Factors that possibly influence variation in the calling song of field crickets: temperature, time, and male size, age, and wing morphology

Konstantine Souroukis, William H. Cade, and Gareth Rowell

Department of Biological Sciences, Brock University, St. Catharines, Ont., Canada L2S 3A1

Received July 29, 1991
Accepted December 11, 1991


The structure of the calling song of the Texas field cricket, Gryllus integer, was studied. Pulse rates, percentage of missed pulses within a trill, numbers of pulses per trill or trill lengths, and intertrill intervals were measured for males singing in the field and in the laboratory. All song parameters were variable and were distributed normally. Intertrill intervals were longer in the laboratory, but all other parameters were similar in laboratory and field populations. Pulse rates varied in a linear fashion with ambient temperature in the laboratory and field. The percentage of missed pulses in a trill decreased with increasing temperature in the field and in the laboratory; intertrill intervals varied inversely with temperature only in the field. In field populations, immediately before and after sunrise male songs had fewer pulses per trill and a greater frequency of missed pulses than songs produced for a few hours following sunset. Song structure did not vary with age, weight, or hindwing dimorphism. Most song parameters were correlated with each other. The data are discussed in terms of female choice and attraction to male song, male competition by way of acoustical interaction, and underlying genetic variation in G. integer.


La structure des chants du grillon Gryllus integer a fait l’objet d’une étude. La fréquence des pulsations, le nombre de pulsations manquantes dans une stridulation, le nombre de pulsations par stridulation ou la longueur des stridulations, et les intervalles entre les stridulations ont été mesurés chez les mâles de populations sauvages et chez des mâles gardés en laboratoire. Les variables du chant subissaient des fluctuations et suivaient une distribution normale. Les intervalles entre les stridulations étaient plus longs en laboratoire, mais toutes les autres variables étaient semblables en laboratoire et en nature. La fréquence des pulsations suivait une courbe linéaire en fonction de la température ambiante, aussi bien en laboratoire qu’en nature. Le pourcentage de pulsations manquantes dans une stridulation diminuait lorsque la température augmentait, en laboratoire ou en nature, mais les intervalles entre les stridulations variaient en fonction inverse de la température seulement en nature. Chez les populations naturelles, les chants des mâles émis immédiatement avant et après le lever du soleil comportaient moins de pulsations par stridulation et la fréquence des pulsations manquantes y était plus élevée que dans les stridulations émises par les grillons durant quelques heures après le coucher du soleil. L’âge des mâles, leur masse ou le dimorphisme des ailes postérieures n’avaient pas d’effet sur la structure des chants. La plupart des variables reliées au chant étaient en corrélation les unes avec les autres. Les données sont examinées en rapport avec le choix des femelles et leur attitude pour les chants des mâles, la compétition entre les mâles par interaction acoustique et la variation génétique sous-jacente.

[Traduit par la rédaction]

Introduction

The calling songs of male field crickets (Orthoptera: Gryllidae) are species specific and attract sexually receptive females, repel other calling males, and act as cues for terminating migratory flights of conspecifics (Alexander 1957a, 1957b; Cade 1989; Campbell and Shipp 1979). Calling songs may also be used by females to assess the quality of potential mates (Simmons 1988). The song of field crickets is an important taxonomic character, but most species are known from recordings of only one or a few males (for example see Otte and Cade 1984). Information on variation in insect mating songs is necessary to understand mating preferences based on songs, the biosystematics of a group, the underlying genetic template, and other factors involved in the evolution of acoustical signalling. The purpose of this study was to determine the amount of variation in the calling song of the Texas field cricket, Gryllus integer, and the possible influence of temperature, time of activity, and male age, size, and hindwing morphology on calling song.

Methods of study

Song parameters

The calling song of G. integer in Texas consists of a series of rapidly produced pulses of sound which are grouped together into trills of varying lengths at a narrow carrier frequency of 5 kHz. Each pulse is produced by a single closure of the forewings. Our analysis of G. integer calling song was based on 4 song parameters: the rate at which pulses are produced, the number of pulses in a trill, the duration of the silent intervals between trills, and the frequency of missed pulses within a trill. Although the name G. integer has been used for this Texas species, this designation may not be correct, since in California, male G. integer have very different songs (Smith and Cade 1987; Cade and Tyshenko 1990; Weissman et al. 1980).

