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PHONOTAXIS IN MOLE CRICKETS: ITS REPRODUCTIVE SIGNIFICANCE¹

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The southern mole cricket, *Scapteriscus acletus*, is known throughout the Southeast as an important agricultural and turfgrass pest. Several decades of research on these insects have not yielded satisfactory control methods, perhaps because little has been learned of their basic biology and reproductive behavior. This lack of knowledge stems from the fact that mole crickets are burrowing crickets, spending most of their lives underground.

Male and female external morphologies are identical except for the forewings. Male *S. acletus*, as in many cricket species, produce sound to attract sexually responsive females (Alexander 1975). The sound producing apparatus is manifest as a black spot on the male's forewing; it consists of a scraper and a stridulatory file on each forewing. Sound is produced during stridulation when the scraper of one wing rubs the file of the other wing.

Although this apparatus is typical of acoustical crickets, mole crickets are unique in their acoustical behavior. Males call from within special burrows they construct each night prior to calling. Using their fossorial forelegs and large pronotum, males pack and shape the opening of their burrow into an exponentially expanded horn. Bennet-Clark (1970) has shown that this shape amplifies male calling songs in 2 European mole crickets, *Gryllotalpa gryllotalpa* and *G. vineae*. This amplification probably holds true for *S. acletus* (Nickerson, Snyder, and Oliver 1979). Male *S. acletus* produce a continuous trill during the calling period. This song is species-specific with a carrier frequency of about 2.7 kHz modulated at 50 pulses per second (Ulagaraj 1976).

I placed individual *S. acletus* males in soil-filled, 19-liter buckets. These buckets were covered with aluminum screen to prevent the male escaping, placed in a pit, and surrounded by a trapping device (Fig. 1). Males could then be observed for calling behavior and responding animals trapped around the buckets. A modification was made to assess flight from buckets: the aluminum screen cover was removed and the entire trap covered with a cylindrical hardware cloth cage. Individuals flying from buckets hit the cage, fell, and were trapped around the buckets.

Twelve *S. acletus* males were monitored for nightly calling period with respect to sunset (Fig. 2a). Individual males differed significantly in their

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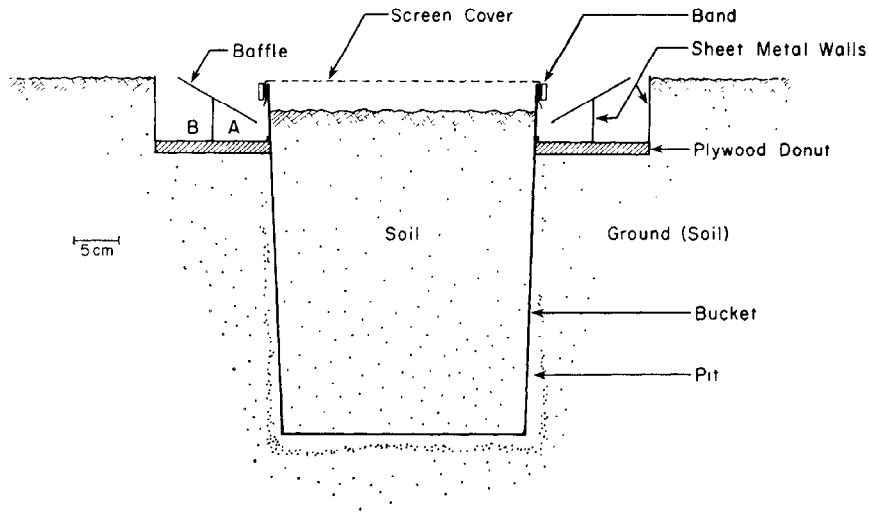


Fig. 1. Bucket trap. *Scapteriscus acletus* males were placed in soil-filled, 19-liter, plastic buckets and observed for calling behavior. Animals attracted to calling males were trapped around the bucket and an aluminum baffle prevented escape. Flying mole crickets were trapped in inner donut A; those crawling toward males were caught in outer donut B.

starting times and each male also showed smaller variation in its starting time than in its stopping times. This smaller variation suggests some importance in starting at this particular time or in not starting prior to the time. Starting of calling correlates with starting of female flights, as measured by observing females confined in buckets (Fig. 2b). Males starting to

