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FACTORS AFFECTING CALLING BEHAVIOUR IN FIELD CRICKETS, TELEOGRYLLUS AND GRYLLUS (AGE, WEIGHT, DENSITY, AND PARASITES)

by

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(With 4 Figures)
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Introduction

The calling of male field crickets (Orthoptera; Gryllidae) attracts females and repels other calling males. Calling males may attract non-calling males, however, which physically attack the caller, or which remain nearby and intercept attracted females. Male-male aggression and other factors influence male calling behaviour (ALEXANDER, 1975; CADE, 1979; BOAKE, 1983; BURK, 1983). This paper reports on some of the factors affecting the amount of calling in 4 species of field crickets, *G. integer* (this species is under taxonomic revision, ALEXANDER & CADE, in prep.), *G. pennsylvanicus*, *G. veletis*, and *Teleogryllus africanus*.

Age affects the amount of signaling in some vertebrates. In the bullfrog, *Rana catesbeiana*, the most regularly calling males are the oldest in the population (HOWARD, 1978). Increased male signaling with age is expected if older males are better at defending signaling sites, and if reproductive effort increases due to declining residual reproductive value (WILLIAMS, 1966). The amount of nightly calling with adult age was studied in the 4 species in the laboratory and in *G. integer* in a large outdoor arena to test the prediction that calling duration increases with age.

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Since some field crickets call only when they have a spermatophore in the spermatophoric pouch (HUBER, 1962), the age at which males first produce spermatophores was determined in the 4 species and compared to the age at which males first called.

Size or weight also may affect signaling behaviour, as in *R. catesbeiana* where the largest males call the most frequently (HOWARD, 1978). Increased calling with size is expected if large size enables males to defend signaling sites more effectively. Large size may also correspond to a good level of health and/or nutrition which leads to increased calling behaviour. Calling duration of individual males of varying weights were determined for the 4 species in the laboratory and for *G. integer* in the outdoor arena to test the prediction that large males call more than smaller conspecifics.

Increased fighting over a limited number of signaling sites should result in reduced male calling (ALEXANDER, 1961). Decreased calling in high density populations of *G. integer* has been reported (CADE, 1979), but no quantitative data are available on the effects of density on calling in crickets. Calling by male *G. integer* at different levels of male density was studied in the outdoor arena to test the prediction that calling duration declines with the number of males.

Attraction of acoustically orienting predators or parasites may also influence calling in crickets. Calling *G. integer* attract and are parasitized by flies, *Euphasiopteryx ochracea* (Diptera; Tachinidae). Parasitized crickets die, and flies may be a selective force against calling in *G. integer*. Satellite males are routinely observed in *G. integer* populations, and remain silent or call irregularly in the vicinity of regularly calling males (CADE, 1975, 1979). *G. veletis*, *G. pennsylvanicus*, and *T. africanus* are apparently not parasitized by acoustically orienting flies, and satellite males are observed much less frequently than in *G. integer* (CADE, unpublished). It is predicted that male *G. pennsylvanicus*, *G. veletis*, and *T. africanus* call more on average and are less variable in their calling behaviour than *G. integer*. The duration and variability of nightly calling in the laboratory is compared among the 4 species to test this prediction.

This and other studies on calling behaviour in crickets present data from laboratory observations. The duration and variability of nightly calling in laboratory and arena populations of *G. integer* are compared to measure the effects of the laboratory environment. It is predicted that male *G. integer* in the controlled conditions of the laboratory call more on average and are less variable in their calling behaviour than males under field conditions.

Methods of study

This study was carried out in St. Catharines, Ontario, Canada, from March 1979 to July 1982. All species except *G. pennsylvanicus* (see below) were raised in the laboratory from adults collected in the following locations: *G. veletis* in St. Catharines; *G. integer* in San Antonio, Texas, U.S.A.; and *T. africanus* in Eshowe, Zululand, Republic of South Africa. Unless otherwise noted, all crickets used in this study were from the first laboratory generation for each species. Cultures were maintained at 30-32°C, and on a 12:12 hr light and dark cycle. Ample food (Purina Cat Chow and lettuce) and water were provided. *G. pennsylvanicus* requires an egg diapause (ALEXANDER, 1968) and is therefore more difficult to raise in cultures than the other non-diapausing species. Late instar nymphs of *G. pennsylvanicus* were collected in St. Catharines in the early summer and raised to maturity under the same conditions as the other species.

