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## 9. Calling Songs and Mate Choice in Mole Crickets

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The study of acoustic communication in insects has undergone a natural progression. Early observations of acoustic signaling were casual and came about from the study of other aspects of the animals' biology. Later investigations became more intensive and distinct signals were associated with the specific behavioral contexts. Calling songs were soon found to be useful in the initial recognition of species as well as determining their geographic distributions (Alexander 1962). With the advent of electronic recording and playback devices, calling songs were analyzed and used to elicit female response. However, most experiments have dealt with the specificity in the response, have used virgin or 'sex-starved' females, and have been carried out under laboratory conditions (Walker 1957, Zaretsky 1972, Morris et al. 1975, Paul 1976).

The fact that females respond to calling males and this response is related to reproduction makes this signaling system amenable to the study of sexual selection and female choice. Selection will favor females that discriminate among males at a distance and reduce time and risk spent locating a mate. Extending this one step further, females may be able to recognize and keep track of individuals for extended periods of time (Lloyd 1981). Conversely, there will be selection on a male's salesmanship, or perhaps his acoustic deception. In recent years, however, theoretical speculations regarding adaptive significance of chorusing (Alexander 1975, Greenfield and Shaw 1982), sexual selection, and reproductive competition in insects (Blum and Blum 1979) have far surpassed their demonstration in the field.

In this chapter, I describe the study of acoustic behavior, phonotaxis, and mate choice in two species of mole cricket, *Scapteriscus acletus* and *vicius*, under natural conditions. Both species were inadvertently introduced into the United States (Walker and Nickle

1981), and because of the lack of specialized predators and parasites they occur in enormous numbers and are considered major pests. Mole crickets inhabit early successional stages such as pastures and cultivated fields. Flight is an important feature of their biology allowing individuals to locate and colonize these ephemeral environments; landing is usually in response to the calling song of a conspecific male.

## METHODS

Observations of male calling behavior and phonotaxis were made in a large bahiagrass pasture at Green Acres Farm, Department of Agronomy, University of Florida. Males of each species, *S. acletus* and *S. vicinus*, were placed individually into 19-liter, soil-filled, plastic buckets. The buckets were covered with aluminum screen wire fastened by a metal band to prevent the males escaping, placed into pits in the ground, and surrounded by trapping devices (Fig. 1A). Calling behavior of individual males could be observed, and responding mole crickets (male and female) were trapped around the bucket.

### Male calling periods

Twelve males of each species were monitored nightly throughout their calling period. Individual starting time (in minutes after sunset) was noted when the male began continuous calling (i.e. did not stop more than 1 min). Each male was inspected every 5-10 min during the calling period until calling stopped.

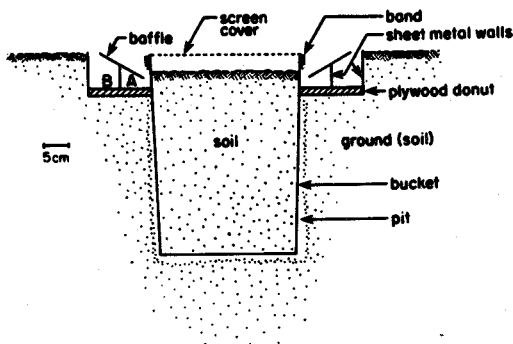
Maximum calling intensities, (dB(A) re .0002 dynes/cm<sup>2</sup>) at a distance of 15 cm above the burrow opening, were measured using a model 2219 Bruel and Kjaer sound level meter. Measurements of intensity for each male were taken within the first 5 min of calling and at each subsequent inspection.

### Flight periods

To assess the start of flight the trapping device (Fig. 1A) was modified by covering it with a 60 cm x 60 cm (dia. x height) hardware-cloth cylinder with lid. Buckets, with screen covers removed, contained one to five females. Females attempting to fly from buckets hit the hardware-cloth cage, fell, and were trapped around the bucket. Time of flight was recorded for individual females.

Landing times of males and females responding to conspecific males were determined by counting the number

A



B

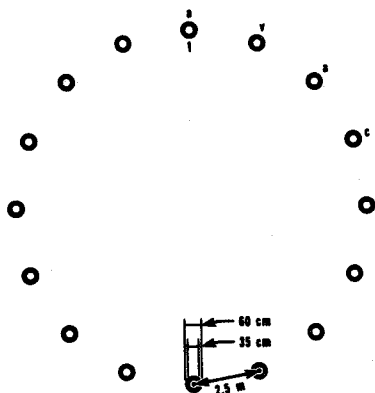


Fig. 1. A. Bucket trap. Crickets attracted to calling males were trapped around the bucket and an aluminum baffle prevented escape. Flying mole crickets were trapped in inner ring A; those walking toward males were caught in outer ring B (from Forrest 1980).

