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Reproductive Behavior and Mating Success of Male Short-Tailed Crickets: Differences within and between Demes

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INTRODUCTION

Acoustically conspicuous animals offer special opportunities for field biologists and students of reproductive behavior. Cicadas, crickets, katydids, and some grasshoppers are the birds and frogs of the insect world. Males loudly advertise their species, sexual readiness, and location. Biologists can use these acoustical displays to detect sibling species, to find local populations and individuals for study, and to determine seasonal, ecological, and geographical distributions. The "songs" can be recorded on magnetic tape and played back with high fidelity and analyzed and synthesized with devices that are simple and inexpensive compared to those needed to do research of equivalent quality with visual and olfactory displays. For ease of study only animals using long-range bioluminescent signals compete with acoustically displaying ones, and a much more limited array of species is involved (Lloyd, 1978).

Unlike birds, frogs, and cicadas, acoustical Orthoptera are easily studied in the laboratory—most species can be maintained in cages with

minimal care, and many can be reared in small space at low cost. Furthermore, some of the behaviors characteristic of free insects outdoors can be elicited in modest cages indoors. Consequently, researchers from many disciplines have used crickets (Gryllidae), katydids (Tettigoniidae), and grasshoppers (Acrididae) to analyze components of acoustical communication and its concomitants: biophysics of sound production (e.g., Michelsen and Nocke, 1974; Sismondo, 1979); neurophysiology of sound production (e.g., Huber, 1975; Walker, 1975; Bentley, 1977; Elsner and Popov, 1978); circadian rhythms (e.g., Nielsen, 1974; Rence and Loher, 1975; Sokolove, 1975; Sokolove and Loher, 1975); audition (e.g., Bailey and Stephen, 1978; Michelsen and Larsen, 1978; Hoy and Casady, 1978); aggression (e.g., Alexander, 1961; Phillips and Konishi, 1973); mating behavior (e.g., Alexander and Otte, 1967; Otte 1970, 1972; Rence and Loher, 1977; Loher and Rence, 1978); phonotaxis (e.g., Popov and Shuvalov, 1977; Bailey and Thompson, 1977; Morris *et al.*, 1978; Cade, 1979*b*; Pollack and Hoy, 1979); genetics (e.g., Hoy, 1974; Elsner and Popov, 1978).

The ease with which some components of communication and reproductive behavior among acoustical insects can be studied indoors has resulted in an unbalanced development of knowledge of the total process. (We know, for example, little about long-range movements of sexually active individuals.) Furthermore, the elements studied in the laboratory evolved outdoors in physical, biological, and social contexts that are poorly, if at all, approximated indoors. As a result, some behavior in the laboratory may be artifactual (never elicited under field conditions and, therefore, without evolved function), or rarely elicited in the field (though adaptive under the specific unusual circumstances that elicit it). For instance, females in laboratory studies of phonotaxis are generally denied all contact with males. The fact that they are often attracted to calls of species other than their own could be related to the fact that they are long-deprived virgins—a class of females rare or lacking in most species in the field. Their behavior may or may not fairly represent how discriminating most wild females are. Obviously, the ultimate tests of hypotheses about female choice, male-male aggression, territoriality, mating frequency, and reproductive “strategies” should be events that occur in the field.

Except for observations of when and where males call, field studies of reproductive behavior of acoustically displaying insects are few and incomplete. (Some recent examples are Gwynne, 1977; Kerr, 1974; Meixner, 1976; Samways, 1977; Ulagaraj, 1975.) The species that have received the most attention in the laboratory—*Teleogryllus commodus*, *Gryllus campestris*, and *Acheta domesticus*—have been largely neglected in the field (but for *T. commodus*, see Browning, 1954; Campbell and Clarke, 1971; Campbell and Shipp, 1974; and for *G. campestris*, see Turcek, 1967; Popov and Shuvalov, 1974; Popov, 1975; Popov *et al.*, 1975).

The most intensive field studies of reproductive behavior of acoustic insects have concerned three species of meadow katydid (*Orchelimum*) (Feaver, 1977) and a field cricket, *Gryllus integer* (Cade, 1976, 1979a). In each case, behavior leading to copulation proved far more complex than previously surmised. In *Orchelimum* spp., males defended calling territories by attacking nearby calling males. Females approached calling males and interacted with them for hours or days before mating. Often the female interacted with the same male on several, though not necessarily consecutive, occasions prior to mating. Silent males occurred near calling males, but females mated only with calling males. In *G. integer*, males sometimes called loudly and defended calling territories but they also adopted two other strategies—soft irregular calling and silent searching or waiting in the vicinity of calling males. Each strategy resulted in some mating with the loud-calling producing the most mating opportunities per unit time and the largest chance of being attacked by a conspecific male or fatally parasitized by a phonotactic fly.

For crickets, *G. integer* is at the r end of the r - K selection continuum (Pianka, 1970). It has two generations each year with the spring generation apparently modest and the fall generation often reaching plague proportions. Adults sometimes fly actively and accumulate about streetlights—a symptom of long-range dispersal and transient or fluctuating habitats. Neither adults nor nymphs burrow extensively. Females lay hundreds of small eggs and invest no further in their progeny.

THE SHORT-TAILED CRICKET

Although it belongs to the same subfamily, the common short-tailed cricket, *Anurogryllus arboreus*,* contrasts with *G. integer* in many respects, and occupies the opposite end of the cricket r - K continuum. All stages live in burrows that they seldom leave except to forage. Throughout its range (southeastern United States), *A. arboreus* has but one generation each year, with adults occurring in spring or early summer and achieving approximately the same abundance each year (see e.g., Fig. 5). Females lack conspicuous ovipositors—i.e., are “short-tailed”—and lay relatively few but large eggs in their burrows rather than inserting them into the soil as do other crickets of the subfamily Gryllinae. They tend the eggs and provide food, including trophic eggs, for the hatchlings (West and Alexander, 1963). Even the male may invest in his progeny, since the female

* *A. arboreus* was long confused with two tropical species of *Anurogryllus* and was incorrectly known as *A. muticus* (De Geer) prior to 1973 (Walker, 1973).

sometimes takes over her mate's burrow for brood rearing. The juveniles disperse soon after their mother dies, each digging a burrow of its own. By winter the juveniles are within two molts of being adults; the following spring they complete their development. All mating occurs during a two-month period. Adults never fly.

Previous studies of *A. arboreus* by others have dealt with their behavior under laboratory confinement (Alexander, 1961; West and Alexander, 1963; Alexander and Otte, 1967) and their life cycle and habits (but not calling and mating) in the field (Weaver and Sommers, 1969; Campbell, 1971). Some aspects of the *A. arboreus* demes that are the subject of this chapter have been reported elsewhere: attraction of predators to calling songs (Walker, 1964, 1979), physical characteristics of calling songs (Walker, 1973), sound fields produced by calling males (Paul and Walker, 1979), deciduous wings (Walker, 1972), energetics of calling (Prestwich and Walker, 1980).

Several features of *A. arboreus* make its reproductive behavior peculiarly susceptible to study. As in other crickets, males make species-specific calls that attract sexually ready females. All calling and mating each 24 hr occurs during the 2 hr beginning at sunset. Calling males are easy to locate because they are generally fully exposed and their song is a loud, continuous trill. Marked males can be located and identified without trapping or handling. Crickets are generally quiet upon mating, but shortly after the male short-tailed cricket inserts the spermatophore tube and while still coupled with the female, he usually resumes his loud, continuous trill.* The pair remain coupled, with the male singing, for 10–20 min (Fig. 1). Males sometimes call for several evenings in succession from the open ground at the entrance to their burrows. These sites can be marked, the activities of the male monitored, and the ultimate fate of the burrow determined.

The reproductive behavior of short-tailed crickets seems likely to involve intense sexual competition, a subject of much current interest but with few data from insects (Blum and Blum, 1979). Short-tailed crickets are outbreeding, and a male can mate up to three times in a single evening.* Because populations are sedentary and dense and females mate during a

* Male crickets insert the tube of a spermatophore into the female's genital tract leaving the sperm-filled bulb outside (Fig. 1). The copulatory trill of *A. arboreus* is given as the bulb empties; since it is identical to the calling song (Walker, 1973), additional females might be attracted to the mating male. I saw the first direct evidence of this May 4, 1979—a coupled pair with an attending female. This trio was inadvertently disrupted, but two days later I found another and spotted a third female 20 cm above. As I watched a fourth female arrived. The male mated successfully with three of the females! (Except for the results nothing seemed exceptional about this male or the one two nights previously. Each was of ordinary size, calling at ordinary intensity from an ordinary perch—on a tree trunk about 1 m up. Other males were calling, without success, as close as 3 m.)



FIG. 1. Pair of mated short-tailed crickets on tree trunk. Abdomens are attached at terminalia. Male (above), with forewings raised, is trilling continuously. Sphere at tip of male abdomen is the bulb of the spermatophore. (Drawing by Art Agnello.)

two-month period, males are seldom if ever in short supply. Females sometimes mate more than once (Alexander and Otte, 1967; Walker, 1973), but since they produce fewer than 130 offspring (Weaver and Sommers, 1969), a single spermatophore should hold more than a lifetime supply of sperm. In Florida, the southernmost portion of the range of *A. arboreus*, the long growing season ahead leaves females maximal time for mate choice, perhaps intensifying competition among males.

DEMES STUDIED

A. arboreus doesn't fly (Walker, 1973), and the habitats it occupies are discontinuous—i.e., bounded locally by habitats in which no *A. arboreus* occurs. The population, or deme, on each island of suitable habitat is evidently largely independent of other such populations. Immigration must be by walking and therefore unlikely for demes that are widely separated or

with streams intervening. Two demes were monitored: the *lawn deme*, 1960–1971, in which the entire population was studied (probably 150–300 adults inhabiting 0.5 ha), and the *woods deme*, 1971–1978, in which a small portion of the population was studied (approximately 150–300 adults inhabiting 0.5 ha of more than 3000 adults inhabiting more than 15 ha).

The lawn deme centered about a centipede grass lawn covering about two-thirds of a 0.24 ha lot at 213 S.W. 41st Street, Gainesville, Fla. On two sides the deme reached its natural limits in open xeric woods dominated by southern red oak, turkey oak, and live oak (*Quercus falcata*, *Quercus laevis*, and *Quercus virginiana*). On the other two sides it was generally limited by residential streets and well-cared-for yards, although a few males sang in the bordering areas. The lawn had scattered shade trees, and between it and the xeric woods were hedges and flowering shrubs. A frame house and a patch of dense, mesic woods further complicated the site.

The woods deme was in closed-canopy mesic woods 7 km to the west (NW $\frac{1}{4}$, sec 31, tp. T9S, R19E). It was dominated by water oak (*Quercus nigra*), basket oak (*Quercus michauxii*), sweet gum (*Liquidambar styraciflua*), laurel oak (*Quercus laurifolia*), hickory (*Carya glabra*), and *Magnolia grandiflora*. The crickets were most abundant where the understory was sparsely developed. The area studied most intensely was 0.5 ha near the deme's southwestern limits of open farmland and poorly drained pinelands. To the east the deme extended approximately 0.3 km and to the north at least 0.5 km.

MALE CALLING STATIONS

Unless an evening is cold or very wet, most mature males call. Once calling, a male usually does not change his site (his *calling station*) that evening. The principal exceptions result from disturbances and from events at the beginning and end of the daily calling period: (1) Males that sing at the entrance to a burrow will retreat into the burrow if approached or illuminated. They sometimes resume calling within the burrow. If their retreat is early, they will often sing again outside the burrow the same evening. (2) Males that call from tree trunks generally ascend and begin to call while ambient light is still high. If approached under such circumstances, they leap from their perch, strike the ground, and freeze. Such individuals may later climb the same or another perch and resume calling. (3) A male ascending a tree trunk may pause and call for a few minutes before continuing his climb to the station from which he will broadcast for the remainder of his evening's song period. (4) Near the end of the evening's song period, a male calling from a tree trunk or other perch may partially descend and call

for several minutes from a lower station. Rarely a male will descend and call from the ground for several to many minutes.

