Singing Schedules and Sites for a Tropical Burrowing Cricket (Anurogryllus muticus)

T. J. Walker

Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611, U.S.A.

and

J. J. Whitesell

Valdosta State College, Valdosta, Georgia 31601, U.S.A.

ABSTRACT

When and where crickets call during a night should have important consequences for their reproductive success, yet little is known of individual calling behavior under natural conditions. This is particularly true in the tropics, where high temperatures throughout the night increase the opportunities for complex adaptations. Collectively males of *A. muticus* at Fort Sherman, Panama, called throughout the night; however, individual males seldom called more than three hours. Some males called close to their burrows and retreated into them when approached; others called on the ground away from any burrow and usually moved 1-6 m at intervals during their calling period. Males remained faithful to type of calling site on consecutive nights, and burrow-calling males used approximately the same calling periods. Individualized specialization as to time of calling may result from calling being energy costly and receptive females flying during most of the night.

IN MOST CRICKET species, males make calling songs, sexually ready conspecific females use the calling song to move to the male, and courtship and insemination ensue. That this scenario is oversimplified is attested by masses of theory and an increasing array of facts—see, for example, Alexander 1975, Otte 1977, Cade 1980, Lloyd 1981, Gwynne and Morris 1982. This paper deals with two simple but generally neglected aspects of cricket calling: when and where males sing.

WHEN MALES SING.—There are surprisingly few data on the daily cycles of calling for crickets outdoors. R. D. Alexander (1956, partly repeated in Dumortier 1963) diagrammed daily calling patterns for 26 species in eastern United States, indicating that all called during most of the night and that 19 called during daylight as well—though to a lesser degree. Alexander's diagrams gave no details as to changes in numbers of callers as a function of the day-night cycle nor did Alexander indicate whether the same individuals call during all times that the species can be heard. Alexander and Meral (1967), monitoring calling in *Gryllus veletis* and *G. pennsylvanicus* in southern Michigan, found that when nights were warm, both species sang chiefly at night; when nights were cold, calling occurred only during daylight. They reported that when nights were warm some *veletis* males (individuals identified by location) called only at night, "while others chirped intermittently during the day and less steadily during the night," implying some individual specialization as to time of calling. Nielsen and Dreisig (1970) studied

populations of *Gryllus brunneri* and *G. bimaculatus* outdoors in Morocco and reported that both called some in the afternoon and mostly at night; nighttime calling was sometimes curtailed by cold. They monitored four males of *brunneri* and one of *bimaculatus* at their burrows or in outdoor cages and learned that two *brunneri* males and the *bimaculatus* male called only at night. Cade (1979a) reported hourly counts of calling males of a Texas *Gryllus* sp. during four nights. Calling occurred all night, and on the three nights that populations were high, he noted a three- to fourfold increase in numbers calling immediately before and during sunrise.

Forrest (1980, 1981) and T. Walker (1980) are apparently the only investigators who have quantified the calling times of numerous individual males outdoors. In the three species they studied, *Scapteriscus acletus*, *S. vicinus*, and *Anurogryllus arboreus*, calling was limited to within two hours after sunset, and all males sang during the minutes of peak calling.

Laboratory studies of cricket calling times have used constant temperatures and sudden lights and have generally focused on the physiology of daily cycles rather than their nature or function (e.g., Loher 1972, Sokolove 1975). Loher (1979) combined data from several laboratory studies in discussing the adaptive significance and integration of circadian rhythms in calling, locomotion, and oviposition in *Teleogryllus commodus*.

Daily calling times of animals other than crickets have been studied. For example, Henwood and Fab-

rick (1979) correlated the dawn chorus of birds and primates with optimal suitability for sound propagation. Young (1981) subsequently extended the correlation to dawn and dusk chorusing by cicadas.

