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Inter- and Intraspecific Variation in Nightly Calling Duration in Field Crickets, *Gryllus integer* and *G. rubens* (Orthoptera: Gryllidae)

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The time that male field crickets spend calling was measured electronically in the laboratory to examine nightly calling duration from different species and populations. Male Gryllus integer *from Davis, CA, and Las Cruces, NM, called approximately 7 h per 24 h, whereas male* G. integer *from San Antonio and Austin, TX, and Norman, OK, and male* G. rubens *from McAlester, OK, and Arkadelphia, AR, called approximately 3 h per 24 h. Variation in duration of calling is discussed in terms of the energetic costs of producing song and selection against calling by acoustically orienting parasites and predators. Duration of calling was also studied in field-collected male* G. integer. *Males were first observed in field populations and then collected. Those males observed calling in the field later called significantly more in the laboratory than males observed showing non-calling, satellite behavior. Flying* G. integer *collected under lights were intermediate in their calling duration to calling and satellite males. These data are discussed in terms of the heritability of nightly calling song duration in field crickets.*

KEY WORDS: calling song; field cricket; *Gryllus;* selection; geographic variation.

INTRODUCTION

Cricket calling song attracts sexually receptive females and attracts and repels conspecific males (Alexander, 1975; Cade, 1979a; Otte, 1977). Calling behavior is expensive energetically (Prestwich and Walker, 1981) and, in some spe-

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cies, attracts acoustically orienting parasites and predators (Cade, 1975; Sakaluk and Belwood, 1984; Walker, 1989). The time that individual males call each night varies among species. Male *Gryllus integer* call approximately 3 h per night on average in the laboratory, but *G. veletis* and *G. pennsylvanicus* call 6 h (Cade and Wyatt, 1984). The song of *G. integer* consists of a series of pulses arranged in a trill, whereas *G. veletis* and *G. pennsylvanicus* produce chirps or repeated bursts of song consisting of a few pulses per burst (Alexander, 1957; Smith and Cade, 1987). Trilling is more expensive energetically (Prestwich and Walker, 1981), and this may be one factor contributing to reduced calling in *G. integer*. *Gryllus integer* calling also attracts flies, *Ormia* (=*Euphasiopteryx*) *ochracea* (Diptera; Tachnidae), that deposit larvae on calling males. Parasitized *G. integer* die in a few days, but *G. veletis* and *G. pennsylvanicus* are not parasitized by acoustically orienting flies. Acoustically orienting flies have probably selected against calling in *G. integer* (Cade, 1975; Cade and Wyatt, 1984). Previous comparisons were between single populations of different species and there is no information on variations in calling duration between populations of a species or between species having similar song types. Such information is necessary to understand the factors influencing the duration of sexual signaling in field crickets. This paper reports on nightly calling duration in the laboratory by male field crickets from three populations of *G. integer* from Texas and Oklahoma and on the calling duration of males of two other species, *G. rubens* and *G. integer*, from California and New Mexico. The name *G. integer* has been used to refer to California and Texas field crickets, but these are probably different species and the designation for the Texas species is incorrect (Smith and Cade, 1987; Weissman *et al.*, 1980). In this paper the Texas and Oklahoma species is referred to as *G. integer* (Texas), and the California and New Mexico species as *G. integer* (Calif.).

This paper also reports on variation in nightly calling duration of *G. integer* (Texas) males from a single population. *Gryllus integer* (Texas) males call and attract mates and they silently intercept females attracted to calling males, so-called satellite behavior (Cade, 1979a). To determine if such intraspecific differences in behavior between males in field populations are reflected in variations in calling time in the laboratory, males were observed in the field; they were then collected and nightly calling durations were determined in the laboratory.

MATERIALS AND METHODS

Experiment 1: Variation Between Species

Cultures of field crickets were established in the laboratory from males and females collected in the following locations: *G. integer* (Texas) from Austin and San Antonio, TX, and from Norman, OK; *G. rubens* from Arkadelphia,

AR, and McAlester, OK; and *G. integer* (Calif.) from Davis, CA, and Las Cruces, NM. Species identification in many crickets is based primarily on calling song structure and sonagraphs for the three species studied here are given by Smith and Cade (1987). Cultures were maintained in the laboratory according to procedures described by Cade and Wyatt (1984). Individuals used in this experiment were the first generation raised from field-collected individuals.

