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Arboreal Singing in a Burrowing Cricket, *Anurogryllus arboreus*

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Summary. 1. *Anurogryllus arboreus* males in north peninsular Florida sing at ground level or above the ground on the trunks of trees or on other vegetation. Their song is a continuous trill at 70–80 pulses/s and 5.0–5.5 kHz. Prevailing singing locations of individual males vary among and within demes (Fig. 2). Males of congeneric West Indian species sing only at ground level.

2. Females are flightless and climb plants only in response to male calls. Therefore the three-dimensional acoustic output of a male may be of less direct importance than the male's *broadcast area* – the area at ground level within which the intensity of his call exceeds the auditory threshold of the average female.

3. Assuming a threshold of 38 dB (SPL re 2×10^{-5} N·m^{-2}) we found that males calling 1 m above the ground had broadcast areas averaging 14 times the broadcast areas of males calling at ground level (119 vs. 1,642 m^2) (Fig. 4A–D, Table 1).

4. In terms of broadcast area, the optimal height for singing is influenced by spreading loss at greater heights, by attenuation due to ground cover and low vegetation, and by acoustical shadows due to rough terrain.

5. On vertical surfaces, such as tree trunks, crickets more often (27:1) sing facing right or left than up or down (Fig. 3) making the broadcast areas asymmetrical (Fig. 4B–D).

6. When crickets singing on vertical surfaces deviate more than 22.5° from the horizontal, they generally (7:1) angle downward (Fig. 3). Facing downward apparently has no acoustical advantage over facing upward since sound levels behind a cricket calling on the ground are at least as intense as those ahead (Fig. 4E).

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Introduction

Anurogryllus arboreus, the short-tailed cricket, is a flightless univoltine species found throughout the southeastern United States. In Gainesville, Florida, adult males are present from April to early June; adult females tend eggs and young juveniles in burrows until late June. Males begin singing at or shortly after sunset and all have ceased about 2 hrs later; individuals sing for an average of 40 min (Walker, 1979a). The call has no long-term variations in intensity and sounds continuous except for brief interruptions, often associated with changes in orientation. It consists of 5.0–5.5 kHz pulses (corresponding to wing closures) at a rate of 70–80 per s (Walker, 1973). Nearly all of the males of the related Caribbean species, *A. muticus* and *A. celerinictus,* sing at ground level; the majority of *A. arboreus* males in north peninsular Forida demes sing above ground on tree trunks, shrubs, or low vegetation. This characteristic varies significantly within and between local populations (demes) (Walker, 1979a). In demes inhabiting open areas, such as lawns and pastures, early season singing is at ground level at the entrance to an extensive burrow system, apparently where the male spent the winter as a juvenile. Males later abandon their burrows and sing on low vegetation or tree trunks. In demes inhabiting closed-canopy woods, males apparently omit the stage at which they sing at burrow entrances, though a few sing at ground level. Males in open area demes that would otherwise sing at ground level will climb sections of logs set vertically near their burrow entrances (Walker, 1979a).

The calling songs of male crickets attract potential mates. Some species have complex behaviors that increase the range of their calling songs. European mole crickets, *Gryllotalpa gryllotalpa* and *G. vineae*, build burrows in the shape of exponential horns which amplify their calling songs (Bennet-Clark, 1970). Pro-

