Nightly and hourly rates of attraction of flying field crickets, *Gryllus integer*, to conspecific song

WILLIAM H. CADE

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

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Nightly and hourly rates of attraction of flying field crickets, *Gryllus integer*, to conspecific calling song were studied in an arena placed in the natural habitat of the species in central Texas. Calling of male *G. integer* in the arena and tape-recorded broadcasts of conspecific song were the sources of cricket song that subsequently attracted flying crickets. Observations were conducted for 10 h from approximately 1.5-2 h past sunset to 3 h past sunrise for 97 nights in 1983 and 1985-1988, using calling males, and for 4 nights in 1988, using taped song. The number of crickets attracted each night varied greatly, significantly more females were attracted, the numbers of males and females attracted decreased near sunrise, and significantly more crickets entered the arena from 2 to 6 h than from 7 to 11 h past sunset. Results are discussed in the context of mating behavior and sexual selection in this and other species.

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Les réactions nocturnes et diurnes de grillons *Gryllus integer* à l'audition d'appels conspécifiques ont été étudiées dans une arène délimitée dans un habitat naturel, au centre du Texas. Les appels de mâles de *G. integer* dans l'arène et des enregistrements d'appels conspécifiques ont servi de sources sonores. Les arènes ont été surveillées durant 10 h, de 1,5-2 h après le coucher du soleil jusqu'à 3 h, après le lever du soleil, durant 97 nuits en 1983 et de 1985 à 1988, au cours desquelles les mâles servaient de source sonore, et durant 4 nuits en 1988, au cours desquelles des enregistrements ont été utilisés. Le nombre de grillons attirés chaque nuit variait considérablement; significativement plus de femelles étaient attirées; le nombre de mâles et de femelles attirées diminuait à l'approche du lever du soleil et significativement plus de grillons gagnaient l'arène durant la période de 2-6 h après le coucher du soleil qu'au cours de la période de 7-11 h après le coucher du soleil. Les résultats sont examinés en relation avec le comportement d'accouplement et la sélection sexuelle chez cette espèce et chez d'autres espèces.

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Introduction

The calling song of male crickets attracts conspecific males and females. In some species of field and mole crickets (Orthoptera: Gryllidae and Gryllotalpidae), macropterous individuals fly to and land near a source of conspecific calling song. The mole crickets Scapteriscus acletus and Scapteriscus vicinus fly for a very limited time after sunset, but in the field crickets Gryllus integer and Gryllus rubens, flying individuals are attracted to calling songs throughout the night (Cade 1979a; Forrest 1980, 1983; Ulagaraj and Walker 1973, Walker 1986). The timing and other aspects of the attraction of flying crickets have important consequences for mating behavior in these species. Previous studies have used broadcasts of synthetic or previously tape-recorded calling song to observe the attraction of flying crickets. This paper reports on the attraction of flying G. integer to both tape-recorded broadcasts of conspecific song and to calling males observed in outdoor arenas.

Methods of study

Observations and experiments on G. integer were carried out at the Brackenridge Field Laboratory, Austin, Texas, at various periods from April to August, 1983-1988 (no data were collected in 1984), in a grassy area enclosed by concrete walls measuring $13.5 \times 13.5 \times 1.2$ m. (The name G. integer is commonly used to refer to this species in central Texas, but that designation may be incorrect (Weissman et al. 1980; Smith and Cade 1987)). A metal barrier (30 cm wide) at the top of the wall prevented crickets from climbing into or out of the arena. The arena was covered with plastic orchard net to prevent entry by birds. Crickets landed on the net and fell to the grass below.

The grass was kept at a low height and crickets were readily visible.

Data gathered by observing cricket attraction to calling males were collected during a study on variations in mating behavior that involved observations on individually marked G. integer (W. H. Cade, in preparation; French and Cade 1987). The arena was observed from 22:00 to 08:00 local time, approximately 1.5-2 h past sunset to 3 h past sunrise. Marked G. integer generally called throughout the observation period. The number of calling males per hour for observations in 1986 is given by French and Cade (1987), and data on the total amount of calling are reported elsewhere (W. H. Cade, in preparation). Observations in 1983 and 1985 were carried out at a high density of 22.4 and 21.3 marked males and females on average, whereas those carried out in 1986 to 1988 had an average of 4.8 and 4.4 males and females each night. Several replicates at each density were performed and consisted of observations over 4-12 nights each for a total of 97 nights. Unmarked male and female crickets were often found in the arena. To determine the frequency of attraction of G. integer to the arena, unmarked crickets were collected and counted hourly by searching the arena using lights.