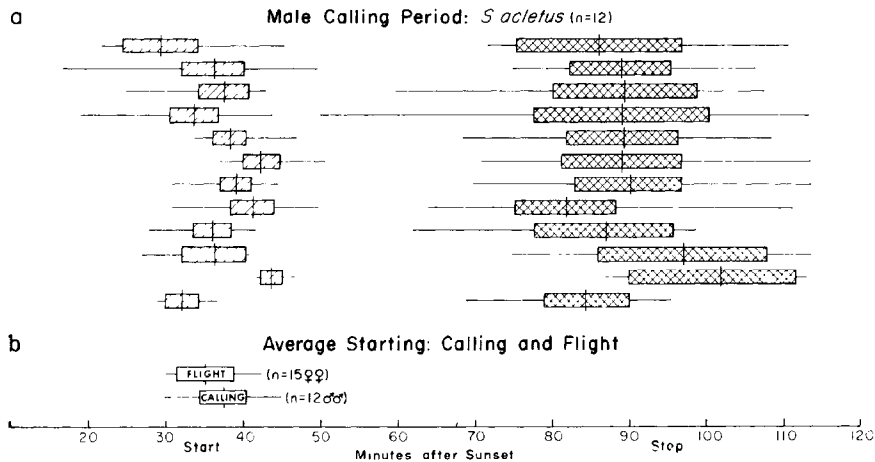


Fig. 2. a) Twelve *S. acletus* males caged outdoors were monitored for calling period with respect to sunset. Vertical lines are means, horizontal lines are ranges, bars represent 95% confidence intervals of means. Significant individual differences in starting times are evident. b) Fifteen *S. acletus* females caged outdoors were observed for start of flight. Starting of flight and male calling are closely correlated.

call too early would be wasting energy whereas those starting too late would not attract early flying females.

Scapteriscus acletus flights occur from April to July in the spring with a smaller flight from October to January in the fall. These flights consist of about 80 percent females, and both males and females respond to calling males (see below). These flights are the major form of dispersal in mole crickets and allow a flying individual to monitor a large number of calling males. If a flying female can hear calling males only if they are closer than 6 m (a conservative assumption), if flight speed is 11.8 km/h (Ulagaraj 1975), $0.01/\text{m}^2$ (Kleyla and Dodson 1978), a female in straight-line flight for 5 minutes should hear more than 60 calling males.

Females therefore have the opportunity to assay a large number of calling males. If there are differences (significant to female reproduction—see below) in these males revealed in their calls, then females should selectively respond to certain males. High nightly variances in numbers attracted to individual calling males in bucket traps suggest that females choose certain males over others. Four males calling within 20 m of each other on 3 nights attracted totals of 66, 32, and 16 mole crickets. Each night 1 of the 4 males attracted a disproportionate share of the totals: 43 (65%), 28 (87%), and 9 (56%) respectively. What parameters of the call do individuals use to selectively respond to the call?

Until recently, prior to the revived interest in sexual selection, the chief concern with acoustical insects was whether females responded principally, or only, to conspecific calls (Alexander 1975). Conspecific attraction was convincingly demonstrated by flying *S. acletus*. Of 179 *S. acletus* attracted to 12 *S. acletus* males and 12 *S. vicinus* males, only 2 were trapped at the heterospecific call of *S. vicinus*, a number equaling that trapped at controls (Table 1). Ulagaraj and Walker (1975) showed that this specificity was due to differences in pulse rates and carrier frequencies of the 2 calls.

Scapteriscus acletus males show so little variation in those 2 parameters (Ulagaraj 1976) that it seems unlikely that females use them to choose among conspecific males. Intensity, however, is one parameter that varies greatly between males and in individual males on successive nights. More than 100 years ago, Charles Darwin noted the importance of intensity in female choice and male competition in acoustical Orthopterans.

“. . . those individuals which were able to make the loudest or most continuous noise would gain partners before those which were less noisy . . .”

Are females actually selecting louder males or is it that a louder call travels farther and is therefore heard by more females? Increasing the intensity at the sound source by 6 decibels (dB) will approximately double

TABLE 1. SPECIFICITY OF RESPONSE TO CAGED CALLING MALES BY *S. acletus*. BUCKET TRAPS (FIG. 1), GREEN ACRES FARM, UNIVERSITY OF FLORIDA, MAY 1979.

Sound source	Number attracted
Conspecific (<i>S. acletus</i>)	175
Heterospecific (<i>S. vicinus</i>)	2
Control (No male)	2

the distance at which the sound can be heard. Sound radiates in all directions from the sound source. Predictions that can be made as to the effect of a 6 dB increase in intensity on response to the call included these 3: 1) If individuals fly in a single plane, maintain straight line courses of flight, and come from outside the area of the sound field, twice as many should respond. This doubling corresponds to the doubling of sound field diameter. 2) If individuals fly in one plane in a randomly changing direction or if they come from within the sound field area, a 4-fold increase would be expected, corresponding to the increase in sound field area. 3) If individuals fly randomly at all heights there would be a predicted 8-fold increase in response, corresponding to the increase in sound field volume. It does not seem likely that this last prediction can hold true. Flying insects increase risks and energetic costs at altitudes above or below some "optimal" height that varies with the insect and the circumstances of the flight. Mole crickets, for example, must fly high enough to avoid obstacles and low enough to detect calls and minimize energetically expensive ascending flight. Most would be expected to fly at nearly the same height on a given evening over given terrain. Small variances in altitude of flight are known to be the case for migrating butterflies (daytime) and migrating moths (night) (e.g. Arbogast 1966, Schaefer 1976).