Field populations

Two sets of recordings were made of calling male G. integer in field populations in and near Austin, Texas. Each recording was approximately 1 min in length and was made using a EPM Electronics (model P200) parabolic microphone, a Sony WM-F46 cassette recorder, and BASF chromondioxid 2 C60 tape. The ground temperature was taken at the approximate location of the calling cricket after the recording was made, thus avoiding any disturbance to the calling G. integer.

The first set of recordings was made between 24:00 and 03:30 local time in May 1986. There are two distinct phases to the activity cycle in G. integer calling behavior: the number of calling G. integer

1Present address: Department of Entomology, Texas A&M University, College Station, TX 77843, U.S.A.
remains relatively constant from sunset to just before sunrise, and increases greatly shortly before sunrise (Cade 1979; French and Cade 1987). These recordings were used to measure the variation in field populations during the first phase of the activity cycle, when the number of males calling is relatively constant and before the increase in calling occurs. Spectrograms of recorded songs were produced on a Kay Elemetrics Sonagraph (model 7029A). Each spectrogram contained 2.4 s of song, and 4–7 spectrograms were produced for each cricket.

The second set of field recordings was made in August 1990. Recordings were made from 20:00 (sunset) to 02:00 local time and from 05:00 (sunrise) to 10:30. Spectrograms were produced using MacSpeech Lab II software on an Apple Macintosh IiX computer and were used to study variation in G. integer calling songs produced for a few hours after sunset and songs recorded at sunrise and for a few hours thereafter.

Measurements of the 4 song parameters were made directly from the spectrograms for both sets of recordings made in the field. Pulse rates, i.e., the number of pulses per unit time, were calculated from the longest trill of each spectrogram. Means and standard deviations were calculated for each male from the several spectrograms of his song. In determining the number of pulses per trill, all trills of a male were used that were represented completely on the spectrograms. Individual means and standard deviations were determined. Intertrill interval was the average time between trills for all complete intertrill intervals on all spectrograms for a male. A missed pulse was defined as a space within the trill of more than 15 ms but less than 35 ms (this is the interval into which a pulse would fit). The percentage of missed pulses was calculated for each individual.

**Laboratory population**

Variation in song structure was also studied in the laboratory using male G. integer raised from individuals collected from Austin, Texas, in spring 1989. These crickets were second- and third-generation laboratory stock. See Solymar and Cade (1990) for details on rearing crickets. Laboratory analysis of song allowed the effects of male size, age, and wing morphology to be measured more carefully. Immediately after the final molt, adult male G. integer were weighed on a Mettler BB240 electronic balance, characterized as macropterous or micropterous, and placed in individual 240-mL clear plastic containers. Each container had a cotton-plugged water vial and food (Purina Cat Chow®). Males were exposed to a 14 h light : 10 h dark cycle. The temperature in the laboratory was recorded at the beginning of the dark portion of the cycle.

_Gryllus integer_ song was analyzed in the laboratory using a specially designed digital signal processor (DSP) that measured pulse rate, number of pulses per trill, intertrill interval, and percentage of missed pulses for up to 5 males simultaneously over a period of several hours. Males were placed in a clear plastic cylindrical chamber (50 × 40 mm) which was covered with screen and provisioned with food and water. Two Archer electret microphones (270090 PC) were mounted at the focus of parabolic reflectors (14 cm in diameter) placed above the cylinders containing individual males. Each cylinder–microphone apparatus was placed inside a particleboard chamber (80 × 40 × 40 cm) that prevented the song of neighboring males from being recorded on adjacent microphones. Data were usually collected for 12-h periods from October to December 1989.

**Results**

The 4 song parameters are illustrated in Fig. 1, a representative spectrogram of G. integer calling song from the 1986 field recordings.

**Variation in song parameters in the laboratory and field**

Figure 2A presents the frequency distributions of pulse rates from the 1986 field recordings and from males in the laboratory. The mean and SD for pulse rates in the field and laboratory were 66.9 ± 8.2 and 70.2 ± 5.9 pulses/s, respectively. These values were not significantly different (t = 1.8, p = 0.1, df = 64). The distributions of pulse rates were not significantly different from the theoretical normal distributions (Kolmogorov–Smirnov, D = 0.3, p = 0.5, df = 2 in the field and D = 0.3, p = 0.5, df = 2 in the laboratory).