Types of Calling Stations

Methods

Males were located by their calling songs. A 6-volt headlight with a dimming device was used as needed. The most intensive work on types of calling stations was during 1967 for the lawn deme and 1977 for the woods deme. Observations in other years were sufficient to have detected major changes in frequencies. Calling stations were classified as (1) on the ground at a burrow, (2) on the ground, no burrow evident, and (3) above ground. If above ground, the height was estimated to the nearest 0.3 or 0.15 m (lawn deme) or measured to the nearest 0.1 m (woods deme). The nature of the substrate was recorded (e.g., tree trunk, leaf of seedling tree, fern frond) and whether the cricket could move higher without detouring (as on an unobstructed tree trunk). If on the ground at a burrow, the cricket was generally within 2 cm of and facing the entrance hole. When approached, he would dart into the burrow, turn about, and investigate the entrance with the antennae. (Occasionally a cricket would search frenziedly before finding the entrance. Crickets not at burrows never made such movements.) Once in the burrow, the male would sometimes resume calling. Rarely, a male was calling within a burrow when first located. In such cases, I could seldom refute the conjecture that he had initially been singing outside. However, in three instances the burrow entrance was loosely plugged with dirt and the muffled sound had been uninterrupted during my search.

Results

Calling at burrows was remarkably more frequent in the lawn deme than in the woods deme (Fig. 2A,B). Approximately 40% of males observed in the lawn deme were at burrows (in 1967, 313 of 755). In the woods deme fewer than 0.5% of calling males were at burrows (in 1977, 1 of 503). In both demes, males not at burrows were generally on perches rather than on the ground.

Determinants of Calling Stations

Temperature

On cool evenings during the calling season fewer males called and a greater proportion of those calling were on the ground. This was true for

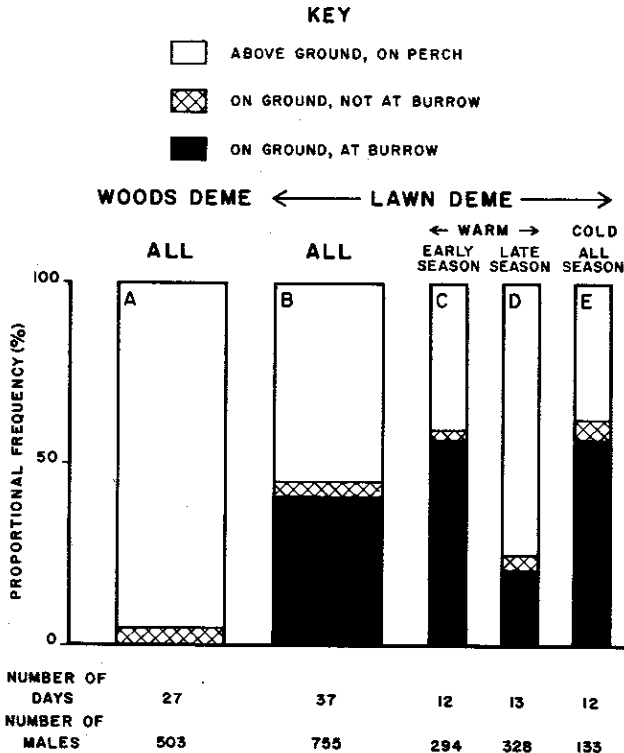


FIG. 2. Proportional frequency of calling stations of short-tailed cricket males. (A) Woods deme, 1977, all evenings. (B-E) Lawn deme, 1967. (B) All evenings. (C) Early season, warm evenings (April 4-17 and 23°C or higher at first calling). (D) Late season, warm evenings (Apr 18-May 13 and 23°C or higher at first calling). (E) Cool evenings ($<23^{\circ}\text{C}$ at first calling: Apr 4, 9, 20, 21, 27-30; May 3, 5, 9, 10).

both the lawn deme (Fig. 2E vs. 2B; Fig. 3) and the woods deme, and in each population the threshold for the effect on a clear evening was an air temperature of approximately 23°C at sunset. When the temperature fell below 20°C , all singing ceased.

The one instance of calling at a burrow observed in the woods deme in 1977 was at 20°C .

As reported above, calling from within burrows was never usual. Most cases were at 20 - 23°C .

Maturity

Most early season calling in the lawn deme was on the ground at burrows even on warm evenings (Fig. 2C). In 1965 and 1967 burrows at which males called were marked with numbered stakes and observed on sub-

sequent evenings. Only early in the season were the burrows monitored closely during the calling period. Of 47 burrows so monitored, what was presumed to be the same male occupied the burrow and usually called each evening for 1-8 nights ($\bar{x} \pm SD = 3.2 \pm 2.0$). Males calling at burrows were difficult to mark because they retreated inside when approached and could seldom be caught without destroying the burrow. I marked four without capturing them using spray paint or a quick paint brush applied to a hind tibia. Three others were captured, marked on the pronotum, and released down their burrows. Of the 7 males marked at their burrows, 1 was never seen again and 5 called at their burrows for 1-5 additional evenings. No nonmarked cricket called at the 7 burrows. Four of the marked crickets were seen calling on tree trunks 1-11 m from their burrows on the 3rd-6th night after marking. None of these called at the burrow again; one was seen on three subsequent evenings at perches 9, 1, and 24 m from the perch occupied before. Two of the seven burrows remained occupied (as revealed by being freshly plugged with dirt each morning) after the male was no longer evident by his nightly calling. One was excavated 6 days after calling had ceased there and proved to be occupied by a female.

Three burrows at which males called more than one night were excavated. All were extensive and had defecation chambers giving evidence of long-term occupancy. Weaver and Sommers (1969) reported that adult males of *A. arboreus* in central Louisiana were in their overwintering bur-

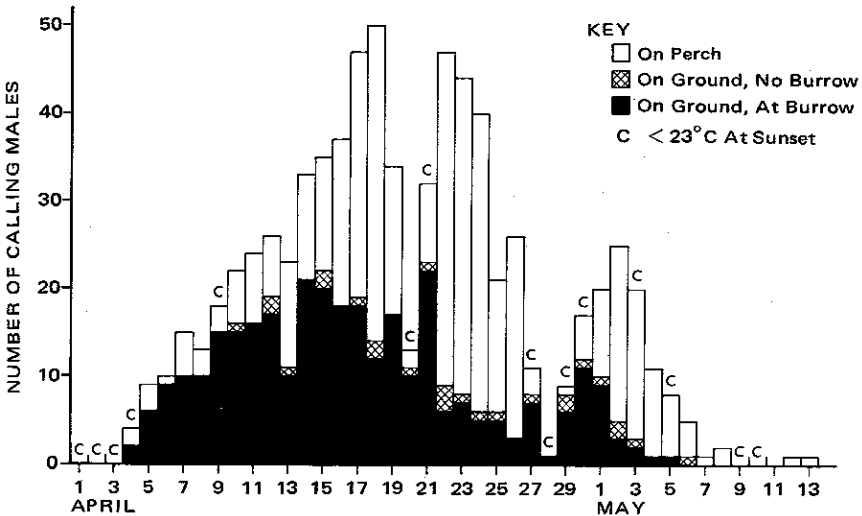


FIG. 3. Number of short-tailed cricket males calling and their calling sites each evening during the 1967 mating season of the lawn drome. (Except for May 3 and 5, which were cloudy, evenings with temperature < 23°C at sunset were clear and temperatures continued to drop.)

rows for about one week. Available evidence suggests that early season calling by males at burrows is their first calling and may be resumed each evening for as long as a week. Males eventually abandon their overwintering burrows and call elsewhere.

Woods deme males almost never called at their overwintering burrows. The ones doing so were generally among the first callers for the year and were along a narrow road and a powerline right-of-way. Five burrows were staked in 1978, but calling occurred on a subsequent night only once.

Access to Perches

A likely reason for the great difference between the lawn and woods demes as to site of first calling is the accessibility of elevated perches.

In 1967 in an effort to determine the relation between burrow and tree trunk calling in the lawn deme, I placed 0.6 m oak logs (15–20 cm in diameter) vertically 3 cm south of 13 burrows where males had called the evening before and left them in place for 1–6 days. Three of the burrows were those of crickets I had managed to mark distinctively. Calling was subsequently observed at 10 of the burrow sites. On 14 of the 20 occasions of subsequent calling, the male was on top of the vertical log ($n = 10$) or on the side of it ($n = 4$). On the other occasions the male was on the ground near the burrow entrance ($n = 5$) or within the burrow ($n = 1$). The crickets calling from the logs were evidently those that had called from the ground previously—at least on the four occasions, at two burrows, that a cricket called on a log placed at the burrow of a marked cricket, the cricket had the predicted mark. There was no correlation between calling from the log and the number of days that the male had been at the burrow site. For the 14 instances of calling on logs, the days elapsed since the cricket first called averaged 4 (range 1–8; $\bar{x} \pm \text{SD}$, 3.9 ± 2.5); for the five instances of calling at burrows in the presence of a log, elapsed days since first calling averaged 4 (1–6, 3.7 ± 2.0). Table I gives data for four representative burrows.

Other Males

The occurrence of other calling males could influence site of calling. This possibility will be considered in the paragraphs below, first for males calling at burrows (lawn deme only) and then for males calling elsewhere (both demes).

In most cases, males calling at burrows were apparently calling at the burrows where they had spent the winter as juveniles. The initial spacing of such callers would depend on prior events. However, once calling began, males with burrows near those of other calling males could leave their burrows sooner (or later) than those in more solitary locations. Burrows of call-

TABLE I. Site of Singing at Four Representative Burrows^a

Burrow number	Date of first singing	Dates log in position	Evenings after log in position ^b					
			1st	2nd	3rd	4th	5th	6th
3 ^c	Apr 5	Apr 10-14	B ^d	L	L	N	L	-
16	Apr 9	Apr 10-13	L ^e	L	B	N	-	-
49	Apr 13	Apr 14-16	N	L	L	-	-	-
77	Apr 16	Apr 17-22	B	L	N	N ^f	B ^f	L

^a After 0.6-m log was placed vertically 3 cm from entrance—lawn deme, 1967.

^b L, log; B, burrow; N, no song.

^c Cricket marked April 6.

^d I.e., the fifth evening since the cricket was first heard.

^e I.e., the first evening since the cricket was first heard.

^f Temperature at sunset <23°C.

ing males in the lawn deme were mapped and monitored closely each evening during the early portion of the calling season in 1965 and 1967. Males calling at burrows within 3 m of another were not significantly less likely to stay and call another evening than were more solitary males (Table II).

Males calling away from their burrows should be more labile in their choice of calling site relative to calling neighbors. Their changing site of singing would not involve leaving an extensive burrow that had proved safe during the previous weeks or months. In theory, one might expect calling males that were not tied to burrows either to approximate regular spacing or to aggregate. The former would occur if males could increase their quota of females by minimizing competition. Under such circumstances, males would maximize intermale distances so long as they did not lose by moving to areas with lesser densities of sexually ready females. Regular spacing with the interval inversely correlated with habitat suitability would result

TABLE II. Frequency of Male's Calling at Burrow^a

Number of neighbors calling within 3 m	1965		1967		Total
	Number of males	Number calling again	Number of males	Number calling again	(proportion calling again)
0	21	14	22	18	0.74
1	8	6	4	3	0.75
2 or more	0	0	8	4	0.50

^a On one or more subsequent evenings, as a function of the number of neighbors calling within 3 m on the evening of male's first calling. Lawn deme, first 7 and 9 days of calling, 1965 and 1967 (beyond these dates other studies interfered with close monitoring of burrows).

[Fretwell's (1972) ideal free distribution]. Aggregation would occur if females preferentially mated with males that were overtly competing with other males. [If this were the case a male should approach or retreat from other males depending on his competitive strength and upon the strength of female preferences for group-calling males. If females mated only with group-calling males, males should, no matter how poor, call in choruses (see Alexander, 1975).]

Obligatory chorusing is easily refuted. Solitary males call readily and for durations that approximate those of males in dense populations. Whether males away from burrows have a tendency either to aggregate or to assume a uniform distribution is more difficult to decide. The available data that are most pertinent to this question are for males calling on tree trunks (Table III). Two, three, or even four males sometimes called from the same tree trunk and individuals calling a few centimeters apart usually behaved the same as those meters apart or on different trees. Two trends are apparent: (1) as more trees were occupied, a greater proportion bore multiple males (Table III); (2) the lawn deme had a higher portion of multiply occupied trees than did the woods deme (0.07 vs. 0.03). Both of these phenomena are in accord with multiple occupancy being a matter of chance and, therefore, more likely at higher densities of tree-calling males and at lower densities of tree trunks.

