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Authors: Hill, Peggy S. M., Wells, Harrington, and Shadley, John R.

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Singing from a constructed burrow: why vary the shape of the burrow mouth?

PEGGY S. M. HILL, HARRINGTON WELLS AND JOHN R. SHADLEY

(PSMH, HW) Faculty of Biological Science, The University of Tulsa, OK, USA 74104. E-mail: peggy-hill@utulsa.edu.
(JRS) Emeritus Professor of Mechanical Engineering, The University of Tulsa, OK, USA 74104.

Abstract

Male prairie mole crickets, *Gryllotalpa major* Saussure, studied in Oklahoma, sing sexual advertisement songs from constructed burrows in the soil. Here we report on variation in shape of the acoustic burrow mouth not previously described for this or other mole cricket species. We have identified six distinct shapes, of which only the 'slit' form has been previously described. Since the surface opening acts as the system 'radiator', we hypothesized that variation in the shape would account for at least some of the measured variation documented since 1993 in the songs produced by the population studied. We looked for patterns in the variation of dominant frequency of advertisement calls and maximum amplitude of calls that were linked to shape of burrow openings, but found none. Future work will focus on the role of previously documented weak higher harmonics in the *G. major* calling song, which might vary with differences in burrow mouth shape.

Key words

Gryllotalpidae, burrow, song, acoustics, radiation

Introduction

Some animals that produce acoustic sexual advertisement signals compensate for limitations in their morphology, or constraints imposed by the environment, by singing from constructed devices. These allow them to increase radiation resistance and thus produce louder sounds (Bennet-Clark 1989, Forrest 1991). Constructed devices are common however, to only a few taxa, such as the mole crickets in the orthopteran family Gryllotalpidae, who sing from constructed burrows in the soil that are typically species-specific in design (Bennet-Clark 1970a, Nickerson *et al.* 1979, Forrest 1983, Kavanagh & Young 1989, Walker & Figg 1990, Daws *et al.* 1996).

Burrow characteristics have not been described for most of the 90 extant described species (Eades *et al.* 2006) in the Gryllotalpidae, nor is the song produced in these burrows always known (Hill *et al.* 2002). Yet the structure of the burrow has been useful as a tool in resolving species-level taxonomic issues where data are available (Bennet-Clark 1970b, Forrest 1983).

The burrow appears to serve as an acoustic transformer, where a male stands with his head in a small 'bulb'-like chamber, with his wings raised so that his body fills the space in a constriction at the base of an exponentially increasing acoustic horn. The horn opens to the surface at ground level through a relatively, with respect to the mole cricket's wing, large mouth. Thus there are two resonators in the system: the harp on the mole cricket's wing and the acoustic horn of the burrow (Bennet-Clark 1995, 1999). The efficiency of this two-stage transduction process in converting metabolic energy

into sound has been estimated at 17 to 34% for *Gryllotalpa vineae* Bennet-Clark (Bennet-Clark 1970a, 1999).

Walker & Figg (1990) first described the acoustic burrow of the prairie mole cricket, *Gryllotalpa major* Saussure (1874), from a sample of seven males. They poured plaster casts of the burrows and found a smooth-walled acoustic horn with a single linear surface opening, or mouth, slit-shaped, of dimensions $\sim 25 \times 85$ mm. The horn of this species narrows to a constriction and then expands into a bulb-like chamber in which the male stands as he sings, the tip of his abdomen visible from the surface opening. The constriction can be felt as a ridge when probing the burrow at the base of the horn. With his wings in the constriction, the "effective source area" is increased (Bennet-Clark 1995, p. 203). The opening to the bulb, where the male locates, is typically in a central position at the base of the horn, equidistant from the extremes of the longest dimension of the horn mouth (Fig. 1, see also Walker & Figg 1990, Hill 1998).

G. major is a native of the tallgrass prairie of the south central United States. Adult males (of this largest of North American crickets, who weigh as much as 2.6 g and measure as long as 5 cm) construct specially designed acoustic burrows in moist springtime soils and broadcast an airborne advertisement call, or calling song, to attract females for mating (Walker & Figg 1990). A substrate vibration, which elicits responses of near calling neighbors in the field, is also produced with the same temporal pattern as the airborne call (Hill & Shadley 1997, 2001). Individuals call for about 30 min just at sunset on nights when climatic conditions are appropriate, and the entire population may call for approximately 1 h (Hill 1999). Thus, they exploit a relatively empty sound window after birdsong dies down and before amphibians begin to call. A statewide study in Oklahoma, comparing 30 sites where *G. major* had been heard chorusing, with 30 where none had been documented, found that soils on *G. major* sites had a silt content of 10-25%, significantly higher than sites where none of the insects were found. Percentage of sand, clay and organic matter were not different between the two treatment groups, suggesting that adequate silt content is probably important to burrow construction (Vaughn *et al.* 1993).

