Hearing and spatial behavior in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae)

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SUMMARY

The prairie mole cricket (*Gryllotalpa major* Saussure) is a rare orthopteran insect of the tallgrass prairie ecosystem of the south central USA. Populations are known to currently occupy fragmented prairie sites in Oklahoma, Arkansas, Kansas and Missouri, including The Nature Conservancy’s Tallgrass Prairie Preserve in north central Oklahoma. Prairie mole cricket populations were surveyed at this site and at another site in Craig County, OK during the spring of 2005 and 2006, using the male cricket’s acoustic call to locate advertising aggregations of males. Five males from one large aggregation were removed in a study to describe (1) the hearing thresholds across the call’s range of frequencies, (2) the distances over which the higher harmonic components of the male’s calls are potentially detectable, (3) the species’ sensitivity to ultrasound and (4) the spatio-auditory dynamics of the prairie mole cricket lek. Results indicate that *G. major* has a bimodal pattern of frequency tuning, with hearing sensitivities greatest at the 2kHz carrier frequency (41 dB SPL) and declining through the call’s frequency range (84 dB at 10kHz). A second sensitivity peak is evident in the ultrasound range at 25 kHz (62 dB SPL). Spatial analysis of *G. major* lek sites indicates that approximately 73% of males within the lek are spaced in such a way as to allow acoustic interaction at the species’ carrier frequency, while any information in higher harmonic overtones in the call appears to be available only to nearest neighbors.

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INTRODUCTION

Crickets and other orthopterans tend to space themselves across the landscape within suitable patches of habitat based in part on the detection of acoustic signals produced by conspecifics (Alexander, 1962; Forrest, 1983; Otte, 1992; Sakaluk et al., 1995). While other critical factors, such as the availability of forage, refugia and mates as well as the intensity of predation pressures, are also assumed to influence the spatial distribution of crickets, most studies have focused on the role of the calling song in driving the spatial dynamics of orthopteran aggregations (Farris et al., 1997). As in most other Orthoptera, the spatial dynamics of advertising male crickets are often well described but poorly understood. In many cases, these spatial arrangements are an outcome of the complex interaction of an animal’s neural capacity for detecting neighboring conspecific signalers and the acoustic interference of environmental factors (Römer and Bailey, 1986).

Mole crickets (*Gryllotalpidae*) are a unique ensiferan clade distinguished from other true crickets by morphological and behavioral adaptations that allow the group to exploit an almost exclusively subterranean ecological niche (Ulagaraj, 1975; Figg and Calvert, 1987). Mole crickets have large, powerful forelimbs (dactyls) that allow for the excavation of complex burrow systems beneath the subsoil. Several species in the group produce advertisement calls from within the burrow complex or from within an acoustic calling chamber located at the terminus of a burrow at the soil surface (Bennet-Clark, 1987). While considerable work has been done in describing the production of acoustic signals in mole crickets (Bennet-Clark, 1970), fewer studies have focused on the hearing of species within the group, other than the morphological description of the tympanum: covered in *Gryllotalpa* species and *Neocurtilla hexadactyla*, exposed in the genus *Scapteriscus* and missing in *Triamescaptor aoeta* (Hill et al., 2002). One early study described a high-frequency sensitivity in several gryllotalpid species, including a 20–30 kHz best frequency in the northern mole cricket (*Neocurtilla hexadactyla*), which was attributed to conspecific calling song detection (Suga, 1968). However, later studies found mole crickets’ advertisement calls to be devoid of high-frequency components (Bennet-Clark, 1989; Forrest, 1983), leaving this high-frequency sensitivity unexplained. *Scapteriscus borellii*, a mole cricket species introduced to the southeastern USA that engages in nocturnal dispersal flights, has been shown to have a bimodal hearing capacity that includes sensitivity within the range of conspecific advertisement calls (3kHz) as well as a second sensitivity peak in the ultrasonic range (25kHz) that probably allows detection of echolocating bats. Additionally, this flying mole cricket species exhibited evasive behavior when faced with ultrasonic stimuli (Mason et al., 1998). *Scapteriscus abbreviatus*, a closely related flightless species, exhibited neither sensitivity to ultrasound nor any behavioral aversion to the stimulus in the same study.