If calling from a tree trunk with other males strongly reduces a male's chance of mating, one would expect it to be rare—alternative calling sites on other vegetation or the ground were always available. The data indicate that males are no less likely to call from trees if unoccupied trees are scarce. In fact, the proportion of males calling from trees went up rather than down at higher densities in the lawn deme (Fig. 3) (most of the above-ground-level calling was on trees).

A final evidence that multiple males calling from one tree trunk is a stochastic occurrence: in 1977 males were captured and allowed to establish burrows in soil in 500 ml jars with screen lids. Two or more such jars were opened and placed at the base of a tree prior to sunset. At sunset or shortly afterwards the males would come out of their jars, ascend the tree, and call. As many as five were induced to call on the same tree in this manner. Never did a male descend the tree until near the end of the calling period. Movements rarely were directly toward or away from other singing males; males generally evidenced no response to one another and did not noticeably space themselves either vertically or radially.

Height of Calling Males

Most males called from stations above ground level (Fig. 4A). Their perches were sometimes at the top of what they had ascended—e.g., stumps,

TABLE III. Frequency of Trees Having More than One Calling Male as Related to the Prevalence of Singing from Trees

Prevalence category	Lawn deme, 1967			Woods deme, 1977		
	Number of nights	Number of trees occupied ^a	% of occupied trees with > 1 ♂ ^b	Number of nights	Number of trees occupied ^a	% of occupied trees with > 1 ♂ ^b
Nights with 1-10 trees occupied	31	135	5	11	67	0
Nights with 11-20 trees occupied	5	65	7	15	229	3
Nights with 21-30 trees occupied	3	72	11	2	52	6
All nights	39	272	7	28	348	3

^a Sum of trees occupied for all nights in the prevalence category. For the lawn deme totals include 252 instances of singly occupied trees, 18 of trees with 2 males, 1 with 3 males, and 1 with 4. For the woods deme the corresponding numbers of trees are 337, 10, 1, and 0.

^b For the lawn deme the proportions of occupied trees that were multiply occupied were not significantly different among the three prevalence categories (G -test; $0.5 > p > 0.1$). For the woods deme the proportions were significantly different (G -test; $p < 0.005$).

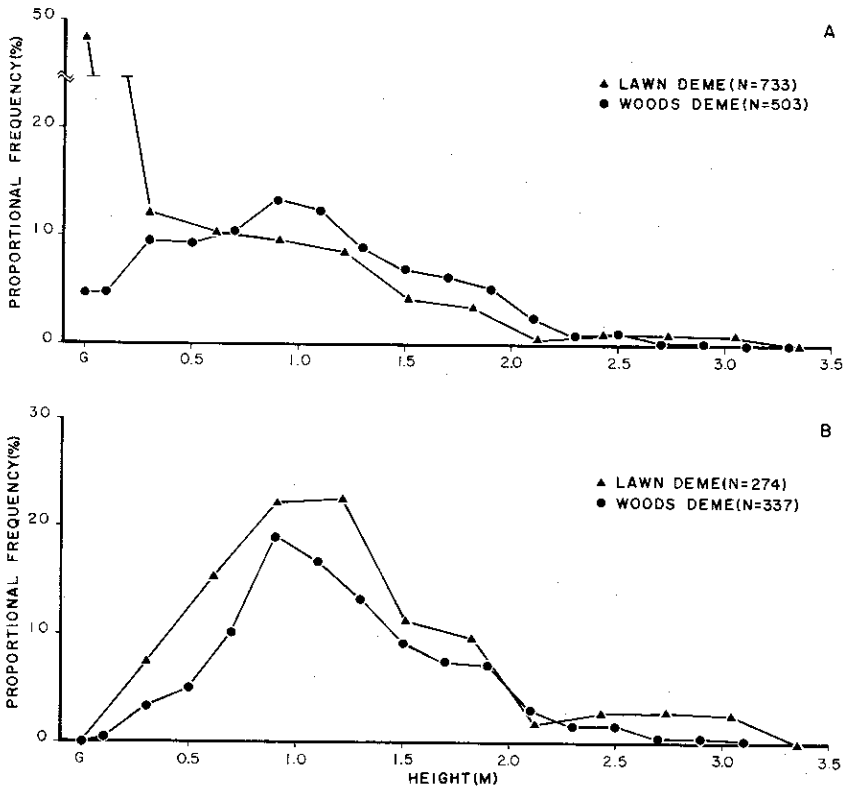


FIG. 4. Proportions of calling short-tailed cricket males at various heights. (A) All calling males. (B) Males calling on vertical surfaces and having free access to greater heights.

the 0.6 m logs described above, ferns, and seedling trees. However, males did not climb to the tops of the most popular calling sites—the unobstructed vertical surfaces of tree trunks. Here the male could reveal what calling height had in the past proved most favorable to reproductive success. In both demes the modal height of males on unobstructed vertical surfaces was approximately 1 m, and more than 60% of such males called at heights between 0.5 and 1.5 m (Fig. 4B).

Site Fidelity and Wandering

That the same male calls at a burrow several nights in succession was shown by marking experiments described above. When I first studied the lawn deme, I noted that a tree would often be the calling site of a cricket several evenings in succession, and supposed that the same cricket called from the tree each evening, perhaps occupying a nearby burrow during the

day. This supposition was refuted by the behavior of marked crickets. Males calling away from burrows were captured, marked on their pronotums with identifying dots of colored paint, and gently released at the site of capture as soon as the calling period was over. Significant numbers were marked and released during 6 years and the results were generally consistent from year to year and from deme to deme (Table IV). Only 7% of marked males that called again did so at the original site. That the lack of site fidelity was not a result of trauma from the marking procedure is shown by the fact that an even lesser percent called at the second site a second time—even though they were undisturbed except for my reading the colored dots as they called. Furthermore, of the four crickets marked at burrows that subsequently called from trees (see above), none called from the same tree twice. When a tree was occupied several evenings in succession, it was generally a different cricket each evening.

Although calling for more than one evening at a site other than a burrow was uncommon, 7% of males were doing so the first time they were resighted and 6% were the second time (Table IV). However, no male ever called at its previous evening's site for both its first and second resighting. Except for instances of repeated calling at the home burrow, only two males (of 332 marked) called more than two evenings at a single site. These remarkable crickets were of the lawn deme in 1965 and 1967. The two were similar in some important respects: each travelled more than 25 m from the tree where it was originally captured and released, each eventually called for eight consecutive evenings without changing sites, each was associated with both a tree and a burrow at this site, and each was active near the end of the calling season.

Details for each male are as follows: The 1965 male was marked April 28 and was next seen on May 4 5 m south. It was seen after that on May 5 14 m farther south and then on May 9 26 m southwest. On May 9–16 this male called nightly 1.2–2.7 m up the trunk of a turkey oak. On May 12 it mated. On May 15 it called from 1.2 m up and then from the entrance of a burrow 0.2 m from the base of the tree. It retreated into the burrow when disturbed, and the entrance was later plugged with dirt. The 1967 male was marked May 5 and the following evening called at a red oak 26 m wsw (across the street from the area monitored for Fig. 3). It continued to call at the same oak each evening through May 13. On May 9 and 10 (cool) it called at a burrow 0.5 m west of the base of the tree; on the other evenings it called from 1.5–4.0 m up the trunk. On May 11 it was watched as it left its burrow and ascended the tree prior to calling. On May 11–13 it was watched in dim light as it completed calling, descended the tree, and moved about on the ground. On May 11 it made a series of short, quick runs within 1 m of its burrow, came within 0.2 m of the burrow, and stopped 0.4 m from it after 4 min. It remained motionless for 1 hr 34 min before moving 0.2 m in one quick burst toward the burrow. At midnight, 43 min later, the

Table IV. Site Fidelity and Distance Travelled (m) by Marked Males of *Anurogryllus arboreus*

Deme	Number marked	Site fidelity ^b		Straight-line distance to new site ^c			
		First time resighted	Second time resighted	1-day interval		> 1-day interval	
				n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$
Lawn							
1965	77	3/31 ^a	0/8	17	9 ± 6	25	15 ± 14
1967	22	0/10 ^a	1/4	14	14 ± 10	3	7 ± 8
Total	99	7%	8%	31	11 ± 8	28	14 ± 14
Woods							
1972	65	0/15	0/6	12	20 ± 12	9	35 ± 16
1973	53	1/14	0/5	3	7 ± 5	15	18 ± 16
1975	54	2/22	0/6	11	20 ± 15	16	18 ± 13
1976	61	2/18	1/7	13	12 ± 8	9	20 ± 18
Total	233	7%	4%	39	16 ± 12	49	21 ± 16

^a Males marked at winter burrow excluded until they called away from this burrow.

^b Number calling at same as previous site/number resighted.

^c Only males that changed sites are included. Original and all subsequent resightings were classified only on the basis of days elapsed between sightings.

cricket was gently touched; it jumped several times before disappearing 2.5 m from the burrow. The next evening it called from the same tree as before, descended, ran in the same erratic manner for 12 min, and disappeared into its burrow. More than an hour later it was just outside its burrow and returned into it. After descending the tree on May 13 the cricket again made sporadic rapid movements within 1 m of its burrow, but was lost from sight after 7 min. On May 14 and 15 it called from a live oak 8 m west of the site occupied for the previous 8 days.

When males changed their calling sites from evening to evening, as they generally did, the distances between successive sites were often substantial. For the 70 instances in which a marked male was seen calling at a new site one day after being seen calling at another site, the average distance between the two sites was 14 m (Table IV).

On five evenings in 1965 and 1967 the site of the lawn deme was closely observed, by dimmed headlight, from the end of calling until midnight or later; more casual observations were made on other evenings. Even at the peak of the calling season few crickets were seen after calling ceased. Most were located by short bursts of sound made by interacting males. On four occasions one male was inside a burrow and another one was at the entrance. The outside male rarely entered the burrow—and generally quickly exited. When marked males were released into occupied burrows they usually left after a brief spat with the occupant, but in one case all was quiet for 40 min before the intruder ran out.

Two of the males seen vying with the occupant of a burrow had been marked where they were calling 4 and 5 m away 4 and 1 hr earlier. Another male, originally marked a week earlier, was observed calling from a tree trunk and 45 min later was seen 16 m away at the base of a large tree. Travel after calling can be rapid and long as well as slow and short.

Pitfall traps operated for another purpose provided some circumstantial evidence of male wandering. No females and 19 males were caught in unbaited traps; 17 of the males were caught outside the calling period (Table VI; Walker, 1979).

To explore further what males did after calling, I embedded the bottom edges of 46-cm-diameter, cylindrical, bottomless screen cages 10 cm into the soil of the centipede lawn and introduced into each a male that had just finished calling from a tree. Of three males so introduced, two dug shallow burrows 4–6 cm deep and apparently occupied them most of the time except when calling from the top of the cage for four or more consecutive evenings; the third sang but made no burrow that I could detect. It apparently concealed itself under the grass during the day and often called on the ground rather than at the top of the cage. (The soil had been moistened in the cages in which the crickets burrowed, but had been left dry in the cage with the burrowless cricket.)

When placed on moist sand in 4-liter jars in the field, males of the woods deme burrowed readily ($n > 100$).

That wandering males will dig burrows in the field was confirmed by finding males of the lawn deme digging burrows and by observing that males calling at burrows on cold evening late in the season were sometimes at "cricket-deep" (20–30 mm) burrows rather than at more elaborate, overwintering burrows.

SURVIVORSHIP

Data from males marked for study of site fidelity and wandering were used to compare survival prospects under various circumstances (Table V). One of seven males marked at the home burrow was not found again, whereas 219 of 325 (67%) of those captured and released at other sites were not. The mean survival times for burrow-released and perch-released males in the lawn deme were 4.4 and 1.8 days, respectively. In both lawn and woods demes fewer than 10% of perch-released males could be located on the third evening after release.

