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Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae)

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Abstract

The prairie mole cricket (*Gryllotalpa major* Saussure) is a native of the tallgrass prairie ecosystem of the south central United States. The largest of North American crickets, its populations have declined with the reduced availability of suitable grassland habitat. Prairie mole cricket populations were surveyed at The Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma in the spring of 2005. We located 95 acoustic burrows occupied by calling males and recorded the calling songs of 55. We measured 3 morphological characters for 8 of these field-recorded males and characterized each male's calling song for 7 key acoustic variables. Statistically significant relationships were discovered between male body length and 2 song parameters: syllables chirp⁻¹ and dominant frequency.

Key words

Gryllotalpidae, morphology, calling song, burrow, size, frequency

Introduction

Many groups of animals make use of advertisement displays to attract mates. Advertising individuals, normally the male of a species, that exhibit the most colorful phenotype, ornate display maneuvers, or robust call characteristics, often gain a measurable mating advantage over less conspicuous signalers (Andersson 1994). For animals that use acoustic display, variation in the advertisement call provides material for both intrasexual and intersexual selection (Darwin 1981, Alexander 1962, Forrest & Green 1991), and selective pressures originating from interspecific predation may also serve to influence various aspects of the display (Alexander 1962, Andersson 1994, Simmons *et al.* 2001, Zuk *et al.* 2001, Bertram *et al.* 2004). Additionally, the morphology of the caller should influence aspects of an acoustic advertisement signal (Brown *et al.* 1996, Gray 1997, Bennet-Clark 1998, Tarano 2001, Burmeister *et al.* 2002, Esteban *et al.* 2002, Lode & Jacques 2003, Gerhardt 2005).

Orthopterans were one of the first animal groups to evolve acoustic structures for use in sound communication (Alexander 1962, Huber *et al.* 1989, Otte 1992), and much of what has been learned in the field of bioacoustics has resulted from various behavioral and neurophysiological studies on crickets (Ulagaraj & Walker 1973, Walker 1975, Forrest 1982, Römer & Bailey 1986, Huber *et al.* 1989, Greenfield *et al.* 1997, Bennet-Clark 1998). One group of crickets that has garnered the attention of both behavioral and neurophysiological research groups is the Gryllotalpidae (mole crickets). While most mole crickets use the typical ensiferan tegmino-tegminal stridulatory apparatus to produce sexual advertisement calls, additional unique morphological specializations, such as robust forelimbs, highly adapted for burrowing and a heavy bullet-shaped

pronotum, segregate them from other gryllids and adapt them for the subterranean lifestyle common for members of the group (Ulagaraj 1975, Bennet-Clark 1987, Walker & Figg 1990, Hill 1998). Much of the work done with mole cricket acoustic behavior has been motivated by the economic significance of introduced pest species now found in the southeastern United States (Ulagaraj 1975, Bennet-Clark 1987, Walker & Forrest 1989, Forrest & Green 1991, Mason *et al.* 1998, Hertl *et al.* 2001, Prestwich & O'Sullivan 2005). Conversely, due to a lack of commercial significance, far less data have been generated by studies seeking to describe the relationship between morphology and sound production in mole cricket species native to North America.

The prairie mole cricket (*Gryllotalpa major* Saussure) is a native gryllotalpid of the tallgrass prairie ecosystem of the south central United States. The largest of the North American crickets, with a length up to 5.0 cm and mass up to 2.6 g (Walker & Figg 1990), its populations have declined with reduction in suitable grassland habitat (Figg & Calvert 1987). *G. major* was recommended for protection as a threatened species under the Endangered Species Act of 1973 (U.S. Fish & Wildlife Service 1990), but a lack of data describing the basic ecology of the species stalled protection efforts (U.S. Fish & Wildlife Service 1992). Populations are known to occupy relict tallgrass prairie sites in Oklahoma, Kansas, Arkansas and Missouri, with sites in northeastern Oklahoma well characterized in the literature (Vaughn *et al.* 1993).