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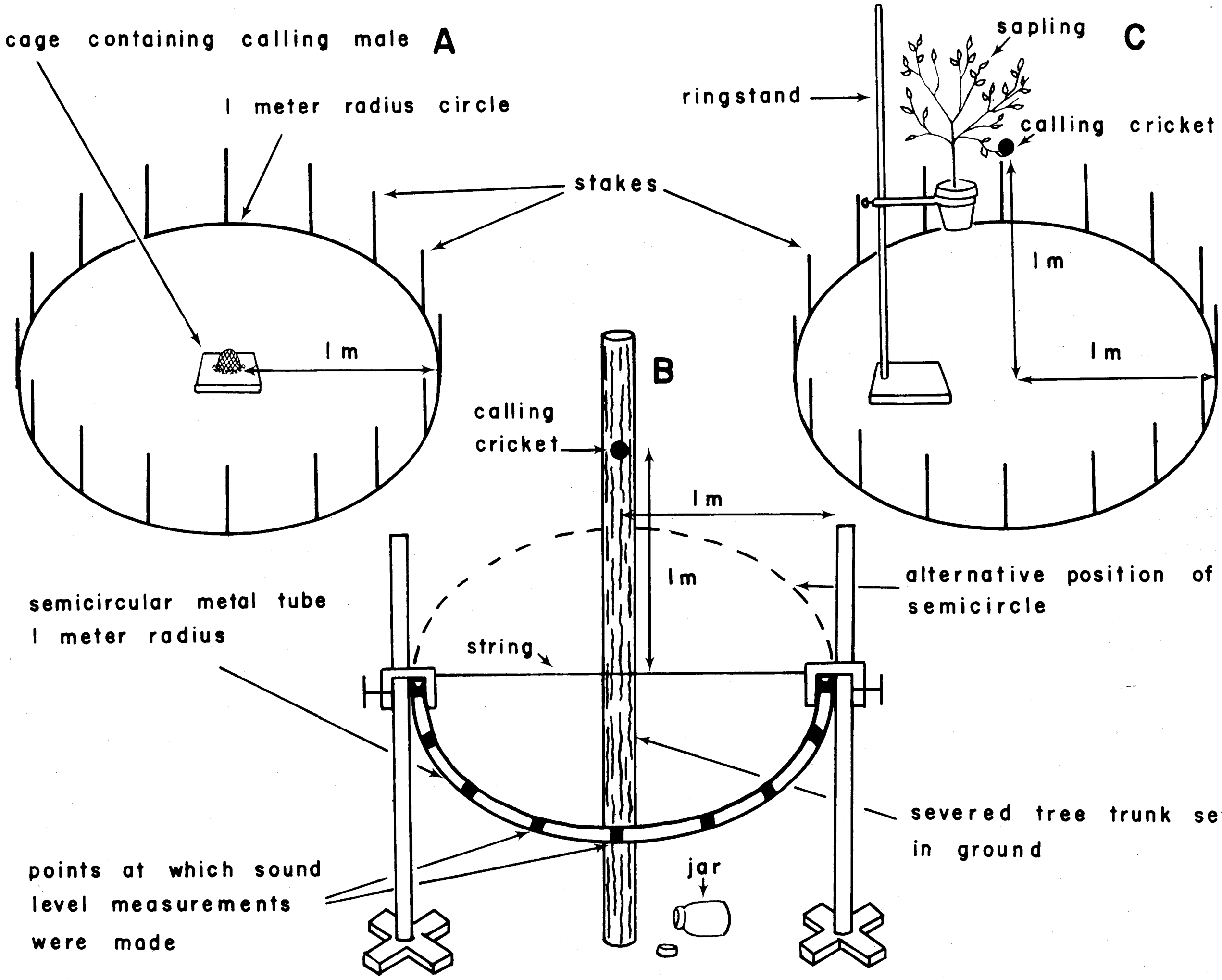


Fig. 1A–C. The measurement of broadcast areas of calling *A. arboreus* males. **A** Males singing on the ground. The male was confined beneath a cup-shaped screen stapled to a piece of plywood; 16 (or 8, see text) measurements were made around a 1 m radius circle at ground level or at 15 cm above ground level. **B** Males singing on trees. A 1 m radius semicircle, made of 2.5 cm dia tubing, was positioned so that 9 measurements were made at distances of 1 m from a point 1 m below the singer. The procedure was then repeated on opposite side of the tree in order to complete a 1 m radius circle of 16 measurements. **C** Males singing on saplings. A potted sapling was raised or lowered so that the unconfined singing male was 1 m above the ground; 16 measurements were made around 1 m radius circle, the center of which was a point 1 m below the singer

zesky-Schulze et al. (1975) found male South African tree crickets, *Oecanthus burmeisteri,* singing in leaf holes that the crickets reportedly had chewed. The uplifted forewings of the crickets fit perfectly within the margins of the holes, and the leaves serve as acoustical baffles, enhancing the loudness of the song. In possibly related observations, tree crickets have been seen singing with their heads positioned in small holes in leaves in New Guinea and in Jamaica, W.I., by J.E. Lloyd (pers. comm.) and T.J. Walker (1969), respectively. (In these instances the holes were significantly smaller than the uplifted forewings.)