As a means of estimating potential survivorship, marked males were released into outdoor cages supplied with soil, food, and moisture. Mean

TABLE V. Survival of *A. arboreus* Males as Revealed by Resightings of Calling Males

Treatment	Number marked	Mean survival (days)	Proportion singing n days after marking		
			1	2	3
Captured at perch, released in outdoor cage					
Lawn (1967)	5	14.2	1.0	1.0	1.0
Woods (1972)	9	— ^a	0.8	0.8	0.6
Woods (1976)	8	22.9	0.9	1.0	0.8
Captured at burrow, released at same					
Lawn (1965, 1967)	7	4.4	0.3	0.4	0.9
Captured at perch, released at same					
Lawn (1965, 1967)	91	1.8	0.20	0.09	0.10
Woods (1972, 1976)	77 ^b	— ^a	0.19	0.13	0.08

^a Observations discontinued before all marked males had ceased to sing.

^b Most marked males in 1976 and all in 1973 and 1975 (Table IV) were excluded here because observations were not continuous enough.

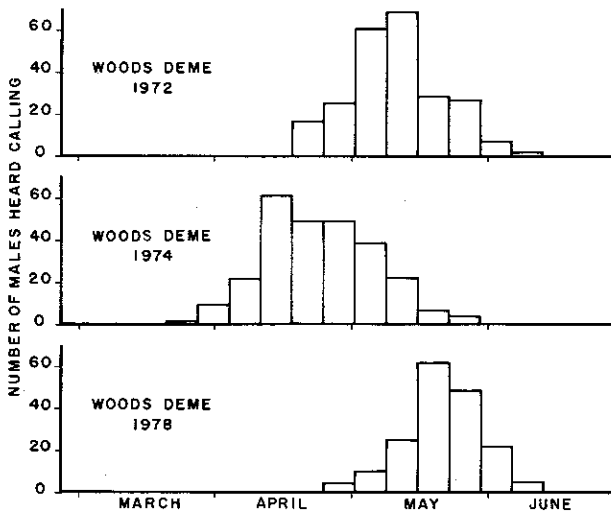


FIG. 5. Variation in seasonal occurrence of calling; woods deme. Each bar represents number of calling males counted weekly by walking a fixed route at 30 min after sunset. Most of the 8 years of observation are similar to 1972. The winter and spring of 1974 were exceptionally mild; of 1978, exceptionally cold.

survival time was 20 days, and caged males frequently called for days after all free males had stopped.

MALE CALLING TIMES

Calling by males in a deme is restricted to a certain *season*. Within this season a given male calls only on certain *days*, and during a 24-hour period, he calls only during certain *hours*.

Seasons

The seasonal occurrence of calling varied significantly from year to year (Fig. 5), and the differences correlated with differences in severity of winter and early spring. During 1971, the only year that both demes were monitored, the number of calling males in the lawn deme peaked 1 to 2 weeks earlier than in the woods deme (Walker, 1980). This correlates with the lawn deme experiencing higher soil temperatures in the spring because of its more exposed site.

The waxing and waning of numbers of calling males during the season is dependent on the number of mature males in the deme and the proportions of such males that sing on particular evenings. The number of mature males depends on recruitment, through maturation or immigration, and on losses, through mortality or emigration. Immigration and emigration are probably of little importance in accounting for variation in counts in the present study because they are unlikely for the lawn deme and should be in equilibrium in the portion of the woods deme studied. The only data on recruitment through maturation are for the lawn deme and are based on these assumptions: (1) Each time a male was detected calling at a burrow that had not been noted previously as a site of calling, another individual had entered the calling population. (2) All males in the lawn deme first sang at burrows. On this basis recruitment lasted for approximately a month in 1967 (Fig. 6). The earliest recruitment was principally in open areas with southern exposure. Later recruitment was in areas with denser vegetation and with varying degrees of shading. Data from caged and marked males were used to estimate that 0.95 of males at burrows survived each day. Survivorship for peripatetic males was approximately 0.7/day.* Using these two figures and further assuming that males stayed in their burrows 3 days after first calling (average observed stay was 3.2 days—see above) and were peripatetic thereafter, I arrived at the estimated population curve shown in Fig. 6. That the trends for estimated population and observed numbers of calling males are similar (Figs. 3 and 6) is surprising, but doesn't prove that the estimated values for recruitment and survivorship are even approximately correct—compensating errors seem likely.

Days

The consistency with which individual males sang evening after evening is difficult to estimate. The best documented influence was that some or all mature males failed to call on cool evenings. Caged males generally called unless the temperature was below 20°C, but the proportion of free males that called was noticeably diminished when temperature at sunset was below 23°C and falling (Fig. 3). Hard rains also diminished calling: both when the soil was saturated from a recent downpour and when precipitation coincided with the calling period. There were no examples in 1967 (Fig. 3), but reduced calling under such circumstances was observed at least 10 times in other years.

* Using this figure gives a *median* time of death of 1.8 days ($0.71^{1.8} = 0.5 = 50\%$)—see Table V, where 1.8 days in the *average* time of survival.

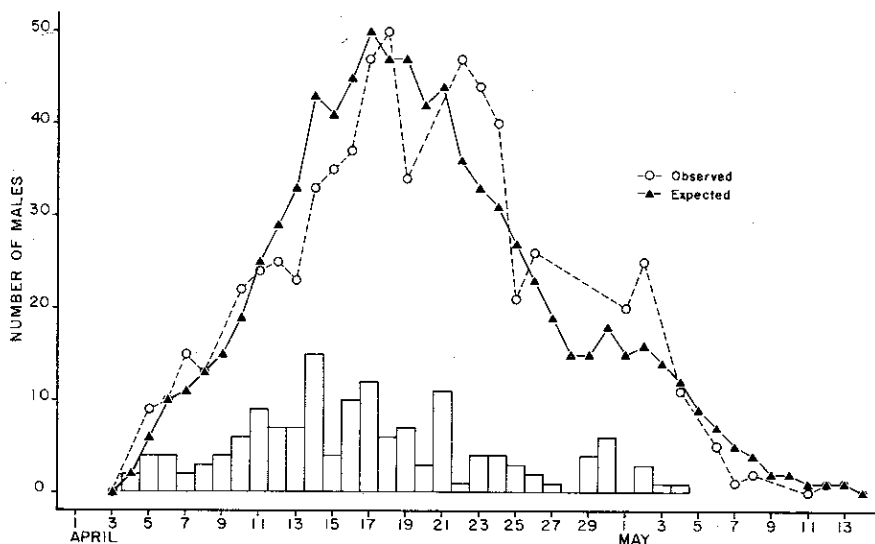


FIG. 6. Estimated number of calling males (solid line) in lawn deme, 1967, based on recruitment (bars beneath) and estimated daily survivorship of 0.95 for first three days (calling at winter burrow) and 0.70 for subsequent days (peripatetic). Recruitment was assumed to equal the number of males calling at burrows that had not been called from previously. Observed number of calling males (dotted line) as in Fig. 3; counts for cool evenings ($<23^{\circ}\text{C}$ at sunset) are omitted because a greater proportion of calling males drop from the chorus then.

If the weather was warm and not too wet, maximum numbers of males called. However, a significant percentage may have refrained from calling under conditions that seemed optimal. Examples of the evidence from free-living, burrow-dwelling males, lawn deme, 1967, are in Table I. For marked, free-living, peripatetic males, there was always the chance that skips in observed evenings of calling resulted from my failure to locate the male rather than his failure to call. However, after making maximal allowances for this uncertainty, I still concluded that males that had been marked while calling from perches often dropped from the chorus for one or more nights. I attempted to quantify this by collecting males from perches, marking them, holding them in individual cages in the field, and monitoring their calling each evening. Several types of cages were used, and both lawn and woods demes were studied. Food and moisture were supplied by various means (e.g., a piece of apple). The results were always similar: more than 90% of the caged males called each warm ($>20^{\circ}\text{C}$), but not drenched, evening. For example, in the most extensive study, involving 25 males of the woods deme in 1976, 19 males never skipped a suitable evening until they permanently quit. The average number of evenings these 19 called was six.

The remaining six males each skipped one evening out of an average of six they might have called—i.e., they averaged five evenings of calling with one gap not accounted for by cold or rain.

The daily calling constancy of males caged outdoors is in contrast to the inconstancy deduced from resightings of free-living, marked males. However, the calling of males caged outdoors was in other respects an uncertain predictor of the calling of free-living males. Caged males often called on cool or wet nights when free-living males were mostly silent. Caged males tended to start calling earlier in the evening and to end later than free-living males in the immediate vicinity. Caged males sometimes called for 15 min or longer after the last of the much larger number of free-living males had ceased. The greater amount of calling by caged males (observed for minutes of calling per day and suspected for days of calling) might be attributed to a larger fuel supply—because of the food furnished and the reduced opportunity for wandering. [Prestwich and Walker (1980), found that males burn fuel approximately 10–16 times faster when calling than when at rest.]

Hours

The hours of calling for individuals were determined in the woods deme in 1977 by assigning an assistant the task of monitoring all males in a limited area for the entire evening's song period. Each calling male was observed in dim light every 5–10 min and scored for calling, position, and mating. Thirty-four perch-calling males were so watched, excluding those that mated or that called during cool evenings ($< 23^{\circ}\text{C}$ at sunset). Their average period of calling was 33 min, with average starting and stopping times of 17 and 50 min after sunset (Fig. 7).

The only comparable data from the lawn deme were taken as a by-product of other studies. The interval between observations of an individual male was sometimes as long as 20 min, especially after 30 min past sunset. Consequently, the stopping times are known less exactly than starting times, and there is a bias toward overestimating stopping times relative to estimates of starting times. The differences between perch-calling males in the woods and lawn deme (Fig. 7) are in the direction of those predicted from the differences in methods, and should be discounted. However, the data for burrow-calling and perch-calling males of the lawn deme are based on the same method; therefore, the differences between the two should be real (Fig. 7). Burrow-calling males started at about the same time but quit sooner than perch-calling males. Average duration of calling for the two types of calling stations in the lawn deme was 18 and 43 min respectively.

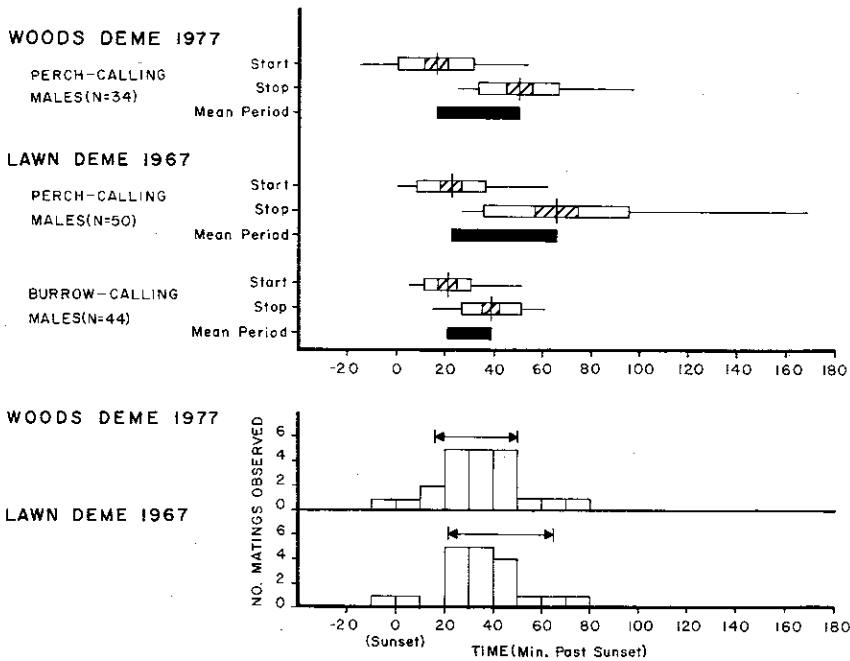


FIG. 7. Times of calling and mating. (A) Calling times. Time of starting and stopping and duration of calling for evenings with temperature at sunset $> 23^{\circ}\text{C}$. Vertical line indicates mean value; horizontal line, range; open box, ± 1 S.D.; shaded box, 95% confidence limits on either side of the mean; black bar, period between mean starting and mean stopping time (i.e., average duration of calling). Woods deme data from observations every 5–10 minutes. Lawn deme data from observations every 10–20 minutes, with stopping times more subject to increased variance than starting times. (Apparent differences between perch-calling males in woods and lawn demes may be attributable to the difference in methods.) (B) Mating times. Frequency of observed matings as a function of minutes past sunset to midpoint of copulation. (Initiation of matings averaged 5–10 min earlier than midpoint of copulation.) Arrows show mean period of calling from perches as determined in (A). When the mating was not monitored beyond initial discovery of a pair in copula, the time of observation was assumed to be the midpoint. This should cause the earliest matings to be judged too early on the average and the latest matings to be judged too late.