The duration of nightly calling in each species was studied by electronically monitoring the calling songs of males kept in individual glass jars (4.2 l). Each jar was covered with a paper top, and food, a water vial, and cardboard shelter were placed inside. Jars were placed from 0.5 to 1 m apart in the laboratory. This distance corresponds to the minimum distance separating calling males in all species in the field (CADE, 1979, 1981a; unpublished). Crystalline microphones were placed inside jars and were connected to either individual sound activated relays which caused a 24 hr clock to operate when a male called, or to a specially designed microprocessor which was programmed to measure the amount of time crickets call. The microprocessor transferred data to a teletype. Both the relays and the microprocessor are sensitive to sounds at 4.5-6.0 KHz, and a minimum sound intensity of 50 dB SPL. This range of frequencies and sound intensity is characteristic of the species studied here (ALEXANDER, 1962; CADE, 1979, unpublished). Preliminary studies were conducted with *G. integer* in jars lined with foam rubber. In these containers which did not have the echoic properties of glass, male calling durations were no different than those of males kept in unlined glass jars. Also, the sound relays and microprocessor produced practically identical results when both devices were used to monitor the same males in preliminary trials (CADE, unpublished).

Adult males were removed from laboratory cultures on the day of their final molt. Each male was placed in a sound monitored jar and the total calling time was recorded every 24 hrs until a male was 17 to 45 days of adult age. Sound monitoring was performed under a 12:12 hr light/dark cycle and at 19-26°C. All species studied occur in areas which have temperatures within this range at night (CADE, unpublished). Each species was studied separately to avoid any effect which heterospecific song may have on calling. To provide a constant acoustical environment in the laboratory, the tape recorded song of the species under study was broadcast for 6 continuous hrs, beginning 3 hrs in the dark period. A Sony TC 105 tape recorder, tape loop, and Realistic 40-1228 loudspeakers were used. The sound intensity of broadcast songs was measured using a General Radio 1465B sound level meter. Song intensities of the broadcast song varied from 40 to 65 dB SPL (A scale; 4-10 kHz) in different areas of the room. The intensity of taped song was always below 40 dB inside the jars such that the signal did not activate song monitoring devices. Song broadcasting was discontinued once several crickets started calling for at least 6 hrs per night. The sound level meter was also placed in jars to measure the intensity of songs produced by males in neighbouring jars. Neighbouring songs were always below 40 dB SPL.

Spermatophore production.

In the field cricket, *Gryllus campestris*, males are able to call only when a spermatophore is present in the male's spermatophoric pouch (HUBER, 1962). To determine if the onset of calling behaviour coincides with the age at which males first produce the spermatophore, a separate sample of males from each species was studied. Males were placed in individual glass jars (without microphones). We removed males from their jars each day and exposed

the spermatophoric pouch by gently squeezing the abdomen. Spermatophores were readily visible when present.

Outdoor arena.

An outdoor arena was used to measure *G. integer* calling times in a more natural environment. The arena consisted of a 13 × 13 m area surrounded by a galvanized steel wall (1 m) and a chain link fence (2 m). Small mesh wire was suspended over the top of the arena to prevent birds from entering. Grass was mowed to a height of approximately 3 cm. The arena was divided into 25 quadrats of 1.9 × 1.9 m. Quadrats were numbered and marked with flags. Fifty shelters were placed in the arena using a random numbers table. The shelters were shallow holes covered with a 8 × 8 × .7 cm piece of wood.

Small numbers (Graze Beekeeping Equipment) were glued on the pronota of males, and their hind femurs were painted with fluorescent paint (Day Glo). The arena was observed each night from precisely 22:00 to 06:00 hrs (EDT) in July and August, 1979 and 1980. These data were used to analyze possible variation in calling duration with age, weight, and male density. Since *G. integer* males increase their calling in the early daylight hrs (CADE, 1979), observations were conducted from precisely 22:00 to 10:00 hrs (EDT) for six nights in August, 1980. Data from this 12 hr observation period reflect more accurately the total amount of time that males called, and these data were used to analyze individual variations in calling. Complete checks of the arena were made at 22:00 hrs and every 3 hrs thereafter. We slowly walked through the arena with a Burgess 165/3 ultraviolet lantern which made the hind legs of males readily visible. Each search took 45 to 60 min, and the positions of all males were recorded on maps of the arena. Crickets did not move in response to the ultraviolet light. Throughout the night, observers remained outside the arena and recorded the presence of calling song and the location in the arena where the song was produced. If a song was heard from a location where a male had not been observed previously, we went into the arena and identified the male. Males were only momentarily silenced by raising the wooden shelters. In some cases 2 or more males were together under a shelter, but only one male was calling. Calling males were always identifiable, however, since they continued to hold their wings at 45°, the characteristic calling position.

