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STRIDULATION OF *GRYLLOTALPA AFRICANA* (ORTHOPTERA: GRYLLOTALPIDAE) ON TURF GRASS IN SOUTH AFRICA

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ABSTRACT

During spring to autumn, *Gryllotalpa africana* males stridulate and produce phonotactic calling songs from specially constructed acoustical burrows. Songs start just after dusk and continue for several hours. The characteristics of the trilling song and sound pressure levels produced were investigated by near field digital recordings made during autumn 2002 and spring 2002 with soil temperatures noted by measuring sound pressures beyond the near field with a sound level meter in spring 2002, respectively. The carrier frequency (2.161-2.477 kHz) and syllable duration (7.340-12.078 ms) of calls showed no significant relationship with soil temperature and no significant differences between autumn and spring with soil temperature constant. Syllable period (10.455-17.221 ms) and inter syllable interval (1.912-9.607 ms) were significantly negatively correlated with soil temperature, and with the latter constant, significantly longer in spring than in autumn. The syllable repetition rate (0.058-0.096 syllables/ms) and duty cycle (43.31-81.72%) showed a significant positive relationship with soil temperature and significant decrease in values with soil temperature constant in spring relative to autumn. Sound pressure levels (re. 20 µPa) at 200 mm from the burrow varied from 77.6 to 89.8 dB.

Key Words: male song characters, seasonal variance, soil temperature, sound pressure level, turf grass

RESUMEN

Desde la primavera hasta el otoño, los machos de *Gryllotalpa africana* vibran (producen canciones de llamado fonotacticos) de madrigueras acústicas construidas especialmente. Las canciones empiezan un poco después del atardecer y continuan por varias horas. Las características de las canciones vibradas y los niveles de presión del sonido producido fueron investigados por medio de grabaciones digitales en un campo cercano durante el otoño de 2002 y la primavera de 2002 (con la temperatura del suelo anotada) por medio de la medida de la presión de los sonidos (mas alla del campo cercano) con un medidor de nivel de sonido en la primavera de 2002, respectivamente. La frecuencia aportada (2.161-2.477 kHz) y la duración de la sílaba (7.340-12.078 ms) de las llamadas no mostraron una relación significativa con la temperatura del suelo y ningún diferencia significativa entre el otoño y la primavera (con la temperatura del suelo constante). El período de sílaba (10.455-17.221 ms) y el intervalo entre las sílabas (1.912-9.607 ms) fueron negativamente significativas correlacionadas con la temperatura del suelo, y con la constante última, significativamente mas largo en la primavera que en el otoño. La tasa de repetición de sílaba (0.058-0.096 sílabas/ms) y el ciclo obligatorio (43.31-81.72%) mostraron una relación positiva significativa con la temperatura del suelo y una diminución significativa en valores (con la temperatura del suelo constante) en la primavera (en relativa al otoño). Los niveles de la presión del sonido (re. 20 µPa) a 200 mm de la madriguera varian de 77.6 a 89.8 dB.

Numerous insect species produce stereotyped acoustic signals that are important in intraspecific communication (Kavanagh 1987). In most species that communicate by sound, the male's calling song, which appears to attract conspecific females, is the most obvious and imperative component of the repertoire (Kavanagh 1987).

Male African mole crickets differ morphologically from females by having a pair of large cells (anterior of which is the harp) on each forewing, known as the stridulatory area (Townsend 1983) (Figs. 1 and 2). Males usually stridulate at night, using the entrance of borrows as sound amplifiers (De Villiers 1985). Singing position of *Gryllotalpa* sp. appears to be very similar, although acoustic burrows may have two (*G. vineae*, *G. gryllotalpa*, and *G. africana*) (Bennet-Clarke 1970a; Brandenburg et al., 2002) to four horn-shaped openings (*G. australis*) (Kavanagh & Young 1989). The division between openings may collapse over time, producing fewer openings (Bennet-Clarke 1970a & Kavanagh and Young 1989).