WHERE MALES SING.—Two aspects are of concern here: the sites within their habitat that males use for calling, and the attachment that males show to particular calling sites during a calling period or from one day to the next. Generally males call from sites that are identical or similar to where they feed and rest. For example, tree- and bush-inhabiting crickets call from trees and bushes; ground crickets call from the ground; and mole crickets call from specially modified burrows (Nickerson et al. 1979). The best-documented exception is Anurogryllus arboreus, a cricket that lives in a burrow and forages on the ground, but generally climbs to a perch (e.g., 1 m up a tree trunk) to call (Paul and Walker 1979, T. Walker 1980). When temperatures are low (< 23° C at sunset) or when suitable perches are not nearby, the male often calls just outside his burrow, facing the entrance. T. J. Walker (1980) studied the night-to-night calling site fidelity of A. arboreus and found that perch-calling males usually call at a different perch each subsequent night. The average distance between consecutive perches was 14 m. Except for movement higher or lower on a perch, males did not change calling sites during an evening (T. Walker 1980). Other examples of crickets known to change calling sites from night to night but not during a night are the mole crickets Scapteriscus vicinus and S. acletus (Kleyla and Dodson 1978). Although ca. 90 percent moved from one night to the next, the average distance between successive calling burrows was only about 0.3 m. Alexander and Meral (1967) concluded (from staking calling sites) that many males of Gryllus veletis and G. pennsylvanicus moved from one calling period to the next but that some males, especially late in the season, called from the same burrow or crevice night after night. Campbell and Shipp (1979) reported that Teleogryllus commodus males usually stayed at calling sites one day or less and that the upper limit of occupancy was 14 days.

In the genus Anurogryllus, females use vestigial ovipositors to lay clutches of eggs in their burrows. They tend the eggs and later feed and guard the hatchlings. Males also live in burrows. Their calling songs are long-sustained trills produced by wingstroke rates from 65-185 per sec., depending on the species and the temperature (Walker 1973, Prestwich and Walker 1981). We studied a population of Anurogryllus muticus at the U.S. Army's Jungle Operations Training Center, Fort Sherman, Panama, 14-18 December 1980, and discovered features of timing and site fidelity of calling not previously reported for any cricket.

METHODS

We identified the Anurogryllus at Fort Sherman as muticus by comparing our specimens with identified specimens from Jamaica and on the basis of wing-stroke rate during calling ($\sim$135 sec^{-1} at 27° C). Anurogryllus muticus was common at Fort Sherman in lawns and along roads and jeep trails. It occurred in lesser numbers along rain forest foot trails and only rarely was heard in the undisturbed rain forest. During other studies in the vicinity of Fort Sherman, 9-13 December 1980, we learned that A. muticus did not call during the day and that calling began each evening 5-40 minutes after sunset and continued beyond 0200 hrs. Temperatures were always suitable for calling throughout the night. All calling males were on the ground and some were within 1-10 cm of burrows that they quickly retreated into when approached; others had no burrows and escaped by running or jumping.

The population we selected for intensive study occupied the lawn adjacent to Building 153, a 20 x 75 m shop being converted to a community center. The study area was between the building and paved roads to the north, east, and west; it included 1250 m^2 of lawn, most of which lay in a single north-south, 12 x 90 m strip. The study area was dimly but constantly illuminated. The east wall of the building was continually lighted by three wall-mounted opal glass fixtures spaced 20 and 26 m apart. We estimated that the light intensity of each equaled that of a bare 40w bulb. The doorways at either end of the building were lighted with pairs of similar fixtures. To determine if the numbers calling at various times of night changed differently in lighted and unlighted areas, one of us made hourly counts of calling males on 16 December, starting at 1850 hrs, while driving through two areas of Fort Sherman—one brightly lighted (NCO housing area) and the other dark.

On the nights of 14 and 15 December we perfected census and mapping techniques, made preliminary observations, and marked 11 calling males for individual recognition. Marking was accomplished by applying a spot of white correction fluid on the pronotum and writing on it an identifying number in India ink (Walker and Wineriter 1981). Three of the calling males were at burrows; the other eight were not.

On the nights of 16 and 17 December we started our observations at sunset and censused calling males