Figure 2B shows the frequency distributions of pulses per trill. The means were 34.8 ± 14.8 and 34.6 ± 14.6 pulses per trill in the field and laboratory populations, respectively. These values were not significantly different (t = 0.1, p = 0.9, df = 64), and the two distributions did not differ from theoretical normal distributions (Kolmogorov–Smirnov, D = 0.4, p = 0.4, df = 2 in the field and D = 0.3, p = 0.5, df = 2 in the laboratory).

Figure 3A shows the frequency distributions of intertrill intervals. The means were 174.9 ± 45.4 and 270.8 ± 79.3 ms in the field and laboratory, respectively. The intertrill interval was significantly longer in the laboratory sample (t = 6.0, p = 0.0001, df = 64), and the two distributions did not differ from the theoretical normal distributions (Kolmogorov–Smirnov, D = 0.3, p = 0.5, df = 2 in the field and D = 0.2, p = 0.7, df = 2 in the laboratory).

Figure 3B shows the frequency distributions of the percentage of missed pulses. The means were 5.6 ± 5.6 and 6.7 ± 5.1% in the field and laboratory, respectively. These values were not significantly different (t = 0.9, p = 0.4, df = 64), and the two distributions did not differ from normal (Kolmogorov–Smirnov, D = 0.3, p = 0.5, df = 2 in the field and D = 0.4, df = 2 in the laboratory).
Temperature

The temperature range was 18–23°C (mean 20.9 ± 1.4°C) in the laboratory and 17–23°C (mean 20.5 ± 2.1°C) in the field. There was no significant difference (t = 1.1, p = 0.3, df = 64). Linear regressions between measurements of song parameters and temperature are given in Table 1. Pulse rates increased with temperature in the laboratory and field, and these two regression lines had the same slope and similar elevations (t = 0, p = 1.0, df = 62; t = 1.7, p = 0.1, df = 63). The X-intercepts were 4.2°C in the field and 5.7°C in the laboratory. The intertrill interval decreased with temperature in the field, and the percentage of missed pulses decreased with increasing temperature in the field and in the laboratory.

Male age

Data from laboratory males that were used to determine if song structure varied with male age are given in Table 1. Males were between 6 and 50 (mean 28.7 ± 11.4) days past the final molt when placed in the DSP-monitored cylinders. To test for possible relationships between pulse rate and age, and between percentage of missed pulses and age, the effect of temperature was corrected by using the residuals from the previous linear regressions. There were no significant relationships between male age and the different song parameters.

Male weight

Data from laboratory males that were used to determine if song structure varied with male weight are given in Table 1. Males had an average weight of 388.8 ± 117.7 mg (range 190–611 mg). Pulse rates and percentage of missed pulses were again corrected for temperature. There were no significant relationships between male weight and the different song parameters.

Calling time in the field

Data from males recorded in 1990 in field populations, given in Table 2, were used to determine if song parameters varied with time of calling. There was no significant difference between temperatures in the two time periods (20:00–02:00: mean 27.1 ± 3.1°C, n = 22; 05:00–10:30: mean 27.5 ± 1.9°C, n = 17; t = 0.4, p = 0.7, df = 37). Significantly longer trills were produced after sunset, and males missed a significantly greater percentage of pulses after sunrise.

Flight-wing dimorphism

Data from laboratory males were used to determine if song structure varied with hind-wing dimorphism and are presented in Table 2. There were no significant differences between micropterous and macropterous male G. integer with respect to the different song parameters.

Phenotypic correlations

The correlation matrix of the various song parameters from data collected in the field (1986) and from the laboratory is presented in Table 3. Significant and positive correlations were found between intertrill interval and percentage of missed pulses, and significant negative correlations were
found between pulse rate and percentage of missed pulses and between number of pulses per trill and percentage of missed pulses in both the field and the laboratory. Significant negative correlations were found between intertrill interval and pulse rates in the field and between intertrill interval and number of pulses per trill in the laboratory.

**Discussion**

The calling song of male *G. integer* attracts females and results in spacing between males, but the song also attracts the parasitoid female fly *Ormia ochracea* (Cade 1975, 1979). There was much variation in the song parameters studied here, and this variation is comparable to that shown previously for *G. integer* (Smith and Cade 1987). The variation between laboratory- and field-recorded songs was similar. Only intertrill intervals differed between laboratory and field populations, with males having shorter intervals in the field. Males in field populations probably have reduced intervals because of acoustical interactions and competition from neighbors. In the laboratory, males were relatively isolated from the songs of other males.