Variation between temporally segregated songs of chirping and trilling mole crickets may

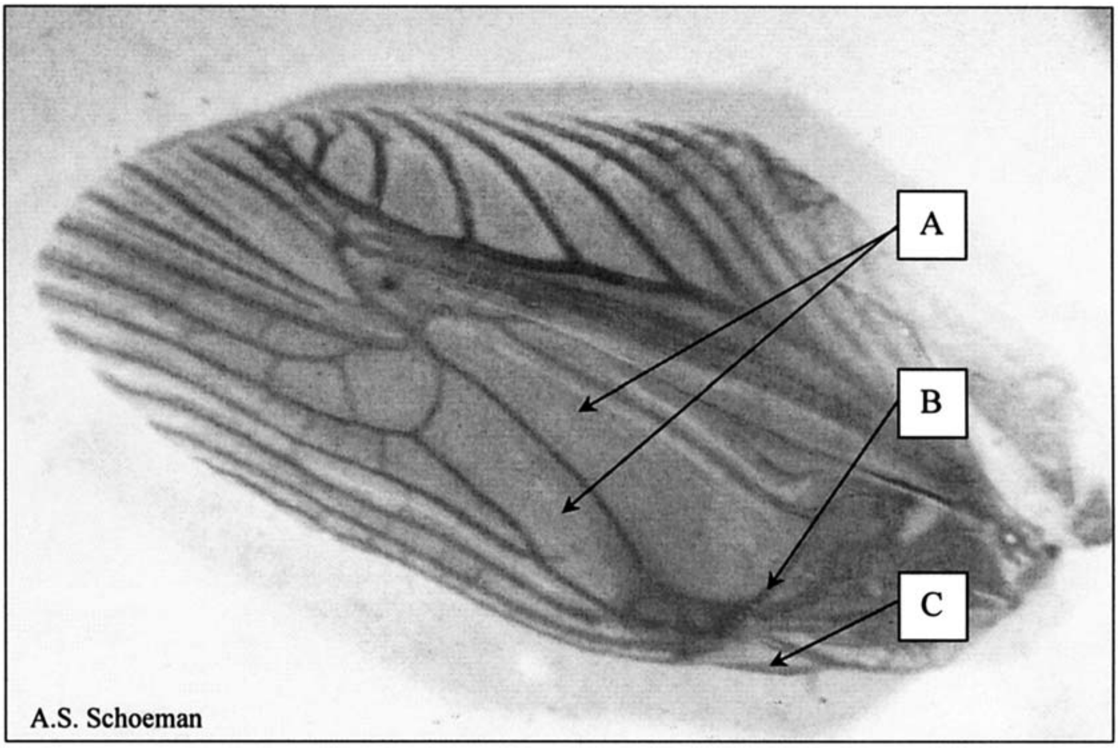

Fig. 1. Ventral view of right male tegmen, showing stridulatory area. A = Stridulatory area, B = File (pars stridens) and C = Scraper (plectrum).

be caused by environmental factor dependence. Chirp rate and syllable or pulse repetition rate in crickets and mole crickets increase linearly with soil temperature over an intermediate temperature range (Bennet-Clark 1970a; Bennet-Clarke 1989; Kavanagh & Young 1989; Doherty & Callos 1991; Ciceran et al. 1994; Hill 1998, 2000). Inter syllable interval is usually negatively correlated with temperature in the Gryllotalpinae and carrier frequency appears to be temperature independent in mole crickets (Bennet-Clark 1989). In the Oecanthinae (Gryllidae), however, the carrier frequency is positively correlated to temperature, but with a smaller slope than for syllable rate (Bennet-Clarke 1989). Walker (1962) also reported carrier frequency to be a regression function of air temperature at low and moderate temperatures for crickets in three genera and three subfamilies. Another potential factor contributing to variation may be physiological, such as size, condition etc. In the Gryllidae, song structure does not, however, appear to vary with male mass or age (Souroukis et al. 1992; Ciceran et al. 1994). In trilling *Gryllotalpa*, the song differences appear to be of fundamental frequency (Bennet-Clark 1970a), while in gryllids, the interval between syllables may be more important (Walker 1962). Male song characteristics in mole crickets are species specific (Bennet-Clark 1970a; Bennet-Clark 1970b; Otte & Alexander 1983; Nickle & Castner 1984; Kavanagh & Young 1989; Walker & Figg 1990; Broza et al. 1998) and provide a key to determine the validity of reports of *G. africana* occurrence.