G. major males produce sounds by rubbing a file of one forewing across the scraper (plectrum) of the other (Hoffart *et al.* 2002, Bennet-Clark & Bailey 2002). The airborne component of the advertisement call is produced as a series of short chirps (Walker & Figg 1990), at a rate of about 1.4 to 3.6 s⁻¹ (Hill 1998), as opposed to a trilling call, which is the most common signal produced by crickets today, and likely the ancestral condition (Alexander 1962, Otte 1992). Only three mole cricket species besides *G. major* produce a chirping advertisement call: *G. marismortui* Broza, Blondheim & Nevo,

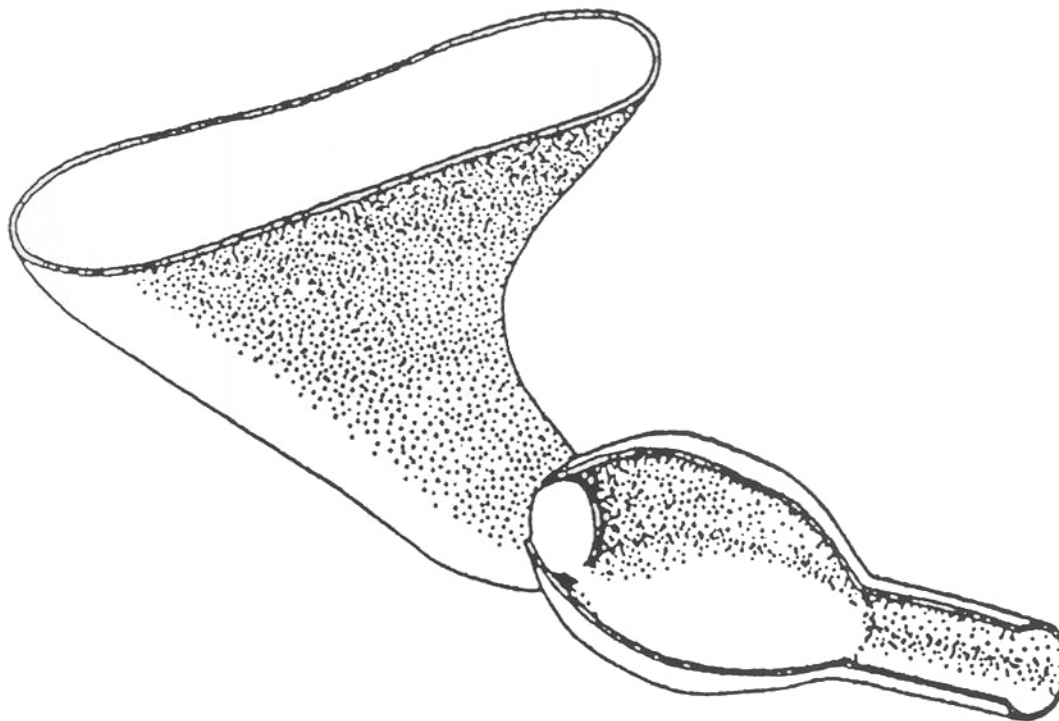


Fig. 1. Prairie mole cricket burrow, redrawn from Walker & Figg (1990) and adapted from Hill (1998).

from Israel, *G. pluvialis* (Mjöberg) from Australia, and *Neocurtilla hexadactyla* (Perty) from the USA (Hill *et al.* 2002). The *G. major* call does show population-level variation, but the dominant frequency is about 2 kHz, and males can produce multiple harmonic overtones (Hill 1998: from the figure and relative to the 2 kHz dominant, 4 kHz = <-19 dB; 6 kHz = <-24 dB; 8 kHz = <-29 dB; 10 kHz = <-36 dB). Because *G. major* males do not change position in their burrows while in full song, they can be recorded at a fixed measured distance from the surface opening, and we can compare harmonic overtones in their calls (Hill 1998). This parameter was sometimes ignored in the past because of the complexity of analysis and potential for introduction of artifacts, or perhaps because of the relatively small contribution of harmonic overtones to the total energy of the call (Hung & Prestwich 2004).

Females fly through the aggregations during the evening calling period at an altitude of 4 to 5 m, before sweeping down for a second pass of 1.5 to 2 m (Howard & Hill 2006), without any constraints on their choice of mates, drop to the ground in the vicinity of a burrow's mouth and enter the burrow (Walker & Figg 1990, Hill 1999). Once on the ground, rather than use a zig-zag mate search strategy (Latimer & Lewis 1986), *G. major* females move around in a circle, like a dog chasing its tail, then select a path towards the male's signal, possibly repeating this circling if they land as much as 1 m from the burrow mouth (Hill pers. obs.) The acoustic burrow is apparently used only for producing the advertisement call. Even though a female enters the burrow mouth and mating likely takes place in the complex of tunnels that lead from the acoustic horn, the female does not remain to oviposit in the male's burrow (Hill 1999).

Bennet-Clark (1987) described 'tuning' of the burrow by the southern mole cricket *Scapteriscus borellii* Giglio-Tos (previously *S. acletus* Rehn & Hebard) in Florida: this has also been observed (Hill pers. com.) in *G. major* in Oklahoma. Before evening calling, a

male will produce 'test chirps' while moving back and forth within the constriction at the base of the burrow horn; modifications are often made to the surface opening or interior of the horn before additional chirps are produced, much as a sound engineer makes periodic 'microphone checks' in preparing for a performance. Bennet-Clark (1970b) described what is apparently the same behavior in *G. vineae* as "warming up"; however, this behavior has not been reported for other species in the Gryllotalpidae.