B. Experimental design (a - *acletus*, v - *vicinus*, c - control)

of mole crickets trapped at calling males during 5-minute intervals beginning at sunset.

#### Mate choice

Sixteen traps, divided into four blocks of four, were placed 2.5 m apart (center to center) around the

circumference of a circle. Each block had a control (bucket containing no male) and three calling males (two of one species and one of the other, depending on the flight season). In each block, buckets with conspecifics were alternated with buckets containing heterospecific males or controls (Fig. 1B).

A treatment within a block was randomly assigned to position one on the circle (Fig. 1B). Blocks were sequentially arranged around the circle, with treatment sequences the same in all blocks. Treatments were sequentially rotated within blocks each night unless no individuals were attracted to any of the males. Block positions were randomly changed after 3 days of treatment rotation. During a 16-day period each bucket occupied every position on the circle. The design served as an outdoor arena where naturally responding mole crickets could choose among neighboring, calling males. Wild calling males within 3 m of the arena were removed.

#### Effects of male size and soil moisture on intensity

Four large (from upper third of male size range) and four small males (from lower third) were monitored nightly (*acletus*, 20 May - 4 June, 1979; *vicinus*, 12 March - 3 April, 1980) for calling intensities, measured as before.

Males call from within acoustic horns constructed in soil (Nickerson et al. 1979), and soil moisture may affect the horn's efficiency in propagating sound. Calling intensities of eight *acletus* and four *vicinus* males were measured for 15 nights (20 May - 4 June, 1979). The occurrence of rainfall between nightly calling periods was noted. Though no measurements of soil moisture were made, it was assumed that after a rain, soil had a higher moisture content than before, and that moisture decreased daily in the absence of rain.

#### Post-flight behavior

In previous experiments males and females trapped at calling males were unable to interact with the caller. In order to observe the calling male and mole crickets responding to and interacting with him, a soil-filled bucket containing a marked male was buried in the ground so that the bucket lip was at ground level. A headlight with a red filter (mole crickets appeared insensitive to red light) was used during all observations.

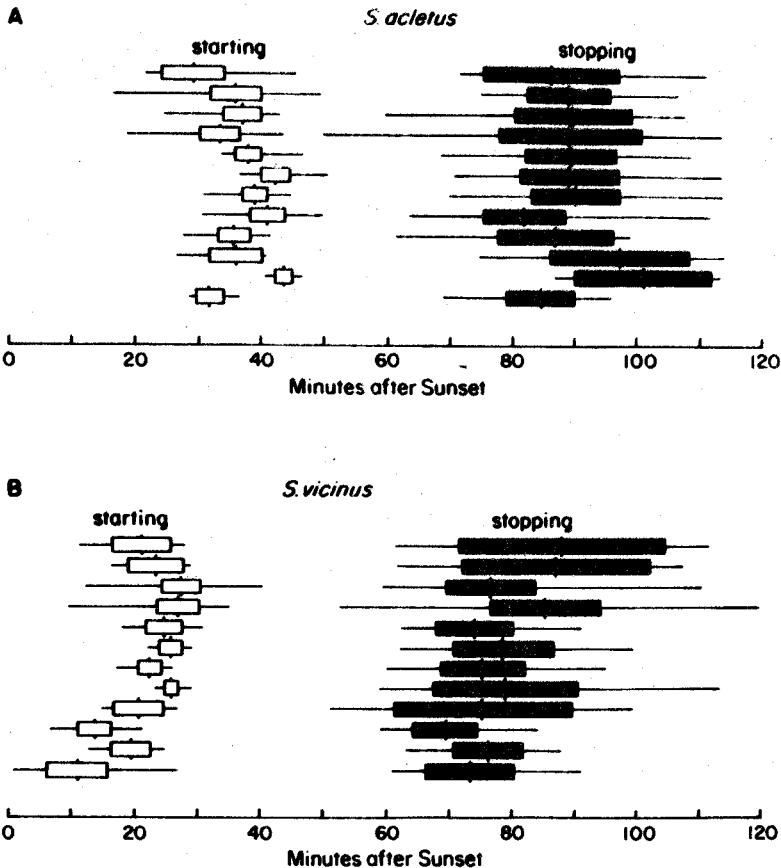


Fig. 2. Individual male calling periods for 12 *acletus* (A) and 12 *vicinus* (B) males. Vertical lines are means, horizontal lines are ranges, and bars represent 95% confidence intervals of means of starting and stopping times of calling by individual males. First eight *acletus* and first four *vicinus* were monitored 18 May - 7 June 1979; the remaining individuals were monitored 10 April - 21 April 1979 (Fig. 2A modified from Forrest 1980).