Sound pressure levels measured just beyond the near field (15-20 cm in line with the burrow, re. 20 µPa) may vary from 65 to 97 dB between trilling mole cricket species, with highest intraspecific sound pressure level variation of 67 to 91 dB (Ulagaraj 1976; Forrest 1983; Bennet-Clarke 1987; Kavanagh & Young 1989; Walker & Forrest 1989). Song intensity of trilling species is positively correlated to male size and usually to temperature, rainfall, and soil moisture (Bennet-Clarke 1970a; Ulagaraj 1976; Forrest 1980; Forrest 1983; Forrest 1991).

Some song characteristics reported for the African mole cricket include a phonotaxis study by Kim (1993) in Hwaseong-gun, Kyonggi-do Korea, who found intensities of calling songs vary between 77 and 80 dB at 150 mm above the openings of calling chambers. The study of Kim (1993) probably does not refer to the "true" *G. africana*. Other song characters of *G. africana* are based on four recordings (Townsend 1983) and vary between reports (Nickle & Castner 1984). Calling

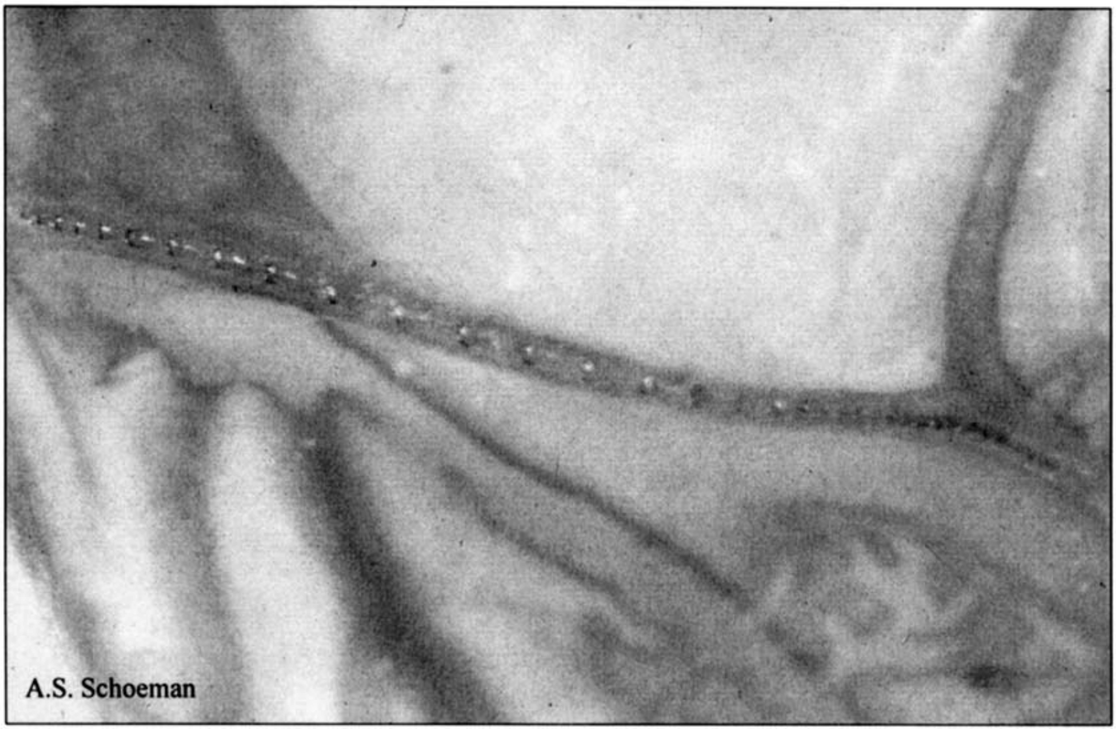

Fig. 2. Ventral view of male tegmen, showing stridulatory teeth arrangement on the file or pars stridens of *G. africana*.

song intensities of *G. africana* from Africa have not been measured.