Cultures were checked each day and newly molted adult males were removed and placed in separate containers. Male field crickets start calling at approximately 4 to 7 days of adult age (Cade and Wyatt, 1984). At 7 to 10 days of adult age males were placed in containers that were monitored automatically for the production of calling song. The duration of calling over 24 h was recorded for 5 to 6 nights for each male. Most calling was during the dark and for a few hours early in the light portion of the photoperiod. This experiment was conducted during 1987–1989 in the laboratory at Brock. Males were kept at a room temperature of approximately 25°C and a light–dark cycle of 12 : 12 h.

Experiment 2: Field-Collected Males

Calling male *G. integer* (Texas) were located and collected in old fields, parks, and grassy areas in and near Austin. The area immediately around calling males was searched and any noncalling males were collected. A third group of male *G. integer* (Texas) was collected under electric street lights where they had flown (Cade, 1979b). Previous acoustical behavior of light-collected males is unknown and these males served as a control. Calling, noncalling, and light-collected males were placed in containers in the laboratory. The duration of calling over a 24-h cycle was recorded for 5 to 7 nights for each male. This experiment was conducted during 1983–1985 at the Brackenridge Field Laboratory in Austin. Males were held at a room temperature of approximately 23°C and placed close to windows and thus exposed to the normal photoperiod of approximately 13 : 11 h, light–dark.

Monitoring Devices

Two types of devices and containers were used to measure male calling time. Males raised in laboratory cultures were studied using a specially modified Apple II+ computer and condenser microphones (Archer Electret 270-092B) placed inside of parabolic reflectors (14.0 cm in diameter at the outside lip). Reflectors were positioned directly above containers with males. Two microphones were placed inside each reflector and each microphone was connected to separate data collection files in the computer. In this way two separate records for each male were collected each day and their accuracy was compared. If the two values did not coincide, the data were discarded. Less than 5% of all measurements had to be discarded. Containers were made of plexiglass cylinders

(7.0 × 15.0 cm) with wire mesh on the top. The cricket's position on the base of the cylinder apparently caused one microphone to receive echos of the song and probably contributed to the occasional discrepancies between the two measurements noted previously. Food and water were supplied.

A second device was a mechanical sound relay that caused an electric clock to run when males called. Males studied in this fashion were placed in 4.2-liter glass jars, food and water were supplied, and a microphone was hung at the top of each jar [see Cade (1981) and Cade and Wyatt (1984) for more information on this monitoring system]. This device was used with field-collected males.

RESULTS

Experiment 1: Variation Between Species

The average time that individual crickets spent calling each 24 h is given in Table I for the various populations of the three species. Comparison of intraspecific values showed that there were no significant differences in mean calling times between populations in any of the three species. Individual measurements from the various populations of a species were therefore combined to compare the mean calling times of the three species (Table I). These means were significantly different (Kruskal–Wallis ANOVA, $H = 52.2$, $P = 0.0001$). *Gryllus*

Table I. The Mean Calling Time per 24 h for Males from Different Populations of *Gryllus integer* and *G. rubens*

Species	*N*	Mean calling time per night (h)	SD (h)	Range	*H*/*U*	P
G. integer (Tex.)						
Austin	37	2.9	3.7	0–12.7	1.4[a]	0.5
San Antonio	23	3.3	4.9	0–9.2		
Norman	25	1.9	2.1	0–8.7		
Total	85	2.8	3.7	0–12.7		
G. rubens						
Arkadelphia	27	3.3	3.1	0–9.7	569[b]	0.[illegible]
McAlester	31	2.7	2.8	0–9.7		
Total	58	3	3	0–9.7		
G. integer (Calif.)						
Davis	35	7.3	2.5	2.1–11.5	281[b]	0.1
Las Cruces	21	6.2	3.6	0–12.7		
Total	56	7.0	3	0–12.7		

[a] Kruskal–Wallis ANOVA.
[b] Mann–Whitney *U*.

integer (Calif.) males called over twice as much as *G. integer* (Texas) or *G. rubens* males.