## RESULTS AND DISCUSSION

*S. vicinus* males began calling significantly earlier than *acletus* males. Once started, males of both species produced continuous trills and rarely stopped during the calling period, which lasted about an hour. Males showed

significant intraspecific variation in their starting times (Fig. 2). Selection could have acted upon variation of this type to produce the species-specific calling periods. Males showed smaller variation in starting times than in stopping times, suggesting that the onset of calling is critical and may be related to a sudden availability of flying females. Males calling prior to the start of flight would waste energy and incur excess risk from phonotactic predators and parasitoids, while those calling after flights had begun would have missed the opportunity to attract females that had already landed.

Flights, consisting mostly of females, were synchronous with calling periods. The beginning of flight was restricted to a brief period (10-15 min) soon after sunset and was similar in timing to the start of calling (Fig. 3). The temporal distribution of landing showed a rapid increase in the number of mole crickets ending flight during the first 15 min and a gradual decline throughout the remaining 30-45 min of the flight period. Flight ceased prior to the end of calling.

Availability of females only in brief synchronous flight periods would not be predicted on the basis of continual maturation of females (see Walker 1982a). For mole crickets that spend most of their lives in the safety of an underground burrow, flight is perhaps the most hazardous activity ever undertaken. Selection pressures from daytime, visual predators (mainly birds) should restrict mole crickets to nocturnal flight. But flight is also endothermic: mole crickets must warm up thoracic muscles to temperatures above 25°C before take-off is possible (Ulagaraj 1975, Prestwich, unpublished data) and they do not attempt to (or cannot) fly when air temperatures are below 17°C. Since *acletus* and *vicinus* inhabit temperate regions where late evening temperatures during the flight season are often less than 17°C, flight would be restricted to warmer parts of the day. Selection from daytime predators and energetic restraints on flight caused by cool temperatures would result in aerial activity occurring at the warmest dark time, i.e. soon after sunset. That male *Gryllotalpa vineae* in France call soon after sunset (presumably when females are in flight, Bennet-Clark 1970) and that flights of *Gryllus integer* in Texas occur only during the first 3 h after sunset (Cade 1979a), support the idea of temperature restraints on flying crickets inhabiting temperate areas.

Climates with little cooling during the night should not impose such temperature constraints on endothermic flights. One species of mole cricket introduced into Puerto Rico from tropical Brazil has been reported to fly late in the evening (Barret 1902), and males of this

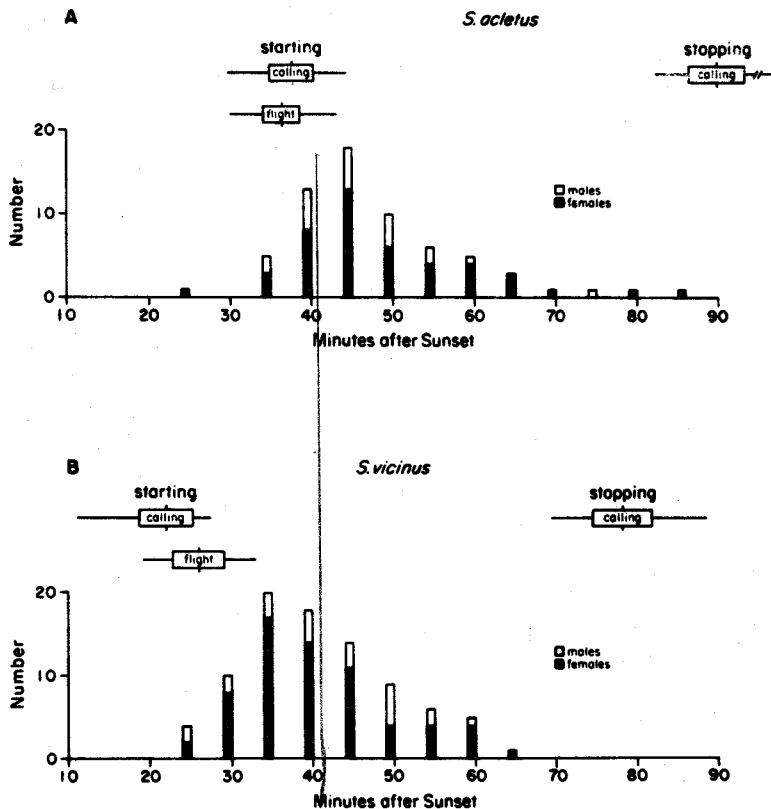


Fig. 3. Male calling and flight periods for *acletus* (A) and *vicinus* (B). Vertical lines are means, horizontal lines are ranges, and horizontal bars are 95% confidence intervals of means of start of calling and flight, and the end of calling. Vertical bars represent the numbers of male crickets landing (i.e. stopping flight) at calling males during 5-min intervals beginning at sunset.

species have been observed calling at times other than twilight (Forrest in prep. a). Also, Walker and Whitesell (1982) found female *Anurogryllus muticus* flying to lights in Panama as late as 0349 hours.

