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The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L.

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Summary. In a field population of *Gryllus campestris*, 209 males and 175 females were marked individually and their migratory and mating behavior was observed. Many females and males mate more than once and both sexes change burrows frequently. All copulations observed were during the day. Automatic recording of calling in 12 selected males, and walking in 7 females, showed that an individual male may call predominantly during the day, during the night, or both day and night, but the females show locomotory activity predominantly during the day. Thus, female locomotion is significantly temporally correlated with copulation but not with male calling.

Introduction

Male crickets emit a species-specific calling song to attract females and receptive females will respond to it by oriented locomotion, i.e. phonotaxis (Huber 1955, 1977; Popov 1972; Popov and Shuvalov 1977; Elsner and Popov 1978; Weber et al. 1981; Thorson et al. 1982).

Males of warm-climate species call during the night (Loher 1972; Walker 1983; Loher and Orsak 1985; Sakaluk 1987). In *Teleogryllus commodus* the pattern of female locomotory activity in the laboratory matches the pattern of male calling, suggesting that the correlation of these two behaviors facilitates encounters between the sexes (Loher 1979a). However, a female starts locomotor activity whenever she hears a male call, in addition to her circadian locomotor pattern (Loher 1979b). This in turn indicates that a male could attract a female whenever he calls. Field experiments on different cricket species have shown that male calling not only attracts females but also attracts other males, regulates territorial spacing, and results in aggregations (Popov 1975; Campbell and Shipp 1979; Cade 1981; Evans 1983). Thus, the male calling song also triggers male locomotion and phonotaxis.

Laboratory experiments on the field cricket *Gryllus campestris* collected in southern Germany have shown that individual males may be active during day, during the night, or night and day (Honegger 1981). This paper examines aspects of male calling and female locomotion in a field population of *G. campestris* from which the animals for earlier laboratory experiments had been collected, in order to test how closely matings are related to these premating behaviors. Our results indicate that in *G. campestris* females rather than males seem to determine the timing of sexual interactions.

Methods

A population of the cricket *Gryllus campestris* was investigated in the field near Radolfzell (Lake Constance) between 16 March and 7 July 1981. The study area was 260 × 60 m, located on a slope facing southwest (Fig. 1). It was subdivided into five areas (A–E) where the population density of crickets was particularly high. The positions of burrows were marked with sticks to which small numbered flags were attached.

In the study area 384 adults (209 males, 175 females) were marked individually with typewriter correction fluid. Most crickets were marked straight after the imaginal moult which in 1981 took place between 22 April and 10 May. The sex of the cricket served as an additional marker. By inserting a blade of grass into a burrow it was possible to lure the inhabitant out of its burrow so as to ascertain its identity.

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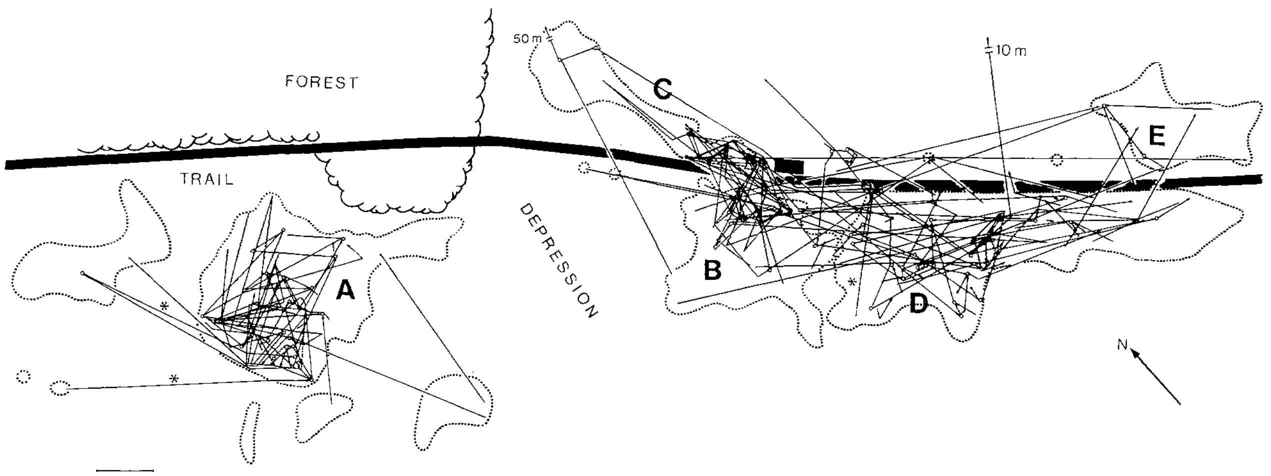