How burrow characteristics contribute to the quality of the song has not been widely studied (but see Bennet-Clark 1989, 1995, 1999), and empirical evidence is available for only a few species (Bennet-Clark 1987, Kavanagh & Young 1989, Forrest 1991, Daws *et al.* 1996). The features actually modified as *G. major* tunes its burrow are not known; however, Bennet-Clark (1987) reported that changes made by *S. borellii* while tuning, modify the pulse envelope, contribute to a gain of up to 18 dB in the sound pressure level of the song, and produce a song of purer tone.

Of special interest to us is any variation in the surface opening of these gryllotalpid burrows and how such variation might contribute to variation in the characteristics of the songs produced. Mole crickets may sing from burrows with no surface openings, or may have up to six openings from an acoustic horn (Table 1). Intraspecific variation in the shape of surface openings has not been reported previously.

Walker & Figg (1990) noted that the length of the 'slit' surface opening of the *G. major* burrows they examined (approximately 86 mm) was essentially half the wavelength of the song's dominant frequency (2.0 kHz, 17.2 cm). We know that the songs of *G. major* males vary in a number of parameters and that variation exists in the surface openings of their burrows. Variation in calling songs and burrow mouths is persistent across calling seasons and generations of individuals.

In this paper we report on the range of variation documented in

Table 1. Number of surface openings for described burrows in the Gryllotalpidae.

Species	Surface openings	Citation
<i>Neocurtilla hexadactyla</i>	0	Forrest 1983
<i>Scapteriscus didactylus</i>	0	Forrest 1983
<i>Scapteriscus borellii</i>	1	Nickerson <i>et al.</i> 1979
<i>Scapteriscus vicinus</i>	1	Nickerson <i>et al.</i> 1979
<i>Gryllotalpa major</i>	1	Walker & Figg 1990
<i>Gryllotalpa vineae</i>	2	Bennet-Clark 1970b
<i>Gryllotalpa australis</i>	4	Kavanagh & Young 1989
<i>Gryllotalpa gryllotalpa</i>	up to 6	Bennet-Clark 1970b

the burrow surface opening of *G. major* and then test the following hypotheses: 1) Variations in burrow surface openings are correlated with variations in call parameters used in mate choice, parameters such as call amplitude and dominant frequency of the call. 2) Variation in length of the longest axis of the burrow mouth is correlated with the dominant frequency of the call for surface opening shapes other than the slit described by Walker & Figg (1990).

Methods

White Oak Prairie in Craig County, Oklahoma, USA (36° 37'N, 95° 16'W) is the site of a long-term study of *G. major* for which we have burrow data since 1993. This prairie supports the largest known continuing population of *G. major*. White Oak Prairie is a privately owned tallgrass prairie remnant, of approximately 65 ha, protected with a conservation easement by The Nature Conservancy. The site includes a ridge top, east-facing slopes, flatter bottomland and two drainage systems, one of which has been dammed to form a pond. The southern boundary is a county road with very light traffic. A two-lane highway with intermittent light traffic and a railroad track are located 500 to 600 m away from the closest *G. major* burrows. The site is burned and mowed for hay, but no known domestic grazing has been allowed. The site is underlain by four soil types: Collinsville-Vinita complex on the steep slopes and rocky hilltop, Dennis silty loam on the gentler east-facing slopes, Parsons silty loam in the flat bottomland, and Verdigris Breaks complex along the drainage areas (US Department of Agriculture 1973). Burrows are aggregated, reflecting a lek mating system, but very little overlap is seen from year to year in the precise location of arenas. Only about 15% of the 65 ha of the site was used for burrow construction over a 3-y period (Hill 1999). All burrows since 1993 have been built in one of the two silty loams. The Dennis and Parsons soils are both silty loams, but the Parsons is poorly drained and may harbor standing water during the early spring calling season in wet years (Hill pers. obs.).

Burrows were located by keying on the males' calls during the sunset calling bouts, and numbered surveyor's flags were used to mark the locations. Each burrow surface opening was measured (long and short axes) with dial calipers and the shape of this mouth noted. Recordings were made of the calling songs, and other sounds, produced at as many marked burrow entrances as was possible each year. Panasonic RQ-L307 minicassette recorders (Matsushita Electric Industrial Co., Taiwan) loaded with Maxell XLII tape were placed on the ground at a measured distance of 20 cm (outside the near field of sound for the 2.0 kHz dominant frequency of the species) from the outermost edge of the burrow mouth, since the mouth of the burrow represents the system's "radiator" or vibrating piston,

rather than the wing surface of the male inside the burrow (Bennet-Clark 1995, 1998). Recorders were placed with the microphone on one end in direct alignment with, and in a plane parallel to, the long axis of the mole cricket's body (Michelson & Nocke 1974); possible since the exact location of the individual is known while he calls from his burrow. Recorders were switched on just prior to the onset of calling for the evening and collected when all calling ceased (about 1 h later).

These simple recorders have a built-in microphone. The amplitude recorded could vary as much as ± 2 dB in the frequency range around 2 kHz for the same signal strength, depending on the sensitivity of an individual recorder. However, Bennet-Clark (1970a) reported that when members of the genus *Gryllotalpa* are in full song, calling song intensity does not vary more than 1 dB (see also Hill 1998).

Recordings made in the field were digitized and analyzed with SIGNAL software (Beeman 1996), which generates oscillograms, sonograms and FFT power spectra from a 2.62-s sample of the recording at a bandwidth of 10.0 kHz (sample rate = 25.0 kHz; frequency resolution = 97.7 Hz; time resolution = 10.2 ms). Sound files produced with SIGNAL were archived and used for further analyses.