The evolution of synchronous, early evening flights may also have been influenced by nocturnal predators (e.g. bats). Individuals flying with large numbers of conspecifics may decrease their chances of being captured (Hamilton 1971). That flights are synchronous not only

with respect to time of night but also with respect to the nights on which they occur support this contention.

Walker (1982a) proposed one other hypothesis for brief synchronous calling by males. If most females respond to males only at certain times of the day, males calling at other times attract few females. Females that respond at the time of maximum calling have the benefit of maximum choice among males as mates. The result can be a positive feedback mechanism in which females force males to display simultaneously by responding only during a brief period on any day. Walker termed such a concurrent display a spree and discussed it as the temporal analog of a lek. Whether or not sprees in mole crickets are maintained by selection in the context of female choice or by selection in the context of predation and energetic constraints on flight is unknown. The two need not be mutually exclusive.

When heavy rainfalls occurred during calling periods, *acletus* males usually called later the same evening, when flights would not be expected. One possibility is that since *acletus* occur in low, poorly drained areas males may call to attract females that have been flooded from their burrows and that will crawl to the safety of a male's burrow and mate with him. Although it is uncertain whether or not females ever walk to calling males without first having flown, calling late at night after a rain and at seasons when flights do not occur (cf. Fig. 1 of Walker 1982b and Fig. 3 of Ulagaraj 1975) is indirect evidence for it.

The response of flying mole crickets to calling males was highly specific (Table 1). Of 150 *vicinus* responding to calling males, 147 (98%) were attracted to conspecifics. Similarly, 284 of 292 (97%) responding *acletus* were trapped at *acletus* males. Numbers of individuals responding to heterospecific calls did not differ significantly from the numbers trapped at

Table 1. Responses of flying mole crickets to males calling outdoors in an experimental arena.

Species calling	Experimental set-up			Number attracted		
	male	male- control	control	con- specific	hetero- specific	con- trol
Year	nights					
<b><i>acletus</i></b>						
1979	12	198	8	175	2	2
1980	4	45	4	109	3	1
Total	16	243	12	284 (193♀)	5	3
<b><i>vicinus</i></b>						
1979	12	140	8	19	0	0
1980	8	87	4	128	2	1
Total	20	227	12	147 (117♀)	2	1



controls. This specificity is due to differences in pulse rates and carrier frequencies of the two calls (Ulagaraj and Walker 1975).

During flights that may last more than 15 min and cover distances over 1.5 km, females are able to hear, assess, and respond to a large number of calling males (Forrest 1980). If differences in males that are important to female reproductive interests exist and are

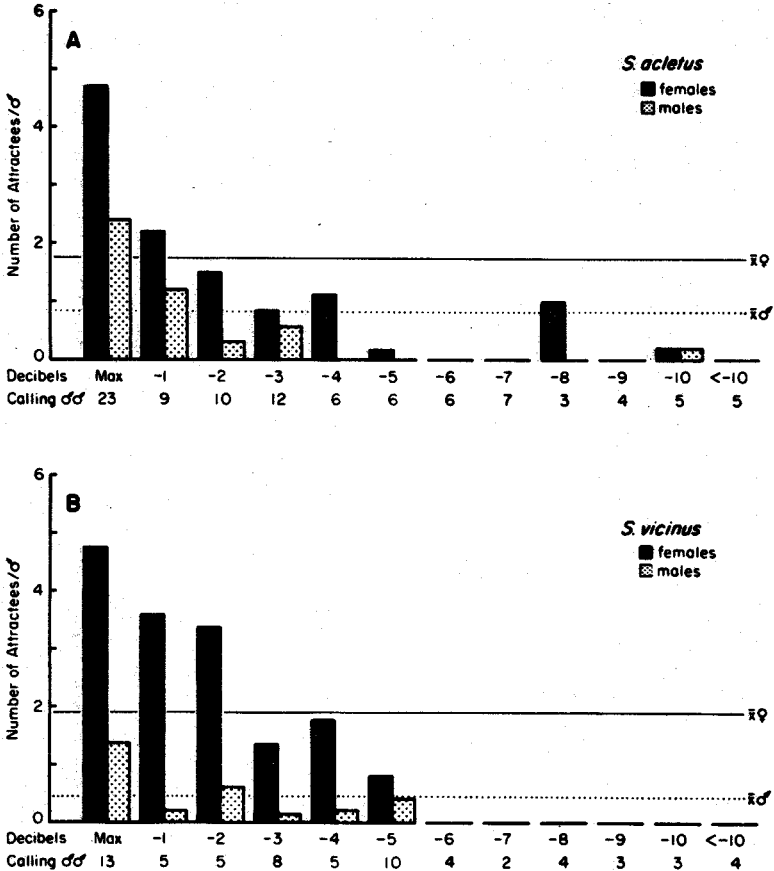


Fig. 4. Effect of calling intensity on the number of individuals attracted for *acletus* (A) and *vicinus* (B). Bars represent the numbers attracted per male to males calling in each rank (number of males in rank indicated below ranking). Solid horizontal line indicates average number of females attracted per calling male each night (calculated by dividing total number of females attracted by total number of male-nights). Dotted horizontal lines are average number of males attracted per calling male each night (from Forrest in prep. b).