Fig. 1. Summary diagram of the paths and directions of migrations by individual crickets in the experimental area. One *straight line* with turning points connects all locations, usually burrows, at which an individual cricket was found. *Lines* start at burrows where crickets were marked. *Arrowheads* indicate last location of discovery (normally a burrow) of a particular cricket. *Circles* indicate burrows which were inhabited successively by different crickets. The *dotted borderlines* surround the densely population areas *A–E*. The *black rectangle* on the trail above area *B* shows the position of the VW bus where the electronic equipment was housed. Scale: 10 m. We found only three females (marked *) that made long distance migrations

A transect was walked 4–5 times each day during the day and migrating animals and matings were recorded. The first survey started between 4:00 and 7:30 a.m. The 4–5 surveys on any day were time-shifted by 1 h relative to the previous day. Additionally, the area was checked during three nights at intervals of 1 h listening for courtship song. For checks of burrows and general observations on interactions of crickets, one of us (R.R.) divided the observations approximately proportionally to the 14 h of daylight and over the whole terrain, so as to minimize the disturbance to any given area. To gain additional information about migrating crickets a 10-cm-deep trench with plastic walls enclosing a 10 × 10 m square was dug in area A. The trench was checked during the surveys each day.

To record the locomotory activity of females automatically, a new recording system was developed (Fig. 2), tested for proper function in the laboratory (Honegger et al. in prep.) and subsequently used in the field. It consisted of a tambourine (31 cm in diameter) which was surrounded by a transparent plastic wall (15 cm high). The tambourine was sunk into the sloping meadow in front of a female's burrow, adjusted to horizontal and connected by a plastic tube with the burrow's entrance. A second cage of transparent plastic prevented other insects from jumping directly onto the tambourine from outside. Under the tambourine three miniature microphones were attached, which picked up the scratching noises of a walking female. The input from the three microphones triggered a pen deflection of one channel of an Esterline Angus event recorder via an interposed amplifier. The amplifier was adjusted so that only the steps of a female, and not the calling of males, triggered a pen deflection. The amplifier and recorder were located in a nearby vehicle. All females were fed once a day at different times with a variety of plants growing in the area. One tambourine was installed without a female as a control device to record the noise of falling rain drops, strong wind, or other artifacts.

To record male calling, three miniature microphones were installed on a wire 5 cm above the burrow entrance. They were connected to the event recorder identically to those for recording female locomotory activity. The amplifier was adjusted so that only the chirping of the burrow's inhabitant triggered the relay. The burrow was surrounded by a circular cage of mosquito netting about 30 cm high and 30 cm in diameter. The top of the cage carried a 5-cm wide collar of transparent foil so that crickets could not climb out of this cage. One of the recording systems was also installed without a male, as a control.

Five and 7 devices, to record female and male activities respectively, were installed in areas B and C. Caged males and females were recorded until 26 June, unless they died in which case the animal was replaced by another one.

For graphical summaries of the amount of activity, the original Esterline Angus recordings were divided into 1-h intervals and the number of minutes during each hour in which activity occurred was determined from the chart.