Individual *S. acletus* males in bucket traps were monitored for nightly intensities during their calling period. Maximum intensity at a distance of 15 cm from the funnel opening was measured using a Model 2219 Bruel and Kjaer sound level meter. Intensity rarely changed more than 1 dB during the nightly calling period. Individuals attracted to the calling males were counted at the end of the calling period.

When calling males were classified nightly as high or low intensity males differing by 3-5 dB, on only 1 night (of 5) did a low intensity male attract any individuals (Table 2). Total numbers attracted to high intensity males were 52 compared to 3 attracted to low intensity males for the 5 nights. High intensity males averaged 10 times as many attracted individuals per male per night as low intensity males (Table 2). Differences other than intensity

TABLE 2. SIX NIGHTS WHEN CALLING MALES NO MORE THAN 20 METERS APART COULD BE SEPARATED INTO HIGH- AND LOW-INTENSITY CALLERS WITH THE GAP BETWEEN THE CATEGORIES 3-5 dB. NO INDIVIDUAL OCCUPIED THE SAME POSITION MORE THAN ONCE IN THE 5 NIGHTS.

Date	Interval (dB)	Number of Callers		Number of Mole Crickets Trapped	
		low dB	high dB	low dB	high dB
11 Apr.	5	1	2	3	29
13 Apr.	4	2	1	0	3
15 Apr.	3	1	3	0	6
18 Apr.	3	1	2	0	6
21 Apr.	4	1	2	0	8
Average		1.2	2	0.6	10.4
Average/Male/Night				0.5	5.2

in male calls were not controlled and could explain some differences in attraction.

Mole cricket calls can be synthesized by electronic "artificial crickets," small, self-contained units that produce identical, constant signals at controlled intensities. With these sound units it was possible to test flying mole cricket response to the equivalent of identical calling males differing in intensity alone.

Two blocks of 3 treatments each were tested for 22 nights. Treatments consisted of: 1) high intensity (range 107-111 dB); 2) low intensity (6 dB below high intensity); 3) control (no sound source). Intensities were measured 15 cm above the speaker. Signal output, calibrated weekly, was a 2.7 kHz carrier frequency modulated at 50 pulses per second.

Catching devices were the same as Ulagaraj and Walker (1975) and were placed on the circumference of a 20 m diameter circle. Each of the 6 positions were 10 m from the circle center and adjacent treatments. Treatments were randomized so that each treatment appeared in every position within a block over a 3 night period. Sound units were assigned a sequence around the circle and this sequence was unchanged with each unit remaining within 1 of its original position.

The numbers caught in similar treatments were summed each night. No mole crickets were trapped in controls during the 22 nights of testing. When the ratio of numbers caught in high intensity traps to numbers caught at low intensity traps is plotted against their sums (Fig. 3), the slope of the regression line does not differ significantly from 0. High intensity traps