revealed in their calls, sexual selection theory predicts that females should respond to certain males in preference to others. High nightly variances in the number of mole crickets attracted to males calling in an outdoor arena indicated that females (and males) are choosing among males on the basis of their calls.<sup>1</sup> A single *vicinus* male attracted as many as 27 *vicinus* females during a calling period, while neighboring males calling within 20 m attracted as few as none. Corresponding figures for *acletus* were 24 and 1.

These high variances were attributable to intensity differences between the males (Forrest in prep. b). Conspecific males calling in an arena were ranked nightly, relative to the intensity of the loudest male (max. dB, Fig. 4). On nights when three or more males

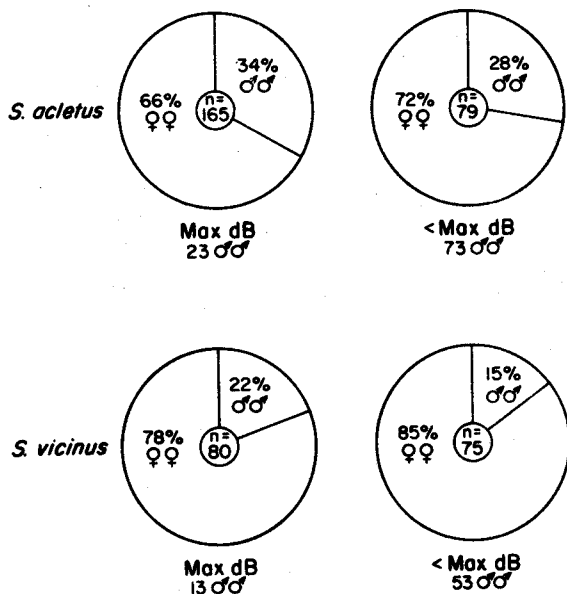


Fig. 5. Sex ratio of mole crickets attracted to loudest (max) and to all conspecifics in lower ranks.

<sup>1</sup> When three or more calling males attracted a total of four or more individuals, the nightly ratios of the variance to the number of crickets attracted per male (i.e. normalized variance,  $s^2/\bar{x}$ ) were  $>1$  on 18 of 20 nights for *acletus* males and 10 of 10 nights for *vicinus* males. The mean ratios were 5.5 (*acletus*) and 3.7 (*vicinus*). That the ratios are greater than 1 shows a nonrandom (clumped) distribution of landing crickets with respect to calling males.

attracted a total of more than three individuals, only males ranked at or near (1-2 dB below max.) the loudest male, attracted above average numbers of mole crickets per male (horizontal lines, Fig. 4). Males ranked 3 or more dB below the maximum intensity male never attracted more mole crickets per male than average, and 20 *vicinus* males ranked more than 5 dB below the loudest male calling the same night, attracted no mole crickets (Fig. 4B). Overall, the loudest males attracted 6.5 times (*acletus*) and 4.4 times (*vicinus*) more mole crickets per male than all other conspecific males (Fig. 5). The sex ratios of mole crickets responding to maximum intensity males and of those responding to all other males were not significantly different (Fig. 5).

Flying mole crickets selectively respond to louder males. If intensity is the cue used in this response, mole crickets must be able to distinguish between the relative intensities of the calls at the source. In other words, mole crickets in flight must be able to recognize distances to individual males and compensate for the attenuation of sound over these distances. Power level received is dependent upon the power level of the source and distance from the source to the receiver. A low-intensity male could be perceived as louder than the most intense male if he, the low-intensity male, were much closer to the receiver.

Morris et al. (1978) showed that sound power was important in the phonotactic response of female *Conocephalus nigropleurum* and gave two possible mechanisms for distance perception by females, frequency mixture and triangulation. The use of frequency mixtures (due to differential attenuation of frequencies in the calling song spectrum) seems an unlikely candidate for distance perception in mole crickets. The frequency spectrum of the calling song has a narrow band and does not contain both audible and ultrasonic frequencies as do calls of *C. nigropleurum*. Since observations on mole cricket flight are difficult, testing the use of triangulation by flying mole crickets to locate males would be difficult and would entail using tethered females in the laboratory. One other possible mechanism exists (T.J. Walker, personal communication). Sound pressure doubles (increases 6 dB) as the distance to the sound source is halved. By flying directly at a source (calling male) and detecting the rate at which the sound pressure increases, a mole cricket could determine the distance to the caller and the source intensity. Repeated orientation need not be involved.