every 10 minutes noting each calling site on a map and marking it by dropping a vial within a few cm of the caller. We tried to locate visually each male and to determine whether it had been marked (and what its number was) and whether it had a burrow nearby. Males calling near burrows nearly always (20 of 21) called from a thumbprint-like depression that amplified the call (Walker, Whitesell, and Forrest 1982). Males calling without burrows generally (14 of 16) called without external amplifiers. This correlation helped in separating the two types of callers. Because males generally called beneath the low tangle of grass that constituted the lawn, they were difficult to locate, and we resorted to classifying calling males as (1) at burrow, (2) not at burrow, (3) undetermined. Observations of marked males not calling at burrows revealed that they generally (7 of 10 male-nights) changed calling sites at intervals during the night. This behavior complicated the interpretation of successive censuses of unmarked males. If a male was heard at a site during one census and not during the next census, a "new" male now calling at a site 1-5 m away was likely the "old" male calling at a new site. Burrowless calling males were so dispersed and the movement of marked, site-changing calling males was so regular that we felt confident in classifying certain unmarked calling males as wanderers. Males that apparently called during only one or a very few census periods during the night were our greatest problem. These males could have moved great distances without calling and then been counted as new males. For example, by interpreting the data first liberally and then conservatively, we concluded that no more than 29 and at least 26 males called in the study area on the night of 16 December.

At the end of each night's observations all burrows that had been located were staked for future identification.

Heavy rains near sunset and at midnight postponed and interrupted calling on 14 and 15 December. The night of 16 December was rainless except for brief drizzles at 2400 and 0106 hrs. The night of 17 December was dry, but calling subsided at *ca* 2000 hrs as 5-15 km^{-1} winds blew from the east and north. We ended continuous observations that night at 0045 hrs after two hours of counting 0-2 males calling. We revisited the area at 0245 hrs and found two males calling. Air temperatures at ground level were suitable for calling throughout the study, ranging from 28 to 24° C.

RESULTS

Counts of calling males made during hourly drives through dark and brightly lighted areas were similar

in their trends (table 1), relieving our concern that the dim illumination in the study area might grossly distort the nightly course of calling.

TABLE 1. *Comparison of trends in numbers of* A. muticus *calling in two areas contrasting in illumination, 16 December 1980, Fort Sherman, Panama.*

Time of census	Counts of callers		Trend $(n/\bar{x})$[a]	
	Dark[b]	Brightly lighted[b]	Dark	Brightly lighted
1850	11	17	1.7	1.1
1950	4	11	.6	.7
2050	6	15	.9	1.0
2150	11	21	1.7	1.4
2350	4	13	.6	.9
0040	3	12	.5	1.0