Materials and Methods

Field recordings (n = 20) of the calling song of *G. africana* males chosen at random but not overlapping were made in a kikuyu grass area of approximately 300 m^2 between and surrounding the putting green and green no. 18 at the Pretoria Country Club from March 2002 to April 2002. Soil temperatures were measured at a vertical depth of 100 mm in the soil profile immediately after recordings were made. Recordings were made between 19h30 and 21h15, local time (GMT + 2 hours). Due to the relative homogeneity including irrigation program, turf grass and soil of the experimental area and relatively short temporal measurement period, soil moisture was assumed to be constant. During October 2002 and November 2002, 20 stridulating males were recorded according to a similar methodology, but at a nearby site comprising a kikuyu grass area (300 m^2) between and surrounding the chipping and bowling green at Pretoria Country Club with a similar irrigation program than the previous site. Recordings between and within the two periods were assumed to be of different males, as no recording sites overlapped. The calls were recorded with a Nomad DAP-3201 digital recorder (Creative Technology Ltd.), with the self-contained microphone held 50 mm from the burrow opening, longitudinal to the long axis of the burrow. Recording distance was within the near field, or distance covered by one wavelength at the carrier frequency of this call (s/2300 cycles × 343 m/s at 20°C = 149.13 mm) (Hill 2000).

All the recordings were analyzed with the computer software program "Canary" V1.2.4 (Cornell Laboratory of Ornithology 1998). A power spectrum (Fig. 3) and oscillogram (Fig. 4) were used to measure three different call characteristics for nine syllables (three successive syllables randomly selected at the beginning, middle and end of each recording, respectively) per recording: Carrier frequency (Fig. 3), syllable duration (Fig. 4) and syllable period (Fig. 4). The inter syllable interval (syllable period – syllable duration), mean syllable repetition rate (inverse of syllable period), and duty cycle ((syllable duration/syllable period) × 100) were calculated from the measured parameters.

The sound pressure level of 20 different calling males which were all assumed to be *G. africana* was also measured according to the methodology for each recording, but at a distance of 200 mm beyond the near field from the burrow opening and longitudinal to the long axis on a night between

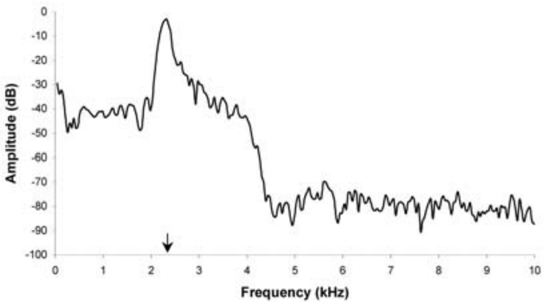

Fig. 3. The power spectrum of a field recorded *G. africana* call (up to 10 kHz), indicating a carrier frequency of approximately 2.3 kHz.

20h00 and 20h30, local time (GMT + 2 hours) in late November 2002. A kikuyu grass area of approximately 300 m^2 including and surrounding of the first tee at Pretoria Country Club was used for measurements. The area sampled had an irrigation program similar to the previous recording sites. Sound level measurements were made with a precision integrating sound level meter (Rion Type NL-14), calibrated by a Rion Type NC-73 sound level calibrator. The equipment was within annual calibration. The sound level meter was used in L_{Aeq} mode, which records the time-weighted average of a series of fast root mean square (RMS) recordings (time constant 125 ms). This gave the A-weighted sound pressure level (dB A scale) (at re. 20 µPa) that was the equivalent continuous level as the fluctuating signal being recorded. A period of approximately 20 s was sufficient to provide a stable level for *G. africana*.

Results

The relationship of call characteristics measured in autumn (March/April) and spring (October/November) of 2002 with soil temperature at 100 mm in the soil profile is represented in Table 1. Soil temperature ranged from 20.7°C to 24.8°C (23.2 ± 1.24°C, mean ± SD) in March/April 2002 recordings and 22.3°C to 26.8°C (23.5 ± 1.16°C, mean ± SD) in October/November 2002 recordings. The data of all the sound characters except syllable period fitted a normal distribution (Kolmogorov-Smirnov test, $P > 0.05$, "Statistica" Version: 5, Statsoft, Inc., 1995) without transformation (Sokal & Rohlf 1997). The syllable period data for both sampling periods was not significantly different from a normal distribution only