How mole crickets select louder males (proximate explanations) is perhaps less interesting than why this selective response has evolved (ultimate explanation, Alcock 1979). Below I discuss some of the reasons why

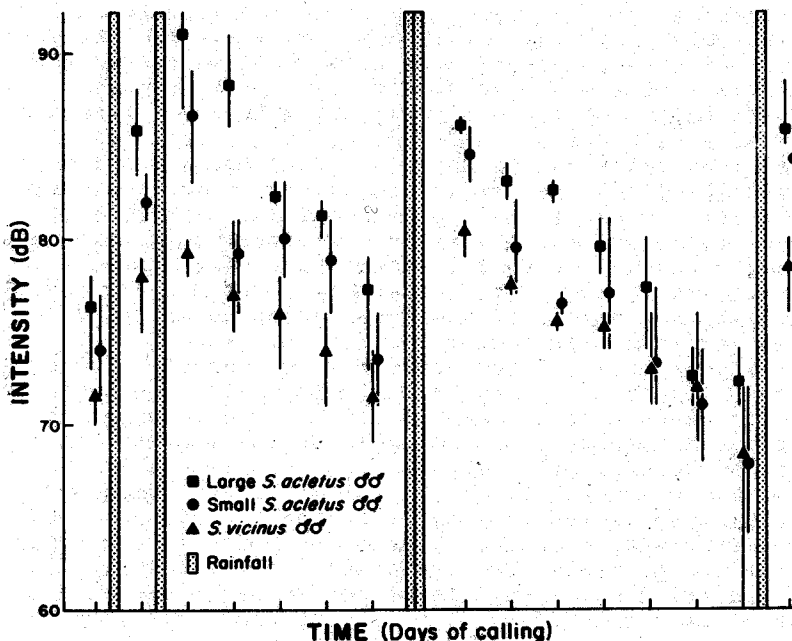


Fig. 6. Effects of male size and soil moisture on intensity of calling. Symbols represent mean intensities and vertical lines are ranges (modified from Forrest 1980).

males and females may show preferential response to more intense calls.

Two factors influenced the intensity of a calling male. After rainfall, calls increased in intensity (Fig. 6). As days passed without precipitation and soil dried, calling intensities gradually decreased over successive nights. Soil moisture probably affected a male's ability to construct an efficient exponential horn; wetter, more rigid horn surfaces probably propagated sound more effectively. Male size also influenced intensity of calls. In 1979 when four large males and four small males were monitored nightly for intensities, the average intensity of large *acletus* males was higher than that for small *acletus* males on every night. ( $n = 15$ , Fig. 6). In 1980 experiments, on 7 of 10 nights the average intensities of large *vicinus* males were greater than for small *vicinus* males. Larger males are probably able to apply more power from large muscles to drive larger wing membranes, and thus produce more intense signals.

Females may use the intensity of calls as a cue to male size. Females responding to high intensity calls (other things being equal) would be responding to larger males that might, on average, be better equipped genetically to acquire resources needed to attain large size. In both *acletus* and *vicinus* the average size of males is significantly larger than that of females (pronotal lengths and mass, unpublished data). Such a sexual difference indicates selection for large size in males and may be related to the correlation between large size and intensity: larger males have higher intensity calls, higher intensity calls attract more females, therefore large males sire more offspring, i.e. make greater genetic contributions to following generations.

Females deposit eggs in chambers at various depths in the soil, and moisture content is an important factor in egg development (Hayslip 1943). Females may use the intensities of calling males to locate moist soil in which to lay eggs. Depths of egg cells, determined by soil moisture, may be an important factor in whether or not newly eclosed nymphs can successfully dig to the surface. *Scapteriscus* females do not care for eggs and young as do *Neocurtilla hexadactyla* females. *Scapteriscus* females ovipositing in moist soil could deposit eggs closer to the surface, avoid the dessication of eggs, and increase survival chances of offspring after eclosion.

Observations of postflight behavior of females that were allowed to interact with the calling male revealed that most females did not enter the calling male's burrow (*acletus*, 68%,  $n = 19$ ; *vicinus*, 71%,  $n = 7$ ; Fig. 7). These females remained on the soil surface 1-10 min and then burrowed into the ground. Some *acletus* females ( $n = 6$ ), captured while burrowing, were placed individually into soil-filled, 19-liter, plastic buckets. Half of these later produced egg cells. Females that entered the caller's burrow left the buckets 1-3 days after entering and never produced egg cells (*acletus*,  $n = 7$ ; *vicinus*,  $n = 2$ ).