Aggregations of advertising males form leks (Hill 1999), a spatiotemporal signaling approach that may provide males with a measurable reproductive advantage (Höglund & Alatalo 1995, Greenfield *et al.* 1997). Upon emergence in the late spring, males construct an acoustic burrow, and return to the burrow nightly to call if weather conditions are suitable. Males produce a long sequence of brief harmonic chirps varying from 1.7 to 2.9 s⁻¹ at a carrier frequency of about 2.0 kHz (Walker & Figg 1990, Hill 2000). Male-male spacing within the lek is thought to be a function of substrate-borne vibration (Hill & Shadley 1997, 2001). Females fly above an aggregation of calling males, drop to the ground and enter a male's burrow (Walker & Figg 1990, Hill 1999).

It is presumed that the female selects a mate based on a combination of passive and active mechanisms, but it is not known if she selects for size, nor if male size correlates with any characteristic of the advertisement call. In this paper we report on an attempt to determine the relationship between call parameters and male size in *G. major*. Based upon previous studies of orthopteran groups and other taxa, we hypothesize that size will correlate positively with calling song intensity and negatively with dominant frequency.

Methods

The Nature Conservancy's Tallgrass Prairie Preserve (36° 49'N, 96° 23'W) in north central Oklahoma is the largest continuous tract of tallgrass prairie remaining in North America, about 16,000 ha. The property, located along the southern fringe of the Flint Hills and within the historic boundaries of the Osage Nation, was purchased by The Nature Conservancy in November of 1989 and consists of approximately 80% tallgrass prairie vegetation and 20% oak woodlands. The long-term management plan for this property includes the utilization of prescribed burns, bison and cattle grazing and limited mowing, to facilitate the restoration of a functional tallgrass prairie landscape (Hamilton 1996, Fuhlendorf & Engle 2001). Prairie mole crickets were documented at various locations within the site during the period 1993-1998, but no continued monitoring of populations has occurred since that time (R. G. Hamilton pers. com.).

Beginning in April 2005, historic *G. major* chorusing sites at the Tallgrass Prairie Preserve were resurveyed. Additionally, a systematic search was conducted to determine populations throughout the preserve. During the 47-d calling season from April 4 to May 20, 2005, 96 acoustic burrows were located and flagged. Approximately 35% of the preserve was inventoried, replicating a method employed in earlier survey efforts and recommended in the literature (Figg & Calvert 1987, Figg *et al.* 1992). Populations were surveyed by using the male cricket's sexual advertisement call as a discrete presence indicator. Aggregations were located by driving county and preserve roads at sunset, during evenings in April and May, stopping about every 800 m to listen for calling. In some cases, due to lack of road infrastructure on the preserve, areas were inventoried entirely on foot. When a calling aggregation was found, the burrow of each calling male was located and flagged. Geographic coordinates of each acoustic burrow were documented, using both a hand-held Garmin GPS unit (Garmin International, Olathe, KS, USA) and a more accurate Trimble Backpack unit (Trimble Navigation Limited, Sunnyvale, CA, USA).

Upon locating the burrow of a calling male, the individual was assigned an alpha-numeric designation; a recording of the male's call was made on a subsequent evening. Recordings were obtained with Sony TCM-150 audio-cassette recorders (Sony USA, New York, NY, USA) using Maxell XLII High Bias 110-min cassette tapes (Maxell Corp. of America, Fair Lawn, NJ, USA). They were placed at a distance of 20 cm from the front of the burrow opening, parallel to the main axis of the burrow, as described in previous acoustic studies of the species (Hill 1998, 2000). Each individual male's alpha-numeric designation, date, time, and lek-site location were noted on the tape at that time. Recorders were placed in this position and activated approximately 15 min prior to sunset and the onset of calling, and collected later that same evening after all males had ceased advertising.