[a]The hypothesis that the numbers calling in the brightly lighted area followed the trend revealed by the numbers in the dark area could not be rejected ($X^2 = 9.06$; $P > 0.1$).
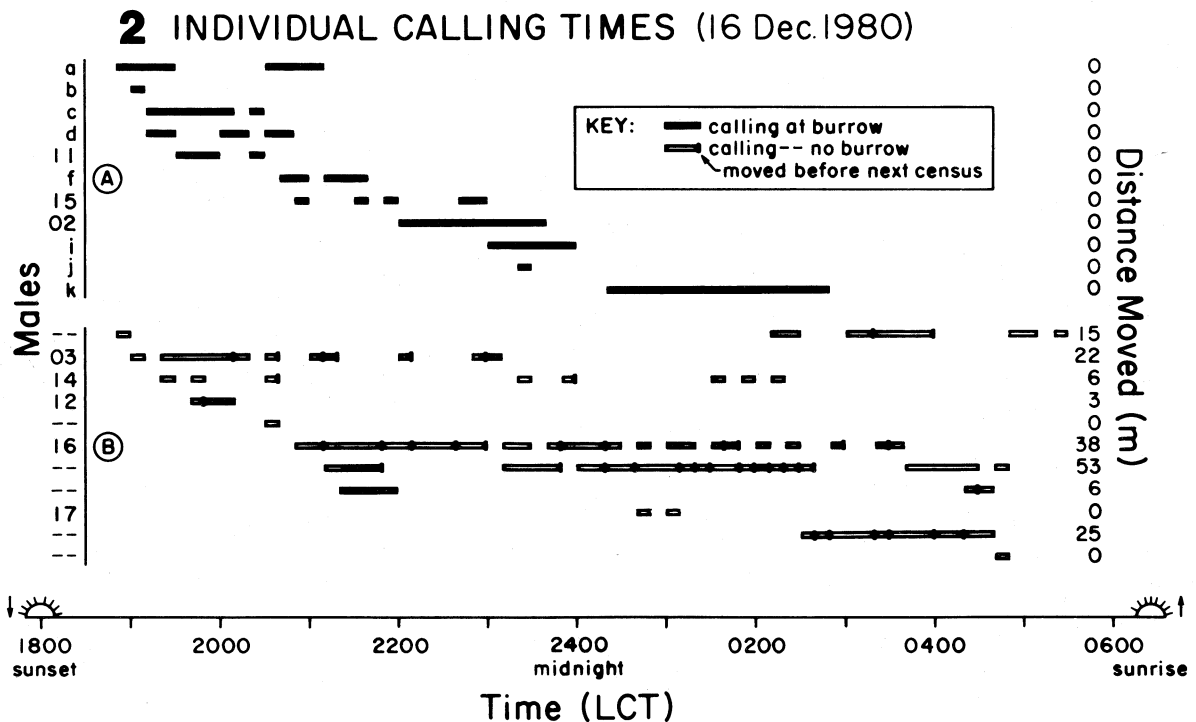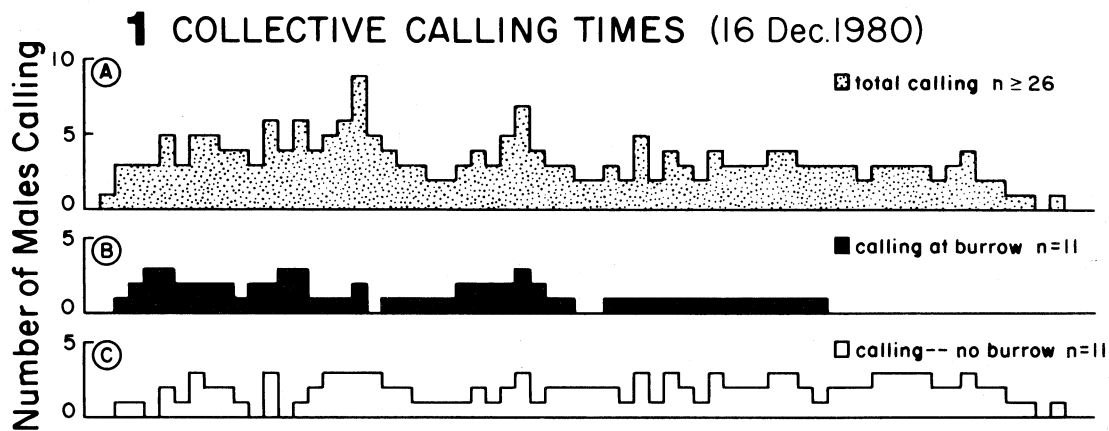[b]The hypothesis that numbers calling in each area did not change during the census period could not be rejected at $P = 0.05$ ($X^2 = 10.1$ and 4.6).

During four nights in the study area, the maximum number of calling males counted during a single period was 10 (14 December, 2120 hrs)—after a heavy rain that inhibited earlier calling. On 16 December, the only night that was rainless and calm, the maximum was nine (fig. 1, 2135 hrs). On 15 and 17 December, it was six.

Except when stopped by heavy rains, calling continued throughout the night. On 16 December males called at every census between 1845 and 0515 (fig. 1). Calling occurred both at burrows and away from burrows during most of the night, but after midnight, calling at burrows decreased (fig. 1).

Many more males called during an evening than called at any one time. For example, on 16 December at least 26 males called but no more than nine at once; on 17 December the corresponding figures were 23 and six. Males calling at burrows and males calling away from burrows were nearly equally numerous— of 22 individuals visually located on 16 December, 11 were at burrows and 11 were not. Of 16 located on 17 December, 11 were at burrows and five were not. (Since many of the burrows were staked, males calling at burrows were on average easier to spot.)

Each individual, especially if calling at a burrow, restricted its calling to a limited portion of the population calling period (fig. 2). No male calling at a burrow called during a period longer than 3 h 20 min—compared to a population calling period of approximately 11 h. The longest period during which a marked male not at a burrow called was 6 h 50

1 COLLECTIVE CALLING TIMES (16 Dec.1980)

Number of Males Calling

(A) 10 5 0 ⊠ total calling n ≥ 26

(B) 5 0 ■ calling at burrow n=11

(C) 5 0 □ calling-- no burrow n=11

2 INDIVIDUAL CALLING TIMES (16 Dec.1980)

Males

a
b
c
d
11
(A) f
15
02
i
j
k

KEY: ▬ calling at burrow
calling-- no burrow
moved before next census

--
03
14
12
--
(B) 16
--
--
17
--
--

Distance Moved (m)