Males were either introduced into the arena on the day of their molt, or were kept in individual glass jars in the laboratory and later used to replace dead or missing males. Replacement males were allowed 3 nights to acclimate to the arena before information on their behaviour was used in subsequent analysis. Males were replaced if they were not seen in the arena for 3 nights. In 1979, *G. integer* was studied with 16 to 19 males in the arena. The number of males in 1980 was initially maintained at 18 to 21 males. To study the effects of density on male calling duration, males were then added to the same arena population to increase their number to 37. Crickets used in the outdoor arena portion of this study were from the second, fifth, and sixth generations from laboratory cultures.

Male weight.

To compare male weight with the amount of calling, males from all species were weighed at 7-15 days of age. A preliminary study demonstrated that male wet weight varied little in repeated measurements (CADE, unpublished). Males were removed from laboratory sound jars, weighed, and returned to the jar. *G. integer* males were also removed from the arena and weighed.

Results

Calling in the laboratory.

The average age at which males began calling in laboratory jars is presented in Table 1. No difference in the mean age at which males from

TABLE 1. Age at which male *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* first called in the laboratory

Species	Age (days) males first called			
	Mean	N	SD	Range
<i>G. integer</i>	6.9	47 ^a	3.3	4-23
<i>G. pennsylvanicus</i>	6.2	24	0.9	4-8
<i>G. veletis</i>	5.8	23	0.7	3-6
<i>T. africanus</i>	4.9	32 ^a	1.7	2-7

^a = 4 *G. integer* and 1 *T. africanus* males did not call.

the different species began calling was found (ANOVA, $F = 1.4$, $p > 0.05$, $df = 3, 122$). (These and subsequent ANOVAS and t tests were performed on log transformed to normal data.)

Mean calling times with increasing age are shown in Fig. 1. Starting at day 5 (the average age at which males first produced spermatophores and were therefore capable of calling; see following), there was no significant increase in calling behaviour with age in *G. integer* ($r = 0.09$, $p > .05$), *G. pennsylvanicus* ($r = -0.1$, $p > .05$), *G. veletis* ($r = 0.1$, $p > 0.05$), or *T. africanus* ($r = 0.02$, $p > .05$).

To compare calling between and within species, mean calling time was determined for each male over the period of 7 to 16 days. This period was chosen since all males produced spermatophores by day 7 (see following), and there was no difference in mean calling times over days 7 to 16 in any of the species. Frequency distributions of individual mean calling times are presented in Fig. 2. The average calling time for all *G. integer* males was 3.1 hrs per 24 hrs ($N = 51$, $SD = 2.6$). (This sample was the parental generation for selection experiments on calling duration, CADE, 1981b). Average calling times for *G. pennsylvanicus*, *G. veletis*, and *T. africanus* were 6.9 hrs ($N = 24$, $SD = 2.7$), 7.5 hrs ($N = 23$, $SD = 1.9$), and 5.5 hrs ($N = 33$, $SD = 2.6$), respectively. Mean calling times for the 4 species were significantly different ($F = 3.94$, $p < .01$, $df = 3, 127$). When *G. integer* was excluded from the analysis, no significant difference among the remaining 3 species was observed ($F = .25$, $p > .05$, $df = 2, 76$).

The shape of a frequency distribution may indicate the type of selection acting on a character. A normal distribution suggests stabilizing selection, whereas directional selection on a character should result in a distribution which is skewed to the left or right from normal (JOHNSON, 1976). Frequency distributions in Fig. 2 were compared to theoretically

generated normal distributions by the χ^2 Goodness of Fit Test. The distribution for *G. integer* was significantly different from normal ($\chi^2 = 18.2$, $df = 6$, $p < .01$), and was highly skewed to the left. The distributions of *G. pennsylvanicus*, *G. veletis*, and *T. africanus* were not different from normal ($\chi^2 = 5.4$, $df = 5$, $p > .05$; $\chi^2 = 3.1$, $df = 4$, $p > .05$; and $\chi^2 = 2.8$, $df = 6$, $p > .05$, respectively).