MATING SUCCESS

All aspects of the behavior of a male short-tailed cricket should reveal what has, in previous generations, increased the probability of siring progeny. The male's calling behavior—including physical characteristics, time of day, calling station, and site fidelity—should be closely related to the odds of reproducing.

Analyzing male mating success depends on detecting matings. All those

detected during this study involved males apparently at their calling stations—The female was sometimes watched going to the calling male; more usually a coupled pair (typically with male singing) (Fig. 1) was where a calling male had been noted minutes earlier, or a coupled pair was found (by the copulatory song) at a site and time that fit the presumption that the female had been attracted to the male's calling song. The possibility that matings occurred without the male attracting the female by his calling is discussed below in the section on sexual selection. The occurrence of such matings should not affect the analysis of relative success of males calling from different stations or at different times, because that analysis can be based on the proportions of the calling males that were detected mating. Frequency and effectiveness of observation should affect the absolute but not the relative values of the proportions, provided they are the same for different classes of calling stations or different times. For one class of calling station—calling at a burrow—the effectiveness of monitoring for mating seemed likely to be lower than for the other classes. Even though 41% of the instances of calling in the lawn deme, 1967, were at the entrances to burrows, only one mating was seen there (1 of 313 = 0.003 matings observed per calling male). For 28 males observed calling on the ground but not at a burrow, the observed mating success was 0.036 (1 of 28), and for 14 instances of males singing on logs placed vertically near their burrow entrances, the observed mating success was 0.214 (3 of 14; pairs coupled on the logs at the site of calling). These results made it important to determine what happens when a female is attracted to a male calling on the ground at a burrow. I therefore released reared virgin females 1 m from males calling at burrows. The first two females released soon contacted the calling male. The male immediately retreated into his burrow, the female immediately followed, muffled courtship and copulatory sounds were heard, and the male departed after 18 and 31 min, respectively. In neither case did he resume calling. In one case he remained within a few centimeters of the entrance for 5 min and started to reenter the burrow only to be met and turned away by the mandible-gnashing female. (A third virgin disappeared on her way toward a calling male—discussed below.) Obviously, the infrequency of observed matings at burrow entrances is an unsafe basis for concluding that males calling at burrows seldom mate. The following analysis, therefore, excludes matings by males singing at burrows; such matings may have been a large proportion of those in the lawn deme. (It should also be noted that mating frequency is not equivalent to reproductive success—the consequences of matings vary greatly.)

The data used in the analysis of mating frequency are from two studies: (1) For the lawn deme in 1967, every calling male was observed each evening as many times as events allowed. Beginning at first calling, I made circuits of the study area recording the location of every calling male. On

consecutive circuits new callers and the presence or absence of previously noted callers were recorded. Intervals between consecutive observations of the same calling male varied between 10 and 30 min. Since mating requires only 5–20 min, some callers surely mated undetected; however, the nature of the calling station should not have influenced the probability of detection. (2) For the woods deme in 1977, approximately 80% of the males were observed only once during an evening. Starting at first calling, I investigated each male heard and noted its position and whether it was mating. When the density of callers was low, I enlarged the area for observations rather than systematically monitoring the same caller more than once. I varied my procedure only when I found more than one male singing on the same tree trunk. I repeatedly checked such males for changes in position and for mating. In addition, an assistant sometimes watched all the males ($n = 3-11$) that called in a limited area and noted their activity at intervals of 5–10 min.

For males not calling at burrows, lawn deme males averaged fewer females per evening of calling than did woods deme males. The raw data do not reveal the difference: 18 matings were observed for 422 lawn deme males ($18/422 = 0.041$) and 21 for 502 woods-deme males ($= 0.042$). However, 3 of the 18 lawn-deme matings were on logs experimentally placed at burrows and might otherwise have occurred out of sight (leaving $15/422 = 0.036$). Furthermore, a smaller proportion of the (in-sight) matings were detected in the woods deme than in the lawn deme, since only 17% of the woods deme males were regularly reinspected while nearly all of the lawn deme males were. Mating success of regularly reinspected males in the woods deme was 0.091 (8/88). When calling apart from a burrow, lawn-deme males were apparently less than half as successful as woods-deme males, supporting the hypothesis that in the lawn deme a major portion of mating occurred within the burrows of males.

The relation of height of calling station to observed mating success was similar for the two demes (Fig. 8). For both, maximal mating rates were at heights above 0.4 m, and neither deme had matings above 2.0 m. Seventy-two percent of all perch-calling males and 85% of those calling on a vertical surface with no impediment to climbing higher were at 0.5 to 2.0 m (Fig. 4). The difference in the two percentages is attributable to a high proportion of perch-calling males within 0.5 m of the ground being on low vegetation with no unencumbered route higher.

The greater mating success of males at 0.5–2.0 may be entirely a result of their having larger *broadcast areas*—i.e., areas on the ground within which the call intensity exceeds the female's threshold of hearing (Fig. 9). Paul and Walker (1979) measured the broadcast areas of males calling from the ground and from perches 1 m up saplings and tree trunks. The latter two had significantly greater areas than the first with the ratio of the mean

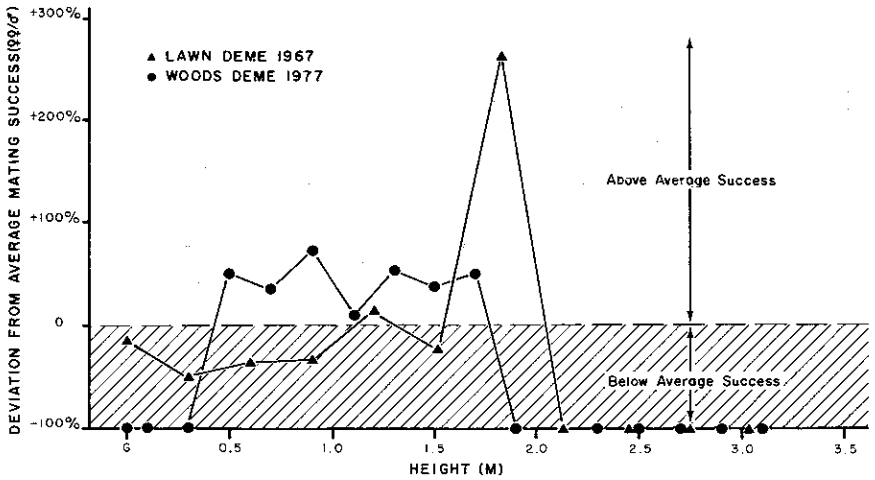


FIG. 8. Observed mating success of male short-tailed crickets as a function of height of calling perch. Mating success is calculated as the number of mating pairs observed at a particular height divided by the number of calling males observed at the same height. The ordinate is expressed as percent deviation from average mating success. Average for the lawn deme (1967) was 0.021 (16/755) and for the woods deme (1977), 0.042 (21/503). (Matings resulting from experimentally placing logs at burrows are excluded.)

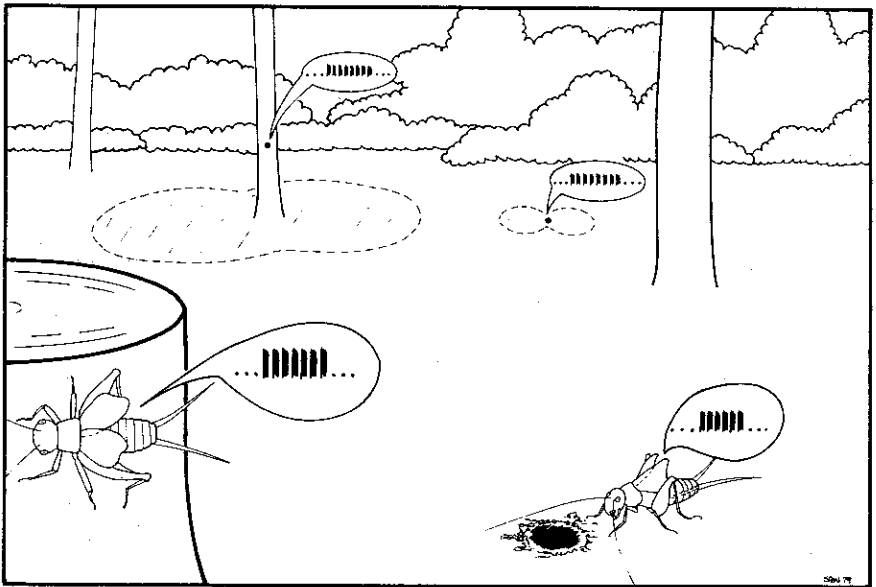


FIG. 9. Comparison of *broadcast areas* (= area on ground in which sound level exceeds threshold of hearing of female) of male calling 1 m above ground on tree trunk and male calling on ground. The former approximates 1642 m² and averages 14 times the area of the latter (Paul and Walker, 1979). Crickets in foreground show usual position of males calling from tree trunk and on ground (note entrance to burrow).

areas being 1:11:14. We attributed the small broadcast area of the former to attenuation from ground cover and low vegetation and to acoustical shadows from uneven terrain. We also noted that there are costs to calling above ground—as the cricket ascends, his broadcast area eventually becomes smaller because of spreading loss and intervening low branches. Furthermore, the sound level is reduced at the base of the perch—where the female elects to climb or to continue at ground level. Even when the male is close to the ground, the female may climb the wrong stem. On two occasions females were seen to make repeated forays up stems adjacent to the one from which a male was singing within 0.8 m of the ground.

In the woods deme, mating success was approximately even between 0.4 and 1.8 m, whereas in the lawn deme, greatest success occurred at 1.1–2.0 m (Fig. 8). The more open understory in the lawn deme may have increased the height yielding the maximal broadcast area for a calling male (Paul and Walker, 1979).

One other measure of attraction of females to calling males was attempted (Walker, 1979). Caged males were suspended about 0.1 m above pitfall traps in the woods deme during the calling seasons of 1977 and 1978. Half the males were muted and the rest called normally. Empty cages over pitfalls served as controls. All females trapped were beneath calling males (Table VI), but the overall catch rate was only 0.02 females/normal male/night. Trap design—perhaps the lack of a silhouette of a stem supporting the male—may account for low catch rate.

The reproductive success of males that call with one or more other males on the same tree trunk is of special interest. In the lawn deme in 1967, 15% of males calling on tree trunks (43 of 295) shared the trunk with at least one other calling male. Of the 12 matings observed on tree trunks none was on a multiply occupied one, but the mating frequencies of solo vs. group-calling males were not significantly different ($\chi^2 = 2.13$; $P > 0.1$).

At first glance, the results from the woods deme (in 1977) seem dif-

TABLE VI. *Anurogryllus arboreus* Caught in Pitfalls Beneath Suspended Cages—Woods Deme, 1977 and 1978^a

	2-hr calling period		Other 22 hr (all traps)
	Normal male ^b	Other ^c	
Trap days	247	494	741
Females caught	5	0	0
Males caught	2	2	17

^a Walker (1979).

^b Cages contained normal males that sang during calling periods.

^c No calling; cages were empty or held muted males.

ferent. Here 6% of males calling from tree trunks (23 of 360) shared the trunk with at least one other calling male, and of the 17 matings observed on tree trunks, 4 were on multiply occupied tree trunks. However, only 1 of the 4 was in progress when the males were first located. In the other three instances, the matings were detected because the males were reexamined periodically in hopes of seeing how a female behaved as she approached two or more males calling from the same trunk. *When first observed*, 1 of 23 calling males sharing trunks with other males was mating (4%) and 9 of 337 males calling singly on trunks were mating (3%). Mating frequencies were not significantly different. In none of the three instances that mating occurred on a multiply occupied tree trunk after the callers had been sighted was the female seen as she approached the males. Each time she coupled with one of the males between subsequent observations. Which male had been successful was deduced from the positions of the males—generally unchanged from the positions prior to mating. Neither the upper nor lower male consistently won the female (Table VII).

Calling during different weeks of the calling season produced different probabilities of mating, and the change with season—at least for males not calling at burrows—was different in the lawn deme, 1967, and the woods deme, 1977 (Fig. 10). Some of the difference between demes may be attributed to a significant proportion of matings in the lawn deme, especially early season ones, being in burrows where they could not be detected. Since calling at burrows was nearly lacking in the woods deme, the observed frequency of matings there may have closely paralleled total frequency.