0
0
0
0
0
0
0
0
0
0
0

15
22
6
3
0
38
53
6
0
25
0

↓ ☼ ☼↑

1800 sunset   2000   2200   2400 midnight   0200   0400   0600 sunrise

Time (LCT)

FIGURES 1 and 2. FIG. 1. Number of *A. muticus* males calling as a function of time, night of 16 December 1980, study area, Ft. Sherman, Panama; censuses were made at 10 min. intervals. At least 26 males called, but no more than nine at once (A); 22 were located visually and classified as calling at a burrow (B) or not (C). FIG. 2. Calling times of individual males, night of 16 December 1980, study area, Ft. Sherman, Panama. Individuals are identified at left by letter (on stake at burrow) or number (on pronotum). A. Males calling at marked burrows. In three instances, the male had been marked too. B. Males calling away from burrows. Five were individually marked (numbers); the others were not (— —) (see text).

min. The longest run of calling without missing a 10-minute census period was 2 h 30 min for a male calling at a burrow and 2 h 40 min for a male calling without a burrow.

Males not calling at burrows generally moved between bouts of calling (figs. 2, 3). The maximum distance traveled by a marked male during an evening of calling was 59 m. This male ended only 11 m from where it started, but others traveled straighter routes.

The marking of individuals and the staking of burrows allowed us to know what certain individuals did on consecutive nights. Of 11 males marked (3 at burrows), three were not seen on subsequent
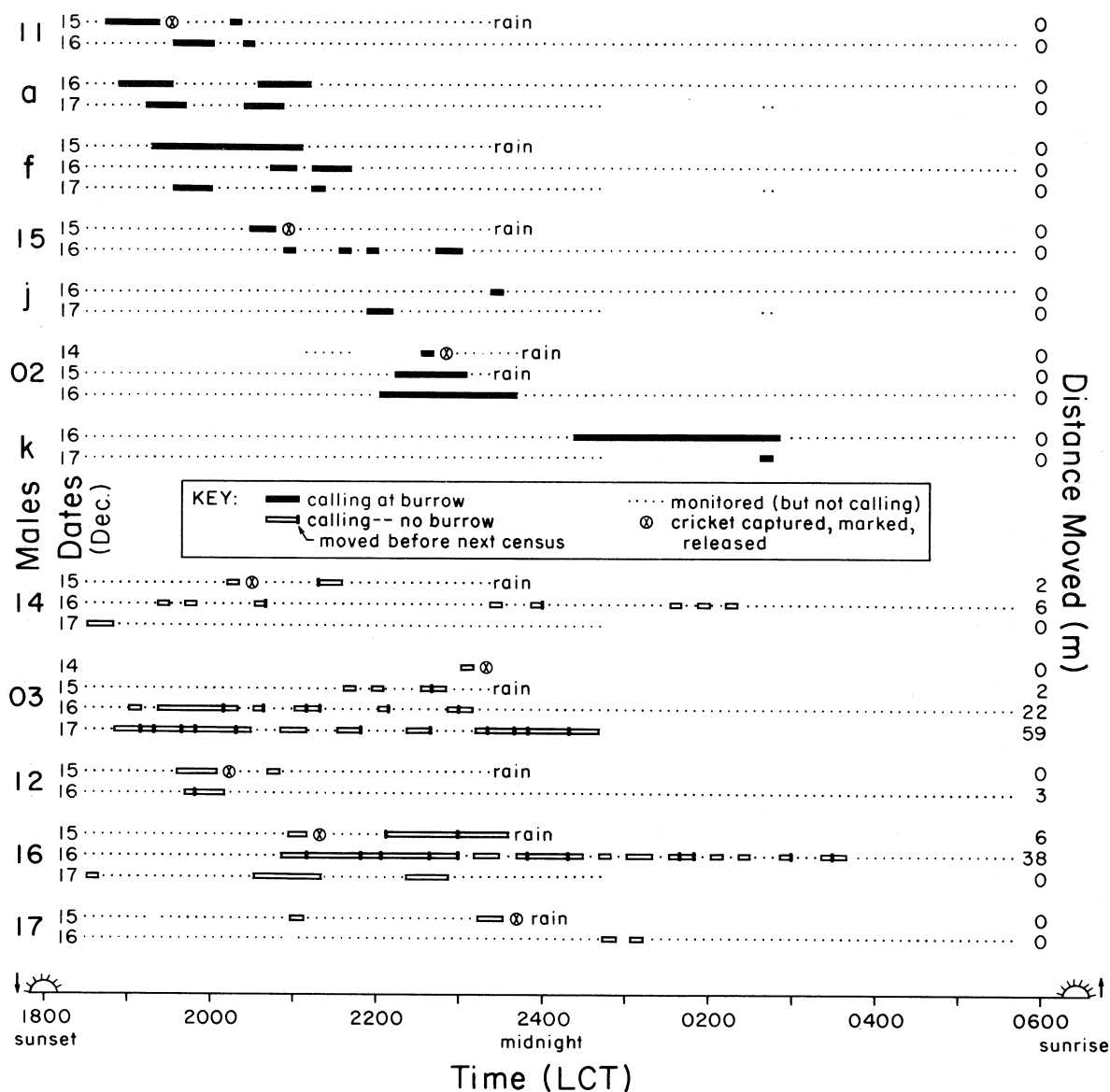
FIGURE 3. Calling times of individual males of *A. muticus* on consecutive nights (dates are small numbers at left), study area, Ft. Sherman, Panama. Above: Males calling at marked burrows (letters at left); three of males had been marked on the pronotum as well (large numbers at left). Below: Males calling away from burrows. All were marked on the pronotum.