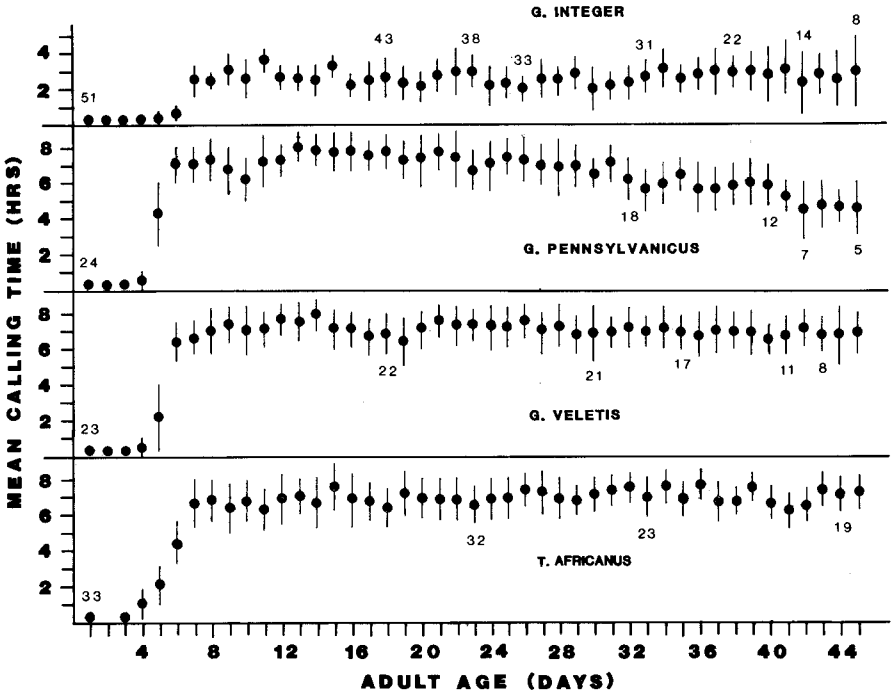


Fig. 1. Mean time calling per 24 hrs with increasing adult age by male *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* in laboratory jars. Sample sizes are shown and represent the number of males measured on the day indicated and on following days.

The coefficient of variation (CV), a measure of the degree of behavioural variability, was determined as $S.D. \times 100/\bar{X}$ (BEKOFF, 1977). Overall CVs for each species were calculated using the mean calling time for all conspecific males. Individual male CVs were also calculated. CVs for calling duration are shown in Table 2, and individual and overall variability in nightly calling duration was the greatest in *G. integer* males.

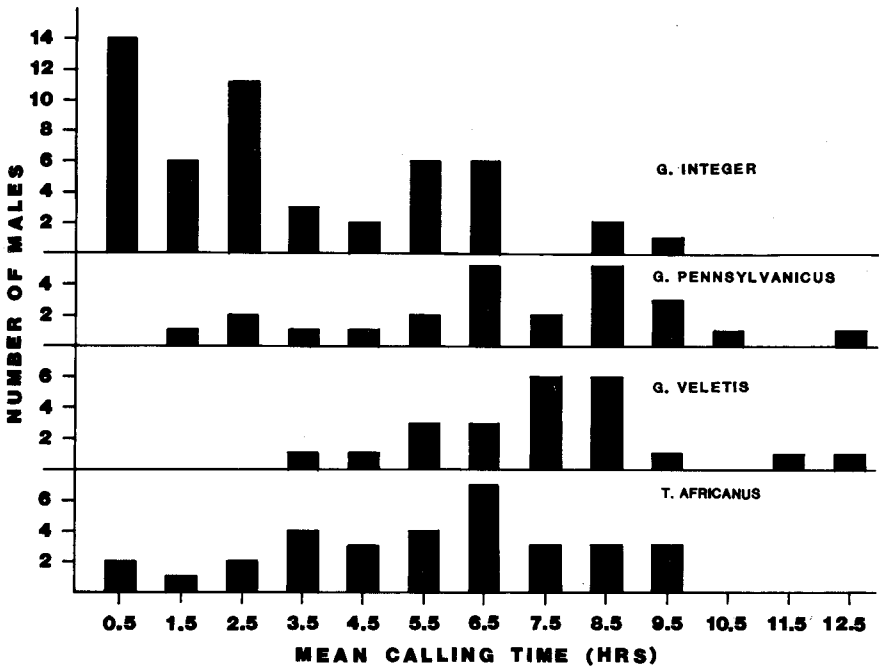


Fig. 2. Frequency distributions of mean calling times per 24 hrs over days 7-16 days of adult age by individual male *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* in the laboratory.

Spermatophore production.

Data on the age at which males first produced spermatophores are presented in Table 3. No difference was found in the average age at which the spermatophore was first produced ($F = 2.2$, $p > .05$, $df = 3, 35$).

Calling in the arena.