Since *A. arboreus* females are flightless and climb plants only in response to male calls, their initial response to sound must be at ground level. We hypothesized that *A. arboreus* males enhance their ground-level broadcast areas by singing from tree trunks and other vegetation rather than at ground level.

Materials and Methods

The crickets we studied were from a deme in a closed-canopy mesic wood near Gainesville, Florida (NW 1/4, sec. 31, tp. T9S, R19E). In 1977, we noted site and orientation of 503 calling males, and for 41 we measured sound level at 15 cm above the dorsal surface using a General Radio (1551-B, A weighting) sound level meter.

In an attempt to estimate the auditory sensitivity of *A. arboreus* females, we observed their phonotaxis in a cylindrical copper-screen

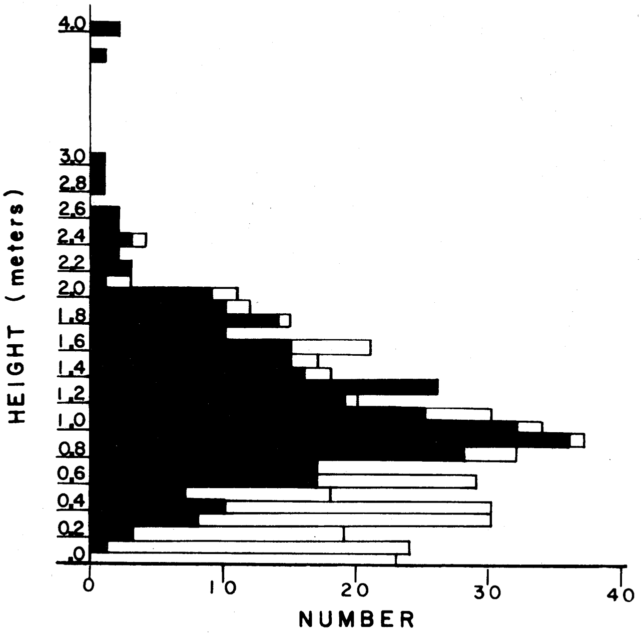


Fig. 2. The vertical distribution of 503 calling *A. arboreus* males in the field in 1977. Solid bars represent those males located on vertical surfaces (tree trunks) in such a way that they could climb farther up ($N = 337$). An additional 166 males (open bars) were singing at ground level or singing on shrubs and branches of trees or saplings from which they could not easily climb higher

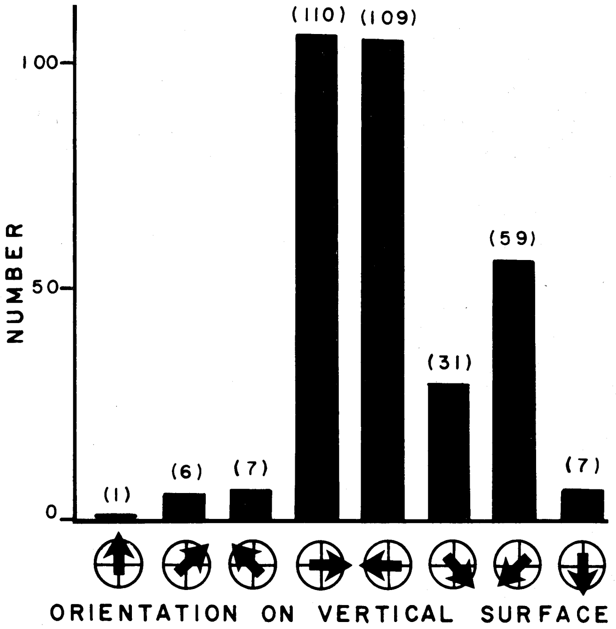


Fig. 3. Orientation of singing males found on vertical surfaces in 1977. Each bar (and the number above) indicates the frequency of males headed within 22.5° of the arrow

cage, 105 cm diam. × 12.5 cm high (cage, with legs added, is figured by Spooner, 1964). The cage was placed in the middle of a pasture and a 7.5 watt red light suspended over its center. Before sundown several plastic cups holding marked females in their burrows were opened and placed in the center of the cage. A caged male was placed nearby in a predetermined direction and distance. After sundown, movements of the females were noted, and the amplitude of the male's song was measured at 15 cm normal to his dorsal surface. During the test period, the position of the singing male with respect to the phonotaxis cage was changed by 90° or 180°. Four females were tested in this manner for four days.