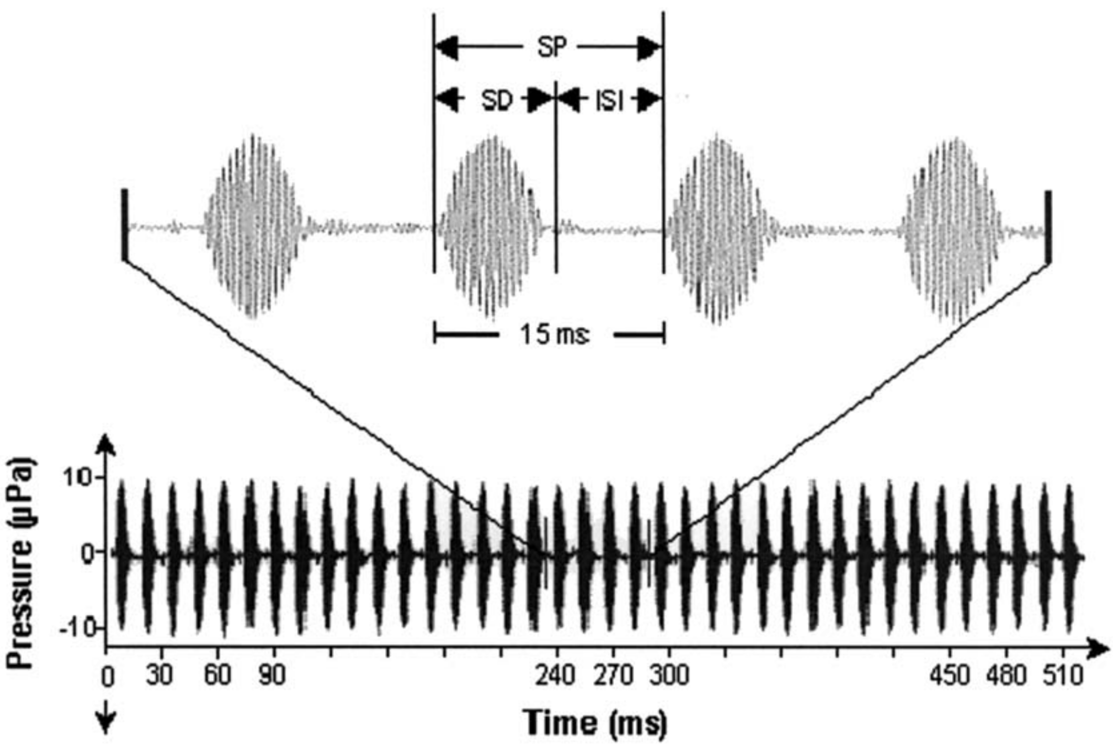

Fig. 4. Oscillogram of a field recorded *G. africana* trilling call over 510 ms. The thickened red lines indicate an approximate eight times shorter temporal scale with the different measurements made. SD = Syllable duration, ISI = Inter syllable interval and SP = Syllable period.

after logarithmic transformation (Sokal & Rohlf 1997) (Kolmogorov-Smirnov test, $P > 0.05$, "Statistica" Version: 5, Statsoft, Inc., 1995).

The multiple regression parametric test ("Statistica" Version: 5, Statsoft, Inc., 1995) showed a highly significant relationship of syllable period, inter syllable interval, syllable repetition rate and duty cycle with soil temperature for both recording periods (Table 1). Carrier frequency variation of *G. africana* males was not significantly related to the tested temperature range. The results show a negative relationship between syllable period and soil temperature for both sampling periods after data were transformed to linear scale before presentation, with soil temperature constantly explaining more than 80% of the variation in the former. The rate of decline in the syllable period was slightly higher in the spring recordings. The syllable duration had no significant relationship with soil temperature. Inter syllable interval was negatively correlated with soil temperature, with R^2 values under 0.50. The rate of decline, however, was slightly higher for the spring recordings relative to those in autumn. The syllable repetition rate was positively related to soil temperature during spring and autumn. In the latter season recordings, the rate of syllable increase was lower than during the spring recordings over a similar range of soil temperatures. Soil temperature was a relatively good predictor (R^2 approximately 0.80) of syllable repetition rate in both recording periods. The duty cycle increased significantly with soil temperature, but with relatively low R^2 values, during both recording periods, respectively. The rate of increase with soil temperature was higher in spring relative to autumn values. Slopes of regression lines should be compared with caution, as they are dependant on the measurement scale.

