Orthopteran
Mating Systems

Sexual Competition in a
Diverse Group of Insects

edited by Darryl T. Gwynne
and Glenn K. Morris

Chapter 11

11. Mating Modes and Female Choice in Short-Tailed Crickets (*Anurogryllus arboreus*)

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Short-tailed crickets owe their name to the female's lack of a conspicuous ovipositor. A female **Anurogryllus arboreus** does not insert her eggs into soil like other grylline crickets but piles them in a chamber of her subterranean home. She tends the eggs as they incubate, and when they hatch, nourishes the juveniles with trophic eggs and food she has foraged on the surface. When the mother dies, the young disperse, and each excavates a burrow of its own (West and Alexander 1963; Walker 1973, 1980).

After overwintering as late-instar juveniles, the crickets become adults and the cycle soon begins again. What happens once each year, between maturing of adults and laying of egg clutches, is the subject of this paper. The events are complex, sometimes surprising, and far from being adequately known or understood.

BIOLOGICAL BACKGROUND

A. arboreus occurs throughout southeastern United States (Walker 1973) but has been studied in the field only in central Louisiana (Weaver and Sommers 1969) and Gainesville, Florida (Paul and Walker 1979; Walker 1979, 1980). It exists in stable, sedentary populations in a variety of habitats. During most of the year, while the young are growing or overwintering, short-tailed crickets are seldom seen because they spend their days in dirt-plugged burrows and venture out at night only in search of food, which they carry back to their chambers to eat. Multitudinous small mounds of tailings that appear after a rain, when individuals repair or enlarge their quarters, are the chief evidence of a dense, maturing population. However, when males come of age the population is suddenly manifest: each evening at sunset males start a loud incessant chorus. An hour later quiet is restored until the following evening. Short-tailed crickets compress not only their daily calling times to

an unusual degree (Fig. 8) but also their seasonal
calling times (Fig. 1). Their calling season lasts for
less than three months with numbers peaking during the
early weeks. Within a single habitat, 95% of calling
occurs in 5-6 weeks (Walker 1980). Other univoltine,
burrow-dwelling crickets at Gainesville, Florida, have
more prolonged calling seasons (Fig. 1).

In open habitats, such as lawns and pastures, a male
first calls at the entrance to his overwintering burrow.
After several nights males abandon their home burrows and
generally call each successive evening from a different
elevated perch, such as a fern, a fence post, or, most
commonly, a tree trunk. In wooded habitats nearly all
calling is from perches (Walker 1980). Modal height of
calling when males have unobstructed access to higher
sites is ca 1 m (Fig. 2).

Unlike two tropical species of short-tailed cricket,
A. arboreus is flightless and all traffic to calling
males is from the surface (Walker 1972, 1973; Walker and
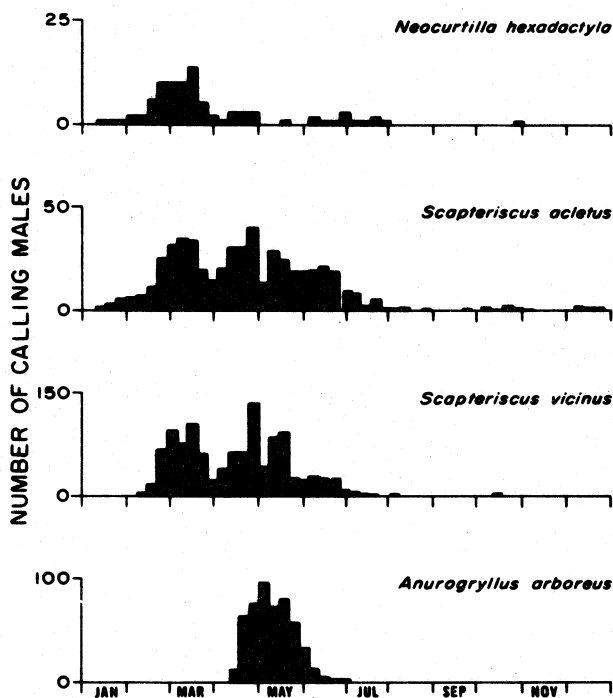Whitesell 1981).

Fig. 1. Seasonal distribution of calling in four
species of burrow-dwelling crickets, Gainesville,
Florida, 1970-1971. Numbers based on weekly or biweekly
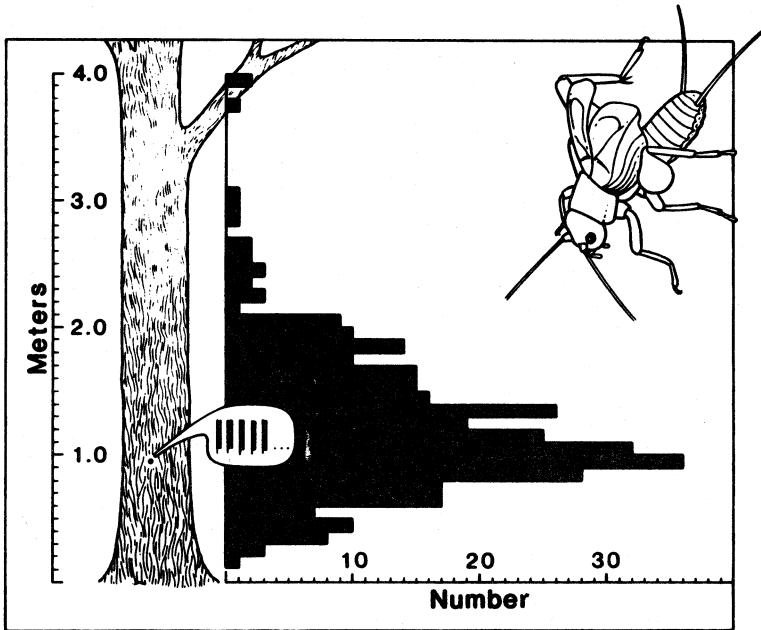censuses at 15 sites.

Fig. 2. Vertical distribution of 337 males of
A. arboreus calling from tree trunks (Paul and Walker
1979). Male at upper right is in typical calling
posture.

Previously reported work and the present study show
that sexual pairing in **A. arboreus** occurs in the male's
burrow, in the female's burrow, or in the open (Table
1). Each mode of mating will be considered separately
below, and a final section will discuss the integration
of the three in the reproductive strategies of males and
females.

MATING IN MALE'S BURROW

In a lawn-inhabiting population of short-tailed
crickets that I studied for more than 10 years,
approximately 40% of calling was by males at their burrow
entrances. When an observer approached, the males dashed
into their burrows and sometimes resumed calling while
still underground. From the first it seemed likely that
females were attracted to males calling at their burrows,

but the only observation supporting that conclusion was
one pair discovered mating near the entrance to a
burrow. Finally, mating by males calling at burrows was

Table 1. Mating modes in short-tailed crickets
           (A.arboreus).