The broadcast areas of males were measured in four situations: 1) Male singing on the ground, sound levels measured on the ground. Males were held individually in small wire cages with wooden bottoms. Encircling each such cage 8 or 16 stakes marked the ends of 1-m radii – every 45° in 1976 and every $22^1/_2$° in 1977. The General Radio sound level meter was used (with a 1-m extension cord) to measure sound level at each stake (Fig. 1A). 2) Male singing on the ground, sound levels measured at 15 cm above ground. In order to estimate the effects of ground vegetation and uneven terrain, we measured the sound level 15 cm up at each of the stakes (Fig. 1A). 3) Male singing on the vertical surface of a tree trunk, measured 1 m below (Fig. 1B). These measurements were in June, 1977, in an open grassy field that had no resident *A. arboreus*. Five sections of tree trunks, each about 2 m high, were set upright in the field. Four had diameters of 0.09–0.15 m at 1 m; the fifth, used only once, had a diameter of 0.40 m. Shortly before sunset, several jars with individually marked males in their burrows were opened and placed at the base of each "tree". After sunset some males would climb the trees and sing. For each tree the most consistent singer above 1 m was selected, and the others were removed. Although over 20 males were caged for testing in 1977, only 4 males were consistent singers, and most of our data are based on experiments with these 4 males. A 1-m radius, semicircular, metal tube was positioned in a horizontal plane 1 m below the cricket. A string connecting the two ends of the semicircle was made tangent to the tree with its midpoint directly beneath the cricket. Sound level was measured at each of the 9 points at 22.5 °C intervals around the semicircle. The semicircle was first placed forward of the side of the tree with the cricket and then to the rear of it. 4) Male singing on the upper side of a leaf, sound levels measured 1 m below (Fig. 1C). Since males sometimes sing on elevated horizontal surfaces, such as leaves of shrubs or saplings, we placed males on the leaves of a sapling held in a flower pot. The pot was held in a ringstand and its height adjusted so that the cricket sang 1 m above the ground. Sound level on the ground beneath was measured at 22.5° intervals around the circumference of a 1-meter-radius circle centered beneath the cricket.

Ambient temperatures during most measurements were 24–26 °C.

Results

Vertical Distribution and Orientation. Figures 2 and 3 show the vertical distribution and orientation of males observed singing in 1977.

Female Auditory Thresholds. Ideally, a male's broadcast area would be the area within which the amplitude of his song exceeds the auditory threshold of the average conspecific female. In our limited testing