At the same time as recorders were activated, meteorological data for the lek-site were recorded: air and soil temperature, relative humidity, dewpoint, barometric pressure, wind speed and direction. All data except soil temperature were obtained using a Kestrel 4000 (Nielsen-Kellerman, Boothwyn, PA, USA) hand meter. Soil temperature at 15-cm depth was measured with a dial thermometer (Cole-Parmer Instrument Co., Niles, IL, USA). An attempt was made to record every male present, but the short calling season combined with the large size of the study site prevented this.

During the period beginning on May 11, 2005 and ending on May 20, 2005 (the last day *G. major* males were observed calling

at the site), 8 previously recorded males were extracted from their acoustic burrows and measured for length, pronotal width, and mass. Length was measured to the closest 0.1 cm and pronotal width to the nearest 0.01 cm using dial calipers (Cole-Parmer Instrument Co., Niles, IL, USA); mass was measured to the closest 0.1 cm using a Pesola 20010 micro-line spring scale (Forestry Suppliers, Jackson, MS, USA). Five males were held for additional observations, and the remaining 3 returned to a location < 1.0 m from their burrow.

The 8 recorded songs were digitized and analyzed with SIGNAL software (Beeman 1996). This package generates oscillograms, sonograms and FFT power spectra from a 2.62-s sample (bandwidth=10.0 kHz, sample rate=25.0 kHz, frequency resolution =97.7 Hz, time resolution=10.2 ms). Each recording was analyzed at the 15-min mark of calling to measure 6 key call characteristics: chirp duration, chirp rate, interchirp interval, syllables per chirp, maximum call amplitude and dominant frequency. The duty cycle was calculated from the chirp duration and interchirp interval data. Since chirp rate in *G. major* is positively correlated with soil temperature (Hill 1998), all calling song parameters were subjected to regression analysis against soil temperature before further statistical analysis. Data were tested for normality, and then for the level of association between each pair of morphological and call variables (SigmaStat for Windows, ver. 2.0, Jandel Scientific, San Rafael, CA, USA). The Pearson Product Moment test was used for normally distributed data, and the Spearman Rank Order Correlation for data sets that failed the Kolmogorov-Smirnov test of normality.

Results

The 8 *G. major* males in this study varied in morphology and calling song characteristics (Table 1) in ways consistent with values reported in the literature (Walker & Figg 1990, Hill 1998, 2000). Linear regression indicated a correlation with soil temperature for all parameters except dominant frequency and maximum amplitude; therefore, these variables were corrected to a standard temperature of 20° C before further analysis. All data were normally distributed except for the number of syllables per chirp.

The greatest variability in calling songs of the 8 males was seen in maximum amplitude, call duration and interchirp interval (Table 1), but this variation could not be explained by our 3 morphological measurements. A strongly negative correlation exists between dominant frequency of the calling song and male body length (Fig. 1). The songs of longer males were significantly lower in frequency (Pearson Product Moment: $r = -0.872$, $p = 0.005$). In terms of song

Table 1. Individual morphology and calling song variation for *G. major* males, expressed as mean, standard deviation and coefficient of variation ($n = 8$).

Variable	\bar{x}	$s_{\bar{x}}$	CV
Male Body Length (cm)	4.625	0.225	4.86
Male Body Width (cm)	1.018	0.053	5.17
Body Mass (g)	2.598	0.225	8.66
Syllables/Chirp	17.150	3.161	18.43
Chirp Duration (msec)	154.618	45.275	29.28
Interchirp Interval (msec)	166.614	35.653	21.40
Duty Cycle	0.476	0.036	7.61
Max Amplitude (v)	0.476	0.119	34.20
Dominant Frequency (kHz)	1.971	0.091	4.63
Chirp rate (chirps/min)	188.500	34.863	18.49