The values for the different measured and calculated sound characteristics at variable soil temperatures and differences between autumn 2002 and spring 2002 recordings with soil temperature constant are summarized in Table 2. Only syllable repetition rate needed to be arcsine-transformed (Sokal & Rohlf 1997) for all the dependant variables to be normally distributed (Kolmogorov-Smirnov test, $P > 0.05$, "Statistica" Version: 5, Statsoft, Inc., 1995). A multi analysis of variance (MANCOVA, parametric test, Sokal & Rohlf 1997, "Statistica" Version: 5, Statsoft, Inc., 1995), with soil temperature entered as a covariate, was used to determine significant song character differences between the two temporally segregated field recordings.

The results showed that the carrier frequency of *G. africana* males was constant between autumn and spring at approximately 2340 cycles per second (Table 2). The power spectrum (Fig. 3, representative for most songs) graphically represents the carrier frequency and shows a low frequency component and no clear harmonics for *G. africana* males. The spectrogram (Fig. 5) of a general sound recording shows the sound structure during and between syllables. Fig. 5 shows the low frequency observed in the power spectrum was also present between syllables and therefore when no mole cricket sound was produced (Fig. 5).

Syllable duration did not vary significantly between seasons and was usually just longer than nine milli-seconds (Table 2). The syllable period,

TABLE 1. RELATIONSHIP BETWEEN MALE *G. AFRICANA* SONG CHARACTERS AND SOIL TEMPERATURES OF 23.2 ± 1.24°C (MEAN ± SD) AND 23.5 ± 1.16°C (MEAN ± SD) AT A VERTICAL DEPTH OF 100 MM PROFILE IN THE SOIL FOR MARCH/APRIL 2002 (RECORDING 1) AND OCTOBER/NOVEMBER 2002 (RECORDING 2), RESPECTIVELY, AT PRETORIA COUNTRY CLUB.

Data		Regression variable				
Song character	Recording	Slope	Intercept	R^2	*F*	*P*
Carrier frequency (kHz)	1	0.001	2.310	0.0004	0.019	0.891
	2	-0.009	2.569	0.0228	0.931	0.340
Syllable period (ms)	1[2]	-1.067	63.826	0.8092	195.174	0.0000001
	2[2]	-1.127	41.089	0.8139	174.960	0.0000001
Syllable duration (ms)	1	-0.079	11.104	0.0118	0.552	0.461
	2	-0.198	13.702	0.0412	1.7205	0.197
Inter syllable interval (ms)	1[2]	-0.874	25.395	0.4521	37.968	0.0000001
	2[2]	-0.929	27.387	0.3913	25.712	0.000009
Syllable repetition rate (Syllable ms^{-1})	1[2]	0.004	-0.031	0.7926	175.781	0.0000001
	2[2]	0.007	-0.084	0.8406	210.990	0.0000001
Duty cycle (%)	1[2]	3.485	-15.920	0.2755	17.495	0.000128
	2[2]	4.245	-37.130	0.2581	13.915	0.000593

[1]$P < 0.05$.
[2]$P < 0.001$.

TABLE 2. VALUES OF MALE *G. AFRICANA* SONG CHARACTERISTICS RECORDED AT PRETORIA COUNTRY CLUB AT SOIL TEMPERATURES OF 23.2 ± 1.24°C (MEAN ± SD) AND 23.5 ± 1.16°C (MEAN ± SD) AT A VERTICAL DEPTH OF 100 MM IN THE SOIL FOR MARCH/APRIL 2002 (RECORDING 1) AND OCTOBER/NOVEMBER 2002 (RECORDING 2), RESPECTIVELY. SIGNIFICANT DIFFERENCES BETWEEN RECORDINGS WITH SOIL TEMPERATURES CONSTANT ARE SHOWN.

Data		Value		MANCOVA variable	
Song character (Unit)	Recording	Range	Mean ± SD	*F*	*P*
Carrier frequency (kHz)	1	2.198-2.476	2.34 ± 0.067	0.096	0.757
	2	2.161-2.477	2.34 ± 0.075		
Syllable period (ms)[2]	1	12.031-17.061	14.3 ± 1.09	21.226	0.00001
	2	10.455-17.221	14.6 ± 1.45		
Syllable duration (ms)	1	7.340-10.959	9.3 ± 0.91	1.826	0.180
	2	7.372-12.078	9.1 ± 1.13		
Inter syllable interval (ms)[1]	1	2.979-9.607	5.1 ± 1.62	11.548	0.00104
	2	1.912-7.779	5.6 ± 1.72		
Syllable repetition rate (Syllable ms^{-1})[2]	1	0.059-0.083	0.070 ± 0.0061	14.724	0.00024
	2	0.058-0.096	0.069 ± 0.0082		
Duty cycle (%)[1]	1	43.31-78.15	64.9 ± 8.25	7.276	0.00845
	2	48.66-81.72	62.44 ± 0.097		