Behavior of Male	Behavior of Female	Mating Site
(1) Calls at own burrow	Goes to male, mates, takes over burrow	In male's burrow
(2) Finds female's burrow	Admits male, mates, retains burrow	In female's burrow
(3) Calls from perch[a]	Goes to male, mates, leaves	In open

[a] May later search on ground at base of perch for
     female that has mated earlier with calling male. If
     found, female may again mate in open (see text).

investigated by releasing reared virgin females 1 m away
(Walker 1980). In two of three trials the female went
directly to the male, he retreated into his burrow, she
followed, and courtship sounds were heard. After an
interval appropriate for completing sperm transfer, the
male left the burrow. When one of the males attempted to
re-enter, the female turned him away with gaping
mandibles.
     In a woods-inhabiting population of short-tailed
crickets, also studied for more than 10 years, less than
1% of calling was by males at burrows, and such calling
occurred only at the edge of the woods and early in the
season (Walker 1980). It seems certain that matings in
the male's burrow in the woods population are a lesser
proportion of the total than in the lawn population.

MATING IN FEMALE'S BURROW

     This mode of mating is difficult to detect under
field conditions, although laboratory observations in
glass-sided burrows suggested that it occurs (Alexander
and Otte 1967, Walker 1973). Field observations gave
indirect evidence for it: once males left their home

burrows they generally traveled each night, as though searching for female burrows to enter. Males could be watched roaming about after the calling period, with distances between successive calling perches of marked males giving conservative measures of nightly movement (Table 2). Pitfall catches of crickets confirmed that after the calling period males moved about much more than females (Table 3) (Walker 1979).

Table 2.   Distances between calling perches for successive sightings of marked males of A. **arboreus** (from Walker 1980).

| Population (years) | Straight-line distance to new perch (m) | | | |
| | 1 day interval | | >1 day interval | |
	n	$\bar{x}$ ± SD	n	$\bar{x}$ ± SD
Lawn (1965, 1967)	31	11 ± 8	28	14 ± 14
Woods (1972, 1973, 1975, 1976)	39	16 ± 12	49	21 ± 16

Table 3.   Numbers of short-tailed crickets captured in pitfalls in a woods population, 1977-1979 (partly from Walker 1979). Some pitfalls had calling or experimentally muted males suspended above them.

	2 h including calling period	other 22 h
Males	8	23
Females	16[a]	0

[a] All but one captured beneath a calling male.

In an attempt to get direct evidence of mating in
the female's burrow I ran a pilot experiment in the midst
of the woods population during May 1980. Eight virgins
reared outdoors were induced to make their burrows
beneath the center of individual 30 x 30 x 15-cm, 3-mm
mesh, hardware cloth cages (Fig. 3A). One old-appearing
virgin, one young-appearing virgin, and a control (no
cricket added) made up an experimental replicate. The
four replicates were at least 10 m apart; cages within a
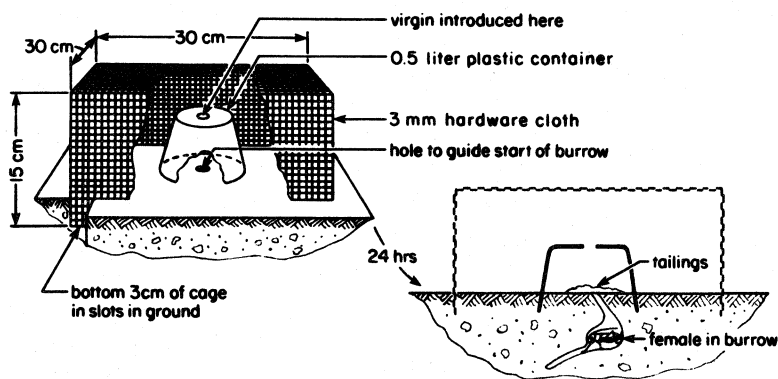replicate were no closer than 1.5 m.

Once the females were established in their burrows
the hardware cloth cages were removed each night after
calling had ceased and replaced the following afternoon
before sunset (Fig. 3B). This procedure made it
impossible for the female to go to a calling male but
allowed searching males access to the female and her
burrow during the remainder of the night. After the
females were exposed 4 or 5 nights (22-26 May), I
excavated their burrows and retrieved five of the eight.
One was dissected and sperm found in her spermatheca;
another was injured as she was unearthed and died and
decayed before spermathecal assay; and the remaining
three were placed in 4-liter jars with soil to see if
they would lay fertile eggs. Two months later two of the
three had produced progeny. The soil beneath the control
cages was also excavated, but no crickets were
recovered. No male appeared in any cage during the
calling period, as might have occurred had one cohabited
with the female during the day. Males most likely mate
and leave the same night.

Since three of four virgin females mated with
searching males within 5 nights, it is likely that mating
in the female's burrow is an important aspect of
reproductive behavior in **A. arboreus.** Walker and
Whitesell (1982) reported evidence for a similar mating
mode in a Panamanian species, a sibling species with
A. arboreus, A. muticus. Loher (1979) reported
that **Teleogryllus commodus** females in the laboratory
mate with introduced males (cf. searching males) 2-6 days
earlier than they begin locomotion indicative of
phonotaxis.

MATING ON PERCHES

This mode of mating, unlike the other two, is easily
studied in the field. The female climbs to the
continuously trilling male and mating occurs in the open,
usually on a tree trunk. After the spermatophore tube
has been inserted, the pair assumes a tail to tail
position with the male holding the female with his
terminalia. The male then resumes calling and generally

A. Set-up

Labels:
- virgin introduced here
- 0.5 liter plastic container
- 3 mm hardware cloth
- hole to guide start of burrow
- 30 cm
- 30 cm
- 15 cm
- bottom 3cm of cage in slots in ground
- 24 hrs
- tailings
- female in burrow

B. Daily routine

Labels:
- remove cage at 2200h
- 4 hrs includes calling period
- 20 hrs (0000-1800h) (2200-2400h)
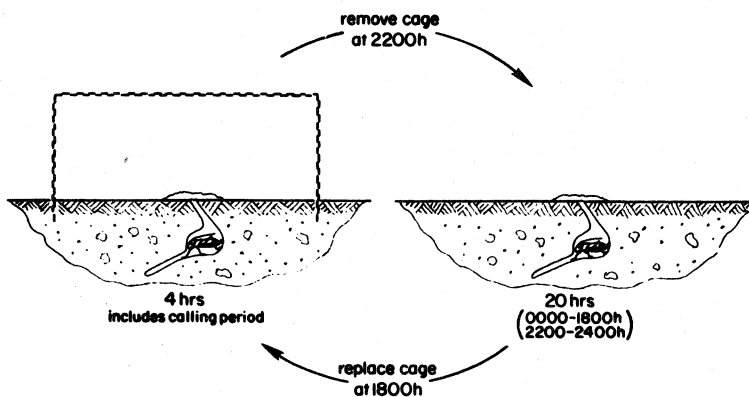- replace cage at 1800h

Fig. 3. Assay for searching males of **A. arboreus.**
A. Method of establishing virgin female in burrow
outdoors beneath a hardware cloth cage. B. Technique
for restraining female during calling period and exposing
her to searching males during the time males roam. At
1800 h each day the cage is replaced and at 2200 h it is
removed. (Sunset and start of calling are ca 2000 h; all
calling ends by 2200 h.)

calls throughout the 10-30 min that he remains coupled to
the female. A brief interruption in calling sometimes
followed by several seconds of intermittent calling is
auditory evidence that a female has arrived at a calling
male and coupling is in progress. If a pair are already
in copula, they can be located by the male's calling as

readily as can a solitary male. If males calling on
perches are inspected at 10-min intervals, practically
all their matings can be detected.