Mean durations of calling per 8 hr observation period for male *G. integer* of known age in the outdoor arena are shown in Fig. 3. In 1979 all males were observed in the arena from the day of their final molt, whereas some 1980 males were kept in the laboratory for a known period and placed in the arena to replace missing or dead males. Male *G. integer* in the outdoor arena started calling 6.3 days on average after the day of their final molt in 1979 and 1980 ($N = 37$, $SD = 7.9$, $Range = 4$ to 19 days). No significant difference in the mean age *G. integer* first called in laboratory jars and in the arena was found ($t = 1.9$, $p > .05$, $df = 1, 82$). There was also no

TABLE 2. Within species and within individual coefficients of variation for the nightly duration of calling for *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* in the laboratory

Species	Within sample	Coefficient of Variation (%)			
		\bar{X}	N	Within individual Range	S.D.
<i>G. integer</i>	83.8	44.4	51	0-212.2	66.4
<i>G. pennsylvanicus</i>	39.1	36.8	24	22.3-57.6	14.7
<i>G. veletis</i>	25.3	34.6	23	26.1-52.6	11.4
<i>T. africanus</i>	47.2	37.2	33	0-48.3	16.3

TABLE 3. Age at which male *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* first produced spermatophores

Species	Age (days) spermatophore first produced			
	Mean	N	SD	Range
<i>G. integer</i>	4.4	9	1.2	3-7
<i>G. pennsylvanicus</i>	4.2	10	1.3	3-6
<i>G. veletis</i>	4.8	8	1.1	3-7
<i>T. africanus</i>	3.7	12	1.3	2-5

significant increase in mean calling time with age in 1979 or 1980 (starting at day 5, $r = .1$, $p > .05$; and $r = .2$, $p > .05$).

Males at the initial density called .63 hrs on average ($N = 20$, $SD = .58$, $Range = 0$ to 1.6 hrs). When the density was increased, males called an average of .47 hrs per night ($N = 37$, $SD = .75$, $Range = 0$ to 3.5 hrs), which represents a significant difference between these 2 densities ($t = 3.4$, $p < .05$, $df = 1, 55$). These data are from observations from 22:00 to 06:00 hrs.

The mean calling times per night for males who were observed from 22:00 to 10:00 in 1980 are shown in Fig. 4. Males called an average of .75 hrs during the 12 hr observation period ($N = 37$, $SD = 1.04$, $Range = 0-4.4$ hrs). The distribution of calling is significantly different from a theoretically generated normal distribution ($\chi^2 = 14.6$, $df = 5$, $p < .01$). Eleven males were not observed calling in the arena, and the distribution is skewed to the left. Overall CV for this sample is 138.6%, and the average CV for individual males is 85.3% ($N = 37$, $S.D. = 34.9$, $Range = 0-145\%$).

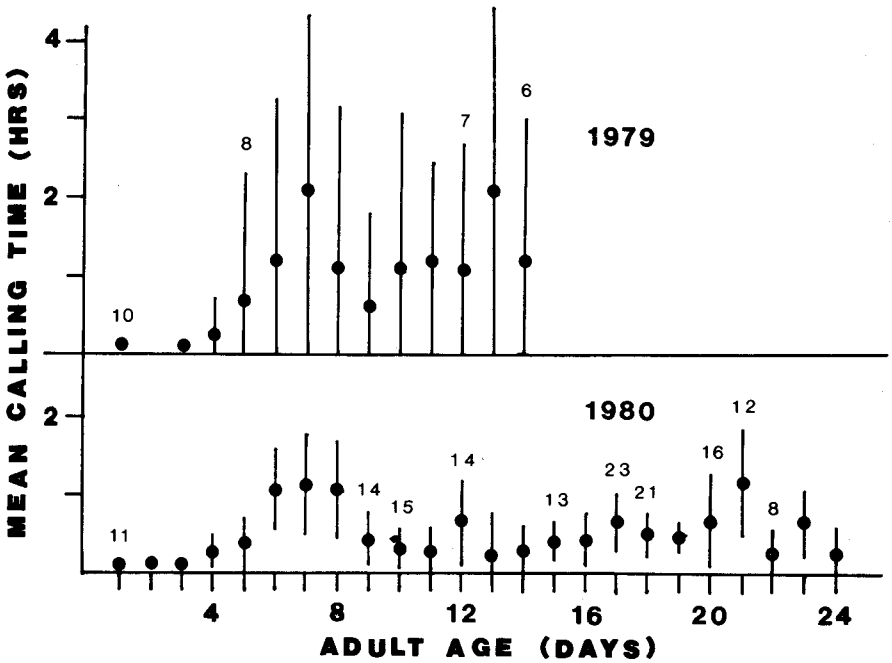


Fig. 3. Mean time calling per 8 hr observation period by male *G. integer* in the outside arena in 1979 and 1980.