[1]$P < 0.05$.
[2]$P < 0.001$.

inter syllable interval, syllable repetition rate and duty cycle were significantly different, with soil temperature constant, between the autumn and spring recordings. The syllable period and inter syllable interval were significantly longer and the syllable repetition rate and duty cycle significantly shorter in spring than in autumn, respectively.

During the spring recordings, one individual was recorded at a soil temperature of 21.9°C with the following sound characters (mean ± SD): carrier frequency: 2.638 ± 0.0068 kHz, syllable period: 17.89 ± 0.085 ms, syllable duration: 7.9 ± 0.30 ms. Inter syllable interval, syllable repetition rate, and duty cycle was calculated as (mean ± SD) 10.00 ± 0.217 ms, 0.0559 ± 0.00026 syllables/ms and 44.1 ± 1.47%, respectively.

The sound pressure levels (re. 20 µPa) of *G. africana* varied from 77.6 to 89.8 dB at 200 mm from the burrow. The ambient - and soil temperature (average of five measurements) at the onset of the experiment were 21.5 ± 0.30°C and 23.24 ± 0.112°C, respectively. At the end of the experiment, ambient - and soil temperatures (average of five measurements) were 21.15 ± 0.263°C and 23.03 ± 0.217°C.

DISCUSSION

Gryllotalpa africana males constructed acoustical burrows with one or two horn-shaped openings observed. Two openings may initially have been constructed, but one opening may have collapsed over time. Male African mole crickets started calling just after sunset and, especially during the warm summer months, called until midnight, attracting flying conspecifics and even walking nymphs. Calling activity was generally limited to soil temperatures exceeding 14°C during late August to late May, when conspecifics flew. Initial calling was characterized by a distinctive warm up period. The sound matured from the initial slow erratic trill to a constant trilling call. Some male callers exploited microclimatical conditions near brick walls and concrete slabs. These spatial orientations, which artificially increased soil temperatures, were especially utilized during times of relatively low soil temperatures. Males called singularly, but were usually observed in calling groups as individuals separated by a few meters during stridulation.

Males randomly selected from the field in spring and autumn and acclimatized for one week at L:D 12 h:12 h, which was a relative shorter daily light cycle, and 28 ± 1°C, did not call in the laboratory, suggesting photoperiod as a factor contributing to stridulation activity. This observation may have been biased by the fact that mole crickets were kept in containers, which have been found to influence their behavior (Walker 1979 & Hudson 1988).

Songs of *G. africana* males were produced at sound pressure levels of 77.6 to 89.8 dB and characterized by a carrier frequency of approximately 2.34 kHz with some variation between males. The latter did not vary significantly between autumn and spring and with soil temperature. If the song had a low frequency component, it could not be distin-