EFFECTS OF 6dB INCREASE: *S. acletus*

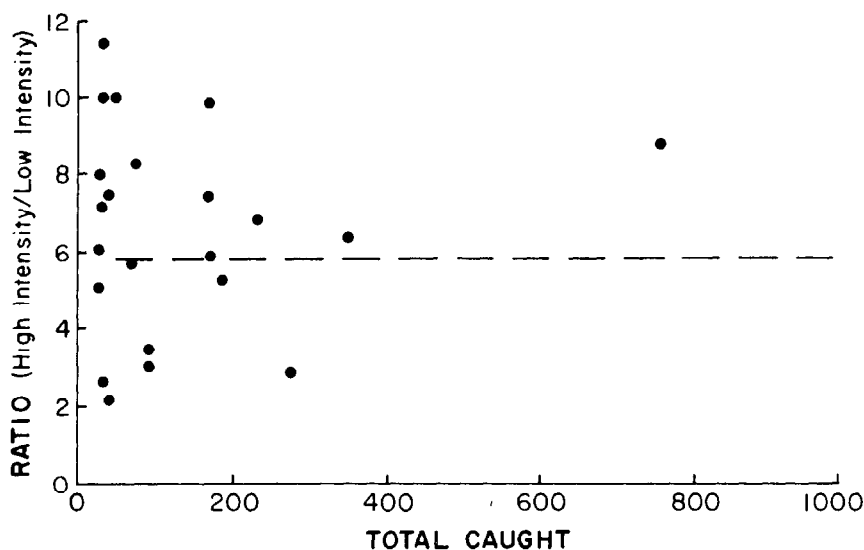


Fig. 3. Results of 22 nights of broadcasting artificial *S. acletus* calls at 2 intensities 6 dB apart. Each dot is a nightly ratio of numbers trapped at high intensity calls to numbers trapped at low intensity calls. Dashed line is overall ratio (5.7). These results differ from those of Ulagaraj and Walker (1975) and can be explained by female choice but not by simple physical models.

showed nearly a 6-fold increase in response compared to low intensity traps. This increase is significantly higher (Table 3) than the 2 or 4-fold increase expected for the 6 dB increase in intensity (see predictions above). Ulagaraj and Walker (1975) reported a doubling in response with a 6 dB increase. They used tape players, amplifiers, and speakers of questionable quality and the calls may have been distorted at higher intensities.

It appears that smaller differences in intensities of naturally calling males make larger differences in response (10-fold for 3-5 dB difference—natural males; 6-fold for 6 dB difference—"artificial crickets"). The artificial crickets, both high and low intensities, were much higher in intensity than natural males; perhaps selectivity decreases when the intensities compared are both abnormally high. Morris et al. (1977) have shown that sound power (intensity) is an important factor in response of females *Conocephalus nigropleurum* to taped male calls. I have shown that flying mole crickets are selectively responding to louder calls and that they must be able to distinguish between relative intensities of calls at the source.

To determine what affects the intensity of males in the field, 4 large males (from the upper third of the male size range) and 4 small males (from the lower third of the male size range) were monitored 15 days for intensity (Fig. 4). Intensities were measured as before.

Two things appeared to affect intensities of males. After rainfall the calls of both large and small males increased in intensity (Fig. 4). As days passed without rainfall, and soils dried, intensities of calling gradually decreased over successive nights. Soil moisture probably affected the males' ability to construct efficient exponential horns, and intensity output lowered. The second factor affecting calling intensity was male size. Although ranges overlapped, the average intensity of the large males was higher than that for small males on every night. Male tegmina have certain sound resonating membranes. A larger male is able to apply more power to larger membranes and therefore would produce a call of higher intensity.

Why do flying mole crickets select louder males? Female mole crickets build egg chambers in the soil and therefore soil moisture is an important factor in egg deposition (Hayslip 1943). Females may use intensities of males to locate areas of moist soil to lay eggs. Females may also use relative intensities of males in an area as a cue to male size. Females responded to higher intensity calls and therefore larger males who on the average are better equipped genetically to acquire needed resources.

Male response to calling or tapes of calling conspecific males have been shown to occur in several acoustical Orthopterans (e.g. *Gryllus integer*, Cade 1979; *Orchelimum* spp., Feaver 1977, Morris 1971; *Scapteriscus* spp.,

TABLE 3. COMPARISON OF NUMBERS OF *S. acletus* TRAPPED AT 107-111 dB ("HIGH") AND AT 6 dB LOWER INTENSITY ("LOW").

Total catch (22 nights)	2979
Total catch (high)	2536
Total catch (low)	443
Ratio estimate (high/low)	5.7
95% Confidence interval	5.2-6.3*