The prairie mole cricket, *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae), is a rare endemic of the tallgrass prairie ecosystem of the south central USA and is currently known only from Oklahoma, Arkansas, Kansas and Missouri (Walker and Figg, 1990; Vaughn et al., 1993). Adult males construct an acoustic calling chamber (see Movie 1 in supplementary material) with an opening to the soil surface that is used exclusively for producing sexual
advertisement calls (Hill, 1999). Unlike most gryllotalpids, males produce a long sequence of brief chirps varying from 1.7 to 2.9 per second at a carrier frequency of ~2.0 kHz (Walker and Figg, 1990; Hill, 2000) and with harmonic overtones up to 10 kHz (Hill, 1998). Variation in the call’s dominant frequency and syllables per chirp correlates with male size (Howard and Hill, 2006). Females are attracted to the calling aggregation, fly over the sound field created by the displaying males and then drop to the ground to enter the selected male’s burrow (Walker and Figg, 1990; Hill, 1999; Howard and Hill, 2006); however, no information is available on whether or not this flying species is able to detect the ultrasonic frequencies emitted by echolocating bats.

In the mole cricket genus Scapteriscus, males are attracted to the calls of other males and are thought to space themselves in a uniform distribution near the periphery of a nearest neighbor’s sound field (Forrest and Green, 1991). Scapteriscus females are known to be preferentially attracted to advertisement calls with greater intensity (SPL), and a male with a louder call is thought to reduce nearest neighbor distances to ensure that the sound field of a less attractive male is contained entirely within his own. Conversely, less attractive males are thought to space themselves further away from the focal male to increase the likelihood of attracting a female (Forrest and Green, 1991).

Gryllotalpa major males mate in leks with statistically significant aggregation at three levels of scale: (1) thelek proper, (2) subsets of clumped burrows and (3) 1–3 burrows within plots of 3–4 m in diameter (Hill, 1999). Prairie mole cricket leks form more often on recently burned sites (Howard and Hill, 2007), and inter-male spacing among the two or three nearest neighbors is thought to be influenced by substrate-borne vibrations produced by advertising males (Hill and Shadley, 1997; Hill and Shadley, 2001). However, the richness of harmonic overtones in the calling song, rather than the call intensity, was the parameter in the airborne component of the call found to be correlated with distance to the nearest neighbor (Hill, 1998). The current study examines spacing in natural aggregations in the context of auditory sensitivity (under idealized assumptions about sound propagation and attenuation). We predict the following: (1) G. major hearing will be tuned to the carrier frequency of the advertisement call; (2) if a flying species potentially exposed to predation by bats, G. major will exhibit hearing at ultrasonic frequencies; (3) all advertising G. major males within a lek will be spaced within the maximum effective signal range of all other advertising males in the lek and (4) because the number of harmonic overtones negatively correlates with nearest neighbor distance (Hill, 1998), some harmonic content of the calling song will be detectable by neighboring males.

**MATERIALS AND METHODS**

**Auditory sensitivity**

Five signaling Gryllotalpa major Saussure males were extracted in 2006 from three lek sites at The Nature Conservancy’s Tallgrass Prairie Preserve in Osage County, OK, USA (36°49′ N, 96°23′ W) and transported live to the laboratory for measurements of auditory sensitivity across the advertisement call’s range of frequencies. After removal of both pairs of wings, specimens were mounted ventral side up on a plastic platform using low-melting-point wax. The prothoracic legs were restrained with the wax to emulate resting leg position. The ventral cuticle of the prothorax was removed, with the leg nerve, including auditory nerve bundles, isolated at the foreleg/prothoracic cavity junction. Summed auditory nerve responses were recorded from whole leg-nerves using tungsten-wire hook electrodes with an indifferent electrode placed in the abdomen. Nerve responses were amplified (AM Systems Model 1600, Carlsborg, WA, USA) and recorded by computer (National Instruments PCI-6040E A/D board, 100kHz sampling rate, Austin, TX, USA).

Acoustic stimuli were tone pulses of 50ms duration with 1 ms rise/fall times, repeated at 2.0s⁻¹. Stimulus generation and data acquisition were controlled by a custom program written in Matlab (The Mathworks, Natick, MA, USA). The stimulus pulses were synthesized and output through a D/A interface (National Instruments PCI-6040E, 200kHz sampling rate, Austin, TX, USA). The tone pulses were attenuated (Tucker Davis PAS 5; Alachua, FL, USA), amplified (Bruel and Kjaer Type 2706; Nierum, Denmark) and then broadcast through loudspeakers (Realistic piezo tweeter and 4 inch woofer; Fort Worth, TX, USA) placed 50 cm from the position of the cricket preparation. Stimulus levels at the position of the cricket were calibrated using a microphone (Bruel and Kjaer type 4939) and sound level meter (Bruel and Kjaer type 2231). The frequency range of the system was 1–35 kHz, and all sound pressure levels (SPLs) given are in dB (re. 20μPa).