Animals were defined as day- or night-active if more than 60% of the total activity occurred during the day or the night, respectively. If activity was more evenly distributed, so that less than 60% occurred during day or night, the animal was defined as day-and-night-active.

Results

Occupation of burrows

Figure 3 shows the duration of occupation of the burrows of 167 males. The mean occupation time was 7.5 days. Females in particular became extremely cautious after their imaginal moult and it was more difficult to lure them out of their burrows: we therefore concentrated on males. Of the 209 males marked, we measured 230 burrow occupation periods for 167 individuals: one occupation period for 122 males, two periods for 30 males, three periods for 12 males, and four occupation periods for 3 males. Where several occupations had been observed for one individual, there was no preference for any given duration of occupation. Several factors influence the duration of occupa-

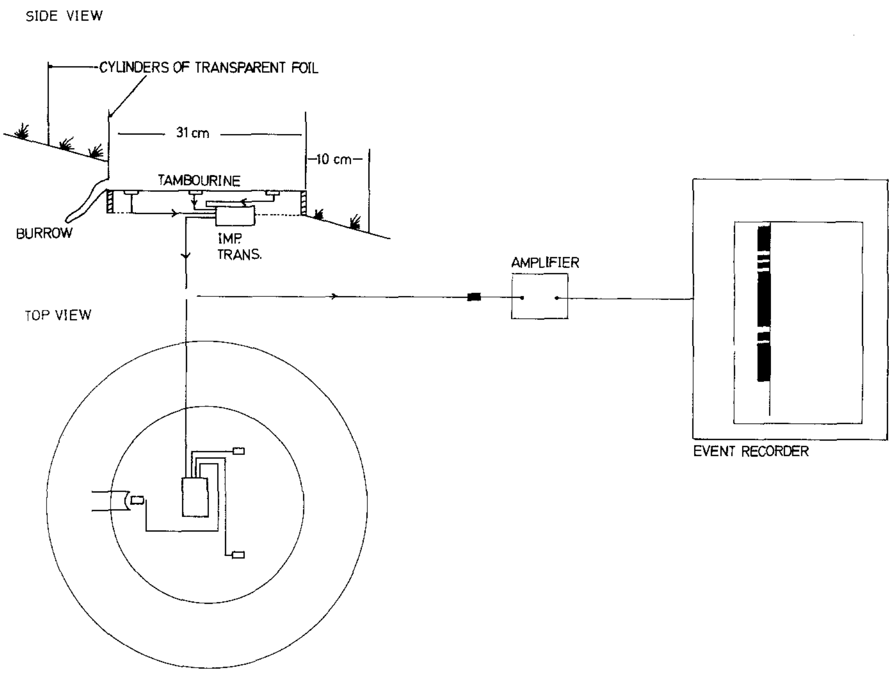

Fig. 2. Schematic side and top views of the automatic recording device for monitoring female motor activity. For further details see text

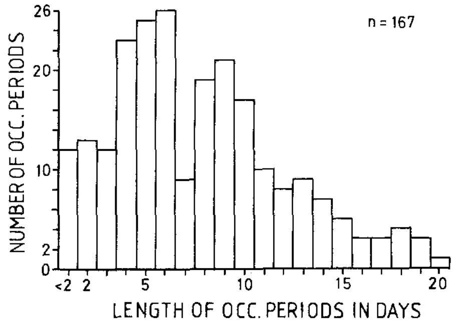

Fig. 3. Number of days for which particular burrows were occupied by male *Gryllus campestris*. The smallest class on the abscissa comprises an occupation time of less or more than 1 day when a particular male was found in two different burrows on the same day or within less than 2 days. For further details see text

tion of a burrow by a given cricket. First, males attack burrow owners in an attempt to occupy their burrows. In the eight attacks observed, however, the owner successfully defended its burrow seven times. Second, males often abandon their burrows after copulation. Third, during rain, all crickets remained in their burrows. Thus, rain extended the time that a burrow was occupied. Periods of rain are indicated in subsequent data presentations (e.g. Fig. 5).