The distributions of mean calling times for *G. integer* (Texas), *G. rubens* and *G. integer* (Calif.) males are shown in Figs. 1, 2, and 3 respectively. Many

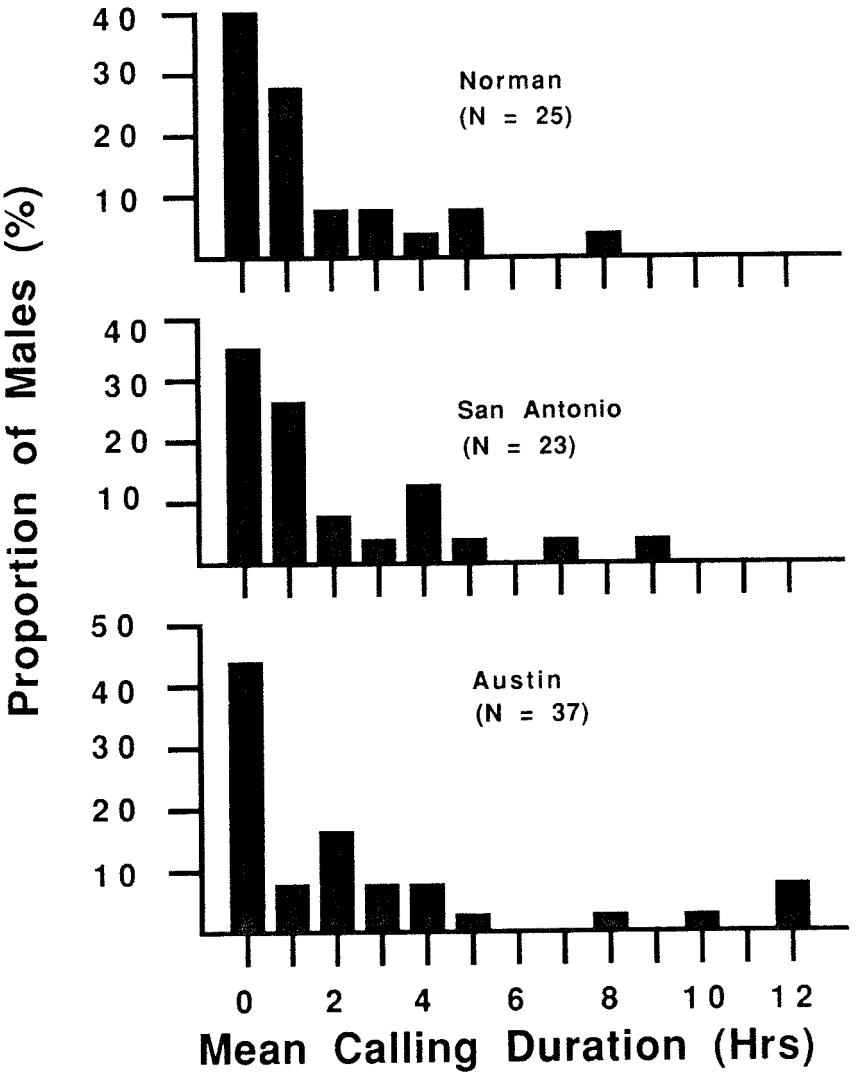

Fig. 1. Average duration of calling per 24 h for individual *Gryllus integer* from populations in Austin and San Antonio, TX, and Norman, OK.