Data were recorded as averaged summed action potentials (SAP; 50 responses averaged). For each frequency, data were collected by recording responses over a range of intensities beginning at 90 dB SPL and stepping down in 3 or 6 dB increments for at least 40 dB, but always until auditory responses were no longer discernible. Smaller intensity increments (3 dB) were used for frequencies near the auditory sensitivity peaks. Responses were quantified in two ways: (1) by measuring the maximum peak-to-peak amplitude in the SAP and (2) by measuring RMS (root mean square) level of the SAP waveform to derive a measure of the relationship between response amplitude and stimulus intensity (intensity–response or IR curves) at each frequency. The two methods of quantifying response amplitudes gave similar results. Data are shown for RMS level measurements. Frequency tuning was measured both as threshold curves and iso-intensity response curves (stimulus amplitude vs frequency for a constant stimulus level). Threshold intensities at each frequency were interpolated from our IR curves as follows. Response amplitudes were measured over a range of intensities from subthreshold levels (no auditory response) to the maximum available stimulus level. We used the RMS levels of subthreshold neural responses as a measure of background activity. We defined threshold as the frequency at which response amplitude exceeded the average level of background (non-auditory) activity by two standard deviations. These values were obtained by interpolation using the ‘interp1’ function in Matlab. We also calculated thresholds using two different methods for pooling the data: (1) thresholds were calculated for each specimen, using the above procedure, and values averaged for the five individuals and (2) intensity–response data were pooled to create global IR curves, and thresholds were calculated from the pooled data (see Fig. 1). Iso-intensity response curves (Fig. 2) show pooled data.

**Male spacing in the field**

To determine the proportion of advertising males within a lek that are spaced within the estimated effective signal range of other lek members, we integrated GIS spatial analysis data from the Tallgrass Prairie Preserve and from White Oak Prairie in Craig County, OK, USA (36°37′ N, 95°16′ W) from the spring reproductive seasons of 2005 and 2006. Leks were located by listening for the male advertisement songs, and only groups of two or more signaling males were included in the analysis. When a group of advertising males was located, each burrow in the group was identified, flagged and numbered. Geographic coordinates of the acoustic burrows were documented using a Trimble ProXRS unit with a TSC1 asset.
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**Spatio-auditory ecology**  

We combined data on male spacing in the field and estimated call broadcast range and auditory sensitivity under two idealized assumptions. (1) Broadcast range can be estimated using the measured intensity of male calls in the field, while also considering the propagation constraints of spatial attenuation due to spherical spreading, frequency-dependent excess attenuation due to temperature and humidity (Beranek and Ver, 1992), and masking noise levels in a complex or noisy environment (US Department of Defense, 1983; Römer, 1993). In other words, we did not measure propagation directly, and our estimates neglect possible effects of absorption by vegetation. These estimates, therefore, can be taken to represent maximum propagation distances for prairie mole cricket calls in native habitat. (2) Auditory frequency tuning curves and hearing intensity thresholds measured in the lab are a reasonable estimate of sensitivity in the field.

Using published spectral data for the *G. major* calling song (Hill, 1998) and relative SPL estimates for each harmonic overtone of the call (Hill et al., 2006), the most conservative maximum signal distance per frequency under ideal conditions was calculated. An inter-burrow distance matrix, produced within the GIS and identifying each burrow’s linear distance from all others within the aggregation, was then queried to determine the number of male pairs within the lek spaced within these maximum signal distances at each of the harmonic frequencies within the calling song. The percentage of the total paired interactions that were spaced within these maximum signal distances was then calculated for each harmonic frequency based upon this queried total.

**RESULTS**  

**Auditory sensitivity**  

The highest hearing sensitivity (mean threshold intensity of 45.4 dB) closely matched the dominant frequency (2.0 kHz) of the male advertisement call (Fig. 1). Intensity thresholds increased across the remainder of the calling song’s harmonic range of frequencies, with the poorest acoustic resolution detected at a threshold of 83 dB at 10 kHz (Table 1). Additionally, intensity thresholds declined steeply at a narrow band within the ultrasound (25 kHz). The threshold intensity curve (Fig. 1) generated by the summed neural responses of the hearing test indicate a clear bimodal hearing pattern, with peak sensitivities correlated with the advertisement song’s carrier frequency, declining sensitivity through the calling song’s harmonic frequency range, and a second sensitivity peak in the ultrasonic range.