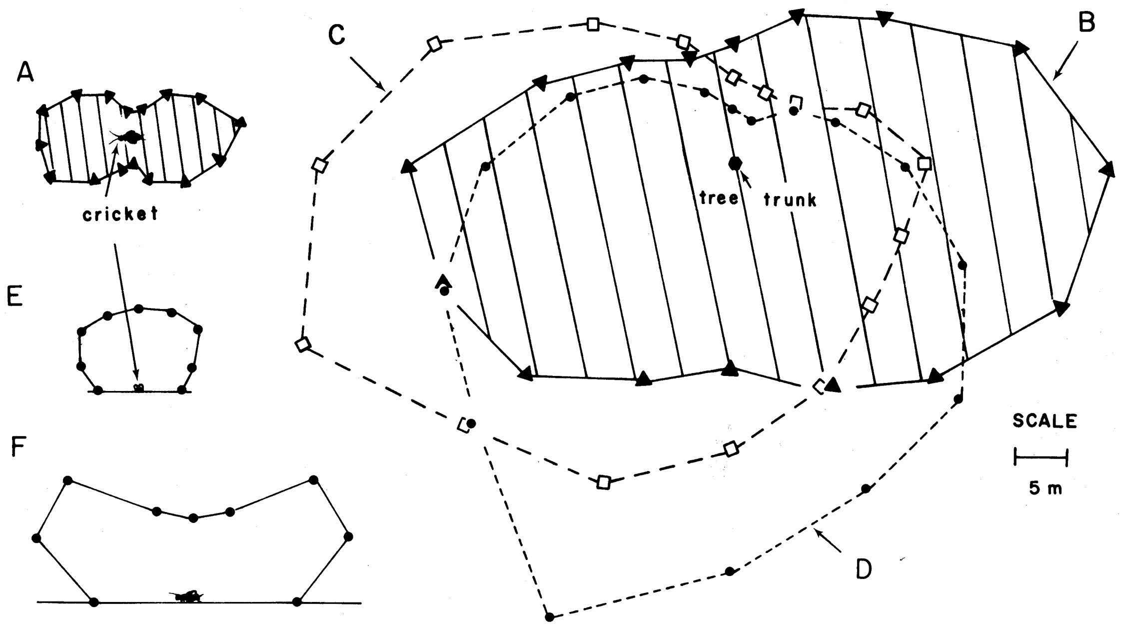


Fig. 4A–F. Sound fields of calling males of *A. arboreus*. Lines mark limits within which SPL is 38 dB or higher. **A–D** Broadcast areas (=ground-level sound fields) and their shapes. **A** Males singing on ground. Area: 119 m^2, the average from Fig. 2. Shape shown is from measurements made 15 cm above ground level of 3 crickets and a total of 7 measurements for each of the 16 radii. (Shapes from ground-level measurements were variable and asymmetrical, probably because of uneveness of ground vegetation and terrain at the test site). **B–D** Males singing on tree trunk, 1 m above the ground. Dot shows the tree's position; cricket is on the side of the trunk toward the bottom of the figure. Areas: 1,642 m^2, the average from Fig. 2. **B–C** Average shapes for males singing with head directly to one side (**B**) or with head 45° down (**C**). Each radius based on 9 or more measurements of 4 or 5 crickets. Data standardized to make all crickets face left. (Since sound fields of crickets facing right or left are asymmetrical but approximately mirror images, we reversed the data for right-facing crickets and averaged them with the data for left-facing crickets to arrive at the shapes illustrated). **D** Shape for male with head straight down. (Each radius from 3 measurements of one cricket; asymmetry may or may not be characteristic). **E–F** Longitudinal (**E**) and cross (**F**) sections through sound field of a male singing on the ground. For each section the plane passed through the midpoint of the cricket and sound level measurements were made at 22.5° intervals 1 m from the cricket. Each radius based on 7 or more measurements of one cricket. Differences between corresponding front and rear or left and right measurements are not statistically significant

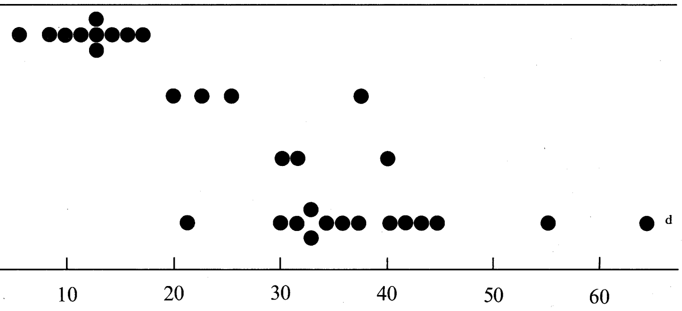
of *A. arboreus* females, two of the four test-females were attracted to the calling songs of single *A. arboreus* males and followed the changes we made in the locations of the singing males. One of the test females clearly responded to the song of a male 6 m away, the greatest distance tested. Field measurements of the amplitude of the calling songs of 41 males gave a median reading of 75 dB. If only spreading loss is taken into account, a song of this intensity attenuates to 43 dB at 6 m. This is probably a high estimate of the auditory threshold of *A. arboreus* females; both the singing male and the responding female were at ground level, and there was certainly excess attenuation due to ground vegetation and uneven terrain (Embleton et al., 1976). A neurophysiological measurement of the auditory threshold of a female Australian field cricket, *Teleogryllus commodus,* was 34 dB (for the most sensitive female tested; Loftus-Hills et al., 1971). With 34 dB and 43 dB as guidelines, we used 38 dB as an arbitrary limit for calculating the broadcast areas for *A. arboreus* song. This sound level fits another criterion: with our equipment, calling song levels below 38 dB could rarely be distinguished from the background noise in our study area.