Attraction of crickets to tape-recorded *G. integer* song was studied in July 1988, by broadcasting previously tape-recorded conspecific song from within the arena. Song was broadcast using a Sony stereo cassette recorder (WMF46), a Realistic MPA-20 amplifier, and two high-frequency loudspeakers (Realistic 40-1228) placed in the center of the arena and pointing directly up. The song intensity varied from approximately 85 to 92 dB as measured 6 cm from the front of each loudspeaker, using a General Radio sound-level meter (1565-D). Song was broadcast continuously from 22:00 to 08:00 on four nights. Attracted crickets were collected from the arena hourly.

In 1983 and 1988, a neighboring arena was also checked approximately every 3 h. There were no calling males or broadcasts of taped song in this arena and it served as a control for the attraction of crickets to the observation arena. The neighboring arena was not used in the other years.

TABLE 1. The total and average number of male and female G. integer attracted each night to the arena for each replicate, in observations using male crickets as a source of conspecific calling song

Replicate	No. of nights	No. of crickets			
		Males		Females	
		Total	$\bar{x} \pm SD$	Total	$\bar{x} \pm SD$
1983 April – May	12	5	0.4±0.27	18	1.5±0.3
1983 May	11	32	2.9 ± 1.1	48	4.3 ± 2.3
1983 July	7	36	5.1 ± 2.1	27	3.8 ± 1.7
1985 July	10	31	3.1 ± 1.6	87	8.7 ± 2.9
1985 August	9	48	5.3 ± 2.2	74	8.2 ± 2.5
1986 April	4	1	0.25 ± 0.18	3	0.75 ± 0.3
1988 June	9	24	2.6 ± 1.4	45	5.0 ± 2.8
1986 August	10	27	2.7 ± 1.9	48	4.8 ± 1.9
1987 June	10	17	1.7 ± 0.7	28	2.8 ± 1.1
1987 August	10	36	3.6 ± 1.3	71	7.1 ± 2.9
1988 May	5	3	0.6 ± 0.2	14	2.8 ± 1.4

Results

Crickets were often observed flying and landing on the bird net over the arena and falling to the grass below. Crickets were never observed to climb into the arena over the concrete walls and metal barrier. A total of 723 G. integer entered the arena during the 97 nights when calling males were present. All crickets were macropterous. There were 260 males and 463 females, and this difference between the sexes is significant ($\chi^2 = 56.9$, p < 0.01, df = 1). The total and average numbers of crickets attracted each night for individual replicates are shown in Table 1. The control arena had a total of three male and eight female G. integer over the 35 nights in 1983 and 1988.

The hourly total number of male and female crickets that entered the arena when calling males were present is shown in Fig. 1A for all replicates combined. The hourly rate for males and females was similar. There were 521 male and female G. integer collected during the first half of the observation period from 2 to 6 h after sunset and 202 crickets were collected from 7 to 11 h. This difference is significant ($\chi^2 = 140.7$, p < 0.01, df = 1).

A total of 41 male and 66 female G. integer entered the arena during the four nights when tape-recorded G. integer song was broadcast. This difference is significant ($\chi^2 = 5.8$, p < 0.05, df = 1). The average number attracted per night was 10.2 (SD = 2.7) for males and 16.5 (SD = 3.2) for females. One male and five females were found in the control arena. The hourly totals for male and female G. integer that entered the observation arena for these four nights are shown in Fig. 1B. Rates of attraction for males and females were similar. There were 63 G. integer collected from 2 to 6 h after sunset and 34 from 7 to 11 h. The difference is significant ($\chi^2 = 8.7$, p < 0.01, df = 1).