Iso-intensity response curves (Fig. 2) indicate that the bimodal frequency sensitivity is also evident at suprathreshold stimulus intensities but further suggest that, as stimulus increases, frequency tuning for *G. major* flattens somewhat to include the harmonic components of the advertisement call. Moreover, at the highest intensities examined (85 dB), the curve shifts toward a lower-frequency sensitivity peak at 1.0 kHz with two additional secondary sensitivity peaks within the curve at 3.5 kHz and 30 kHz. This shift may occur due to the recruitment of responses from subgenual organs.

**Spatio-auditory ecology**  

Overall, the majority (74%) of the 300 males were spaced so that they could detect the dominant frequency of a neighbor’s calling song, but only a small proportion (<11%) were spaced such that effective signal range for the frequencies found in the advertisement call of *G. major* (2–10 kHz).

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**Table 1. Estimated effective signal range of the carrier frequency and harmonic frequencies of the advertisement call and mean percentage of males located within that range on 11 *Gryllotalpa major* leks**

<table>
<thead>
<tr>
<th>Call component (kHz)</th>
<th>Estimated effective signal distance</th>
<th>Mean % ± s.e.m.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>76.8</td>
<td>73.6±8.9</td>
</tr>
<tr>
<td>4</td>
<td>6.4</td>
<td>10.7±3.5</td>
</tr>
<tr>
<td>6</td>
<td>4.3</td>
<td>8.6±3.3</td>
</tr>
<tr>
<td>8</td>
<td>1.6</td>
<td>1.4±0.9</td>
</tr>
<tr>
<td>10</td>
<td>0.8</td>
<td>0.1±0.06</td>
</tr>
</tbody>
</table>

Percentages were calculated based upon spatial distribution of males, estimated effective signal range for the species, and frequency-specific signal attenuation properties.
they could detect the highest frequency components of a neighbor’s song (Table 1). It was more common for males to be spaced at or beyond the estimated maximum signal range of other males within small leks \( (N<7 \text{ males}) \), while in larger leks nearly all males tend to be within the estimated maximum signal range of the entire lek membership at the dominant frequency.

Only a small proportion of males within the leks surveyed were spaced close enough to potentially detect the higher-frequency components of a neighbor’s calling song (based on overlap of concentric circles representing frequency in Fig. 3). At the first harmonic overtone of the advertisement call (4kHz), 10.7% of males were spaced close enough to potentially interact acoustically with a neighbor, while 8.6% of males could potentially detect a neighbor’s second harmonic overtone (6kHz). Even smaller proportions of advertising males could potentially detect the calling song’s two highest harmonic overtones (1.4% at 8kHz and 0.1% at 10kHz) (Fig. 4; Table 1). Regardless of the population size of the lek examined, small groups of 2–4 males were consistently seen distributed across the lek in clusters spaced closely enough together to potentially detect some harmonic overtones of the other males in the cluster. A greater proportion of these intra-lek clusters was spaced to allow for the potential detection of the member’s second and third harmonics rather than of the fourth and fifth harmonics, and generally only nearest neighbor pairs were spaced close enough to potentially detect these high-frequency call components.

**DISCUSSION**

Overall, the results suggest that *G. major* hearing is tuned to frequencies found within the male advertisement call. The greatest sensitivity is at the dominant frequency of the call, with absolute sensitivities comparable to previously studied gryllotalpids (Mason et al., 1998). While males do appear to space themselves, at least in larger leks, within earshot of other singers, our data do not support the prediction that they make use of higher harmonic components of the call in spacing their burrows on a lek. Even assuming optimal signal propagation (attenuation due to spherical spreading and excess attenuation only) (see Römer, 1993; Beranek and Ver, 1992), few individuals were close enough for any call components above the fundamental to be audible.

A rather narrow sensitivity in the ultrasonic range suggests that *G. major*’s hearing allows it to avoid echolocating bat predators. Oklahoma has 22 native bat species (Caire et al., 1989), and at least five species are common to the area of our two field sites (W. A. Caire, personal communication). Echolocation frequencies for two of these, the big brown bat (*Eptesicus fuscus*) and hoary bat (*Lasiurus cinereus*), were measured in Arizona to be as low as 26kHz (Fenton and Bell, 1981) but vary at the population level across North America:
and lower frequencies are not suitable for detection of small prey (Jones, 1999). Measured echolocation frequencies for both the big brown bat and hoary bat are in the range of the higher tuned hearing sensitivity in *G. major*, which is the largest cricket in North America (Walker and Figg, 1990) and apparently an appropriate prey size for larger bats. Thus, ultrasound hearing should be advantageous in this species, even if a secondary adaptation for detecting and evading bat predators (Hoy 1992; Mason et al., 1998).