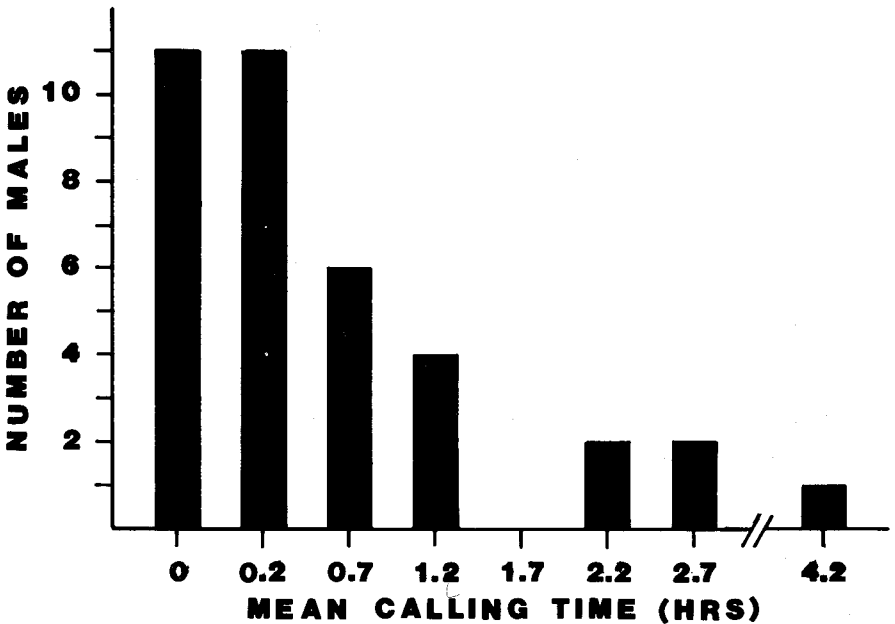


Fig. 4. Frequency distribution of mean calling times per 12 hr observation period by individual male *G. integer* in the outdoor arena.

TABLE 4. Mean time calling by male *G. integer*, *G. pennsylvanicus*, *G. veletis*, and *T. africanus* of varying weights in the laboratory and in the outdoor arena

Species	Weight range (mg)			
	300-399	400-499	500-599	600-750
<i>G. pennsylvanicus</i>				
\bar{X} hrs	5.2	7.7	5.9	7.9
(SD; N)	(1.9; 4)	(1.6; 9)	(2.2; 6)	(1.3; 5)
<i>G. veletis</i>				
\bar{X} hrs	6.7	7.6	8.7	7.2
(SD; N)	(1.8; 3)	(2.4; 12)	(2.6; 5)	(2.1; 3)
<i>T. africanus</i>				
\bar{X} hrs	6.3	6.2	5.4	5.7
(SD; N)	(1.7; 7)	(1.4; 12)	(1.6; 9)	(2.4; 5)
<i>G. integer</i> - laboratory				
\bar{X} hrs	2.9	3.1	3.6	2.8
(SD; N)	(1.2; 11)	(1.8; 19)	(2.1; 11)	(2.3; 10)
<i>G. integer</i> - arena				
\bar{X} hrs	1.1	0.6	0.7	1.0
(SD; N)	(1.1; 6)	(0.5; 11)	(0.8; 8)	(0.8; 6)

Male weight and calling.

Mean calling times with individual weight from the laboratory and for *G. integer* from the arena are presented in Table 4. There was no significant increase in the average duration of laboratory calling in the different weight classes in *G. integer* ($r = .1$, $p > .05$), *G. pennsylvanicus* ($r = .1$, $p > .05$), *G. veletis* ($r = .04$, $p > .05$), or *T. africanus* ($r = .1$, $p > .05$). No significant increase in the mean duration of calling by males with increasing weight was observed in the arena ($r = .09$, $p > .05$). Weights were not available for all males studied in the outdoor arena.

Discussion

The age at which males first produced spermatophores was significantly less than the age at which males first called in each species. Spermatophores were produced from 1 to 2 days earlier than the calling song. This difference is small relative to the length of adult life in all species. Calling may be delayed by a requirement for hardening of the exoskeleton or other maturational processes which affect calling. HUBER (1962) demonstrated that the presence of a spermatophore in the spermatophoric pouch is necessary for calling to occur in *G. campestris*. In

functional terms, spermatophore and song production are related since males should only call when it is possible to inseminate females.