Burrow mouth shape, call amplitude and dominant frequency.—We used archived data from four years (1997, 1998, 2000, 2001), chosen because those data sets were the most complete, to compare the maximum amplitude of the calling song from 106 males with the dominant frequency of those songs with respect to shape of the burrow mouth. Maximum amplitude was measured directly from graphs created with SIGNAL. Dominant frequency was measured with a DOMFREQ program designed in our laboratory that we have added to the SIGNAL software.

Length of the longest dimension of the burrow mouth and dominant frequency.—Walker & Figg's (1990) report that the long axis of the mouth of the *G. major* acoustic horn (which in their study was represented only by the slit shape) was being scaled to the wavelength of the song produced by the occupant male, suggests that dimensions of the burrow opening might also show a relation to the dominant frequency of the call produced within it for other burrow mouth shapes. We used the same data set as above (1997, 1998, 2000, 2001) to compare length of the burrow mouth's longest dimension and the dominant frequency of the calling song produced in it with respect to mouth shape.

Data analysis.—A multivariate linear model (regression model) was created to test for effects of burrow mouth shape and length of the longest dimension of the burrow mouth on advertisement call dominant frequency and maximum amplitude for the four years of archived data. Specifically, maximum amplitude and dominant frequency were response variables (response vector), and length, shape and the length by shape interaction were explanatory variables. A MANOVA was used to test for significant explanatory variable effects (Sall & Lehman 1996).

Results

Our work with the prairie mole cricket in the early 1990's at White Oak Prairie in Oklahoma revealed variation in the burrow surface opening not described by Walker & Figg (1990). In addition to the 'slit' in their description, the shape of the burrow opening can be a smoothly curving 'crescent', or a sharp, V-shaped, 'boomerang' (Fig.

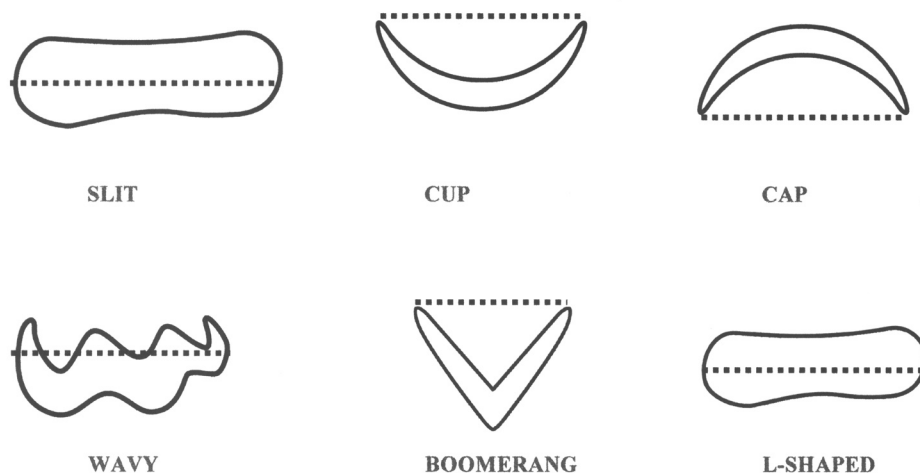


Fig. 2. *G. major* burrow-mouth shapes observed at White Oak Prairie in Oklahoma, 1996-2004. Drawings were made by Craig Stelle, MFA, The University of Tulsa, and are not to scale. Dotted lines indicate the axis measured for mouth length of each shape.

2). Further observations in subsequent seasons determined that the crescent is sometimes curving away from the body of the singing male in a 'cup', but may also curve toward the male in a 'cap'. A few burrows each season appear on the surface to be the 'slit' type, but internally the bulb containing the male is located on one end of the slit instead of being in the center, to form an 'L' shape. Some burrows will have a 'wavy' appearance to the mouth, while still other burrows each year defy classification and have been grouped together in our data as 'other'. The 'slit' type burrow opening is the most common construction observed (Table 2).

In addition, a few burrows each year (1 to 4 in the years documented in Table 2) have a soil bridge, like a drawbridge over a moat, bisecting the 'slit' type surface opening. Superficially this construction resembles the burrow of *G. vineae* (Bennet-Clark 1970b). However, the two mouths of the *G. vineae* acoustic horn are lacking, and the bridge often erodes rather quickly to reveal a typical linear opening.

Archived sound files were used to examine variation in advertisement call maximum amplitude and dominant frequency with respect to the shape of the burrow mouth and the length of the longest dimension of the burrow mouth from which the call was recorded (Fig. 3, 4). The model was not a significant predictor of the response vector (whole model test: $F = 0.6321$; $df = 26, 182$; $p = 0.9164$), which is to say that all regression coefficients associated with length and shape were not distinguishable from zero. Correspondingly, shape ($F = 0.5489$; $df = 12, 182$; $p = 0.8800$), length ($F = 1.6320$; $df = 2, 91$; $p = 0.2012$) and shape \times length ($F = 0.3884$; $df = 12, 182$; $p = 0.9665$) were not significant factors in predicting maximum amplitude and dominant frequency.