In a study of *Scapteriscus* species, signal intensity was the call component correlated with male spacing (Forrest and Green, 1991). *Gryllotalpa major* call intensity varies among males, but inter-male distance does not correlate with calling song intensity. Harmonic content of the calling song does correlate negatively with nearest neighbor distance (Hill, 1998); however, it is not known if males can modulate harmonics in the calling song, only that males advertising at the closest inter-male distances produced songs with a greater number of harmonic overtones. Regardless, less than 11% of the males in the current study were spaced at distances to potentially detect the second harmonic of a calling neighbor. This result lends support to the argument (Hill and Shadley, 1997; Hill and Shadley, 2001) that *G. major* males space themselves based on cues from the substrate-borne vibrational component of the calling song. Further, males are not known to respond to the airborne component of the advertisement signal of a conspecific neighbor once the acoustic burrow has been constructed and the male has begun to actively signal (Hill and Shadley, 2001). Theory suggests, however, that airborne females, who fly 4–5 m above a lek and then swoop down to a height of 1.5–2 m for a second pass (Howard and Hill, 2006), can use the harmonic overtones to assess the proximity of advertising males, as the rapid attenuation of these higher-frequency call components provides distance cues. A signaler with more harmonic overtones will be perceived as closer in space than a signaler at an equal distance and an equally intense calling song, but with fewer harmonics (Römer and Lewald, 1992). Thus, males with more harmonic calls may be considered more attractive to females than males with less spectral richness in the calls.

Two unexpected results of this study require additional data before strong conclusions can be drawn. Tuning of the hearing within the range of frequencies in the calling song is broader at higher stimulus levels. Stronger responses at low frequencies might suggest that vibration receptors are being recruited and therefore hint at a more important role for substrate components in this species than we have so far documented. Additionally, males advertising on leks of less than seven individuals tended to be more broadly spaced than males on larger leks. In katydids, central nervous processing of signals allows individuals to filter out all but the two closest singing conspecifics in a chorus (Römer, 1993), and other orthopterans may attend to only one or two closest or loudest neighbors (Römer, 1993; Greenfield, 1994) or even sing from less than half the maximum estimated signal range (Römer and Bailey, 1986). Thus, *G. major* males may only be interacting with nearest neighbors, even on leks with the fewest individuals, where we found inter-burrow distances to be relatively greater.

In many orthopteran groups, the detection of conspecific advertisement song is known to mediate inter-male spacing and pair formation (Alexander, 1967; Morris, 1979; Latimer and Sippel, 1987; Snedden and Sakaluk, 1992; Tuckerman et al., 1992; Farris et al., 1997; Forrest et al., 2006), while signal detection is under constraint by both biological and environmental factors (Römer, 1993). As in other ensiferan species, hearing in *G. major* is tuned to the carrier frequency of the calling song, and females are phonotactic. While orthopteran signal transmission and detection in natural environments is well described (Römer and Bailey, 1986; Römer and Lewald, 1992; Cooley, 2001; Couldridge and von Staaden, 2004), less is known about which components of the advertisement call are actually used in inter-male spacing, or in female choice, especially in *G. major*. A general trend, however, is that temporal patterns of a signal to be used in species recognition, while the frequency spectrum is used more to detect predators, to discriminate mates at close range or to estimate distance to a conspecific singer (Stumpner and von Helversen, 2001). This interpretation is supported by empirical evidence in bushcrickets that prefer louder, harmonic songs, where the higher harmonics could be useful in estimating distance to the signaler (Latimer and Sippel, 1987), and female *Teleogryllus oceanicus*, who preferred calls with additional harmonics in two-choice tests between pure tone calls and those with harmonic overtones (Latimer and Lewis, 1986).

While distinct from other mole cricket species in aspects of its advertisement call structure, habitat requirements and lek mating system, *G. major* fits a generalized ensiferan model with regard to its hearing. As in *Scapteriscus* species (Mason et al., 1998), *G. major* has bimodal hearing sensitivity that allows efficient detection of conspecific calling songs as well as the ultrasonic signals of potential microchiropteran predators. This study also supports the hypothesis of a bimodal signaling system (Hill and Shadley, 1997) whereby the airborne component targets flying females and the substrate-borne component provides spacing cues used in inter-male spacing. Higher-frequency harmonic overtones in the calling song may be important in female choice as females estimate distance to the nearest male, but additional study is required before a role is found for harmonic overtones in nearest neighbor interactions among closely spaced males. Such studies might test a harmonic-mediated male spacing model by assessing male response to simulated closely spaced nearest-neighbor calling songs that exhibit differential harmonic overtones at high amplitude and the corresponding female preferences for the same.

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