Migration distances

Migration distances between different burrows were computed as straight lines between the bur-

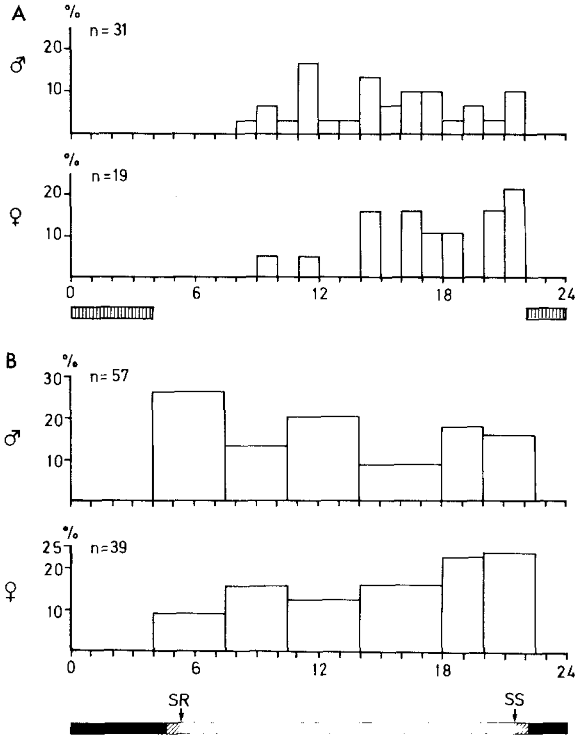

Fig. 4 A, B. Numbers of male and female crickets which were caught traveling through the grass **A** by surveys of the whole experimental area and **B** by inspection of the trench in area A. Numbers of crickets per time interval are expressed as percent of the total number *n* caught between 25 April and 27 June. *Hatched bars* below A indicate times in which no surveys of the experimental area were made. The *bar* below the histograms shows the natural light-dark cycle with dawn, dusk, sunrise (*SR*) at 5:25 a.m. and sunset (*SS*) at 9:25 p.m. (daylight saving time) at 20 June. For further details see text