TABLE VII. Matings on Tree Trunks Occupied by More Than One Calling Male—Woods Deme, 1977

Date	Number of males on trunk	Positions of males		Successful male
		Heights of males (m)	Horizontal separation (cm)	
May 8	2	0.8, 0.8+	2	"lower" ^a
May 9	2	1.2, 1.3	0	lower
May 15	3	0.4, 1.5, 1.5+	8, 0	"upper" ^b
May 17	2	0.9, 0.9+	10	"upper?" ^c

^a Mating in progress when crickets were first found. Mating male was 1 cm below other male which was 1 cm to left of female.

^b When first seen, upper two males were 1 cm apart and tail-to-tail. Eight minutes later, female was coupled with one of the upper males.

^c The left male was approximately 3 cm above the right male when first seen; 25 min later, the left male was mating and was 1 cm below the right male (now 30 cm away).

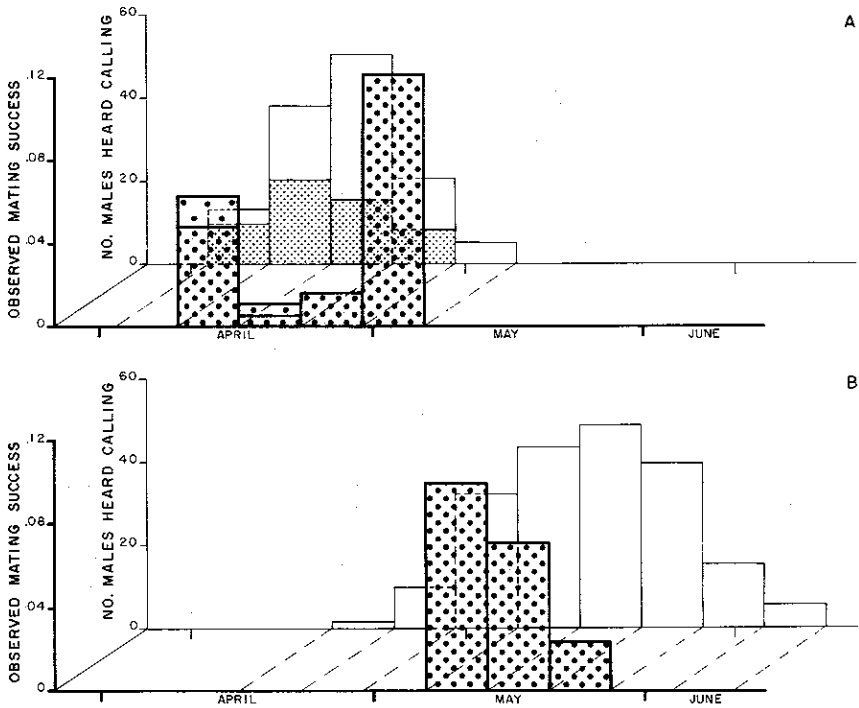


FIG. 10. Weekly changes in observed mating success (front bars) of calling males, other than those at burrows, compared with number of males calling (rear bars). Front (dotted) bars show the proportion of calling males observed other than at burrows, that were detected mating. (Males calling at burrows were omitted because their matings were generally undetected.) Rear bars are based on weekly censuses of calling (as in Fig. 5). Stippled areas in rear bars represent males that were calling at burrows. (A) Lawn deme, 1967; 18 matings for 442 males observed at 10–30 min intervals throughout evening calling period. Three of the nine earliest matings (upper areas of first two front bars) are doubtfully included in the analysis because they were by males calling from logs experimentally placed at their burrows. They might otherwise have called at the burrow entrance and mated within. (B) Woods deme, 1977; 21 matings for 502 males, 415 of which were observed only once during the evening calling period. The heights of the front bars should be approximately doubled to make them comparable to those for the lawn deme—because males in the woods deme were watched less closely than those in the lawn deme (see text).

The profitability of calling also changes with the time of evening, but the times of mating initiation (as opposed to the period in copula) and the minute-to-minute changes in numbers of calling males are too inexactly known to justify calculating probabilities of mating as a function of time of calling. It is evident, however, that the number of pairs in copula in both demes reached a maximum 20–50 min past sunset, corresponding to the period when most males were calling (Fig. 7B).

DISCUSSION

Sexual Selection

Only recently has the theory of sexual selection been developed relative to acoustical insects (Otte, 1972, 1977; Alexander, 1975; Cade, 1976, 1979a; Morris, 1979; Morris *et al.*, 1978; Lloyd, 1979b, Fig. 3). Now theory is well-advanced relative to the field studies needed to test and direct it. Cade (1976, 1979a) and Feaver (1977) have been the first to entertain explicit hypotheses relative to sexual selection as they investigated the reproductive behavior of acoustic insects in the field. The sexual behavior of short-tailed crickets differs in important ways from the other acoustic insects that have been studied.

Selection directly related to sexual reproduction is traditionally partitioned into intrasexual selection (generally interference competition among males for a limited supply of females) and intersexual selection (generally the choice by the female among those males that are available as sexual partners). While this classification conceals some subtleties (e.g., see Lloyd, 1979a), it suffices to organize the present discussion.

Intrasexual Selection

One of the striking aspects of the reproductive behavior of male short-tailed crickets is the lack of overt interference competition among males. Though the populations are often dense, each male seems to pursue his reproductive goals without regard to the similar efforts of others. Males calling at burrows were sometimes as close as 0.5 m; and having one or more neighbors calling at burrows within 3 m did not significantly change the probability that a male would call from the burrow on a subsequent evening (Table II). As many as four males (Table III) called from the same tree trunk without overt aggression—and mating success data refutes the contention that males calling from the same tree trunk greatly improved their individual chances of mating.

Calling males of some acoustic insects do not tolerate nearby competitors—they either go elsewhere or drive their competitors away or otherwise silence them. Cade (1976, 1979a) found that calling males of *G. integer* were never closer than 1.0 m. When he broadcast the calling song within 2 m of calling males, most ceased calling and either ran toward the speaker, attacking a male if one was tethered there, or behaved like a satellite male (see below). Morris (1971, 1972) and Feaver (1977) demonstrated that males of *Orchelimum nigripes*, *Orchelimum gladiator*, *Orchelimum vulgare*, and *Conocephalus nigropleurum* travel as far as 0.7–8 m to attack a calling male and that dominating males of these species actively maintain a space free of conspecific callers.

The failure of male short-tailed crickets to attack or to move away from other calling males may be related to the brief period each evening that females respond to calling (Fig. 7B). The cost to a male of going elsewhere or attacking is not merely the chance of finding a poorer place or losing the fight but a failure to advertise to sex-ready females for an important portion of that evening's mating period. Since time is so brief, a male displaced by an attack would not be expected to travel far before resuming calling, and the successful attacker might once again be faced with the choice of giving up valuable calling time or tolerating a competitor. Attack may prove unadaptively spiteful rather than selfish. In contrast, males of *G. integer*, *Orchelimum* spp., and *C. nigropleurum* evidently call for many hours each day making the time required to clear an area of competitors relatively inexpensive. Cade (1976, 1979a) reported that females of *G. integer* are attracted to calling during 9 hr between sunset and sunrise. Feaver (1977) noted that males of *Orchelimum* spp. established their general spatial arrangement and dominance relationships by midday—prior to the time she observed mating.

The only evidence of interference competition between male short-tailed crickets concerns the occupation of burrows after the evening's calling is completed. A male in a burrow (not necessarily one that he constructed) will defend it from other males. The effect of such intolerance is a diminished chance that the burrow-holding male will have competitors calling nearby the following evening. Defending a burrow has a high probability of success, low risk, and at least some payoff. The payoff would be even greater if wandering males can detect by contact chemoreception the home ranges of females that are likely to mate within 24 hr (Otte and Cade, 1976; Paul, 1976; Rence and Loher, 1977). They could then establish themselves in burrows in the vicinity and call with enhanced chance of success the following evening.

The possibility of wandering males detecting the home range of receptive females suggests yet another male strategy. A male might find and enter the burrow of such a female and mate with her there. (The advantages and disadvantages to the female of such a mating are considered in the next section.) Mating in the female burrow could be of common occurrence and be undetected. Laboratory studies provide evidence for its occurrence: Alexander and Otte (1967) and Walker (1973) introduced males into cages having a burrow occupied by a female and observed silent mating in the burrow.

If unrestricted females often mate in their own burrows, the following are logical consequences: (1) Males should spend significant time searching. (2) Males should drop from the chorus for one or more evenings (if cohabitation lasts at least 24 hr). (3) The number of matings observed per calling male per evening should be significantly less than predicted from

data on sex ratio, matings per female, efficiency of observation, and male longevity. Evidence that the first two occur was given above. The third is also true, at least for the woods deme. The sex ratio approximates 1:1 (Weaver and Sommers, 1969; and my rearing results) and females mate one or more times (Walker, 1973; and below). Therefore, males should average more than one mating each. In the woods deme, where males so rarely called at their burrows that mating in male burrows should be negligible, the efficiency of observation was approximately three times greater for 88 males systematically reinspected than for 414 males observed only once: average calling period was ~ 40 min (Fig. 7); copulation lasted 10–20 min; $40/10\text{--}20 \approx 3$. If males observed but once had additional matings at the predicted rate (39 matings/414 males rather than 13/414), their success rate was 0.094. This agrees well with the success rate observed for regularly reinspected males ($8/88 = 0.091$). Both of these rates indicate that males must average 10–11 nights of calling for each copulation realized. Mean survival of marked males (Table V) suggests that males average less than five nights of calling.

Excavating burrows is a direct method of testing for cohabitation. J. E. Weaver excavated burrows in Louisiana (personal communication, 1978) and recalled no instance of finding more than one adult in a burrow. Of 96 cricket-containing burrows excavated between April 3 and June 5 (mating season), each had but one adult cricket. No excavations were made during the 2 hr immediately following sunset, when mating in the male's burrow sometimes occurs.

If mating resulting from silent searching is assumed, then males must divide their total reproductive effort between searching and calling strategies. The mix of the two should depend on the costs and benefits under similar circumstances in the past, and the male may have inherited the ability to switch between the two behaviors or to change the mix in response to specific environmental cues (e.g., Alexander, 1975, Fig. 1).

A male with another male calling nearby generally calls without overt response to the competition. The possibilities of attack or retreat were discussed above. A third alternative is for the male to remain silent and attempt to intercept and mate with females on their ways to the calling male. Such satellite behavior is known for a variety of acoustic animals including at least one cricket species (Alexander, 1975; Cade, 1976, 1979a; Perrill *et al.*, 1978). Satelliting would seem particularly easy in short-tailed crickets since the only path to many calling males is a herbaceous stem or slender tree trunk. The fact that marked males sometimes skipped evenings of calling (see above) is compatible with satelliting. However, observational evidence is chiefly negative: I routinely searched the vicinity of calling males for females and occasionally spotted one; I spotted no silent males.

The observed behavior closest to satellite behavior was apparently an artifact. When a calling male was brightly illuminated, he would often cease singing until the light was turned away. Rarely he would remain silent for several or many minutes. The following incident (woods deme, 1978) illustrates this behavior and gives negative evidence for the success of satellite behavior, if adopted. Two males were observed calling on the same 0.3-m-diameter water oak, one at 1.5 m and the other directly beneath at 0.3 m. The lower male quit calling when illuminated and did not call again during the following 17 min. He kept his wings raised in singing position, however. A 500 ml jar with a reared virgin female was opened on the ground directly beneath the two males. After 8 min the female left the jar and ascended the tree toward the calling male. She passed within 5 cm of the rear of the silent male veered to the left and stopped her ascent at 1.0 m. She investigated a small swelling on the trunk and descended the tree to the ground almost opposite the point of release. (The upper male was singing a somewhat sputtery song during this episode, and the lower male remained silent with wings raised.) The female moved in spurts and made a nearly circular 2-m path on the ground ending at the base of the tree near the point of release. She ascended again, passing within 4 cm of the head of the silent male, and 9 min after originally leaving the jar coupled with the calling male. The silent male did not change his station, but during the next 7 min he resumed calling.