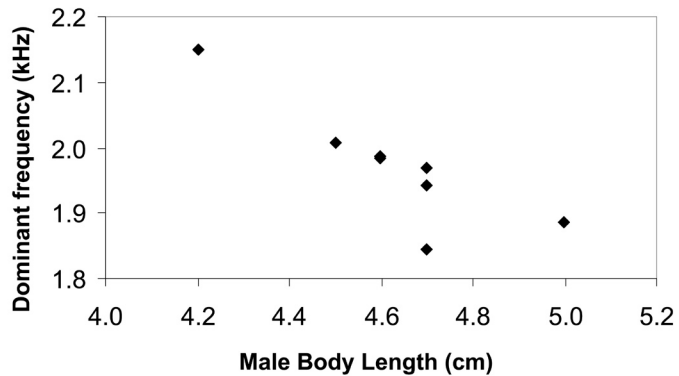


Fig. 1. Correlation analysis of the dominant frequency of the calling songs of *G. major* males and the body length of the males who produced the songs (Pearson Product Moment: $N = 8$, $r = -0.872$, $p = 0.005$).

structure, a significant positive correlation exists between length of the male and syllables per chirp in his song (Fig. 2), with longer males producing songs of more syllables (Spearman Rank Order Correlation: $r = 0.835$, $p = 0.005$). Other than these 2 relationships, morphology did not explain the variation seen in the other 5 measured calling song parameters.

Discussion

The results of this study support our initial expectation that a certain level of species-level homogeneity would be observed in each of the 7 call parameters measured for the 8 individuals. Preliminary analyses of the results indicate a greater heterogeneity in temporal aspects of the prairie mole cricket's calling song and minor dissimilarities in song structure and spectral characteristics. Nonetheless, the observed variability in these temporal parameters was not closely correlated with variation in morphology. Correlation analyses revealed a relationship between a male's length and the dominant frequency of his calling song, and between male length and the syllables per chirp component of song structure.

Previous unsuccessful attempts to link call amplitude to social or environmental factors had encouraged us to look for some aspect of morphology to predict inherent individual ability to produce a louder call (Hill 1998). While our hypothesis concerning the relationship between dominant frequency and morphology was supported, we found no such support for a relationship between morphology and advertisement call intensity. In other words, while the males of greater overall length produced lower-frequency songs with more syllables per chirp, they did not necessarily produce louder songs.

Variation in the dominant frequency of calling songs of advertising males across taxa is often correlated with some aspect of body size (Gray 1997, Burmeister, *et al.* 2002, Lode & Jacques 2003, Hodl, *et al.* 2004, Lardner & Lakim 2004, Larson 2004, Gerhardt 2005, Honda-Sumi 2005). The characteristics of the advertisement song are limited both by the overall size of the individual, and by the morphology and musculature of the sound-producing apparatus (Bennet-Clark 1998). In mole crickets, as in other cricket groups, the size and structure of the tegmina are crucial in determining the dominant frequency produced during calling episodes (Bennet-Clark 1970).

Additionally, and differing in this regard from most other Ensifera, mole crickets often employ an acoustically-tuned burrow

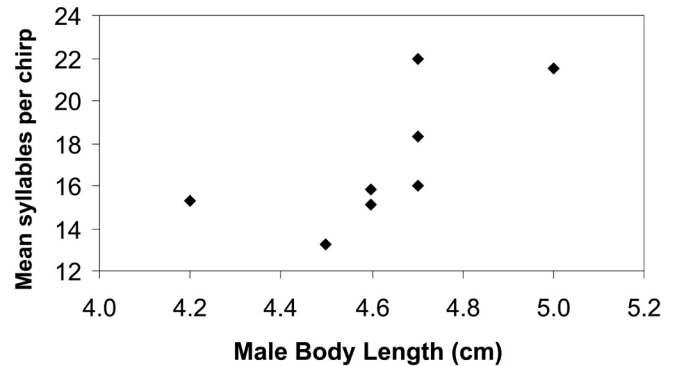


Fig. 2. Correlation analysis of the mean syllables per chirp in the calling songs of *G. major* males and the body length of the males who produced the songs (Spearman Rank Order Correlation: $N = 8$, $r = 0.835$, $p = 0.005$).