Yet another aspect of the behavior of **A. arboreus**
makes its mating on perches easy to study. Males calling
from perches can be captured and kept individually in
500 ml containers with 400 ml of soil, where they
excavate burrows and call from the surface each evening.
If the lid of such a container is removed prior to
sunset, the male will leave approximately at sunset,
ascend whatever tree or post has been made handy, and
call. If more than one container is opened at the base
of a single tree, all males will climb the trunk and
call. Under natural circumstances two, three, or four
males sometimes call from one tree trunk, but more than
95% of the trees in the habitats studied had one or
none. Experimentally caged males can be used to
establish choruses or solo callers on predetermined trees
(Paul and Walker 1979, Walker 1980).

FEMALE CHOICE EXPERIMENTS

During spring 1980, in the midst of the woods
population, I attempted to determine if females preferred
males calling in choruses to those calling singly and
gathered preliminary data on whether other attributes of
a male predict his success in attracting females.

Methods

The study site had three, 0.2-m diameter-breast-
high (DBH), water oaks **(Quercus nigra)**, designated
north, center, and south, that formed an obtuse isosceles
triangle (legs 2.25 m, base 4.0 m) (Fig. 4). Each
evening prior to sunset, open containers with males in
their burrows were placed at the bases of the oaks in
numbers designed to establish a chorus on one tree and a
solitary caller on one or each of the others (Fig. 4A).
The first night of every two, a coin flip determined
whether the north or the south tree would be used for the
chorus; the next night the opposite tree was used.
During the first 8 nights of the study, the center tree
was a control (no container placed at its base);
subsequently it was used for a second solitary caller.
Four males were placed at the base of the chorus tree the
first 12 nights of the study; 4-6 (usually 5) were used
for the remaining nights. Males released had been caught
calling from perches in the vicinity of the study site,
marked for individual recognition (Walker and Wineriter
1981), and, in most cases, weighed. They were held
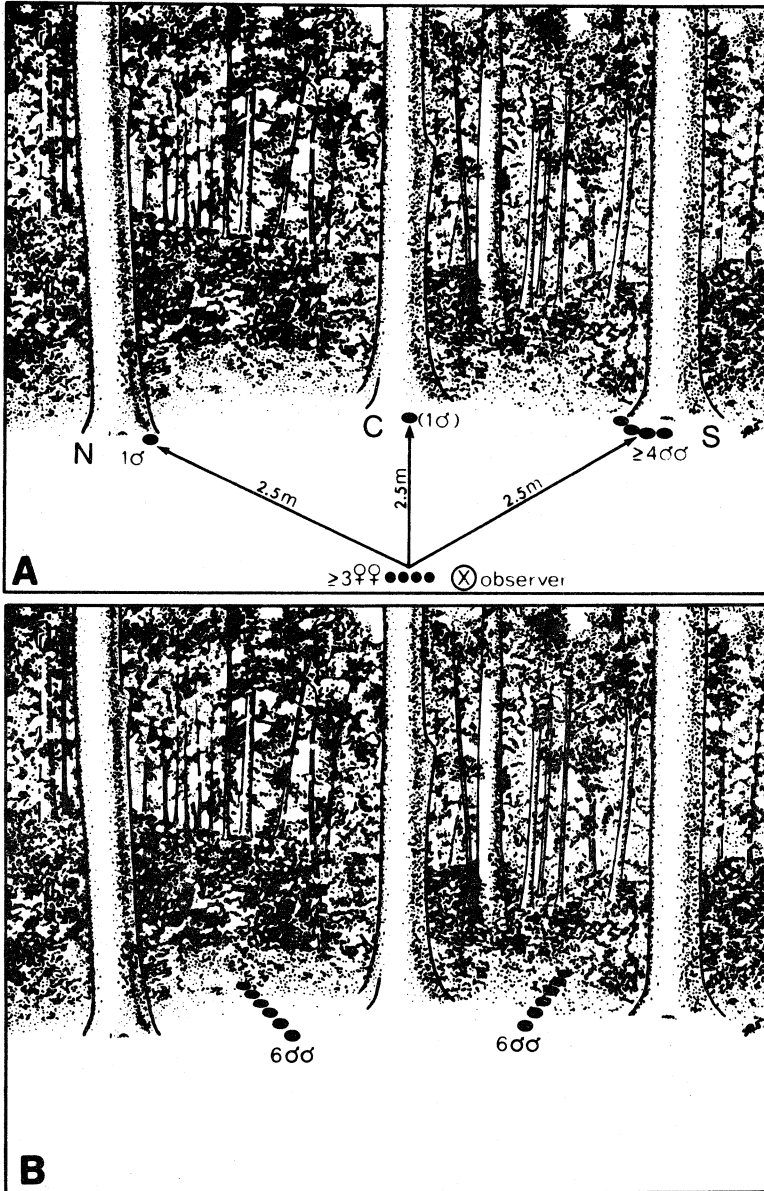outdoors for 1-18 days prior to use.

Fig. 4. 'Three-tree' site and set-ups for studying female choice (A) and male chorus formation (A & B). The chorus tree in female choice studies was north (N) instead of south (S) on 9 of the 18 nights of observations.

Closed containers with outdoor-reared, individually marked females in their burrows were placed at a site 2.5 m from the bases of the trio of water oaks (Fig. 4A). Shortly before sunset the lids were removed and continuous observations begun. Early each evening I remained seated behind the female release site. As it became dark, I could approach calling males and mating females and read their marks using a rheostat-controlled head light. The trees were faintly striped at 0.1-m intervals vertically and at 60° intervals radially to facilitate identifying the positions of crickets. Sound levels of calling males were read with a Bruel and Kjaer Model 2219 meter held 15 cm dorsal to the cricket's body. Readings could not be made until ~25 min after sunset because the male would leap from the tree. By that time many males had climbed too high to be measured, and I was often pressed to keep up with other types of observations even though aided by a hand-held tape recorder.

Results

General. Released crickets generally performed as expected: 79% of the males climbed the intended tree and called, and 61% of the females chose a male from those in the experimental array. Noteworthy details and deviations are described in an Appendix (p. 262) that includes Table 7.