Pulse rates increased with temperature in *G. integer*, and there was no difference in the rates of increase in laboratory and field populations. This relationship between pulse rate and temperature is well known in gryllids and other acoustical Orthoptera and was first demonstrated by Walker (1962). Walker found that the X-intercept was approximately 4°C in laboratory- and field-recorded songs was similar. Only temperature is well known in gryllids and other acoustical Orthoptera.

There was much variation in the song parameters studied here, and this variation is comparable to that shown previously for *G. integer*. In this study, intertrill intervals also varied inversely with temperature in the field, and similar findings have been reported in crickets with a chirping type of song (Doherty 1985; Doherty and Huber 1983). The percentage of missed pulses decreased with increasing temperature in both the field and laboratory. Missing pulses resulted in the interval between pulses being more irregular. Males singing at a faster rate therefore tend to produce songs with more regular intervals between pulses. Missing pulses may result from failure of the central pattern generator to fire or from the failure of the two forewings to engage properly. Various features of cricket song are thought to result from central pattern generators in the central nervous system (Bentley and Hoy 1974; Ewing and Hoyle 1965), and the firing of these generators may vary with temperature.

There was no variation in song structure with weight in this study of male *G. integer*. In male *Gryllus bimaculatus*, however, pulse rates and song intensities increase with body size, and females prefer to mate with larger males (Simmons 1988). Fighting success does vary with body size (Cade and Cade 1992). Fighting success does vary with body size in *G. integer*, and large males win many more fights than small competitors (Dixon and Cade 1986). Small

### Table 1. Linear regressions (r-values, F-statistic, and significance level) of temperature in the field and the laboratory, and age and weight of male *G. integer* in the laboratory, against parameters of song structure

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Temperature Field</th>
<th>Temperature Laboratory</th>
<th>Male Age</th>
<th>Male Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pulse rate</td>
<td>0.8 (40.4)</td>
<td>0.8 (49.6)</td>
<td>0.3 (3.7)</td>
<td>-0.2 (0.8)</td>
</tr>
<tr>
<td>No. of pulses/trill</td>
<td>0.2 (1.1)</td>
<td>0.3 (3.6)</td>
<td>-0.3 (3.5)</td>
<td>0.3 (2.5)</td>
</tr>
<tr>
<td>Intertrill interval</td>
<td>-0.5 (8.6)</td>
<td>-0.1 (0.4)</td>
<td>0.1 (2.0)</td>
<td>-0.3 (3.4)</td>
</tr>
<tr>
<td>% of missed pulses</td>
<td>-0.4 (5.1)</td>
<td>-0.5 (10.1)</td>
<td>0.3 (2.2)</td>
<td>0.3 (2.4)</td>
</tr>
</tbody>
</table>

**Note:** n = 33 males in each category.

### Table 2. Comparison of parameters of male *G. integer* song (means, standard deviations, t-values, and significance levels) at different times of activity in the field, and for males with varying hind-wing length in the laboratory

<table>
<thead>
<tr>
<th>Parameter</th>
<th>n</th>
<th>Pulse rate mean ± SD</th>
<th>No. of pulses/trill mean ± SD</th>
<th>Intertrill interval mean ± SD</th>
<th>% of missed pulses mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period of activity</td>
<td></td>
<td>X ± SD</td>
<td>X ± SD</td>
<td>X ± SD</td>
<td>X ± SD</td>
</tr>
<tr>
<td>20:00–02:00</td>
<td>22</td>
<td>90.8±6.4</td>
<td>60.8±29.2</td>
<td>119.8±36.8</td>
<td>2.5±4.0</td>
</tr>
<tr>
<td>05:00–10:30</td>
<td>17</td>
<td>87.9±8.8</td>
<td>43.0±22.2</td>
<td>139.7±28.5</td>
<td>9.5±3.7</td>
</tr>
<tr>
<td>Hing-wing length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macropterous</td>
<td>20</td>
<td>69.1±6.7</td>
<td>34.5±13.7</td>
<td>267.8±79.9</td>
<td>7.0±5.2</td>
</tr>
<tr>
<td>Micropterous</td>
<td>13</td>
<td>71.9±4.1</td>
<td>34.7±16.5</td>
<td>275.3±81.4</td>
<td>6.2±4.9</td>
</tr>
</tbody>
</table>