Broadcast Areas. Our raw data consisted of sound level meter readings corrected by a factor to compensate for using the 1-meter extension cord. Taking only spreading loss into account, we calculated the distance at which the sound level at each radius would equal 38 dB (in theory, spreading loss results in 6 dB attenuation for each doubling of distance). Thus, if one of our 16 readings was 44 dB at 1 m, it would attenuate to 38 dB at double the distance, or 2 m; a reading of 50 dB would yield a distance of 4 m, and so on. These distances were used to calculate the broadcast areas as follows:

a) Male Singing on the Ground. From the 1977 sound level readings, distances for the 16 radii around the

Table 1. Normalized broadcast areas of calling crickets. Each point represents one *determination*, defined as the average broadcast area for one male at one site of singing on one date

Site of singing / Sound measured	Sample size: Indiv.	Sample size: Determ.	Mean broadcast area (m^2)	Normalized broadcast areas ($|\sqrt{m^2}|$) (scale beneath)
Ground on ground	8	10	119	
Ground 15 cm up	4	4	753[a]	
Sapling 1 m down	2	3	1,274[b]	
Tree trunk 1 m down	4	14	1,642[c]	[d]



[a] Differs significantly from "ground", $0.01 > P > 0.002$
[b] Differs significantly from "ground", $0.02 > P > 0.01$
[c] Differs significantly from "ground", $0.002 > P$
[d] Only one determination was made on the largest tree (0.6 m dia.)

singing male were generated (see Fig. 4A). Lines connecting the radii were drawn, resulting in 16 triangles. Their areas were calculated and summed to give the total broadcast area.

In 1976 only 8 measurements were taken around the males singing on the ground (at 45° intervals). When we calculated our 1977 broadcast areas on the basis of 8 rather than 16 radii, we found that the areas averaged 0.8 as large. We therefore multiplied our 1976 8-measurement areas by 1.2 to make them comparable to our 1977 (16-measurement) areas.

b) Male Singing 1 m Above the Plane of Measurement. In these experiments, the actual distance of sound level measurement from the singing male was not 1 m, but 1.41 m (the hypotenuse of a right triangle with a base and height of 1 m). In this case, the 6 dB attenuation due to spreading loss occurs at a hypotenuse of 2.82 m, and this corresponds to a base of 2.65 m. Using this method, the 16 radial distances at which the sound levels would be 38 dB around the tree or sapling were determined (see Fig. 4B–D). Again, triangular areas were determined and summed.

Square roots were taken of each of the areas to normalize them. Statistical comparisons were made directly from the graphed data (Table 1), using the Mann-Whitney U-test (Sokal and Rohlf, 1969). The broadcast areas of males singing on the ground were significantly smaller than the areas of males singing in saplings, males singing on trees, and males singing on the ground but measured 15 cm above the ground. The broadcast areas of males singing on trees and of males singing on saplings did not differ significantly.

Shape of the Sound Field. Fig. 4A–D shows the ground-level shapes of the broadcast areas of males singing on the ground (A), and males singing on trees (B–D). Figure 4E and 4F are sections of the above-ground sound field of a male calling from the ground.

Discussion

Males of *A. arboreus* that sing on tree trunks or other vegetation rather than on the ground increase the range of their calling songs (Table 1) and therefore ought to attract more females. However, Alexander and Otte (1967) suggest that the male's burrow may be a significant resource for the female since oviposition and egg-tending must be carried out in burrows. Were such the case, females should mate more readily with males singing at their burrows (i.e. males making offerings of the time and energy expenditures their burrows represent) than with males singing on trees (i.e. males offering no burrow). Field observations of two demes near Gainesville were inadequate to compare mating success of burrow-singing vs. tree-singing males, but did confirm that males singing from 0.5–2.0 m above the ground were more successful in attracting mates than males singing higher or lower (but not at burrows) (Walker, 1979a).

Embleton et al. (1976, Fig. 2) showed that sounds above 2 kHz are greatly attenuated as they travel between a sender and receiver that are both near ground level and separated by more than a meter of mown grass. For example a 2 kHz sound travelling 4.6 m drops 22 dB below the level predicted by the inverse square law. Consequently our estimates of broadcast areas of ground-level males are likely exaggerated and the broadcasting advantages of climbing 1 m prior to singing are probably understated. (Marten and Marler's, 1977, measurements of sound transmission at "ground level" were actually at 15 cm and are not applicable to transmission between crickets on the ground).