Further, if we used a calculation of relative dB instead of maximum amplitude of the call in our analyses, the model was still not a significant predictor of the response vector (whole model test: $F = 0.6714$; $df = 26, 182$; $p = 0.8848$). Correspondingly, shape ($F = 0.6023$; $df = 12, 182$; $p = 0.8358$), length ($F = 1.5458$; $df = 2, 91$; $p = 0.2187$) and shape \times length ($F = 0.3949$; $df = 12, 182$; $p = 0.9642$) were not significant factors in predicting relative dB and dominant frequency of the call.

No clear relation between dominant frequency and amplitude of male calls could be attributed to the shape of the opening. Likewise, we did not see a relationship between dominant frequency and the

longest dimension of the burrow mouth that was predicted for the 'slit' shape described by Walker & Figg (1990) when we included all six of the known shapes of *G. major* burrow surface openings in the analysis.

Discussion

This look at burrow mouth shapes in *G. major*, and a possible relationship between variation in the shapes and variation in the sounds produced within the burrows, leaves us with more questions than answers. There is no simple thread linking burrow mouth shape with distributions of sounds that are louder or softer, of lower or higher frequency. The distributions are not clumped by shape of surface opening. A statistically significant relationship between the longest dimension of the mouth and dominant frequency, as suggested for the slit-shaped openings by Walker & Figg (1990), did not hold when other shapes were included (Fig. 4), nor did we find statistical significance between these parameters for the slit-shape mouth alone. Further work is needed before we can determine whether this relationship holds for some shapes, or whether mouth surface area is tied to the burrow's dominant frequency. The slit-shaped opening's surface area is easily estimated from long and short-axis measurements of the mouth, and further investigation may reveal surface area as the basis of any relationship between burrow mouth measurements and dominant frequency. Walker

Table 2. *G. major* burrow opening shapes expressed as % of total.

Year	Slit	Cup	Cap	Wavy	L	Boomerang	Other	Total (n)
1996	57.1	20.0	10.0	4.3	5.7	0	2.9	70
1997	59.3	13.6	1.7	13.6	5.1	5.1	1.7	59
1998	56.3	25.0	2.1	8.3	4.2	4.2	0	96
1999	38.0	43.0	7.0	4.0	2.0	2.0	4.0	100
2001	59.3	25.0	6.3	3.1	3.1	1.6	1.6	64
2002	52.2	23.2	10.1	1.4	2.9	2.9	7.2	69
2003	61.8	23.6	12.7	0	0	0	1.8	55
2004	46.2	31.7	7.7	2.7	7.7	0	4.4	91

Fig. 3. Scattergram comparing amplitudes (expressed as sound level in decibels relative to sample mean maximum amplitude) of *G. major* male calls with dominant frequencies from the same recordings (distinguished by shape of burrow mouth). Mouth shape does not predict dB level or dominant frequency (n = 106; slit=♦, cap=■, cup=△, boomerang=x, wavy=⋈, L-shape=o, other=+).