Satellite behavior by burrow inhabiting males is difficult to envision but could involve near neighbors of calling males refraining from calling and waiting with open burrows. One observation supports this possibility. In studying the behavior of burrow-calling males, I released a long-deprived, lab-reared virgin female 1 m from each of two males calling at burrows 0.5 m apart. she started toward one of the males and at 0.5 m disappeared, apparently down a hole I had not noticed. My attention was directed toward the hole by a few brief bursts of song. I surmised that the female had entered a burrow occupied by a noncalling male. No other song was heard and 20 min later the burrow was plugged with soil.

Intersexual Selection

Female choice is sometimes based on the investment the male offers toward feeding or protecting the female or her offspring; in other instances it may be based on the male's apparent genetic fitness—either in general terms (translating into increased probability that the female's offspring will survive and be reproductively successful) or in specific terms of effectiveness in fertilizing females (translating into reproductively more successful male offspring) (Thornhill, 1976, 1979).

Choice based on both investment and apparent fitness may occur in short-tailed crickets but neither has been demonstrated. West and Alexander (1963) and Alexander and Otte (1967) pointed out that the burrow of a male short-tailed cricket may be a resource of value to the female, and their laboratory evidence and my field evidence establishes that females that mate with a male in a burrow generally gain sole possession of it. For this to be accepted as an example of female choice, it should first be demonstrated (1) that females mate with males with burrows in preference to those with no burrow to offer, or (2) that females use burrow quality as a criterion for deciding among burrow-associated males. Data relevant to (1) are that males with burrows will climb logs placed nearby and that females will often (3 ♀♀/14 ♂-nights) climb the logs and mate with them. (Could the female locate the male's burrow prior to mating? In one instance the burrow below a pair mating on a log was subsequently occupied by a female.) Furthermore, males more often call away from burrows than at burrows, even though they spend the daylight hours individually ensconced in burrows. The only data concerning (2) are of doubtful relevance because they are from observing a long-deprived virgin. When released 1 m from a male calling at a shallow, shelter-type burrow, the female followed the male into the burrow and mated without delay (even though I was peering in with a light). The female excluded the male shortly thereafter, and the next morning a large mound of dirt indicated that she had spent some of the night enlarging her new quarters. (When soil is moist, a burrow can be constructed quickly, and a male that tenders a female his burrow is not offering much. Male burrows and burrow quality may be of greater importance to female choice when burrowing is difficult.)

Female choice based on the male's general fitness or apparent effectiveness in gaining other copulations was not proved either. The restricted period of evening calling, in which many males call simultaneously, has the effect of exposing each male to comparison with others. However, it is unknown whether females monitor males and compare them either sequentially or simultaneously as to intensity, steadfastness, choice of calling station, etc. One female was observed that appeared to be monitoring a male and the outcome was surprising. At 3 min past sunset, too early for mating to have been completed, I located a male calling at 1.0 m on a 0.4-m-diameter tree (woods deme, 1977). Only 0.12 m below the male was a motionless female. The male continued to call with occasional shifts in orientation. After 11 min a second female appeared, climbed directly to the male and mated with him. Copulation lasted 17 min; during all but the first few seconds the male produced the copulatory song, which is indistinguishable from the calling song. The mated female departed, and the female 0.12 m below kept her station as the male continued calling. (If she was monitor-

ing the male for mating success, what better proof could she have had?) At 36 min past sunset the female ran down the tree. She was caught and later dissected; her spermatheca contained sperm.

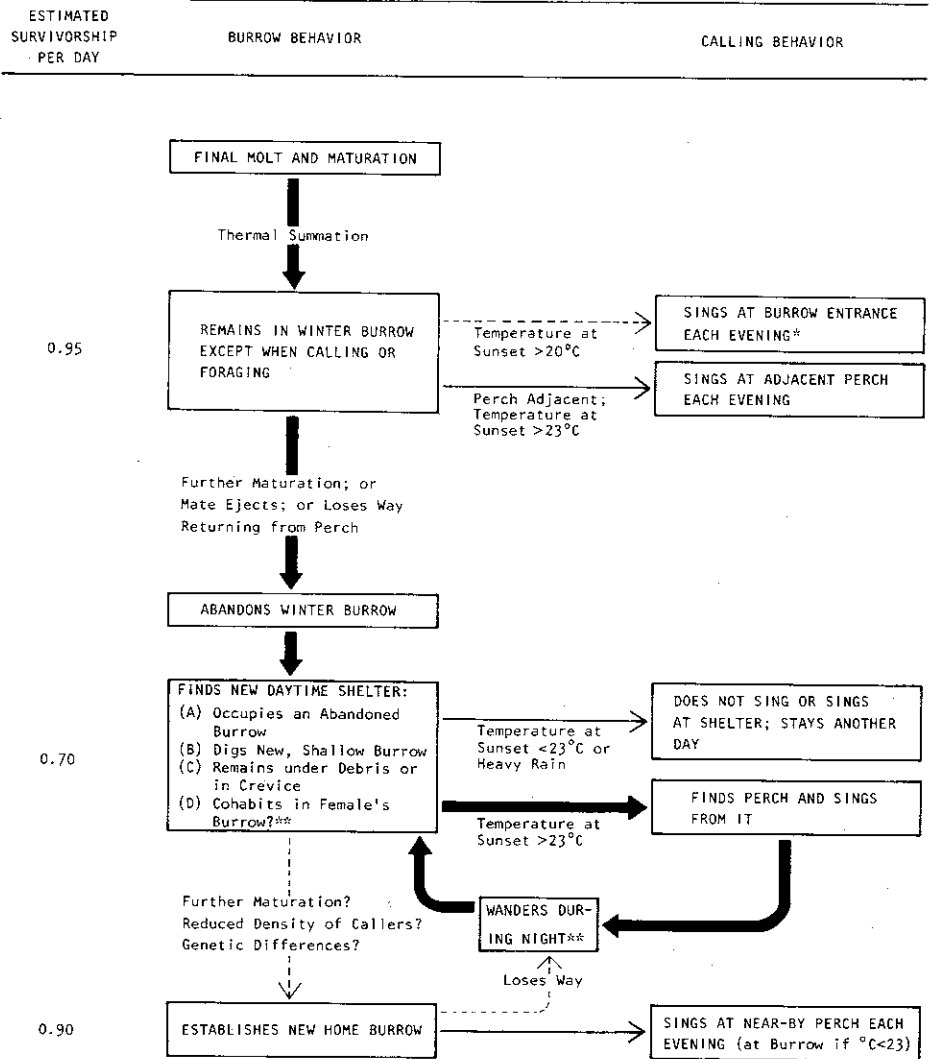
Mating more than once may be an important aspect of female choice. A single spermatophore should contain far more sperm than required to fertilize the fewer than 130 eggs a female produces (Weaver and Sommers, 1969). Consequently a second mating, other than with the same male, could change the sire of all the female's progeny (Parker, 1970). Evidence that females mate with more than one male under field conditions comes from dissecting four females attracted to males calling in cages above pitfall traps (Walker, 1979) (Table VI). Three had sperm in the spermatheca. A female might gain from initiating a second mating if the second male was of higher quality than the first (but see Maynard Smith, 1978, p. 170). She would also be insuring against the possibility that the first male's sperm were inviable, and, depending on the degree of sperm precedence, she might beneficially increase the genetic diversity of her progeny (but see Williams, 1975, p. 129).

If males search for and find the burrows of females (see above), female choice in terms of male quality becomes more complicated. If the female has not mated previously but is ready to do so and if sperm precedence can later cancel the effects of the mating, the female loses no future options by admitting the male and copulating with him in her burrow, and she safeguards against finding no males in the future or having to travel dangerously far to reach one. If the female has already mated [as in the laboratory instance reported by Walker (1973)], her optimal behavior depends not only on male quality and whether there is sperm precedence, but also on the cost of expelling the male without accepting a spermatophore from him and the possible rewards—other than sperm—contained in a spermatophore. The spermatophore is too small (Alexander and Otte, 1967) for its caloric value to be important [cf. *Ephippiger*, in which spermatophore weight is up to 33% of total male weight (Busnel and Dumortier, 1955)], but it could contain scarce substances useful in small amounts [e.g., soluble proteins (Friedel and Gillott, 1977)].

Male Reproductive Behavior

Figure 11 summarizes the major modes of behavior of male short-tailed crickets during their adult lives. Possible functions and determinants of changes from one mode to another are discussed below.

The onset of calling is significantly later when the winter and spring



*Characteristic of barren or mowed sites.

***During a male's nocturnal wandering he may find the burrow of a female that is ready to mate, or soon will be, and gain entrance. The prevalence of such behavior and the duration of cohabitation, if any, are unknown (see text).

FIG. 11. Flow chart of reproductive behavior of male short-tailed crickets. Broad arrows indicate usual progression. Dashed arrows indicate behavior that is sometimes omitted. See text for details.

are unusually cold (Fig. 5), suggesting that completion of the final nymphal instars depends on thermal summation rather than a photoperiodic switch. Many plants show a similar response, and the crickets maintain a predictable relation to the phenology of their community and hence their food plants.

In the lawn deme, males usually called at the entrances of their winter burrows for several evenings. Such behavior was rare in the woods deme, most observations of it being in exposed sites with little litter or covering vegetation. The role of nearby perches in determining the calling stations of young males was demonstrated by placing perches next to the winter burrows of lawn-deme males. Natural perches are generally close for males of the woods deme, and they may have used them and returned to their winter burrows for several evenings. Four factors can be cited as making calling at burrows a better strategy for a young male in the lawn deme than in the woods deme: (1) Females would be maturing in nearby burrows, and the advantage of greater broadcast area gained by climbing perches at the edge of the lawn would be cancelled by the reduced chance that females would be near. (2) Calling at burrows is always safer than calling from perches, and the longer the trip to the perch the more the increased danger from predators [e.g., wolf spiders (Walker, 1979)]. (3) Calling from the ground results in smaller broadcast areas because of attenuation from leaf litter, vegetation, and uneven terrain. Such attenuation would be less on a lawn than in a woods. (4) Burrows are more valuable to the female in the lawn deme because the soil dries more rapidly and burrowing is more often difficult. (This leads to the prediction that burrow-associated calling would be more prevalent in dry weather: it was not conspicuously so.)

In both demes, males eventually assumed a peripatetic existence. Abandoning the winter burrow could be a direct result of ejection by a female that the male had attracted and mated with or of inability to find the burrow after calling from a perch. However, without either event intervening and in spite of a low mortality (estimated at no more than 5%/day), males still abandoned their winter burrows. Local differences in exposure caused different soil temperatures that in turn caused females to mature at different times in different sites. Males that emigrated to sites where females were continuing to mature would improve their chances of mating. (Movement should occur from lawn to wooded borders—it did.)

Males that had left their overwintering burrows generally called from perches each evening and then wandered—perhaps in search of signs of females (see above)—and surely in search of a shelter for the following day. Mortality was high; perhaps 30% of wandering males permanently dropped from the pool of callers each night. Two marked males (see above) exhibited a second sedentary phase in their final days, suggesting that the costs vs.

benefits of wandering change either with age or with density of competing males.

EPILOGUE

These studies of reproductive strategies of *A. arboreus* began in 1965, when I tried to learn how lawn-deme males found their ways back to their burrows each evening after calling from nearby trees. I soon discovered that they didn't—only to find later that they sometimes did. (I still do not know how, nor what are the reproductive consequences of the opposing strategies.) For the varied questions I have since put to *A. arboreus*, my answer-of-the-moment has proved wrong or inadequate again and again. The present summary and collation of such answers constitutes a model of reproductive behavior that is, at best, incomplete. It could well be improved by investigating the clues uncovered in its construction.

Questions that now seem important and answerable include the following: Do peripatetic males detect females chemically? Do virgin females admit and mate with males in their burrows? Does food limit the calling of males? What features are important to differential success among males calling on the same tree? What proportion of females attracted to perch-calling males have mated before? Does that last mating negate earlier ones? Are between-deme differences in calling stations entirely attributable to differences in environment?

Though much remains to be discovered, as much is known of the reproductive behavior of *A. arboreus* under natural conditions as for any other acoustically broadcasting insect. What has so far been determined differs greatly from what was surmised from casual field observations and from what would be predicted from published laboratory and field studies of other calling species.