No difference was observed between species in the age of production of the first spermatophore or the age at first calling. Also, the arena and laboratory samples of *G. integer* did not differ in the age at which they began calling. The lack of differences between these otherwise very different species (ALEXANDER, 1968) in the age of spermatophore production and calling suggests these are basic physiological processes, and the values reported here may characterize similar gryllines. In this connection, McFARLANE (1968) demonstrated that male house crickets, *Acheta domesticus* (Orthoptera; Gryllidae), generally produce their first spermatophore by 5 days of adult age.

The results reported here are the most complete signalling records with age for any insect. Once males had a spermatophore and were therefore capable of calling, they did not differ in the amount of nightly calling with increasing age in any species. *G. integer* males in the outdoor arena also did not show significant variation in calling with age. NIELSEN & DREISIG (1970) measured calling time in 1 individual of *Tettigonia viridissima* (Orthoptera; Tettigoniidae) in a laboratory situation similar to the one used here. This male did not sing regularly in the laboratory, producing only a few seconds of song for the first few weeks of adult life and increasing to a few hours per day at about 16 days of age. Thereafter, no change in the amount of daily calling occurred. No data were reported by NIELSEN and DREISIG on the age at which *T. viridissima* produce spermatophores.

Age related changes in male signaling behaviour are important in the context of alternative mating tactics. For example, older bullfrogs, *Rana catesbeiana*, call to females and defend territories against other males. Young bullfrogs call less frequently and often remain silent near calling males (EMLEN, 1968, 1976; HOWARD, 1978). HOWARD (1978) and RUBENSTEIN (1981) (see also WALTZ, 1982) proposed that most cases of alternative male signaling behaviour were the result of ontogenetic differences between competing males. Calling and non-calling or satellite males occur in *G. integer* (CADE, 1979, 1980), a situation similar to that in *R. catesbeiana*. Our data demonstrate that intraspecific variations in *G. integer* acoustical behaviour are not age related. HOWARD (1978), RUBENSTEIN (1980), and WALTZ (1982) did not distinguish between vertebrates and invertebrates in developing theoretical predictions on age specific variation in reproductive behaviour. In long lived vertebrates which become larger and more experienced with age, pronounced age related variations in behaviour are expected. In species with a short

reproductive lifetime, environmental and genotypic influences should be more important than age in producing particular behavioural patterns. In this regard, CADE (1981b) demonstrated that the realized heritability of nightly calling duration in *G. integer* is approximately 50%.

In addition to attracting mates, the calling song of crickets is a territorial signal which, along with fighting, results in the spacing of males (ALEXANDER, 1961, 1962; CADE, 1981a). Weight might confer an advantage in fighting with other males such that larger males may call more than smaller conspecifics. Relatively heavy weight may also indicate general good health and thus influence the amount of calling behaviour. There was, however, no relationship between weight and the amount of calling in any of the species studied in the laboratory or in *G. integer* outdoors. Also, ALEXANDER (1961) found no correlation between weight and fighting ability in laboratory observations on field crickets.

ALEXANDER (1961) proposed that calling in crickets should decrease with increasing male density since at high density the amount of fighting by calling males is increased and calling sites are limited. Also, males and females should encounter each other more often by chance when crickets are numerous. ALEXANDER's study was on a small laboratory population, and previous field studies of calling and male density did not quantify the amount of calling by individuals (CADE, 1979). Our data demonstrate that male calling decreases with density in an area which resembles the field environment.

Average calling duration per night over days 7 to 16 of adult life is a measure of a male's tendency to call under controlled conditions in the laboratory. All species except *G. integer* called roughly the same amount of time per night on average. *G. integer* called 2 to 4 hrs less per night than males in the other species. Reduced calling in *G. integer* might reflect energetic differences in the types of calling songs among the 4 species. The songs of *G. pennsylvanicus*, and *G. veletis* are composed of sound pulses organized into distinct chirps with quiet periods in between. The song of *G. integer* is composed of pulses organized into long trills with infrequent breaks. PRESTWICH & WALKER (1981) demonstrated a positive relationship between wing stroke or pulse rate and oxygen consumption in crickets. The trilling song of *G. integer* is probably more expensive to produce than the chirping songs of *G. pennsylvanicus* or *G. veletis*, such that reduced calling in *G. integer* may result. *T. africanus* however, has a song consisting of an introductory chirp followed by a trill (OTTE & CADE, in prep.), and thus has characteristics of the songs of *G. integer* and the other species. Calling duration in *T. africanus* was not significantly different

from calling in *G. pennsylvanicus* and *G. veletis*, and energetic differences alone probably do not account for reduced calling in *G. integer*.