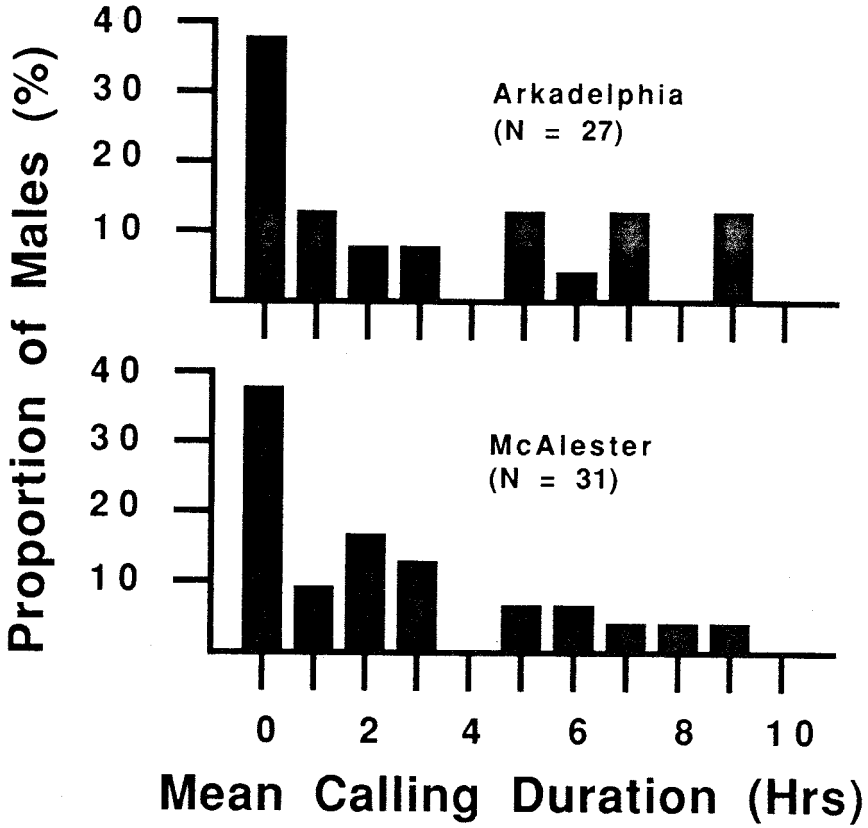

Fig. 2. Average duration of calling per 24 h for individual *Gryllus rubens* from populations in Arkadelphia, Arkansas, and McAlester, Oklahoma.

G. integer (Texas) and *G. rubens* males did not call or called less than 1 h per night, whereas only 1 *G. integer* (Calif.) male did not call.

Experiment 2: Field-Collected Males

The mean nightly calling times for *G. integer* (Texas) males collected in the field are given in Table II. The means are significantly different (Kruskal–Wallis ANOVA, $H = 9.1$, $P = 0.01$). There is no significant difference between the mean calling duration of male *G. integer* (Texas) that were collected after flying to lights and while they were performing satellite behavior (Mann–Whitney test, $z = -0.2$, $P = 0.83$). The frequency distribution for these mean calling times is shown in Fig. 4.

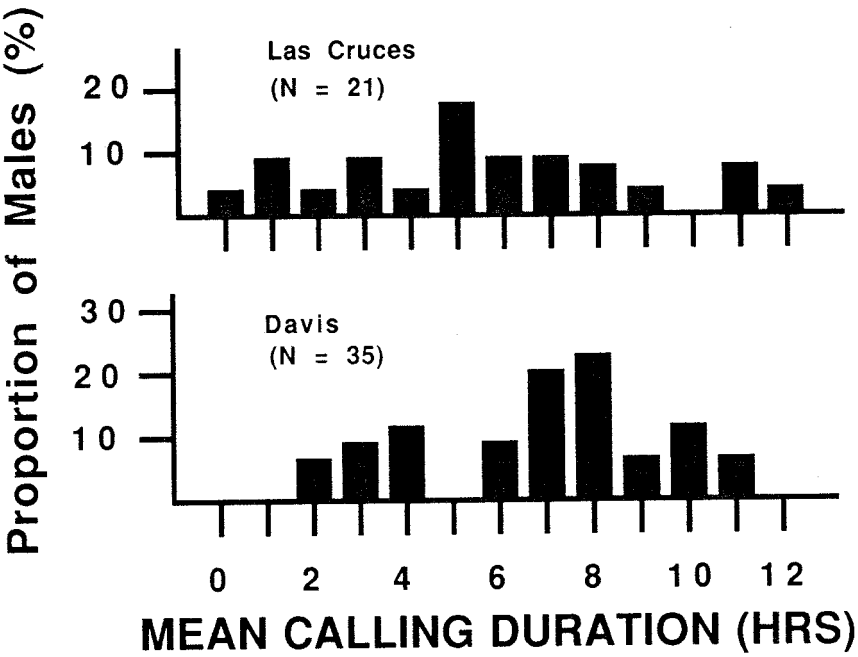

Fig. 3. Average duration of calling per 24 h for individual *Gryllus integer* from populations in Davis, CA, and Las Cruces, NM.

Table II. The Mean Calling Time per 24 h for *G. integer* Males Collected in Austin, Texas, After They Were Observed Calling, Behaving as Satellites of Calling Males, or Flying to Lights

Male behavior	*N*	Mean	SD	Range
Calling	41	4.2	2.8	0–9.6
Satellite	20	2.1	1.3	0–5.3
Flying	16	2.7	2.2	0–7.9

DISCUSSION

Male *G. integer* (Texas) and *G. rubens* showed reduced calling times compared with *G. integer* from California and New Mexico. These values and the shape of the frequency distributions for *G. integer* (Texas) and *G. rubens* are very close to those reported previously for *G. integer* (Texas) from the Austin population (Cade and Wyatt, 1984). All three species produce trilling type songs (Smith and Cade, 1987), but *G. integer* (Calif.) has the fastest pulse rate and thus might be expected to use more energy in song production than *G. integer*