that can influence the intensity and spectral dynamics of the calling song to some degree (Bennet-Clark 1987, Bailey *et al.* 2001). Complicating matters further, behavioral cues may also contribute to spectral variance. Although not within the scope of this study, a correlation has been found between the number of harmonic overtones in the calling song of male prairie mole crickets and the distance to their nearest calling neighbor (Hill 1998). However, most likely it is the slight distinctions observed in the phenotypes of individual calling males that best explain the variation observed in the dominant frequencies produced by the signaler. Moreover, it is this same phenotypic variation, specifically emerging as individual variability in the plectrum and pars stridens, which also appears to best explain observed dissimilarities in the number of syllables per chirp produced in the *G. major* call. In either case, perhaps the larger question should focus on any female detection or discriminatory response to these variations.

Preferences of *G. major* females, in terms of male advertisement call characteristics, appear predominantly as anecdotal references in the literature (Walker & Figg 1990; Hill 1998, 1999, 2000). In field studies of the species, females are seldom seen, and comments on the reproductive behavior of females are sparse. Laboratory experiments attempting to elucidate female choice preferences with this species have not been fruitful, and so we are left to analyze what has been noted from the few field records made by workers. From these we learn that airborne females detect the presence of a calling aggregation of males from a distance, and while in flight, evaluate species-recognition cues based on temporal and structural elements of the calling song that fall above the general hearing frequency threshold of the species. Females may then preferentially isolate one of the calling males from the aggregation based on characteristics of the call that signal fitness, or conversely based solely on proximity of the signaler.

On the evenings of 14 and 15 April, 2005 at 2 prairie mole cricket leks within the Tallgrass Prairie Preserve study site, and on 4 different occasions, airborne *G. major* females approached an aggregation of calling males at a height of about 4 to 5 m and then descended to a height of about 1.5 to 2.0 m, while flying directly over the acoustic burrows and through the sound fields produced by the calling aggregation of males. All of these females landed on the substrate near (<0.5 m) an individual male's burrow and approached the burrow, stopping occasionally to redirect their approach, and then entering the burrow. Here they were greeted by

a change from calling song into the male's subtle courtship trill as noted previously in the literature (Hill 2000). After approximately 20 s of antennae contact within the acoustic chamber, courtship descended beyond view into the burrow complex, and burrow openings were found sealed the following morning.

It is hypothesized that during the approach at higher altitudes the female prairie mole crickets are passively selecting for specificity and proximity. During the lower-level flight it is our hypothesis that females may be actively assessing aspects of the calling song that, in addition to proximity, may reveal aspects of the male's fitness. Whereas we have noted in this study that individual variation in both dominant frequency and in syllable structure (*e.g.*, syllables per chirp) can be correlated with aspects of male morphology, we suggest that these 2 call parameters may be assessed by females as a component of the complex and poorly understood process of active mate selection in *G. major*.

While a statistically significant relationship was found for body length and 2 call parameters, pulses per chirp and carrier, it is not known whether these findings are ecologically relevant. It is common for subterranean organisms to exhibit a somewhat filiform body design, as it lends efficiency to subsoil movement. Additionally, the mechanical tuning of the acoustic burrow in mole crickets can increase call intensity by a significant proportion (Bennet-Clark 1987), and may be responsible for some of the variance documented in dominant frequency (Bailey *et al.* 2001). However, the data provide useful insights into the primary question regarding the relationship between morphology and specific parameters of the advertising call. Moreover, the results provide evidence to support the idea that *G. major* females may employ some measure of active selection, in conjunction with passive mechanisms, to isolate a preferred mate within the dynamic acoustic environment of the prairie mole cricket lek. Further studies are needed to address unanswered questions regarding the neurophysiological contributions to intersexual acoustic interactions, as well as to improve our understanding of the basic behavioral mechanisms that females deploy in locating and selecting mates.

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