Solo vs. assembled males. On 13 nights the necessary conditions were met to determine if calling on the same tree with other males influenced a male's likelihood of mating: two or more males called from one of the trees; one male called from one or each of the other two trees; and one or more females chose a caller. Although 20 of 29 females went to chorus trees, males calling from chorus trees were on average no better than males calling solo in inducing females to come and mount (.42 vs .45 females per male; Table 4).

Choices among concurrently calling males. If calling in choruses is no better or worse than calling solo, the next question of interest is whether particular males are chosen more often than others. The more females that select among the males calling on a single night, the easier it is to detect biases that exist in favor of particular males. On 10 nights two to five females chose among three to seven males (Table 5). Never were more than two males chosen on a single evening. The combined probability (p<.05) shows a significant bias in females' choice of males.

Table 4.   Results of allowing **A. arboreus** females to
           choose between trees with one calling male and
           with more than one calling male (i.e. solo and
           chorus trees); 13 nights.

	solo tree(s)	chorus tree[a]
Tree preferred (no. of nights)[b]	5	8
Total females choosing	9	20
Total males calling	20[c]	48
Females/male	.45	.42

[a] Two to five males calling, $\bar{x}$ = 3.7.
[b] On each of the 13 nights more females went to one
    category of tree than the other. On 6 nights one solo
    tree competed with the chorus tree; on 7 nights two
    solo trees competed.
[c] See footnote b; (6x1) + (7x2) = 20

     Male phenotype and female choice.   Since females are
apparently choosing certain males and rejecting others,
it becomes important to learn what aspects of a male's
phenotype make him likely or unlikely to be selected.
Three features were examined: intensity of call, weight
of caller, and height called from. Method of analysis
was to compare the chosen male (i.e. the one first
mounted) with other males calling from the same tree at
the same time (Fig. 5). Designating the first male
mounted as the chosen male was appropriate because,
except when the male was already in copula or when the
female fell from the tree, a female never gave up a male
she was mounting for another. Comparisons of chosen and
unchosen males were limited to males calling on the same
tree because they were easily accessible to the choosing
females in the last minute prior to mounting.
     Intensity of call (Fig. 5A) seemed likely to be a
potent predictor of female choice for several reasons:
males varied substantially in loudness (Fig. 6); females
could locate loud males easier than faint ones; louder
males ought to be larger and more vigorous (demonstrating
quality genes); previous studies (especially those of
Forrest 1980, 1982) had shown intensity to be important
to females of other calling species. Nonetheless,
intensity did not predict success for **A. arboreus**
males.

Table 5.   Choices of **A. arboreus** females among
           concurrently calling males. Males listed in
           order of success (i.e. numbers of females that
           chose to mount them first). Dash indicates no
           male in that category.

Date	Males on Chorus Tree					Males on Solo Tree(s)[a]		p[b]
(1980)	A	B	C	D	E	Y	Z	
			(numbers of females)					
24 May	2	1	0	–	–	0	–	.62
26 May	2	1	0	0	–	0	–	.52
27 May	2	1	0	–	–	0	–	.62
1 June	0	0	0	0	–	2	1	.44
3 June	3	2	0	0	0	0	–	.06
4 June	1	1	0	0	–	0	0	1.00
5 June	2	0	0	0	0	1	0	.39
6 June	0	0	–	–	–	2	0	.25
7 June	3	0	0	–	–	–	–	.11
8 June	1	0	0	–	–	2	–	.62

[a] On 4 nights solo males called on two trees while
    two or more males called from a single chorus tree.
    On 7 June no male called solo.
[b] Probability, for each date, of a distribution
    with equal or greater bias in female choice.
    Lancaster's (1949) modification of R.A. Fisher's
    method for combining probabilities yields $.04 < p < .05$.

Indeed, males with weaker calls were chosen more often,
though not significantly so, than their loud neighbors
(Fig. 5A). Because intensity was difficult to measure
under the experimental circumstances, the number of
comparisons was small (n = 26).
    Weight of calling male (55 comparisons) also failed
as a predictor of female choice (Fig. 5B). Since weight
is a predictor of intensity (Fig. 6), the failure of
weight to correlate with female choice is further
evidence that intensity of call does not predict female
choice.
    Heights of calling males were always known;
consequently, comparisons between chosen and rejected
males are complete. On 13 evenings a total of 27 females
chose among three or more males calling on the same
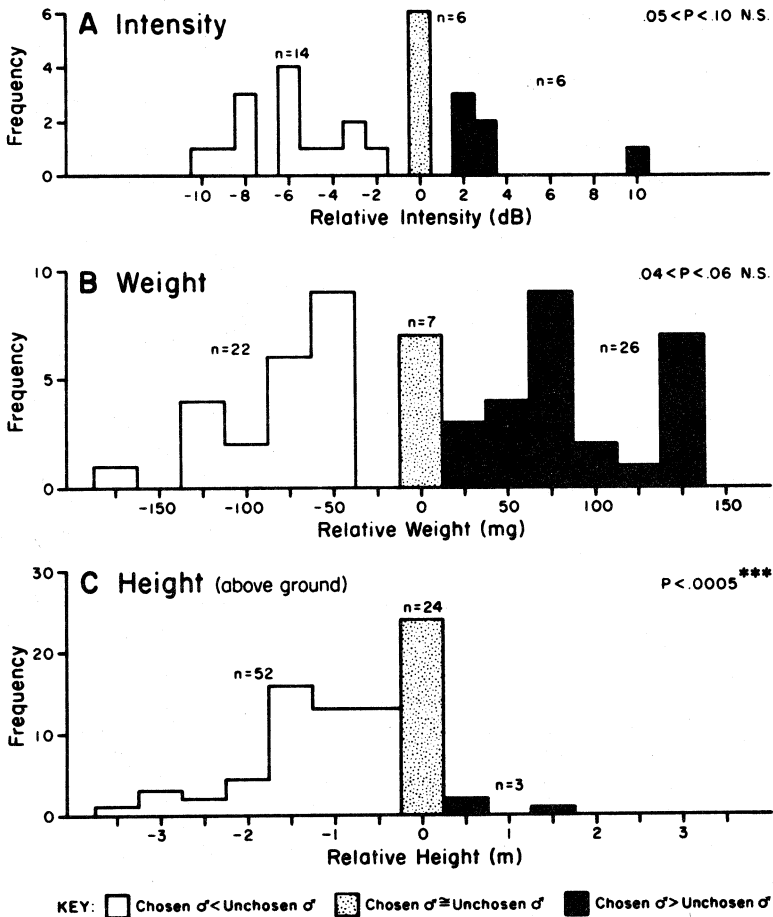tree. Pairwise comparisons (n = 79) between chosen and