### Table 3. Pearson product moment correlation coefficients matrix for the four song structure parameters for the 1986 field data (top value) and the laboratory data (bottom value)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>% missing pulses</th>
<th>Intertrill interval</th>
<th>No. of pulses per trill</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pulse rate</td>
<td>-0.50*</td>
<td>-0.49*</td>
<td>0.20</td>
</tr>
<tr>
<td>No. of pulses per trill</td>
<td>-0.49*</td>
<td>-0.17</td>
<td>0.23</td>
</tr>
<tr>
<td>Intertrill interval</td>
<td>-0.39*</td>
<td>-0.33</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.58*</td>
<td>-0.59*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.54*</td>
<td>0.42*</td>
<td></td>
</tr>
</tbody>
</table>

*p < 0.05 (F-test).*
male *G. integer* initiate fights as readily as large males, which suggests that males do not assess an opponent’s body size before fighting. In any case the parameters studied here do not convey information on the body size of competing males.

The number of calling *G. integer* increases greatly before sunrise and declines a few hours later. The time of increased calling corresponds to greatly increased mating frequency and a decrease in long-range phonotaxis of female *G. integer*. Females attracted during the previous night are often found very close to calling males at dawn, and calling at this time may function as a stimulus for females to mate rather than to attract mates from a distance (Cade 1979; French and Cade 1987). Our data demonstrate that males produced longer trills and had lower frequencies of missed pulses during the night than during the dawn. Longer trills and fewer missed pulses should reflect increased expenditure of energy on the part of males at night and may lead to increased rates of female phonotaxis. If so, males may reduce their trill lengths and drop more pulses from their trills when females are nearby, and long-range phonotaxis of females is reduced or absent. Female *G. integer* from California show increased phonotaxis to males producing longer bouts of song (Hedrick 1986), and female *G. bimaculatus* are attracted more readily to songs with evenly spaced pulses (Doherty 1985). No information is available on phonotaxis of female Texas *G. integer* to songs with varying trill lengths or missed pulses.

Zuk (1987) demonstrated that female *Gryllus veletis* and *Gryllus pennsylvanicus* are attracted more readily to older conspecific males, but that the total duration of calling per night does not vary with age in these species (see also Cade and Wyatt 1984). The cues used by female *G. veletis* and *G. pennsylvanicus* to identify older males are not known, but may involve variations in song structure. In this study there was no variation in song structure associated with relative age of male *G. integer*. It is not known if female *G. integer* from Texas or California are attracted preferentially to older males. Our data demonstrate, however, that females receive no information from the song parameters studied here that allows them to assess relative age differences between males, at least in the laboratory. Hedrick (1986) also found that trill length did not vary with age in California *G. integer*.

Female crickets might also pick mates on the basis of flight-wing dimorphisms. Although no data are available on female choice based on wing dimorphism in field crickets, wing dimorphism is heritable, and long-winged flying field crickets are able to colonize new habitats, so mate choice based on wing dimorphism might benefit females (Walker and Sivinski 1986; Zera and Rankin 1989). In any case there was no variation in song structure with wing morphology in *G. integer*, so females cannot use song to identify males according to wing length.

The overall similarity in song structure between field and laboratory populations, despite major differences between these two environments, suggests that environmental sources of variation may be relatively unimportant compared with genetic variation. In this connection Hedrick (1988) demonstrated that bout lengths in *G. integer* from California have narrow-sense heritabilities of approximately 74%. There is underlying additive genetic variation in nightly calling duration in Texas *G. integer* (Cade 1981), but nothing is known about the heritabilities of the song structures studied here. If song structures are heritable in Texas *G. integer*, then the phenotypic correlations between many of the variables may arise from the sharing of genes responsible for these song features. Information is needed on the heritability of song structure and the incidence of phonotaxis of females to songs of varying pulse rates, trill lengths, intertrill intervals and missed pulses in *G. integer*.

**Acknowledgements**

This research was supported by the Natural Sciences and Engineering Research Council of Canada (grants to W.H.C.) and by a Brock University fellowship (G.R.). The laboratory data were part of an honours thesis submitted in partial fulfillment of the B.Sc. degree (K.S.). A. M. Murray commented on the manuscript. The DSP was designed and built by J. Ross, J. Rustenburg, T. MacDonald, A. Struyk, and G. McDonnell, Department of Technical Services, Brock University. J. Crutchfield and L. Gilbert provided access to the Brackenridge Field Laboratory, University of Texas at Austin.


