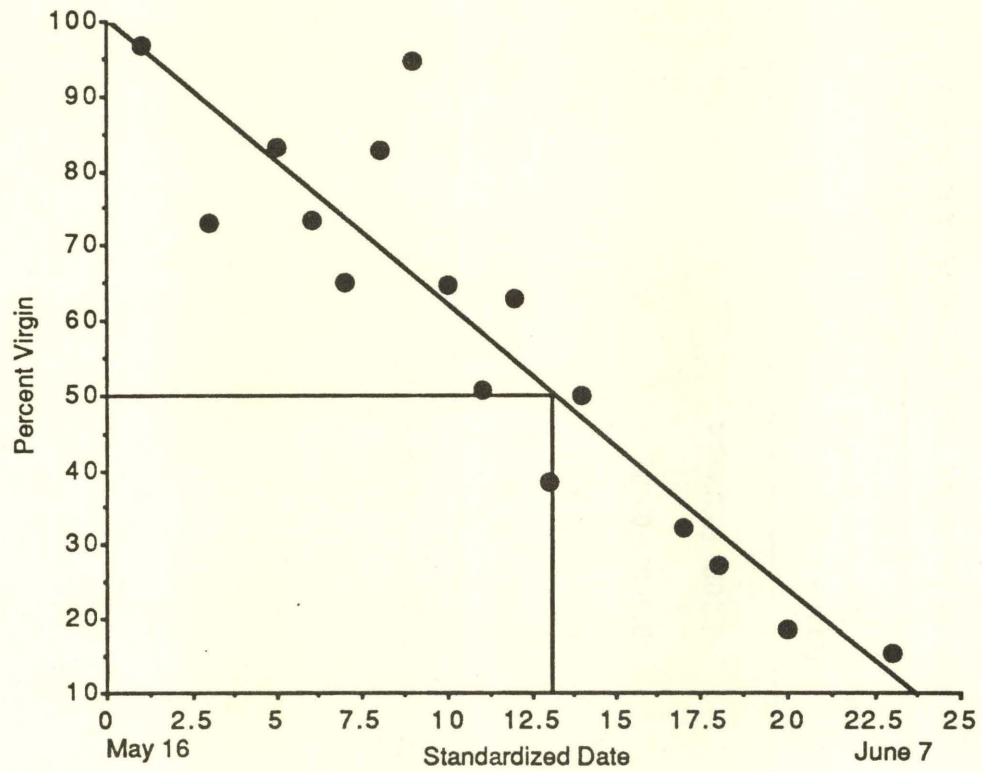


Figure 1. Percentage of virgins in field surveys regressed on standardized date (day 1 = May 16). This relationship was used to predict the date at which virgins represented 50% of the male population.

Table 2. Nightly calling durations of virgin and non-virgin male *Cyphoderris strepitans*.

Group	Calling Duration (hours) (mean \pm SD)
Early season virgin	1.165 \pm 0.83abc
Early season non-virgin	0.343 \pm 0.48a
Late season virgin	0.198 \pm 0.41b
Late season non-virgin	0.453 \pm 0.83c

Means with the same letter are significantly different (Fisher PLSD, $P < 0.05$).

the relative number of virgin females is highest.

Literature Cited

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