Fig. 5. Female choice as related to three properties of calling males. In each case that the property of the chosen male was known, it was compared pairwise with known properties of rejected males calling on the same tree. For example, when a female chose (i.e. attempted to mount) one of four males calling on the same tree, she generated 0, 1, 2, or 3 pairwise comparisons depending on how many of the males were known as to the property being evaluated. For each successive property (intensity, weight, height), a larger proportion of males was known, accounting for increasingly large samples: n = 26, 55 and 79. A. Intensity of call as measured dorsally at 15 cm. B. Weight of male prior to marking. C. Height of male at time of female choice.
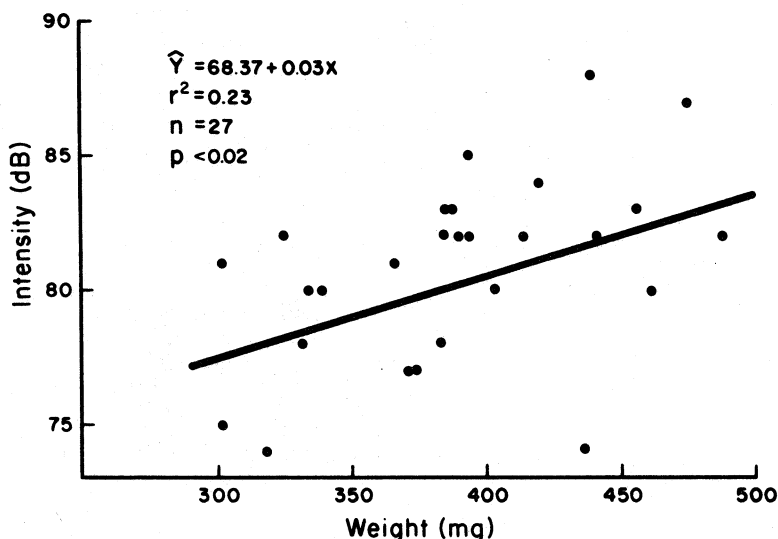
Fig. 6. Weight of wild males as a predictor of calling intensity. Sound levels were measured in the field; the males then were captured and weighed. Slope of regression is 3 dB/100 mg.

rejected males showed that chosen males called from lower perches than rejected males (Fig. 5C). The 27 chosen males were at an average height of 0.8 m (SD = 0.5 m). The highest male classified as chosen was at 2.4 but may not have been the female's first choice, since she was not seen until in copula with him. Another male was mating at 0.9 m on the same tree, and in other cases (see Appendix), females that chose males already mating went much higher before mounting another male. The second highest chosen male in this study was at 1.6 m and was the lowest of five males on its tree. Average height of unchosen males was 1.7 ± 0.9 ($\bar{x}$ ± S.D., n = 79).

Discussion

Finding that females choose certain calling males over others agrees with results of studies on other orthopteran species (e.g. Forrest 1980, 1982; Gwynne 1982). Finding that the female usually mates with the lowest male among those calling on the same tree was unexpected. It leads to the hypothesis that sexually responsive females mount the first calling male they come

close to, regardless of how else that male compares with
other males calling close by. Several types of
observations throw doubt on such an explanation. (1) On
three occasions females seen at the base of a tree with
callers, chose instead a male calling from another tree
2.2 m away. (2) Neither of two females, watched choosing
among two or three males calling within 10 cm of one
another, mounted the closest male. (3) Three of five
females that failed to mate the first male they mounted
because he was already in copula, passed within 4-20 cm
of other calling males on their ascent to mate with
higher males. (4) Males do not initially take up
positions beneath competitors already calling from the
same tree (instead males move higher during the early
minutes of calling) nor do males subsequently move down
to take such positions. An alternative hypothesis is
that the males that would be chosen if height of calling
were uniform are usually the ones calling lowest. In
simple terms the two hypotheses are, 'lowness makes males
desirable' and, 'desirable males call low'. Supporting
the latter idea is that chosen males were calling near
the modal height of wild males (Fig. 2); unchosen males
generally called much higher ($\bar{x} \pm 95\%$ CI = 1.7 $\pm$ 0.2;
cf. 0.8 $\pm$ 0.2 for chosen males).

The alternative hypotheses are testable by allowing
females to choose among the same two or three calling
males as the males' relative heights are experimentally
varied.

SELECTION OF TREES TO CALL FROM

In the previous experiments males emerged from their
burrows to find an obstacle-free tree trunk towering
above. Most climbed it and called, as required in the
experimental protocol. Only 4, of 92 that called, made
the trip of 2.25 m across unfamiliar territory to call
from another tree. To learn something of how males
select a tree or other calling perch I released caged
males equidistant to two or three trees. In the first
test, ten males in their burrows were exposed at the same
site as used for female release, i.e. 2.5 m from each of
the three trees (Fig. 4A). No male called from a test
tree: five of those released called from their
containers, one called 7 m SE of the release site, 0.1 m
above the ground on a fallen branch, and four called 8 m
SSE, at heights of 0.4-0.8 m on 10- and 4-cm DBH trees,
20 cm apart.

On four subsequent nights males were placed in
groups of six between the center and outside trees of the
study area (Fig. 4B). On 3 of these nights additional
males in individual 10 x 10 x 10-cm screen cages were

Table 6. Choice of trees by **A. arboreus** males released
          midway between trees 2.25 m apart (Fig. 4B.)

Date (1980)	Males Calling From		
	Tree S	Tree C	Tree N
10 June	0	4	1
11 June	1aaa	5	3bbb
12 June	1bbb	5	3aaa
17 June	0bb	5aaaa	5bb

a Cage with live male strapped to tree at 1.0 m (aaa
  = 3 cages, etc.).
b Empty cage strapped to tree at 1.0 m (bb = 2 cages,
    etc.).

attached at 1.0 m to one of the trees. Empty cages were
attached to one or two control trees. Caged calling males
or control cages had no effect on the choices of the trees
by experimental males (Table 6). Even though males had to
walk >1.0 m prior to climbing the tree selected, their
average height at calling (1.3 m) did not differ
significantly from the average height in the female-choice
tests (1.5 m).