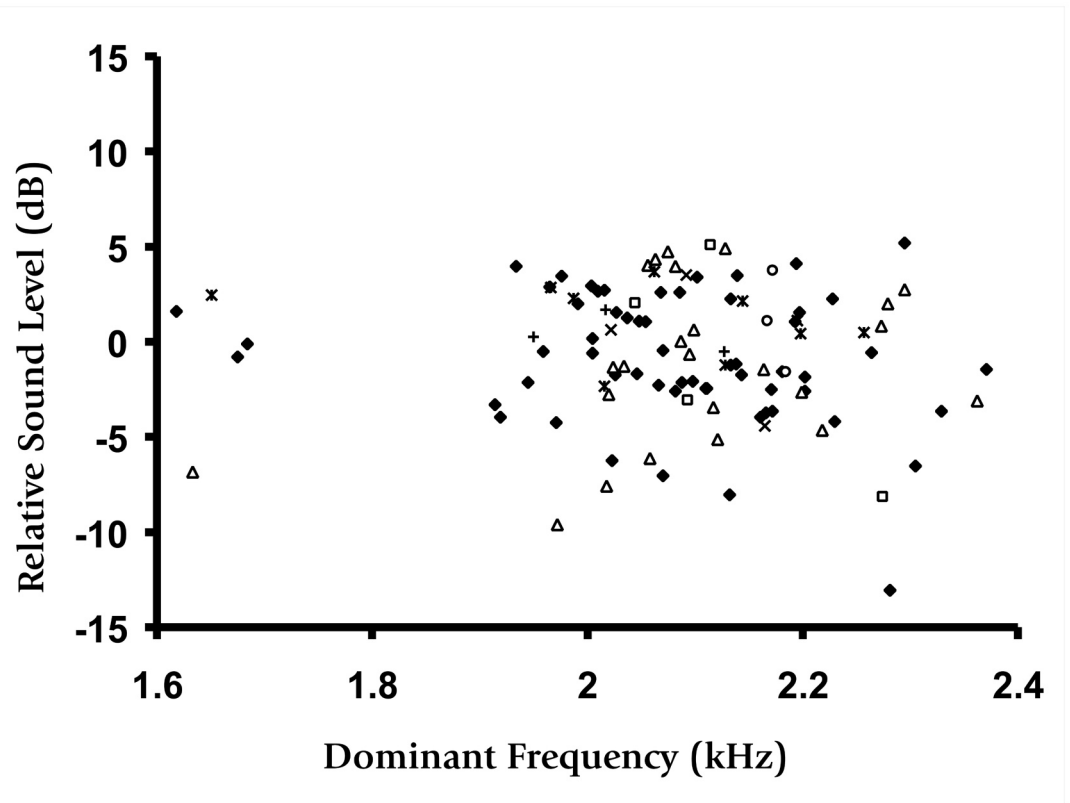
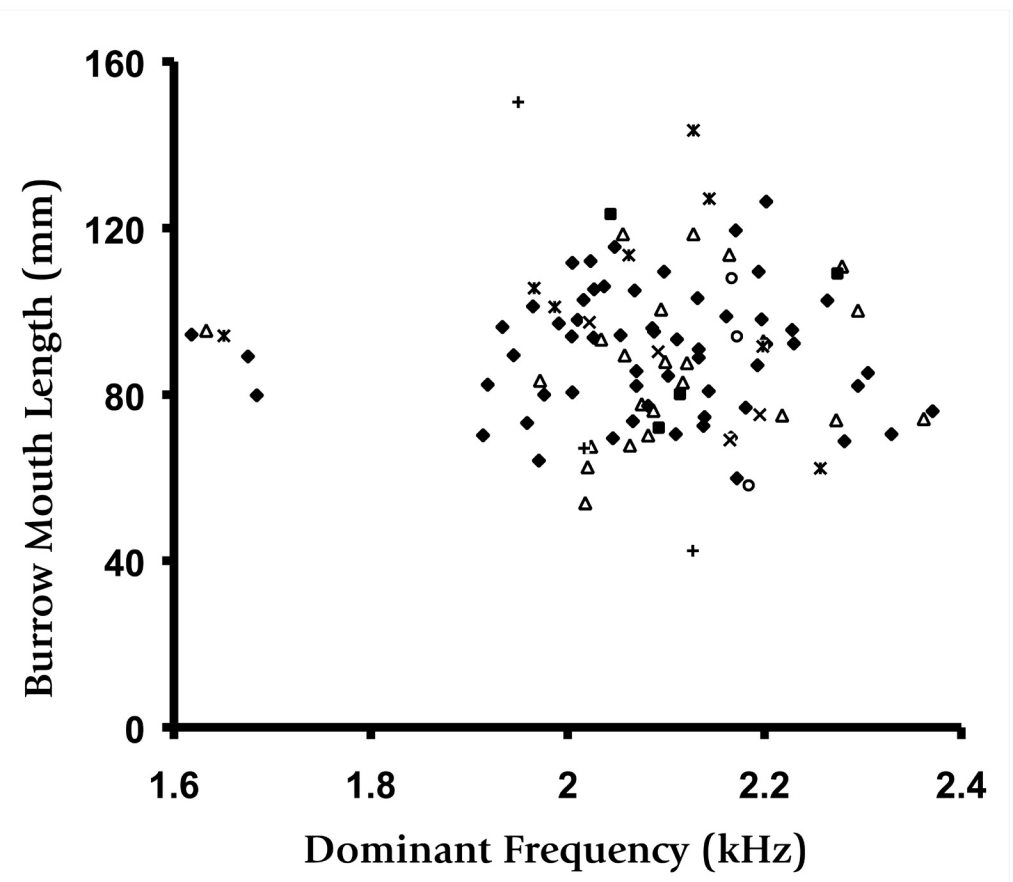


Fig. 4. Comparison of the length of the *G. major* burrow mouth with the dominant frequency of the call produced in that burrow, distinguished by burrow mouth shape. A linear relationship of slope 1/2, per Walker & Figg's (1990) hypothesis for the slit shape, is not seen when additional shapes are considered (n = 106; slit=♦, cap=■, cup=△, boomerang=x, wavy=⋈, L-shape=o, other=+).



& Figg's (1990) first description of the calling song and acoustic burrow of this rare species was based on only eight recordings and seven plaster burrow casts; of course such a small sample could not reveal much about internal variation in horns or mouth shapes.

We can hypothesize that the male "fits" his burrow to his own dimensions in order to produce the highest quality signal (Bennet-Clark 1987), but we still do not know how the variations we see in burrow mouth shape might contribute to this signal quality. Nor do we know if a male will construct a burrow of the same dimensions and surface-opening shape should his first burrow become damaged, or abandoned for some other reason. And since hearing has yet to be studied in *G. major* females, we also do not know if females can discriminate among male calling songs based on the variation observed in parameters such as dominant frequency, maximum amplitude and harmonic overtones of the calling song. We only know that females respond to the male's calling song while in flight (Walker & Figg 1990, Hill 1999, Howard & Hill 2006).

Two South American species of mole crickets that live in the southern United States as pests, *Scapteriscus borellii* Giglio-Tos and *S. abbreviatus* Scudder, have low frequency hearing maxima of 3 kHz and 2 to 4 kHz, respectively, tuned to the acoustic signals they produce, with a threshold under laboratory conditions of about 50 dB at these frequencies (Mason *et al.* 1998). The carrier frequency of the *S. borellii* sexual advertisement call is about 2.7 kHz, and although *S. abbreviatus* does not sing an advertisement call, it does have an abbreviated file with which it produces short pulses of courtship song (Walker & Moore 2006).