Females do not take over male burrows as in *Anurogryllus* (West and Alexander 1963). Using specialized forelegs, *Scapteriscus* females (and males) can construct burrows more rapidly than *Anurogryllus* females and thus reduce risk of predation. The benefits to females received from a male's burrow are probably much less for *Scapteriscus*. Female mole crickets may also have to fight with larger males and risk injury in order to take over a burrow.

When a female entered a calling male's burrow, the courtship song of the male was soon heard. After this, males (one *acletus* and one *vicinus*) sometimes returned

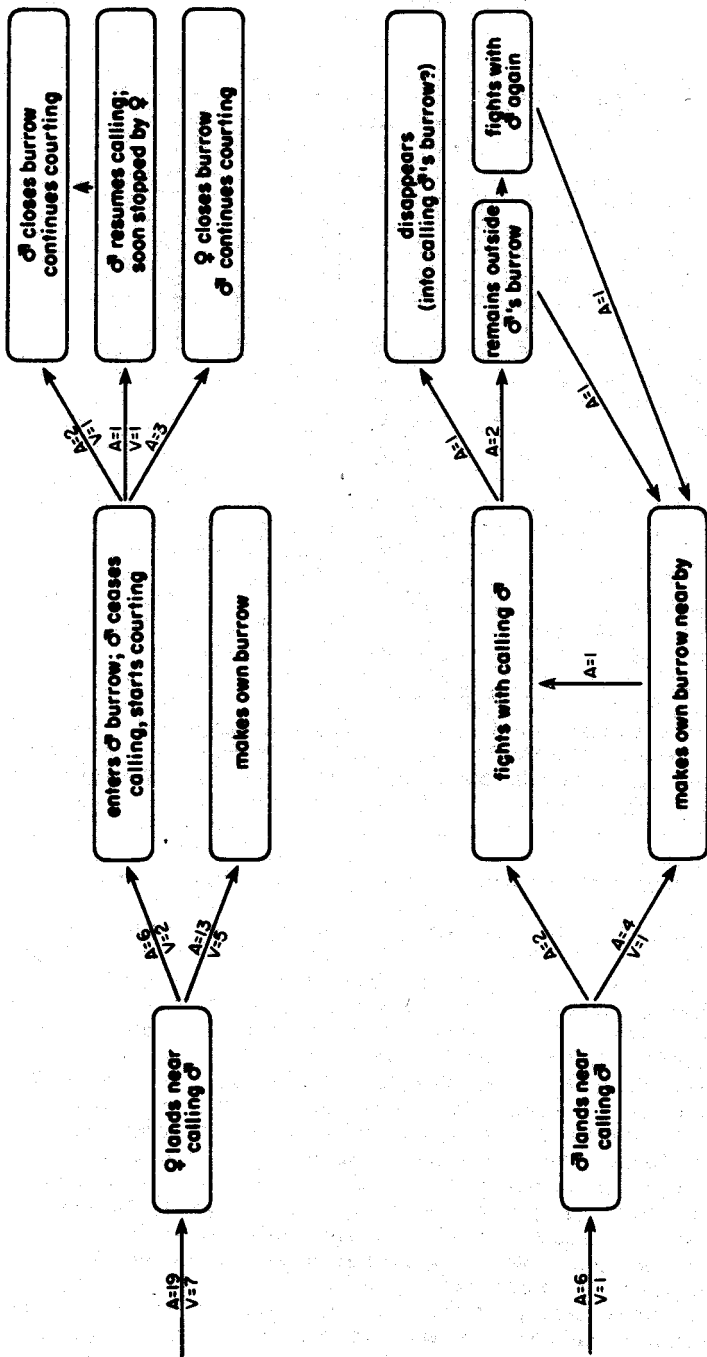


Fig. 7. Postflight behavior of males and females. A (acletus) and V (vicinus) identify number of individuals observed for behaviors shown.

to the burrow opening and closed it by filling it with dirt; males generally close burrows at the end of a calling period (Kleyla and Dodson 1978). Males (one *acletus* and one *vicinus*) also returned and continued calling. In both instances the female confronted and fought with the male. The males stopped calling and closed the burrow entrance. Before he stopped calling, the *acletus* male attracted another female but she did not enter his burrow. On three occasions *acletus* females closed the male's burrow (Fig. 7).

A conflict of interest seems apparent. Males should be selected to continue to call, attract, and sequester as many females as possible during a brief calling period, but females should be selected to monopolize superior males and oviposition sites, avoiding competition from other females. By stopping male calling or by closing the male's burrow, females make the attraction of other females unlikely.

Male mole crickets that fly do not have the opportunity to call for mates but certain benefits obtained through flight would outweigh the costs. Flying male mole crickets may use the calls of males as a cue to locate suitable habitat. Responding to louder calls, males land in areas with high soil moisture (i.e. good calling sites). Increased soil moisture increases a male's intensity; by calling in moist soil a male may increase intensity 15 dB over that in dry soil (Fig. 6), while increases of as little as 3 dB are effective in attracting large numbers of females (Fig. 4).