nights; four (2 at burrows) were seen the next night only; three (1 at a burrow), on the next two nights; one on the next three nights. The eight marked males resighted (for a total of 13 male-nights) were faithful to their original calling modes—i.e., the burrow-calling males continued to call at their burrows, and the males that had been marked away from any burrow did not subsequently call from a burrow (fig. 3).

At the seven burrows where calling was noted for two or more nights, its time of occurrence was approximately the same each night (fig. 3, top). For two or three nights some burrow-calling crickets remained early-evening callers, others remained middle-

of-the-night callers, and one was an early-morning caller. Crickets calling away from burrows called during longer periods and for longer durations and were not as likely to utilize the same period on consecutive nights (fig. 3, bottom).

DISCUSSION

The calling behavior of *A. muticus* is surprisingly different from that of other crickets: some males frequently change calling sites during a night, and males specialize by calling at different times of night. Understanding these differences is part of a larger problem—how insects have adapted in their calling behavior to constraints of space, time, rivals, and enemies (Alexander 1960, 1975; Gwynne and Morris 1982; Walker 1982a).

Before the functions of *A. muticus* calling behavior can be discussed profitably, female reproductive behavior must be inferred. An important feature of *A. muticus* females is that they are either winged (with long metathoracic wings i.e., macropterous) and flightworthy or dealated (with stumps of metathoracic wings) and flightless (Walker 1972). The five winged females we captured were at light; two of the three dealated females were dug from brood-containing burrows and the other was spied on the lawn at night. The three winged females we allowed to make burrows in soil-filled containers dealated within a week. The one we kept isolated from males, as well as the two we put with males, laid fertile eggs, and tended the hatchlings. We hypothesize that (1) females disperse by flight before producing a clutch of eggs, (2) they usually mate prior to flight (cf. *Scapteriscus acletus*, Ulagaraj 1975) as females that colonize temporary openings in the forest would be rash to fly without sperm, (3) they generally land at a burrow-calling male, mate with him in his burrow, take over his burrow, dealate, and use the burrow for brood rearing (in *A. arboreus*, dealated females walk to burrow-calling males, mate, and take over their burrows—T. Walker 1980), (4) they may mate again (cf. *Gryllus* spp., Cade 1979b), and (5) they may rear one or more additional broods. This last speculation is substantiated by a female that we excavated from a juvenile-containing burrow and kept in a glass-sided observation burrow for 27 days. We then added a male; two weeks later she produced a clutch of >40 fertile eggs and subsequently tended the hatchlings for three weeks.