CONCLUSIONS

Male and Female Reproductive Strategies

     Male reproductive behavior was analyzed in an
earlier paper (Walker 1980). The present study resolved
some of the doubtful aspects of the previous schema and
raised new issues (Fig. 7). It confirmed the
speculation that males search for females after the
evening calling period, but did not prove conclusively
that the resultant matings were in the female's burrow
nor, if so, establish how long the pair cohabit. It
produced evidence that males calling beneath other males
mate with more females than the males above but offered
no explanation as to how genes that contribute to
"calling above" maintain their frequencies. The finding
of three males mating silently on the ground with females
that had earlier mated (with other males) on a close-by
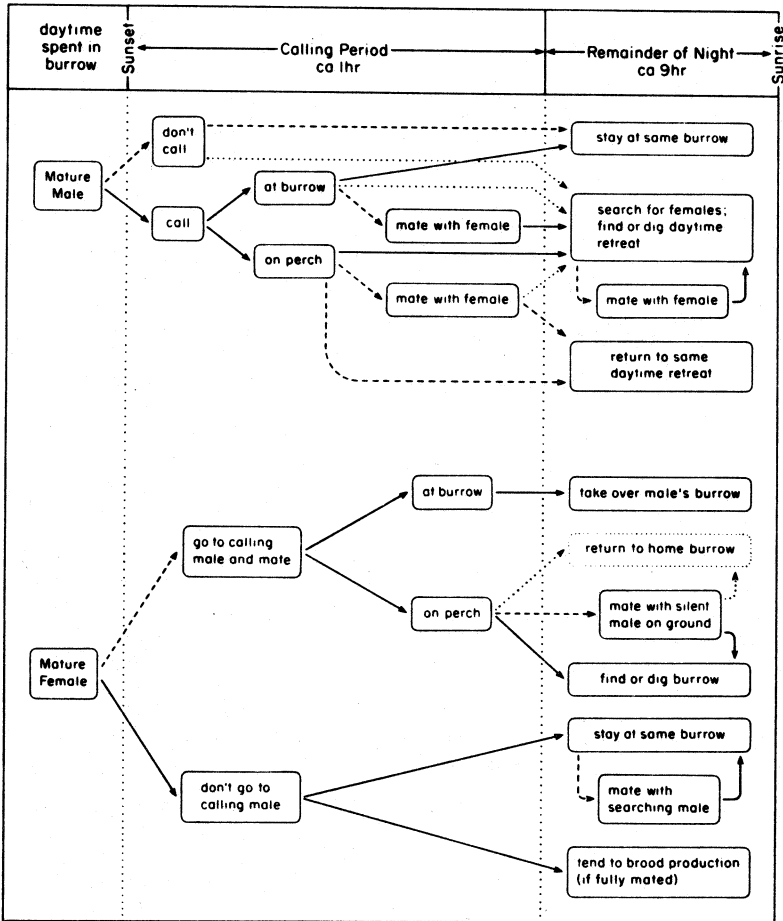tree trunk suggested that males benefit from patrolling

Fig. 7. Nightly reproductive activities of
A. arboreus. Dashed lines indicate less frequent
activities. Dotted lines indicate activities that may
occur but have not been demonstrated.

at the base of tree trunks where females may have mated
during the calling period. Only three of 34 females were
detected mating in this fashion, but the incidence could
have been higher since the couplings were silent. On the
other hand, the experimental females were long-deprived
virgins; wild females may seldom if ever mate with more
than one male per night.

Cade (1980) discussed three ways that a mixture of reproductive modes could be maintained in a population: (1) a single conditional strategy, i.e. males behave appropriate to their age and environmental circumstances, (2) a single mixed strategy, i.e. males mix modes unconditionally, and (3) a stable genetic polymorphism, i.e. males use different modes as a result of genetic differences. The evidence in **A. arboreus** suggests that at least (1) and perhaps (2) are involved. For example, young males that mature in open areas call for several nights at their burrow entrances whereas those in wooded areas do not. When logs were placed vertically near burrows in the open, males often climbed up to call but on some suitable nights did not (Walker 1980). In regard to (3), Cade (1981) reported evidence of a significant genetic contribution to determination of calling vs noncalling behavior in **Gryllus 'integer'** males. Conditional determination of behavior should be expected whenever the consequences of the alternative behaviors are predictable from aspects of the environment that the male can monitor. A mixed strategy or genetic polymorphism should be expected when they are not.

In any case, the male's reproductive success depends on the combined results of all his various behaviors. Three unknowns are critical in determining how much particular males contribute genetically to succeeding generations of **A. arboreus:**   (1) how many males, using which behaviors, do individual females mate with; (2) in what sequence(s) do females yield to various male stratagems; (3) how does a female utilize the sperm she garners (W. Walker 1980)?

Many of the uncertainties about male reproductive strategy in **A. arboreus** stem from ignorance of reproductive behaviors of individual wild females (Fig. 7). The females in the present study were unnaturally deprived of mating opportunities until the date of release, and they had no opportunity to become familiar with a normal home range about their burrows. Wild females probably mate more than once: three of four females trapped beneath males calling over pitfalls carried sperm in their spermatheca (Walker 1979). Also, seven of 38 females that mated in this study were observed mating a second time. Perhaps wild females usually mate first in their burrows with a searching male. Supporting this idea is the fact that two teneral virgins in the present study stayed in their burrows for 11 days and for 5-10 days before traveling 2.5 m to perch-calling males (Table 7, note d); other female grylline crickets, such as **Teleogryllus** spp. and **Gryllus** spp., are sexually receptive within a few days after the final molt (e.g. Loher 1979: **T. commodus** females will mate less than 24 h after their imaginal

molt). Mating with a searching male could be viewed as
an insurance mating and/or as a means whereby females
produce at least some sons that are good searchers.
Mating subsequently with a perch-calling male might yield
a genetically more diverse brood for the female or it
might mean that all or most of her male progeny would
have maximum genetic opportunity to behave in the
superior female-attracting manner of the male the female
selected. The evidence supported the contention that
females choose certain males from among those calling,
though the basis of choice was not established. Fisher's
(1958) runaway sexual selection process could establish a
substantial advantage for females choosing males that
have whatever is important to female choice.
     Since females are flightless and at least generally
tied to a home burrow, females are unlikely to benefit
from assemblies of competing males (leks). The nightly
movements of most males result in their advertising to
different females from one night to the next and provide
the sedentary female with a temporal sequence of
choices. Given an adequate memory a female might mate
with any male that was superior to the last one she had
mated with (or even with a remembered individual that
proved his worth by coming around a second time -- Lloyd
1981).

Why do males call briefly and simultaneously?

     Although competing **A. arboreus** males do not
assemble spatially, they do so temporally. Their calling
periods are brief ($\bar{x}$ ~ 33 min for perch calling; $\bar{x}$ <20
min for burrow calling -- Walker 1980) and nearly
synchronous (Fig. 8). In most other crickets, males
collectively call for much of the night, and individual
males call for hours rather than for minutes (Walker
1982). Walker and Whitesell (1982) monitored
A. muticus calling throughout the night in Panama and
verified individual calling durations of 2 h and longer
(Fig. 8).
     Walker (1982) proposed that the brief calling
period of **A. arboreus** resulted from positive feedback
between males calling when the greatest number of females
are available and females limiting their phonotaxis to
times when they have maximum numbers of calling males to
choose among. Such a process should result in females
restricting their susceptibility to calling to a brief
period when all sexually ready males call. Such
concurrent display is the temporal equivalent of a lek
and may be termed a **spree** (Walker 1982).
     Other factors that could be causal to
A. arboreus' brief evening outburst are temperatures,
predation, energy reserves, sedentary females, and
competing reproductive modes.