A possible disadvantage for crickets singing and mating on tree trunks is their increased exposure to predators. Predation of short-tailed crickets active on tree trunks has been observed only once (domestic cat: Walker, 1964) in more than 100 observation-hours logged by us and a number of University of Florida students. Potential native predators that could use hearing to locate singing crickets on exposed tree trunks include bats, owls, racoons, lizards, tree frogs, various spiders, and certain tettigoniids. All occur in the study areas; however, an attempt to experimentally verify the importance of certain of these by pitfall trapping failed (Walker, 1979b). *A. arboreus* males on tree trunks respond to human observers by ceasing singing, changing singing positions, or even climbing farther up the tree. Sometimes, particularly in the period of failing light shortly after sundown, they leap to the ground. These responses suggest that predation has played a role in the evolution of the behavior of *A. arboreus* males on tree trunks. Differences in predation could explain, in part, species differences in preferred singing heights; perhaps the West Indian species of *Anurogryllus* are more subject to predation by acoustically-orienting predators. (Alternatively, males broadcasting from the ground may be maximizing their broadcast "volumes" (Fig. 4E, F) rather than their broadcast area: Females of the West Indian species may fly to the male).

The modal height of males singing on tree trunks was 0.9 m (Fig. 2). This is high enough to minimize excess attenuation due to ground cover, low vegetation, and rough terrain. The upper limit of singing height may be influenced by attenuation due to greater spreading loss with greater height, by the increased likelihood of being above branches at greater heights (branches would further attenuate and scatter sound and might disorient approaching females), or even by the sound intensity a female requires before she will climb a tree trunk from which a male is calling.

The diameter of the tree may influence a male's broadcast area. The data for the one trial on a tree trunk substantially broader than the other four trunks suggest that large tree trunks further enhance the broadcast area (Table 1). However, singing on a large tree trunk also results in a large acoustical shadow on the side opposite the cricket. This is potentially disorienting to a female approaching the tree on the side of the acoustical shadow.

We have insufficient information to understand why the predominant singing positions are "right", "left", "left-down" and "right-down" (i.e., singing with the body perpendicular to the tree's vertical axis, or with the body headed 45° downward from this position; Fig. 3), or why singing with the head aimed upwards is so rare. One possibility is that the preferred singing positions reflect selection favoring singers that maximize the convex outer perimeter of their broadcast areas rather than merely favoring singers with the greatest broadcast areas. Wandering females are more likely to encounter a broadcast area of a given size, for example, if it has the shape of an elongate ellipse rather than a circle. (Otte, 1977, refers to a "surface of attraction"). This model requires that females move without acoustic input until they encounter a song. Considering the high population densities and close synchrony of maturation in *A. arboreus*, this possibility seems unlikely. We have no broadcast area data for the "up", "left-up", or "right-up" singing positions, and we cannot say whether singing in these positions results in smaller broadcast areas or edges of attraction. The shapes of the sound field on the ground (Fig. 4A, E,F) suggest that facing upwards would yield a broadcast area at least as large as facing downwards. Perhaps the preferred positions allow the male to sing while extending his antennae downwards where they can detect any cricket or predator approaching from below. The anterior lobe of the sound field is much better developed, relative to the rear lobe, in *A. arboreus* (Fig. 4F) than in *Gryllus campestris* (Nocke, 1971, Fig. 8B). This is congruent with the more erect position of the forewings (Walker, 1979a, Fig. 1) and with the head-down orientation on vertical surfaces of the calling male of *A. arboreus*.

Individuals of other predominantly ground-dwelling crickets occasionally sing from elevated perches. We have seen males of several *Gryllus* species (*G. pennsylvanicus*, *G. firmus*, *G. fultoni*) singing on tree trunks. Males of *G. fultoni* populations in northern Florida sing from tree trunks as frequently as males of *A. arboreus*, which occur in some of the same habitats. There are ecological circumstances, not yet fully understood, that allow ground-dwelling crickets of some populations to take advantage of the increased broadcast areas gained by singing from perches.

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