If our inferences about female reproductive behavior are correct, males calling at burrows have a different clientele than those calling away from bur-

rows. Males calling at burrows are directing their sounds upward (Walker, Whitesell, and Forrest 1982) toward flying females, much as certain mole crickets do (Forrest 1980, 1982). Males calling away from burrows are not primarily seeking flying females —their calling postures are generally less appropriate, and when they walk a few meters from time to time, as they usually do, they are unlikely to improve their odds of attracting airborne females. We propose that wandering males are seeking terrestrial females of two sorts: winged virgins and dealated matrons. Both would be ensconced in burrows and could be sought out by silent males, as in *A. arboreus* (Walker 1982b). However, calling while searching has the advantage of making the male known to terrestrial females that are at many times the distance that a male can detect their presence (even if the females deposit pheromones while foraging—cf. Paul 1976). If the female is virgin and ready to fly or dealated and storing inadequate or inferior sperm (W. Walker 1980), she may gain by going to the male rather than waiting to be found. Our most direct evidence that male *A. muticus* search for female burrows is that on two occasions we went to an unusual discontinuous buzzy sound (*ca.* 0.5 sec. buzz every sec.) and found a male digging away the plug to a burrow. In each case the head of the occupant appeared, and the excavating male was repulsed and moved quickly away. We dug up one of the burrows the next day and found a female with more than 20 young juveniles 3-5 mm long. Calling by searching males may also give them a chance to attract flying females, but we doubt that such a female, if already mated, would mate again upon landing without the nuptial gift of a burrow.

We have no convincing evidence that males switch between calling at burrows and calling away from burrows. None of the marked males we resighted had switched (fig. 3). If flying females do take over male burrows, the displaced males could either start calling without a burrow or dig another burrow—which males captured at burrows will do if placed in soil-filled containers. When we captured *A. muticus* males calling without burrows and placed them in soil-filled containers, they too dug burrows and called—proving that a switch in that direction is also possible. T. J. Walker's (1980) studies of *A. arboreus* revealed that male-calling site and wandering can be a function of age. In some populations males first call at their burrows for several evenings; eventually they abandon their home burrows, call from perches each evening, and wander during the rest of the night.

The second aspect of calling behavior in *A.*

muticus that deserves special attention is the restriction of different burrow-calling males to calling at different times of night (fig. 3, top). Timing of burrow-calling should relate to timing of female flights. Four females were collected at lights at various times prior to midnight, and one female arrived at 0349 hrs. We suspect (for good theoretical reasons, Walker 1982a) that the availability of flying females during the night follows a pattern resembling the total number of males calling from burrows (fig. 1). If females fly most of the night, why don't individual males call for the entire period? A likely answer is that 8 hrs of calling would require more energy than the cricket could replace by the next night. A burrow-inhabiting cricket is limited to the vicinity of its burrow for foraging, and calling and foraging are mutually exclusive. The high wingstroke rate and intensity ($\sim$100 dB at 15 cm) of *A. muticus* predict that metabolic rate during calling is >25 times that at rest (Prestwich and Walker 1981). Daytime foraging is apparently dangerous; burrows were closed with plugs of dirt and vegetation during daylight hours. Visually searching predators, such as birds, are one type of hazard; high surface temperatures may be another (Bell 1979).

If calling continually all night is not energetically feasible, why do individual males not call at intervals throughout the night with the intervals more widely spaced after midnight? This procedure would produce the temporal equivalent of Fretwell's (1972) ideal free distribution. Calling at intervals inversely proportional to availability of flying females may seriously reduce a male's probability of success: if a flying female requires a signal lasting x min to orient, land, and find the male, then each time a male temporarily ends his call he loses any female that first heard him <x min before. The best tactic for an isolated, burrow-dwelling male would be to call continuously for one or a very few long periods rather than for many short ones. If the male can hear the calls of burrow-dwelling neighbors, his calling times could be adjusted to fit the immediate, local temporal distribution of male calling as well as the average, area-wide temporal distribution of female landing. Our data refute the notion that burrow-inhabiting males usually wait for opportunities to be solo callers. Males with burrows closer than 10 m often sang simultaneously (8 cases; 2 as close as 2 m); however, males with burrows closer than 2 m (2 cases, 1.5 and 0.3 m apart) never called simultaneously. Complicating the question of whether males should sing solo or in choruses is the possibility that a flying female will judge a habitat poor if she hears only one male calling there.

As is usual in short-term field research, we found it easier to identify important questions after we had left than to answer them while we were there. Further study of *A. muticus*, in Panama or elsewhere, and of its sibling *A. celerinictus*, should be rewarding.

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