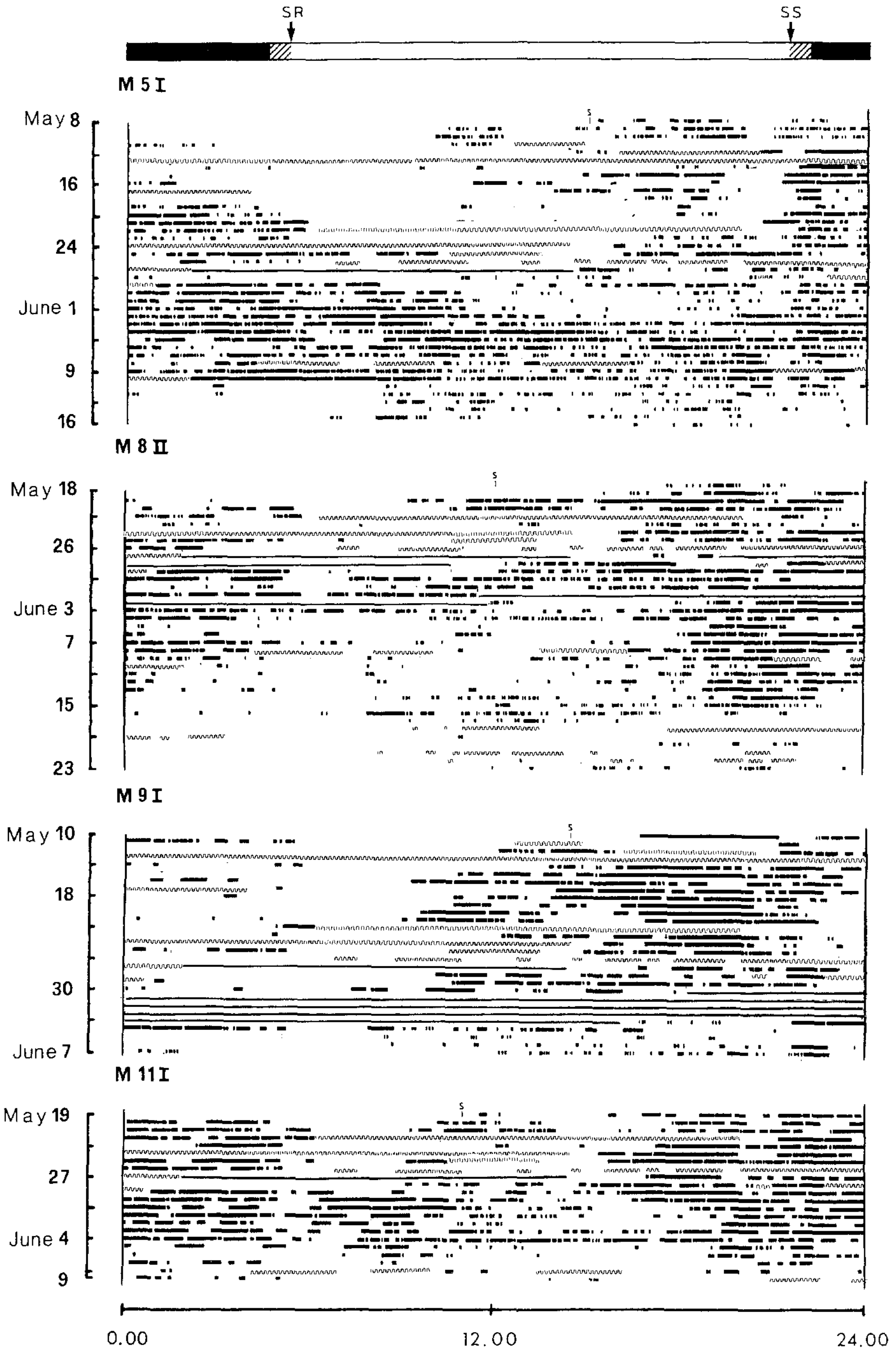

Fig. 5. Drawings of event recorder displays of stridulation (calling song) of 4 males recorded between 8 May and 23 June 1981. Each *horizontal line* from hour 0–24 represents the singing activity record of 1 day. Successive days are presented one below the other. *Blocks* indicate high calling activity. *Thin lines* indicate failure of the electronic equipment, *sinusoidal lines* indicate rain. Since the original records suffered from the moisture all records were redrawn. Apparent calling activity which was duplicated on a concurrent control channel (see Methods) was eliminated from the drawings. *Bar* above the actograms indicates natural light-dark cycle as in Fig. 4. The period of recording for each of the males is indicated on the left side of the actograms

rows because we do not know the actual paths taken by the crickets (Fig. 1). When changing burrows, a large fraction of the crickets moved relatively short distances in restricted areas (see also Table 1). This is particularly obvious in areas A, B, and C. Males and females frequently moved from border areas into these already densely populated areas early in the season, shortly after the imaginal moult. From the end of May on, a few crickets emigrated from these high-density areas and occupied the flat terrain (area E) northwest of areas C and D, which was a fertilized meadow. The first crickets were found there on 28 May.