We are still working to understand sound and vibration thresholds for *G. major* and how the apparent pure-tone tuning of the *G. vineae* and *Scapteriscus* species burrows (Bennet-Clark 1995, 1999) are related to the acoustic behavior we observe in *G. major*. However, we have previously argued that the *G. major* calling song, which has been sampled at 20 cm from the outer margin of the burrow mouth at a mean 96 dB, would have an effective signal range as great as 100 m (Hill 1998). This assumed a 40-dB practical threshold (Bennet-Clark 1989) rather than the 50-dB threshold measured by Mason *et al.* (1998).

A *G. major* acoustic burrow appears with a characteristic mouth shape on the first night a male calls from it. Depending on the social and environmental factors of a given year, a male may sing from the same burrow for a number of nights. We have recorded a single male from the same burrow for 13 nights during one season (Hill 1998). Males maintain their burrows throughout the time that they sing from them, and the first clue that a burrow has been abandoned during the day is that debris has accumulated in the acoustic horn. After a male is successful in attracting a female to his burrow, the next morning the acoustic horn is always filled in a characteristic way with small beads of soil, and the burrow abandoned (Hill 1998). Likewise, burrows are abandoned if the burrow mouth becomes eroded by rain or wind so that the dimensions are too much changed, or if the walls of the acoustic horn become too dry (Hill 1999). How much change or drying can be tolerated is not known. Males may construct their acoustic horn too near a competing singer, so that they stutter, stop and start and never achieve full song in the evening calling bout. The next evening one or both of the 'too-near' neighbors have abandoned the field.

Acoustic theory predicts that the frequency of the calling song should vary with the size of the male producing the sounds, but not be changed significantly by burrow geometry at the mean dominant song frequency (Kinsler *et al.* 1982) of 2.0 kHz used by prairie mole cricket males. Individual morphology of a male's wings should

contribute to variation in the dominant frequency of his songs, and males with larger wings should produce lower frequency sounds.

Variations in the burrow mouth shape should not contribute to variations in the amplitude of the calling song at the dominant frequency when the wavelength at that frequency is much greater than the dimensions of the opening (see Beranek 1986). The surface area of the burrow opening would affect the amplitude of the calling song, and Bennet-Clark (1987) found that tuning of the *S. borellii* burrow resulted in a marked increase in relative sound pressure level. However, the only way that the shape of the surface opening would affect amplitude is by affecting the directivity of the sound emanating from the opening, and at 2 kHz the sound would be nearly omnidirectional for most, if not all, of the dimensions of the surface openings described above.

Individual morphology of the male's wings should also contribute to the relative amplitude of harmonics present in the calling song. The shape of the surface opening could affect the directivities of the higher harmonics of the song escaping the burrow and thus also contribute to variations in the sound fields above the burrows through which the females are flying. A manuscript discussing theoretical aspects of burrow mouth shape and call frequency is in preparation.

S. borellii decreases the relative amplitude of the second and third harmonics during tuning of its burrow and thereby produces a purer-toned calling song (Bennet-Clark 1987); but there is a non-trivial difference that cannot be overlooked when comparing what we report here with the literature on mole cricket bioacoustics: every previously published analysis on mole cricket burrows and the relative energy in the frequency spectrum of their calls has been with species that produce a trilling call, while *G. major* and only three other species worldwide are known to produce an advertisement call of chirps (Hill *et al.* 2002).

When Hung & Prestwich (2004) examined the frequency spectra of four cricket, two mole cricket and two katydid species, in all but one case the carrier frequency accounted for over 97% of the audible and ultrasonic energy in the call. This single case was also the only chirping species in the analysis.

The *G. major* calling song includes multiple harmonic overtones, and previously we have found a correlation between a richer harmonic content of the song and a closer distance between nearest calling competitors for mates (Hill 1998). Still in *G. major*, the calculated energy available in harmonics at 4, 6 and 8 kHz is only 3.4% of the total (K. Prestwich, pers. obs. made in review). So the contribution of the harmonics may appear to be trivial. However, when *Teleogryllus oceanicus* (Le Guillon) was presented with two-choice tests of pure-tone songs or those with harmonic overtones, females preferred songs with additional harmonics. Interestingly, *T. oceanicus* songs are chirps (Latimer & Lewis 1986).

Thus a seemingly insignificant call component might provide significant signal information; however, the point remains that the magnitude of variation reported here for burrow mouth form is not consistent with predominant pure-tone output, unless the variation is some sort of artifact. Significant and compelling questions remain to be answered through mathematical and biophysical modelling. Perhaps work with other members of the Gryllotalpidae being conducted worldwide will reveal that this variation in burrow construction is not restricted to *G. major*.