Reduced calling in *G. integer* relative to the other species probably reflects the attraction of acoustically orienting parasitic flies to the calling song of this species (CADE, 1975). Possible attraction of flies to the song of *T. africanus* has not been studied, but fly larvae have never emerged from over 30 collected males of this species. Also, over 80 hrs of taped song broadcasting and the examination of 153 *G. veletis* and *G. pennsylvanicus* males for fly larvae indicate that these species are not attacked by parasitic flies in southern Ontario during the study period (CADE, unpublished). CADE (1975, 1979) proposed that the attraction of acoustically orienting flies was a major selective factor influencing the amount of calling in *G. integer*. Comparison of calling duration in *G. integer* with the other 3 species is additional evidence that acoustically orienting flies is one factor influencing reduced calling in *G. integer*. Furthermore, in all species except *G. integer* calling durations were normally distributed. The skewed distributions of *G. integer* calling times in the arena and the laboratory may reflect directional selection by flies.

Coefficients of variation for *G. pennsylvanicus*, *G. veletis*, and *T. africanus* were similar for the sample populations and for individual crickets. CVs for *G. integer* in the laboratory are greater indicating more overall and individual variability than in the remaining species. Higher CVs for *G. integer* resulted, in part, from 5 males who called infrequently and therefore had low mean calling times, large SDs and CVs greater than 100%. Nonetheless, *G. integer* is more variable in acoustical behaviour than the remaining species, and routinely has calling and satellite males in the same field population (CADE, 1979). Satellite males occur in *G. pennsylvanicus*, but only at very high density. Satellites apparently do not occur in *G. veletis* or *T. africanus* (CADE, unpublished).

CVs for calling duration in crickets are high compared to signals such as strutting in sage grouse, *Centrocercus uropasianus* (WILEY, 1973), notes in bird songs (SCHLEIDT, 1974), or signals from a variety of species (BARLOW, 1977). Although CVs are generally used to analyse signals lasting no more than 10 sec (SCHLIEDT, 1974), the CV is dimensionless and is an absolute measure of variability (SIMPSON *et al.*, 1960). The total duration of cricket calling lasts up to several hrs each night, however, and is expected to be more variable in length than signals of short duration.

Male *G. integer* in the laboratory and in the arena were similar in several respects. Both groups began calling at similar ages, showed no change in calling duration with age or weight, and had similar distribu-

tions of individual calling times. Males called much less in the arena than in the laboratory. This difference probably resulted, in part, from observations on this Texas species under the cooler temperatures in Ontario. Also, isolation from other males (as in the laboratory jars) results in increased calling in crickets (ALEXANDER, 1961). CVs for arena males were greater than those for males studied in the laboratory. Measurement of cricket calling in the laboratory jars provides an accurate description of this complex motor pattern without the complicating variables of a fluctuating abiotic and social environment.

Summary

The duration of calling by male acoustical insects should reflect the selective forces of mating success and longevity. Nightly calling durations were studied in the field crickets *Gryllus integer*, *G. pennsylvanicus*, *G. veletis*, and *Teleogryllus africanus*. Immediately after the final molt, males were placed in individual jars in the laboratory. Jars were monitored electronically for the production of calling song. Males started calling at 4 to 7 days on average in each species, and there were no significant changes in duration of calling with increasing age. *G. integer* was also studied in a large outdoor arena. Arena males first called at approximately the same age as males in the laboratory, and the duration of calling did not change with age. Onset of first calling followed initial production of the spermatophore by a few days in separate samples of each species. Absence of ontogenetic changes in the amount of calling demonstrates that calling and satellite males in field populations of *G. integer* do not result from age differences. Mean calling duration per night was determined for each male, and there was no difference in mean calling duration with male weight in any species in the laboratory, or *G. integer* in the arena. *G. integer* called significantly less on average than the other species. Individual calling durations in *G. integer* were highly skewed, whereas distributions of the other species were normal in shape. Reduced calling in *G. integer* may result from the attraction of acoustically orienting parasitic flies, *Euphasiopteryx ochracea*, to the calling song of this cricket species. Coefficients of variation demonstrated that *G. integer* is more variable in acoustical behaviour than the remaining species, an observation confirmed by previous field studies.

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