Discussion

Crickets were regularly found in the arena that contained calling males or loudspeakers broadcasting conspecific song, but few were in the control arena. Male and female G. integer are known to fly to conspecific calling song. All of the unmarked crickets collected in the arena probably were flying

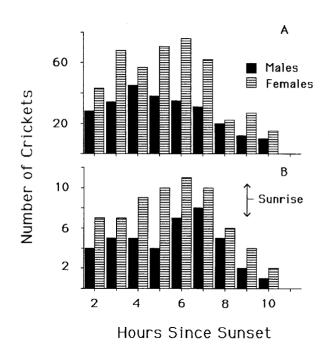


Fig. 1. The total number of male and female *G. integer* attracted each hour to (A) the calling of conspecific males and (B) the tape recorded broadcast of conspecific song.

individuals attracted by conspecific calling song, since any other unmarked crickets were removed during regular inspections of the arena in the day and at the start of observations. The rates of attraction varied greatly between and within replicates, and phonotaxis in field and mole crickets is very dependent on sound intensity and the time of year (Cade 1979a; Ulagaraj and Walker 1975; Walker 1986). The number of females attracted was greater than the number of males in this study, and this finding agrees with previous studies on phonotaxis in this and other field and mole cricket species (Cade 1979a; Forrest 1983; Ulagaraj and Walker 1973; Walker 1986). In one replicate using calling males, however, there were more male G. integer attracted than females. Gryllus integer also flies to electric lights and in this situation females generally outnumber males. This difference in numbers

is less pronounced, however, at the start of a period of several nights during which crickets are flying (Cade 1979b).

The hourly rates of attraction for male and female G. integer to calling males and to broadcast song were similar, and the numbers of attracted crickets decreased in the second half of the 10-h observation period. Walker (1986) demonstrated that G. rubens males and females in Florida fly to synthetically produced conspecific song throughout the night. He found no difference in the number of crickets attracted before and after midnight when conspecific song was broadcast from traps over many nights. On two nights, Walker sampled the number of attracted G. rubens at regular intervals from sunset to sunrise and there was no significant difference in the number of attracted crickets in each time period. Although this study showed that G. integer fly significantly less in the second half of the observation period, Walker's findings for G. rubens are similar to those obtained in this study on G. integer in that the number of G. integer attracted was relatively stable throughout the night, with the greatest decline occurring right before and after sunrise. Walker's study did not continue into the period after sunrise.

Hourly rates of attraction of flying G. integer and G. rubens to conspecific song are very different, however, from the hourly rates of flying G. integer attracted to electric lights. Attraction of G. integer to electric lights is greatest at approximately 1-2 h past sunset and has stopped by 4 h past sunset (Cade 1979b). No information is available on the distance that flying G. integer travel. Relatively long dispersal flights may occur at the beginning of the night, however, and short orientation flights to calling males may occur all night. Insect dispersal is often characterized by relatively long-distance flights shortly after sunset (Johnson 1969). Variation in rates of attraction of flying G. integer to lights and to conspecific song may also arise from differences that light and sound present as stimuli to flying crickets. No data are available to test these hypotheses.

Field studies of *G. integer* show that calling males are usually spatially aggregated and that females and noncalling satellite males occur in these aggregations (Cade 1979a, 1981). Flying crickets attracted to calling song join these aggregations, and attracted females oviposit, feed, and mate. Male *G. integer* attracted to the calling of other males may adopt a range of behavioral patterns: some males start calling at least 1 m from the nearest calling male, some males walk or remain motionless in the vicinity of calling males. These males do not call, but court and mate with females attracted to the other male's song. Silent males also orient to and physically attack calling males (Cade 1979a, 1981).

Mating behavior is not distributed evenly throughout the night in *G. integer*. Males begin calling soon after sunset, and the number of *G. integer* calling is relatively constant until sunrise, when a large increase occurs. The number of callers decreases sharply a few hours after sunrise. The increase in calling behavior at sunrise coincides with a large increase in the number of matings and a decrease in the rate of walking by males and females in an aggregation (Cade 1979a; French

and Cade 1987). The data presented here show that flying phonotaxis also declines at a time when calling and mating increase in frequency. Attracted crickets thus join aggregations before the time at which matings are most likely. The variability in the number of crickets attracted each night, however, may contribute to much variation in mating frequency. Many factors probably influence the evolution of temporal sequences of phonotaxis and mating and related behavior in crickets. One possibility is that female crickets postpone mating until dawn and thus have more time available throughout the night to observe and evaluate males as mates (Walker 1983).

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