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REFERENCES

- Alexander, R. D., 1961, Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae), *Behaviour* **17**:130-223.
- Alexander, R. D., 1975, Natural selection and specialized chorusing behavior in acoustical insects, in: *Insects, Science and Society* (David Pimentel, ed.), pp. 35-77, Academic Press, New York.
- Alexander, R. D., and Otte, D., 1967, The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera, *Misc. Publ. Mus. Zool. Univ. Mich.* **133**:1-62.
- Bailey, W. J., and Stephen, R. O., 1978, Directionality and auditory slit function: A theory of hearing in bushcrickets, *Science* **201**:633-634.
- Bailey, W. J., and Thompson, P., 1977, Acoustic orientation in the cricket *Teleogryllus oceanicus* (Le Guillou), *J. Exp. Biol.* **67**:61-75.
- Bentley, D., 1977, Control of cricket song patterns by descending interneurons, *J. Comp. Physiol. A* **116**:19-38.
- Blum, M. S., and Blum, N. A., eds., 1979, *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York.
- Browning, T. O., 1954, Observations on the ecology of the Australian field cricket, *Gryllulus commodus* Walker, in the field, *Aust. J. Zool.* **2**:205-222.
- Busnel, R.-G., and Dumortier, B., 1955, Etude du cycle génital du mâle d'*Ephippiger* et son rapport avec le comportement acoustique, *Bull. Soc. Zool. France* **80**:23-26.
- Cade, W. H., 1976, Male reproductive competition and sexual selection in the field cricket *Gryllus integer*, Ph.D. thesis, University of Texas, Austin, 120 pp. (Xerox University Microfilms, Ann Arbor, Mich.).
- Cade, W. H., 1979a, The evolution of alternative male reproductive strategies in field crickets, in: *Sexual Selection and Reproductive Competition in Insects* (M. S. Blum and N. A. Blum, eds.), pp. 343-379, Academic Press, New York.
- Cade, W. H., 1979b, Effect of male deprivation on female phonotaxis in field crickets (Orthoptera: Gryllidae), *Canad. Entomol.* **111**:741-744.
- Campbell, D. J., and Clarke, D. J., 1971, Nearest neighbour tests of significance for nonrandomness in the spatial distribution of singing crickets (*Teleogryllus commodus* (Walker)), *Anim. Behav.* **19**:750-756.
- Campbell, D. J., and Shipp, E., 1974, Spectral analysis of cyclic behaviour with examples from the field cricket *Teleogryllus commodus* (Walk.), *Anim. Behav.* **22**:862-875.
- Campbell, T. E., 1971, Pine seed and seedling depredations by short-tailed crickets, *J. Econ. Entomol.* **64**:1490-1493.
- Elsner, N., and Popov, A. V., 1978, Neuroethology of acoustic communication, *Adv. Insect Physiol.* **13**:229-355.
- Feaver, M. A., 1977, Aspects of the behavioral ecology of three species of *Orchelimum* (Orthoptera: Tettigoniidae), Ph.D. thesis, University of Michigan, Ann Arbor, 199 pp. (Xerox University Microfilms, Ann Arbor, Mich.).
- Fretwell, S. D. 1972, *Populations in a Seasonal Environment*, Princeton University Press, Princeton, New Jersey.
- Friedel, T., and Gillott, C., 1977, Contribution of male-produced proteins to vitellogenesis in *Melanopus sanguinipes*, *J. Insect Physiol.* **23**:145-151.

- Gwynne, D. T., 1977, Mating behavior of *Neoconocephalus ensiger* (Orthoptera: Tettigoniidae) with notes on the calling song, *Can. Entomol.* **109**:237-242.
- Hoy, R. R., 1974, Genetic control of acoustic behavior in crickets, *Am. Zool.* **14**:1067-1080.
- Hoy, R. R., and Casady, G. B., 1978, Acoustic communication in crickets: Physiological analysis of auditory pathways, in: *Ontogeny of Behavior* (G. Burghardt and M. Bekoff, eds.), pp. 45-62, Garland, New York.
- Huber, F., 1975, Sensory and neuronal mechanisms underlying acoustic communication in Orthopteran insects, *Adv. Behav. Biol.* **15**:55-97.
- Kerr, G. E., 1974, Visual and acoustical communicative behavior in *Dissosteira carolina* (Orthoptera: Acrididae), *Can. Entomol.* **106**:263-272.
- Lloyd, J. E., 1978, Insect bioluminescence, in: *Bioluminescence in Action* (P. Herring, ed.), pp. 214-272, Academic Press, New York.
- Lloyd, J. E., 1979a, Sexual selection in luminescent beetles, *Sexual Selection and Reproductive Competition in Insects* (M. S. Blum and N. A. Blum, eds.), pp. 293-342, Academic Press, New York.
- Lloyd, J. E., 1979b, Mating behavior and natural selection, *Fla. Entomol.* **62**:17-34.
- Loher, W., and Rence, B., 1978, The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control, *Z. Tierpsychol.* **46**:225-259.
- Maynard Smith, J., 1978, *The Evolution of Sex*, Cambridge University Press, Cambridge.
- Meixner, A. J., 1976, Acoustical behavior and spacing in the Nebraska conehead *Neoconocephalus nebrascensis* (Bruner) (Orthoptera; Tettigoniidae), Ph.D. thesis, Iowa State University, Ames, 160 pp. (Xerox University Microfilms, Ann Arbor, Mich.).
- Michelsen, A., and Larsen, O. N., 1978, Biophysics of the ensiferan ear. I. Tympanal vibrations in bushcrickets (Tettigoniidae) studied with laser vibrometry, *J. Comp. Physiol. A.* **123**:193-203.
- Michelsen, A., and Nocke, H., 1974, Biophysical aspects of sound communication in insects, *Adv. Insect Physiol.* **10**:247-296.
- Morris, G. K., 1971, Aggression in male conocephaline grasshoppers (Tettigoniidae), *Anim. Behav.* **19**:132-137.
- Morris, G. K., 1972, Phonotaxis of male meadow grasshoppers (Orthoptera: Tettigoniidae), *J. N. Y. Entomol. Soc.* **80**:5-6.
- Morris G. K., 1979, Mating systems, paternal investment, and aggressive behavior of acoustic Orthoptera, *Fla. Entomol.* **62**:9-17.
- Morris, G. K., Kerr, G. E., and Fullard, J. H., 1978, Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae: *Conocephalus nigropleurum*), *Can. J. Zool.* **56**:1479-1487.
- Nielsen, E. T., 1974, Activity patterns of *Eugaster* (Orthoptera: Ensifera), *Entomol. Exp. Appl.* **17**:325-347.
- Otte, D., 1970, A comparative study of communicative behavior in grasshoppers, *Misc. Pub. Mus. Zool. Univ. Mich.* **141**:1-168.
- Otte, D., 1972, Simple versus elaborate behavior in grasshoppers: An analysis of communication in the genus *Syrbula*, *Behaviour* **42**:291-322.
- Otte, D., 1977, Communication in Orthoptera, in: *How Animals Communicate* (T. A. Sebeok, ed.), pp. 334-361, Indiana University Press, Bloomington.
- Otte, D., and Cade, W., 1976, On the role of olfaction in sexual and interspecies recognition in crickets (*Acheta* and *Gryllus*), *Anim. Behav.* **24**:1-6.
- Parker, G. A., 1970, Sperm competition and its evolutionary consequences in the insects, *Biol. Rev.* **45**:525-568.
- Paul, R. 1976, Acoustic response to chemical stimuli in ground crickets, *Nature* **263**:404-405.
- Paul, R. C., and Walker, T. J., 1979, Arboreal singing in a burrowing cricket, *J. Comp. Physiol. A* **132**:217-223.

- Perrill, S. A., Gerhardt, H. C., and Daniel, R., 1978, Sexual parasitism in the green tree frog (*Hyla cinerea*), *Science* **200**:1179-1180.
- Phillips, L. H., II, and Konishi, M., 1973, Control of aggression by singing in crickets, *Nature* **241**:64-65.
- Pianka, E. R., 1970, On *r*- and *K*- selection, *Am. Nat.* **104**:592-597.
- Pollack, G. C., and Hoy, R. R., 1979, Temporal pattern as a cue for species-specific calling song recognition in crickets, *Science* **204**:429-432.
- Popov, A. V., 1975, Acoustic behaviour and migrations of field crickets *Gryllus campestris*, *Zool. Zh.* **54**:1803-1809.
- Popov, A. V., and Shuvalov, V. F., 1974, The spectrum, intensity, and direction of the calling song of the cricket *Gryllus campestris* under natural conditions, *J. Evol. Biochem. Physiol.* **10**:61-68.
- Popov, A. V., and Shuvalov, V. F., 1977, Phonotactic behavior of crickets, *J. Comp. Physiol. A* **119**:111-126.
- Popov, A. V., Shuvalov, V. F., Svetlogorskaya, I. D., and Markovich, A. M., 1975, Acoustic behavior and auditory systems in insects, *Rheinisch-Westfael. Akad. Wiss. Natur. Ing. Wirtschaftswiss. Vortr.* **53**:281-306.
- Prestwich, K. N., and Walker, T. J. 1980, Energetics of singing in crickets: Effect of temperature in three trilling species, *J. Comp. Physiol. A.* (submitted).
- Rence, B., and Loher, W., 1975, Arrhythmically singing crickets: Thermoperiodic reentrainment after bilobectomy, *Science* **190**:385-387.
- Rence, B., and Loher, W., 1977, Contact chemoreceptive sex recognition in the male cricket, *Teleogryllus commodus*, *Physiol Entomol.* **2**:225-236.
- Samways, M. J., 1977, Bush cricket interspecific acoustic interactions in the field (Orthoptera, Tettigoniidae), *J. Nat. Hist.* **11**:155-168.
- Sismondo, E., 1979, Stridulation and tegminal resonance in the tree cricket *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae), *J. Comp. Physiol. A* **129**:269-279.
- Sokolove, P. G., 1975, Locomotory and stridulatory circadian rhythms in the cricket, *Teleogryllus commodus*, *J. Insect Physiol.* **21**:537-558.
- Sokolove, P. G., and Loher, W., 1975, Role of eyes, optic lobes, and pars intercerebralis in locomotory and stridulatory circadian rhythms of *Teleogryllus commodus*, *J. Insect Physiol.* **21**:785-799.
- Thornhill, R., 1976, Sexual selection and paternal investment in insects, *Am. Nat.* **110**:153-163.
- Thornhill, R., 1979, Male and female sexual selection and the evolution of mating strategies in insects, in: *Sexual Selection and Reproductive Competition in Insects* (M. S. Blum and N. A. Blum, eds.) Academic Press, New York.
- Turcek, F. J., 1967, Ecological studies of the field cricket, *Gryllus campestris* L., *Biologia* **22**:808-816.
- Ulagaraj, S. M., 1975, Mole crickets: Ecology, behavior, and dispersal flight (Orthoptera: Gryllotalpidae: *Scapteriscus*), *Env. Entomol.* **4**:265-273.
- Walker, T. J., 1964, Experimental demonstration of a cat locating orthoptern prey by the prey's calling song, *Fla. Entomol.* **47**:163-165.
- Walker, T. J., 1972, Deciduous wings in crickets: A new basis for wing dimorphism, *Psyche* **79**:311-314.
- Walker, T. J., 1973, Systematics and acoustic behavior of United States and Caribbean short-tailed crickets (Orthoptera: Gryllidae: *Anurogryllus*), *Ann. Entomol. Soc. Am.* **66**:1269-1277.
- Walker, T. J., 1975, Effects of temperature on rates in poikilotherm nervous systems: Evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*) and reanalysis of published data, *J. Comp. Physiol.* **101**:57-69.

- Walker, T. J., 1979, Calling crickets (*Anurogryllus arboreus*) over pitfalls: Females, males, and predators, *Env. Entomol.* **8**:441-443.
- Walker, T. J., 1980, Seasonal life cycles of crickets and katydids of northern Florida and their geographical variation, (in preparation).
- Weaver, J. E., and Sommers, R. A., 1969, Life history and habits of the short-tailed cricket, *Anurogryllus muticus*, in central Louisiana, *Ann. Entomol. Soc. Am.* **62**:337-342.
- West, M. J., and Alexander, R. D., 1963. Sub-social behavior in a burrowing cricket *Anurogryllus muticus* (De Geer) (Orthoptera: Gryllidae), *Ohio J. Sci.* **63**:19-24.
- Williams, G. C., 1975, *Sex and Evolution*, Princeton University Press, Princeton.