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References

- Alexander R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution* 16: 443-467.
- Beeman K. 1996. SIGNAL. Engineering Design, Belmont, MA, USA.
- Bennet-Clark H. C. 1970a. The mechanism and efficiency of sound production in mole crickets. *The Journal of Experimental Biology* 52: 619-652.
- Bennet-Clark H. C. 1970b. A new French mole cricket, differing in song and morphology from *Gryllotalpa gryllotalpa* L. (Orthoptera: Gryllotalpidae). *Proceedings of the Royal Entomological Society of London B* 39: 125-132.
- Bennet-Clark H. C. 1987. The tuned singing burrow of mole crickets. *The Journal of Experimental Biology* 128: 383-409.
- Bennet-Clark H. C. 1989. Songs and the physics of sound production, pp. 227-261. In: Huber F., Moore T. E., Loher W. (Eds) *Cricket Behavior and Neurobiology*. Cornell University Press, Ithaca and London.
- Bennet-Clark H. C. 1995. Insect sound production: Transduction mechanisms and impedance matching, pp. 199-218. In: Ellington E. P., Pedley T. J. (Eds) *Biological Fluid Dynamics*. Symposium of the Society of Experimental Biology. No. 49. Company of Biologists, Cambridge, UK.
- Bennet-Clark H. C. 1998. Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society of London B* 353: 407-419.
- Bennet-Clark H. C. 1999. Resonators in insect sound production: How insects produce loud pure-tone songs. *The Journal of Experimental Biology* 202: 3347-3357.
- Bennet-Clark H. C., Bailey W. J. 2002. Ticking of the clockwork cricket: The role of the escapement mechanism. *The Journal of Experimental Biology* 205: 613-625.
- Beranek L. L. 1986. *Acoustics*. The American Institute of Physics, Inc., New York, 101.
- Daws A. G., Bennet-Clark H. C., Fletcher, N. H. 1996. The mechanism of tuning of the mole cricket singing burrow. *Bioacoustics* 7: 81-117.
- Eades D. C., Otte D., Naskrecki P. 2006. Orthoptera Species File Online. Version 2.21. Online: [<http://osf2.orthoptera.org>].
- Forrest T. G. 1983. Phonotaxis and calling in Puerto Rican mole crickets (Orthoptera: Gryllotalpidae). *Annals of the Entomological Society of America* 76: 797-799.
- Forrest T. G. 1991. Power output and efficiency of sound production by crickets. *Behavioral Ecology* 2: 327-338.
- Hill P. S. M. 1998. Environmental and social influences on calling effort in the prairie mole cricket (*Gryllotalpa major*). *Behavioral Ecology* 9: 101-108.
- Hill P. S. M. 1999. Lekking in *Gryllotalpa major*, the prairie mole cricket (Insecta: Gryllotalpidae). *Ethology* 105: 531-545.
- Hill P. S. M., Shadley J. R. 1997. Substrate vibration as a component of a calling song. *Naturwissenschaften* 84: 460-463.
- Hill P. S. M., Shadley J. R. 2001. Talking back: Sending soil vibration signals to lekking prairie mole cricket males. *American Zoologist* 41: 1200-1214.
- Hill P. S. M., Hoffart C., Buchheim M. 2002. Tracing phylogenetic relationships in the family Gryllotalpidae. *Journal of Orthoptera Research* 11: 169-174.
- Hoffart C., Jones K., Hill P. S. M. 2002. Comparative morphology of the stridulatory apparatus of the Gryllotalpidae (Orthoptera) of the continental United States. *Journal of the Kansas Entomological Society* 75: 123-131.
- Howard D. R., Hill P. S. M. 2006. Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *Journal of Orthoptera Research* 15: 53-57.
- Hung Y. P., Prestwich K. N. 2004. Is significant acoustic energy found in the audible and ultrasonic harmonics in cricket calling songs? *Journal of Orthoptera Research* 13: 63-71.
- Kavanagh M. W., Young D. 1989. Bilateral symmetry of sound production in the mole cricket, *Gryllotalpa australis*. *Journal of Comparative Physiology A* 166: 43-49.
- Kinsler L. E., Frey A. R., Coppens A. B., Sanders J. V. 1982. *Fundamentals of Acoustics*, 3rd ed. John Wiley, New York.
- Latimer W., Lewis D. B. 1986. Song harmonic content as a parameter determining acoustic orientation behaviour in the cricket *Teleogryllus oceanicus* (Le Guillou). *Journal of Comparative Physiology A* 158: 583-591.
- Mason A. C., Forrest T. G., Hoy R. R. 1998. Hearing in mole crickets (Orthoptera: Gryllotalpidae) at sonic and ultrasonic frequencies. *The Journal of Experimental Biology* 201: 1967-1979.
- Michelson A., Nocke H. 1974. Biophysical aspects of sound communication in insects. *Advances in Insect Physiology* 10: 247-296.
- Nickerson J. C., Snyder D. E., Oliver C. C. 1979. Acoustical burrows constructed by mole crickets. *Annals of the Entomological Society of America* 72: 438-440.
- Otte D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research* 1: 25-49.
- Sall F., Lehman A. 1996. JMP IN, SAS Institute, Inc. Ducksberry Press, Belmont, California.
- Saussure H. de. 1874. *Recherches zoologiques pour servir a l'histoire de la faune de l'Amerique centrale et du Mexique*. 6th part. Imprimerie Imperiale, Paris 3: 293-516.
- U.S. Department of Agriculture. Soil Conservation Service. 1973. *Soil Survey: Craig County, Oklahoma*.
- Vaughn C. C., Glenn S. M., Butler I. H. 1993. Characterization of prairie mole cricket chorusing sites in Oklahoma. *American Midland Naturalist* 130: 364-371.
- Walker T.J., Figg D. E. 1990. Song and acoustic burrow of the prairie mole cricket, *Gryllotalpa major* (Orthoptera: Gryllidae). *Journal of the Kansas Entomological Society* 63: 237-242.
- Walker T. J., Moore, T. E. 2006. Singing insects of North America. Online: [<http://buzz.ifas.ufl.edu>]