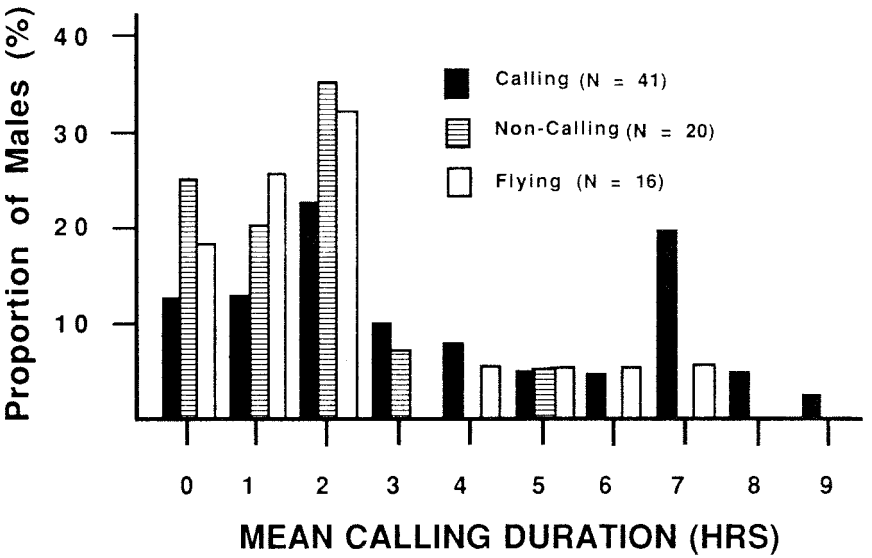

Fig. 4. Average duration of calling per 24 h for *Gryllus integer* males collected in the field after the males were observed, calling, behaving as satellite males, or flying to lights.

(Texas) and *G. rubens*. Alternatively, *G. integer* (Calif.) produces very brief pauses between groups of pulses and the total number of pulses produced over a few minutes may be less than that for *G. integer* (Texas). More information on this possibility is necessary, but calling times and shape of the frequency distribution for *G. integer* (Calif.) are comparable to those reported earlier for *G. veletis* and *G. pennsylvanicus* (Cade, 1981; Cade and Wyatt, 1984). The chirping songs of *G. veletis* and *G. pennsylvanicus* have a much slower pulse rate than the song of *G. integer* (Calif.). These observations suggest that energetic considerations are not of major importance in determining the amount of time males spend calling in these species. Males in these experiments had ample food and water, however, and the energetic cost of producing song may be important in determining male calling durations in field populations.

Selection by acoustically orienting parasitoid flies may have resulted in reduced calling in the *G. integer* (Texas) and *G. rubens* populations. The shapes of the distributions for *G. integer* (Texas) and *G. rubens* suggest that directional selection in some form has operated against calling behavior. Cade and Wyatt (1984) proposed that such skewed distributions reflect a history of parasitism by acoustically orienting flies. Males in Austin and San Antonio populations of *G. integer* (Texas) are routinely parasitized by *O. ochracea* (Cade, 1975 and unpublished data), but it is not known if flies parasitize males in populations of crickets in Oklahoma, California, New Mexico, or Arkansas. *Ormia ochracea*

is readily attracted to the song of *G. rubens* in Florida, and it is likely that *G. rubens* is a host of *O. ochracea* (Walker, 1986, 1989). More information is needed on the incidence of parasitism in cricket populations to assess the importance of acoustically orienting flies as selective agents. Rates of female phonotaxis to calling males, habitat suitability, and other factors may also influence the amount of time that male crickets spend calling.

This study also demonstrated that male *G. integer* (Texas) observed calling in field populations call more each night than males showing noncalling, satellite behavior before being taken to the laboratory. The duration of nightly calling in the laboratory has a narrow-sense heritability of approximately 50% in *G. integer* (Texas) (Cade, 1981). Although many environmental factors influence the amount of time that males spend calling, the data presented here suggest that males having alleles that enhance calling time in the field continue to express these alleles in the laboratory. There was no difference in nightly calling duration between males collected under lights and those showing satellite behavior. Light-collected crickets are probably dispersing individuals that would ordinarily land in established aggregations of calling males. Some flying male *G. integer* (Texas) begin calling, while others perform satellite behavior after they land in an aggregation (Cade, 1979a,b, 1990). Data from field-collected male *G. integer* (Texas) also indicate that laboratory measurements of calling time provide an estimate of a male's tendency to call under more natural conditions. This technique is therefore useful in estimating the amount and type of behavioral variation present in natural populations.

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