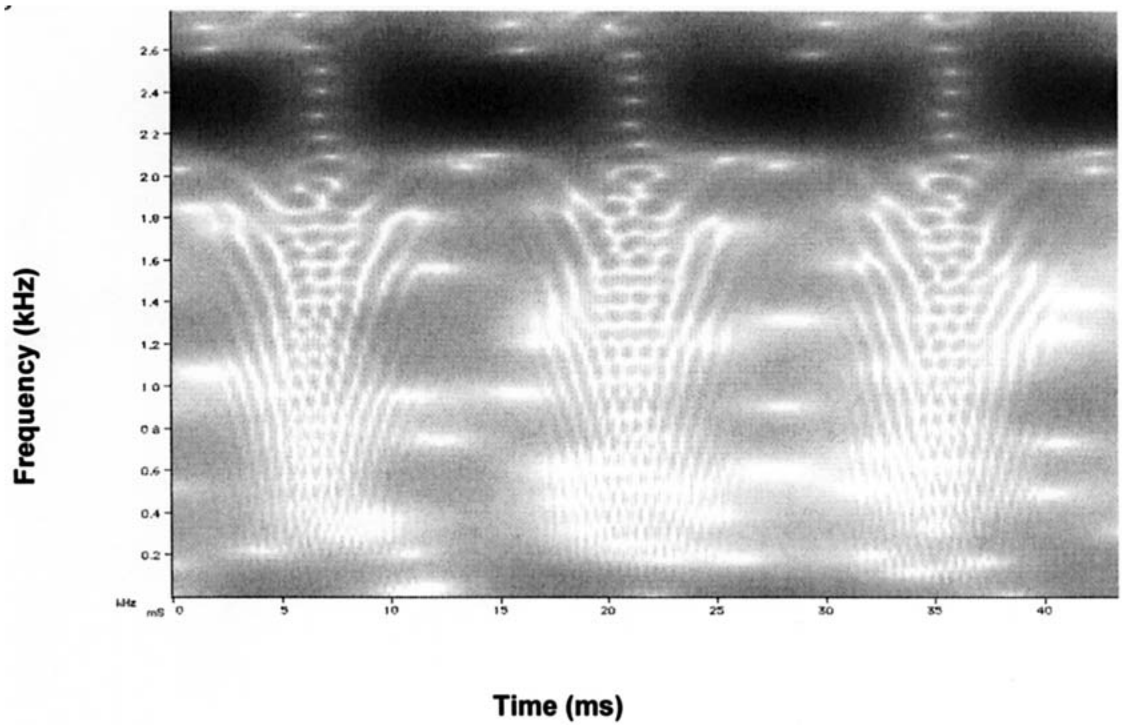

Fig. 5. The spectrogram presenting two complete syllables of a field recorded *G. africana* call (up to approximately 2.7 kHz).

guished from background noise in the current study. Harmonics, which were generally not clearly visible, are usually at a relatively low level in the family (Bennet-Clark 1987). African mole cricket males usually stopped calling, usually less than one minute, when the burrow opening was approached within a one meter radius (personal observation), and the mole cricket was deemed to show some seismic sensitivity. Males in full song were usually less sensitive. Trilling species are generally not very sensitive to substrate vibrations (Bennet-Clarke 1970a; Forrest 1991), although Bennet-Clark (1970a) reported *G. gryllotalpa* to be highly sensitive. Sensitivity may be related to sound pressure level, which may saturate mechano-receptors at high intensities (Bennet-Clark 1970a).

The syllable duration of male *G. africana* calls did not vary significantly between autumn and spring nor with soil temperature, but did show some variation between males. Syllable period was negatively related with soil temperature and varied significantly with soil temperature constant between autumn and spring. Additional sound characters calculated from the syllable period or syllable period and syllable duration, reflected their relationships with the tendencies of the measured variables.

Townsend (1983) reported a mean syllable repetition rate of 49.1-57.8 per second and a mean carrier frequency of 2.1-2.4 kHz for the calling song of *G. africana* based on four recordings. No temperature values or other variables were annotated during these recordings. The calling song frequency of *G. africana* reported from Hawaii is 3.3 kHz, with a syllable repetition rate of 56 per second (Nickle & Castner 1984). Although syllable repetition rates were similar between the two reports, it is not comparable without any temperature information. The carrier frequency values of the present study correspond with that reported by Townsend (1983). Differences in calling song carrier frequency have been used to distinguish between *Gryllotalpa* species (Bennet-Clark 1970b; Nevo & Blondheim 1972). These stridulatory character differences support reports that the Hawaiian species is in fact not *G. africana*. Frank et al. (1998) also stated that the immigrant mole cricket to Hawaii was misidentified as *Gryllotalpa africana*. According to Frank et al. (1998), the species occurring in Hawaii is *G. orientalis*, a species originating from Asia, not Africa.

It appears that a mole cricket species, other than *G. africana*, also inhabited Pretoria Country Club in spring 2002. The distinction of the species was in its higher carrier frequency values. *Gryllotalpa robusta* has a carrier frequency of 1.6 kHz, based on one recording, and *G. parva* has a carrier frequency of 2.9-3.3 kHz, based on two recordings

(Townsend 1983). Hence, the carrier frequency of the unidentified species does not correspond to known values of species occurring in South Africa.

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