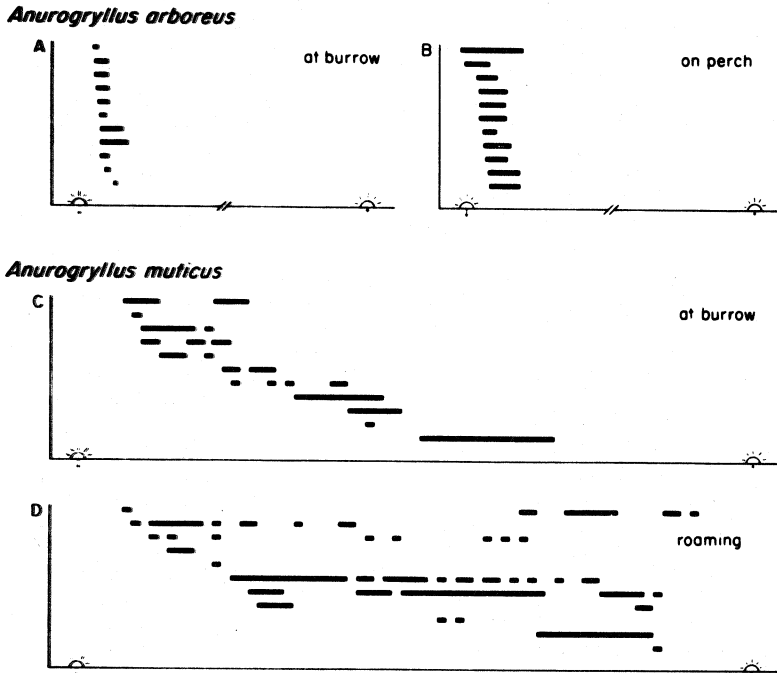*Anurogryllus arboreus*

Anurogryllus muticus

Fig. 8. Representative nightly distributions of
calling in two species of **Anurogryllus**. Eleven males
are plotted for each circumstance for each species.
Symbols on abscissa (time) indicate sunset and sunrise.
A, B. **A. arboreus**, Gainesville, Florida (Walker 1980).
C, D. **A. celerinictus**, Ft. Sherman, Panama (Walker and
Whitesell 1982).

Nights are often cold in north Florida during the
season that **A. arboreus** calls. When temperatures are
less than 23°C, perch calling is inhibited, and at
temperatures less than 20°C other calling ceases as
well. Evening twilight is more likely to be warm enough
for calling than any other dark period. However, some
nights are warm throughout, and no additional calling
occurs. In other crickets, males that restrict their
calling to dusk do so only when the rest of the night is
too cold for females to come (Walker 1982).

Predation could cause **A. arboreus** to limit calling
to evening twilight because their most dangerous
predators are active only in greater darkness, because
callers can use dim light to see and escape predators, or

because only so long as all males call are callers
superabundant enough to saturate or confuse acoustically
orienting predators. However, predators were not
observed to cause significant mortality to calling
A. arboreus males, and the fact that females will remain
coupled to males that resume calling suggests that pairs
are nearly safe from acoustically guided enemies.
Another grylline cricket, **Gryllus fultoni**, calls from
tree trunks during a longer season and in habitats
similar to those of **A. arboreus**; G. fultoni does not
restrict its calling to a brief twilight spree (unpub.)
     Calling in **A. arboreus** uses 10-16 times as much
energy as resting (Prestwich and Walker 1981).
Nonetheless, males apparently have ample energy reserves
to call for longer periods than the usual 30-40 min.
Starved males called approximately the same as fed males
for 8-11 days (Prestwich and Walker 1981).
     Since females generally occupy a home burrow and
never fly, it could be argued that all females that are
prepared to respond to a call on a given evening should
easily do so in 30 min. Males calling the rest of the
night would gain little for their efforts because no new
females would enter their broadcast areas (Paul and
Walker 1979). However, **A. muticus** males roam and call
(Walker and Whitesell 1982); **A. arboreus** males might do
the same if females were responsive to calls other than
in evening twilight.
     Lastly, males may call only during twilight because
at other times other activities, like searching for
females, have greater reproductive benefits. Even if
they do, why should silent searching be superior to
alternating calling and searching? At each new stop a
male could call to a new group of potential mates.
     Although a variety of advantages may accrue to
A. arboreus males because they call briefly and
simultaneously each evening, their chorusing most likely
derives from the fact that females will leave their
burrows to go to calling males at no other time. The
function of females restricting their phonotaxis to a
brief period may be to optimize their choices among
calling males.

ACKNOWLEDGEMENTS

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APPENDIX

Behavior of males

Of 107 males released, 92 called: 84 from the
intended tree, four from one of the other two trees, and
four from the surface of their container. Of the 15
males that did not call, 13 had abandoned their
containers by the end of the calling period. Of the 101
males leaving their containers only one called in the
study area on a subsequent night: a male that called from
the north tree when first released called from the south
tree 11 nights later. Four wild males joined the study,
two ascending chorus trees and two ascending solo trees
(making duets). Only once did a male call first from one
tree and later the same evening call from a second tree:
the male called solo on the north tree for 48 min,
descended, walked to the center tree, where a pair was
mating at 0.55 m, climbed to 0.35 m, called briefly,
returned to the ground, called briefly again, ascended to
0.5 m (about 12 cm from the mating pair) and called for
10 min. The mating pair broke up and on her way down the
tree the female contacted the new male. She did not
mount but stayed in his vicinity for ca 20 min. He then
called again for several minutes, descended to the ground
where he encountered yet another male (which earlier had
called from the south tree!). The two called tail to
tail for about a minute; the male that had mated was
nearby.

Males on chorus trees generally called indepen-
dently, i.e. they gave no evidence of being influenced by
other callers on the same tree. However, if calling
males were within 10-20 cm of one another they often
moved toward one another, made antennal contact, turned,
and called tail-to-tail. Apparently each was behaving as
though the other was a female. Rarely more than two
males interacted resulting in three or four males calling
within a few cm of one another, sometimes in symmetrical
positions (e.g. an equilateral triangle facing out).
When a female approached such a group, she generally went
directly to one of the males, mounted, and mated. Males
that were not chosen did not change their behavior,
apparently acting toward the mating pair as toward an
unattached calling male.