To investigate the possibility that males use calls to locate suitable calling sites two *acletus* males were marked as they burrowed into the soil near a calling male. On subsequent nights all calling males in the area were located and captured; neither of the two males was found.

Males may also respond to calling males because of the females attracted there. Selectively responding to louder calls would bring males into areas abundant with females. Cade (1979b, 1980) has demonstrated alternative male tactics in *G. integer*. Silent males remained in the vicinity of a calling male and courted females responding to the caller. Cade suggested that this alternative behavior is maintained in the population because of opposing selective forces: callers attract females, but they also attract aggressive conspecific males and acoustically orienting parasitoid flies.

Of six *acletus* males watched upon landing, two entered the calling male's burrow but were expelled. These males remained just outside the opening to the caller's burrow and one of the two re-entered and fought with the caller once more. Males remaining outside the

entrance to the burrow may have been waiting to follow females as they entered the burrow, therefore avoiding conflict with the resident male and possibly stealing fertilizations. Both expelled males subsequently made their own burrows nearby (Fig. 7). Other males responding to calling conspecifics made their own burrows upon landing. On one occasion a male excavated his tunnel from one side of the caller's acoustic horn. The caller continued calling. The respondent's digging activity filled the horn with dirt and lowered the caller's intensity 3 dB. The caller soon detected the intruder and the two fought. The resident male resumed calling. The intruder was not found in his side tunnel and may have been in the caller's burrow system, possibly awaiting the arrival of females attracted by the caller. Had the intruder completed the construction of the side tunnel, females entering the caller's burrow might have been diverted away from the caller by the dirt filling the horn entrance. Behavior involving trickery, deceit, and cuckoldry are known in a few insect species (e.g. Thornhill 1979, Lloyd 1980), but more observations are needed to fully understand the significance of phonotaxis in male mole crickets. Nothing is known about the subterranean habits of these crickets. Perhaps males (both callers and noncallers) search for, locate, and mate with females underground. Male *Anurogryllus arboreus* are known to search for and mate with females in their burrows during the evening after calling has stopped (Walker 1982b).

Calling male mole crickets appear to have a high possibility of attracting a mate; a loud male may attract as many as 27 females in one calling period. There are, however, many other factors that must be considered: (1) Relatively few (32% *acletus* and 29% *vicinus*) females attracted to a calling male enter his burrow. (2) Upon entering a caller's burrow, females often prevent the male from calling, decreasing his time spent calling and the number of females he can attract. (3) Although females mate with the male, there is little assurance that his sperm will fertilize her eggs. Females may fly to and mate with other males on a subsequent night. Spermathecae of almost all females responding to males already contain sperm that could compete at the gametic level for fertilization of ova (Parker 1970, Sivinski 1980), or females might manipulate their sperm stores to their own advantage (Lloyd 1979). (4) Calling males also attract other males that fight with the caller, reducing his chances of attracting more females. These responding males may ultimately compete for females and calling sites.

The average number of females attracted per male-night was 0.794 for *acletus* males and 0.515



for *vicinus* males (Table 1). Corrected for females not entering the male's burrow (approx. 70%), a male must call an average of 4.2 nights (*acletus*) or 6.5 nights (*vicinus*) before a female enters his burrow. However, these averages count for little when considering the high variances in numbers of mole crickets attracted to individual males calling in close proximity. If the number of crickets attracted to a male is in some way correlated with a male's reproductive success, then this system offers an accessible measurement of variances in male reproductive success. And if phenotypic differences used by females to choose mates are heritable this would lead to evolutionary change via sexual selection. The fact that large numbers of nonvirgin females from wild populations respond with such variances to calling males night after night, makes this system unique for the examination of female choice (of calling song parameters) and the relation of choice to acoustically mediated pair formation.

#### SUMMARY

Male acoustic behavior and resulting phonotactic responses were observed in two species of mole crickets under natural conditions. Calling periods began soon after sunset and lasted about an hour. Calling periods corresponded to female flight activity.

High nightly variances in numbers of mole crickets attracted to individual calling males (in an outdoor arena) indicated flying mole crickets use calls to discriminate among calling males. A calling male attracted as many as 27 females during a calling period while another male calling within 20 m attracted none. Flying mole crickets selectively responded to higher intensity calls.

Calling intensities were correlated with male size and soil moisture. Observations on post-flight activities of responding mole crickets revealed that females use calls to locate oviposition sites as well as mates, soil moisture being an important factor in egg development. Males, by responding to louder calls, locate areas with numerous females and moist soil (i.e. good calling sites).

Because large numbers of nonvirgin females from wild populations respond preferentially to certain males, this system is unique among acoustically mediated, pair-forming systems in its potential for the study of sexual selection and female choice.

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