*Binomial distribution $p=0.85$

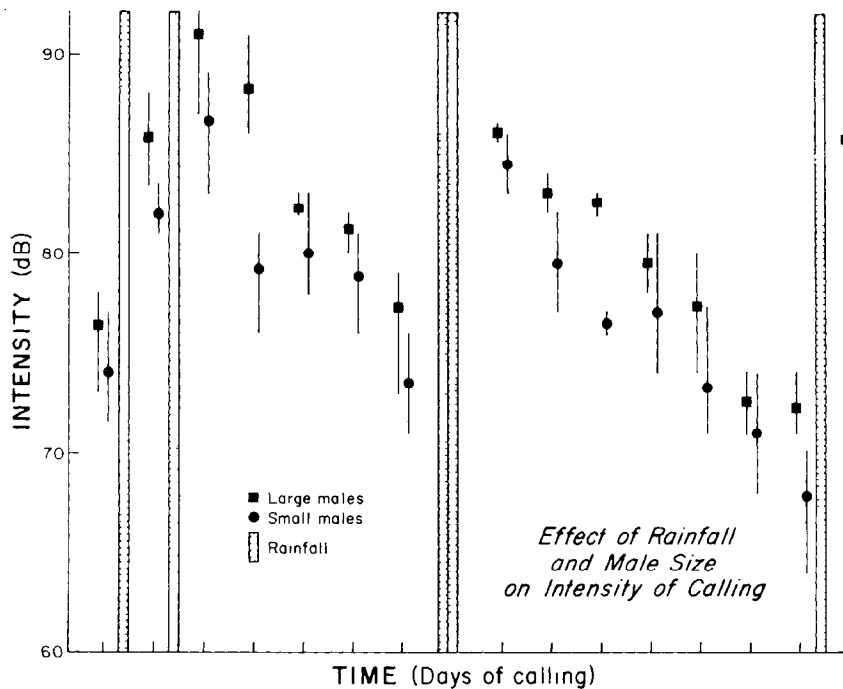


Fig. 4. Effects of soil moisture and male size on intensity of calling by *S. acletus* males: large males ($N=4$) and small males ($N=4$) were monitored nightly (20 May-4 June 1979). Squares and circles are mean intensities of large and small males respectively. On any given night the calls of large males were more intense than small males. Intensities increased for males of both sizes after rainfall and gradually decreased over subsequent successive dry days.

Ulagaraj and Walker 1973). Ulagaraj and Walker (1973) and Mangold (1978) have shown that males of other acoustical Orthopteran species (*Neonemobius mormonius*, *N. cubensis*, *Oecanthus niveus*, *O. celerinictus*, and *Gryllus rubens*) respond to taped calls of *S. acletus*. These cricket species have mating calls with pulse rates similar to *S. acletus* and are all flying crickets. This suggests that male response may be widespread, especially in crickets that disperse by flight. Flying males can monitor calls to locate suitable habitats to land. Flying male mole crickets may respond to louder males to locate areas of high soil moisture and thereby good calling sites. Increased soil moisture increases intensity of calling resulting in increased numbers of females responding. Flying males may land near calling males because of the females that are attracted. Most females have mated before the first seasonal flight (Ulagaraj 1975). This raises the possibility that males and females are able to find each other by other means—underground or walking on the surface. Flying males may land near calling males and search for females. Cade (1979, 1980) has demonstrated alternative male tactics in the field crickets (*Gryllus integer*). Reasons for these alternative behaviors include pressures on calling males who attract parasitoid flies, *Euphasiopteryx ochracea*, and other conspecific males that may attack the

caller. These parasitoids are also attracted to *S. acletus* calls (Mangold 1978); this result may be due to similarities in pulse rates of *S. acletus* and *G. integer* calls.

The mating system of *S. acletus* appears to have a high amount of female choice resulting in high variances in the numbers attracted to individual calling males. This selectivity correlates with calling intensity to a degree greater than is predicted by physical models about sound fields. I have shown that calling intensities are affected by soil moisture and male size, and I have suggested reasons why intensities may be important in the response of flying mole crickets. There are, however, questions that must be asked but can not be answered at this time. 1) Can males mate with or sequester more than 1 female on a given night? The individuals responding to a male calling in a trapping device were unable to influence the male's behavior. A male may stop calling after only 1 female enters his burrow and therefore no other mole crickets may enter that evening. Preliminary tests were inconclusive. 2) Do all females that respond to a male's call mate with that male? Females responding to calls have previously mated. They may use calls to locate suitable habitats and lay eggs fertilized by another male. 3) What do responding males do once they have landed near a calling male? Do they run into the burrow and fight with the caller? Do they search for females that the male is attracting? Are they using his call to locate a good calling site and will they wait until the following night to compete for females by calling?

These questions and others must be addressed before male reproductive success can be evaluated by the response of mole crickets to calls. This system, because of its high amount of female response, offers an unparalleled opportunity to study female choice in phonotaxis to male calls of acoustical Orthopterans.

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DIVERSITY IN THE NESTING BEHAVIOR
OF MUD-DAUBERS
(*TRYPOXYLON POLITUM* SAY; SPHECIDAE)*

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The pipe-organ mud-dauber, *Trypoxylon politum* Say (Sphecidae: Larrinae), constructs long tubular mud nests under bridges and in tree holes. The female provisions each cell of her nest with paralyzed spiders, lays an egg and seals the cell with a plug of mud (Cross et al. 1975). Building a new mud nest is the commonest method of acquiring one, but there are at least 4 other ways. A female may abandon her nest at any stage in the nesting sequence and another female may take it over. Sometimes a wasp moves into a nest that is occupied by another, and the 2 then jointly provision the same brood cell. Occasionally a wasp parasitizes a conspecific by

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