Behavior of females

Table 7 summarizes the behavior of outdoor-reared
females exposed to males calling from three trees ca
2.5 m away. Of females that were known or likely virgin,
41 of 45 left their home burrows and never returned
(although one was discovered, after mating, in a nearby
burrow that another female had abandoned the same night).
Females that were watched as they left proceeded toward
the trees with calling males but not necessarily toward a
particular tree. Females last seen heading toward one
tree were sometimes next seen at another tree. On three
occasions a female seen at the base of one tree (with
callers) did not ascend that tree but went to another
tree, ascended, and mated. Time from leaving the home
burrow until reaching a tree 2.5 m away ranged from 1-
43 min ($\bar{x} \pm SD = 7 \pm 12$; n = 14).
Of 49 females that left their home burrows, 36 were
soon seen mounting, or mating, with a calling male, i.e.
they chose a male the same evening they left; only one
waited until the next evening to make a first choice
(Table 7). The approach to the calling male was usually
quick and direct. Of 57 female choices recorded, 23 were
detected only after the female had contacted the male,
suggesting a rapid, direct approach; in 22 the female was
observed prior to contact and the approach was
straightforward and without long delay. Of the 12
choices that were less direct, six were subsequent
choices caused by the first choice being a male coupled
with another female, two were by females mating a second
time with the same male after a 4-min intermission, and
the remaining four were as follows: (a) the female took
3 min to ascend to a male at 2.4 m; (b) the female took 3

Table 7. Behavior of outdoor-reared **A. arboreus** females
exposed to males calling on trees 2.5 m away,
21 May - 8 June 1980, Gainesville, Fla.

| | Type of Female | | |
	Authen-ticated Virgin[a]	Likely Virgin[b]	Likely Non-virgin[c]
Freed	32[d]	13	16
Left home burrow	30	11	8
Chose calling male on night of leaving	26[e]	9[f]	1
Chose calling male subsequent night	0	3[g]	0
Mated more than once	5[h]	2[i]	0

[a] Reared in isolation.
[b] Reared with other individuals, but no males at time
female was removed (one could have mated with female,
then died and decayed).
[c] Reared with other individuals; male present when
female removed.
[d] Not including two teneral virgins: one exposed every night
until she left and mated on the 11th night; the other
exposed for 5 nights, not exposed for the next 4 nights,
and exposed and mated on the 10th night.
[e] Of the four that left but did not choose, three were
not seen after their departure; the fourth climbed
toward a male at 2.3 m but another female coupled
with him first (her second mating with that male
that night). The original female came within 1 cm of
the mating pair but did not mount. She remained
nearby for 11 min and took 2 min more in descending
to the ground (never to be seen again).
[f] Only eight mated; one mounted three males but failed
to copulate: she kept falling to the ground.
[g] One had mounted and failed to mate the first night
but succeeded the next night; another mated 5 min
before sunset ca 24 h after leaving its home burrow;
the third reappeared 5 nights after her first mating and
mated again.

Table 7.   (continued)

[h] Two of these five females mated twice with the same
male with intervals of 4 and 14 min between matings.
The other three mated with different males. One
mated with one male at 0.6 m during the peak of
calling and 43 min later mated with another male on
the ground. Another female behaved essentially the
same (1.6 m, 46 min), but then mated yet again with
the male she had mated on the ground (4-min
interval). The fifth female mated at .25 m, 7 min
after sunset with one male. After 9 min, she leapt
to the ground as I came close to read her mark.
After 22 min, I spotted her on the same tree mating
at 2.3 m with another male. (She had passed near the
male she chose first, but he was coupled with another
female.)

[i] One mated twice, 5 days apart, the other mated at 8
min past sunset with a male at 0.65 m and 74 min
later mated with another male on the ground near the
base of the same tree (in silence).

min to spiral once around the tree and mate with a male
at 1.5 m; (c) the female climbed 10 cm above two males
calling within 2 cm of each other, came down, first
contacted the upper male, did not mount when he backed
toward her, then mounted the other male when he backed
toward her a second time (the first male did not
interfere); (d) the female climbed above 2.5 m on a tree
where a male at 1.0 m had quit calling before she reached
0.6 m; when the male resumed calling 1 min later, she
came down and mated with him.

   Females that chose males already in copula showed a
variety of subsequent behaviors: (a,b) a female tried to
mount a mating male for 4 min even though another male
was calling 10 cm away; she finally started toward the
other male only to encounter another female; the two
females tried to mount each other and then the new female
coupled with the male; the original female attended the
sexual pair for more than 8 min, returned to the first
male (no longer in copula), and mated with him; (c) a
female mounted a mating pair at 0.9 m, fell to the
ground, returned, persisted in mounting for 3 min more
before ascending toward three males calling above; she
took 4 min to reach and mate with a male at 2.4 m after
passing other males at 2.0 and 2.2 m; (d) a female tended
a mating pair for 14 min, sometimes mounting and falling
0.6 m to the ground, sometimes waiting; she finally mated
with the male when he uncoupled from the first female;
(e,f) a female attended a mating pair for 3 min, then
went 10 cm to another mating pair and attended it for 14
min; she then started up toward two higher males, and

jumped from the tree at 1.2 m (because of my dim light?);
5 min later she was seen ascending the tree again; she
passed within 12 cm of the first two males (neither
mating now), passed within 6 cm of one higher male,
within 20 cm of another, and mated with the highest male
(at 2.1 m); (g) a female tended a mating pair at 0.25 m
for <15 sec before proceeding upward toward three higher
males; at 2.1 m she veered right toward a duo at 2.4 m
but passed 4 cm to their left; at 3.5 m she passed by the
highest male and was lost from sight at 7 m; 8 min later
she came down and mated with the male at 3.5 m.

For first matings, duration of coupling averaged 16
min (n = 27, SD = 5, range 9-31). Second matings the
same evening by either males or females were not
significantly longer ($\bar{x}$ ± SD = 19 ± 9 for 12 males and 16
± 7 for six females). Uncoupling was usually uneventful,
but on two occasions the female dragged the male down the
tree for more than 0.5 m. Once uncoupled the male nearly
always remained and continued calling. On the other
hand, the female quickly descended from the mating site
(38 of 46 cases), usually on foot; but one female walked
to the tip of a dead leaf and dropped 2.3 m to the
ground. In two of the eight remaining cases, once on the
ground and once on a tree trunk, a female stayed near the
male for 4 min and mated with him again. In the other
six instances, the female remained on the tree trunk for
13-52 min ($\bar{x}$ ± SD = 26 ± 15) before descending. In the
52-min case, the female was seen 11 min later mating
silently on the ground with another male.

Of 34 females that mated the evening of release, 28
mated once, five mated twice, and one thrice. Three
females were seen subsequent to the first night: two
mated for the first time the second evening (one had
mounted three males the first evening but repeatedly fell
to the ground during attempted coupling); and one
returned to mate again 5 nights after her first mating
(Table 7).

Three females mated twice with the same male in one
evening. One of these had mated with another male
first. In three instances in which a female mated with
two different males in one evening, she mated first with
a perch-calling male (at 0.6, 0.7, 1.6 m) and subse-
quently with a male on the ground at the base of the same
tree. In two cases the male on the ground had been
calling from a higher perch (2.0 and 2.1 m) when the
female chose her first mate. In the third case the
ground male had started calling at 1.5 m, 15 min after
the female's first mating ended. In every case the
ground matings began after the peak of calling, viz. 68,
82, and 85 min after sunset. In the latter two cases
calling had ceased and the mating pair was located
because another male had come across the couple and

emitted a brief burst of sound. Prior to the earliest
on-the-ground mating, the male had called for a few
minutes at the base of the tree. Once coupled he called
intermittently, but the mating ended in record time (7
min); 4 min later the pair coupled again, this time for
14 min and almost entirely in silence.

No wild (i.e. unmarked) female joined the study.