Timing of migration

Figure 4A shows the timing of migration for a total of 50 crickets (31 males and 19 females) which were found moving through the grass. No crickets were found between 4:00 and 8:00 a.m. There was

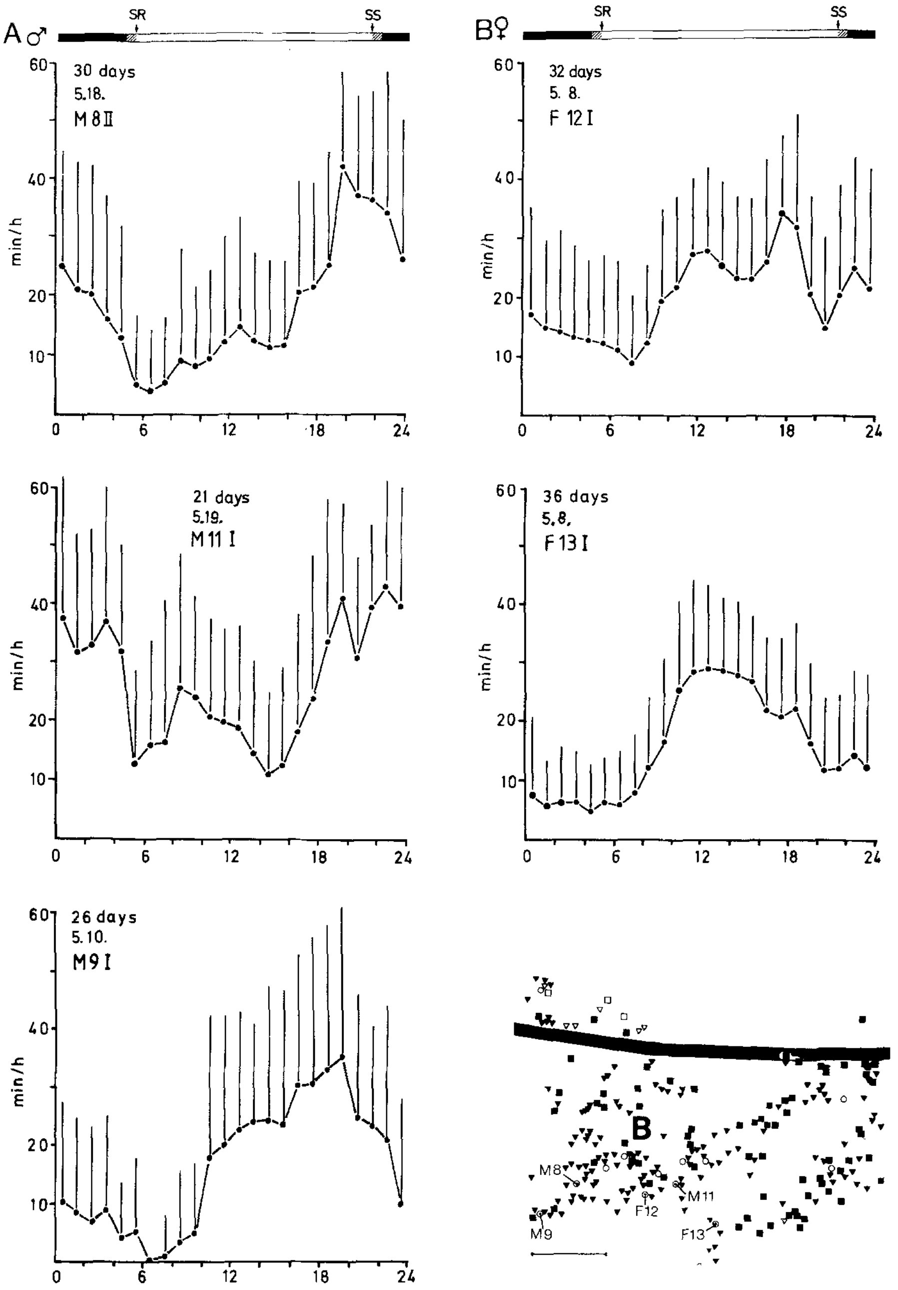

Fig. 6A, B. Mean diel activity in min per h of **A** 3 males and **B** 2 females during the 24-h nature light-dark cycle. Number of recorded days with the date of the first recording day are indicated in the graphs. *Vertical lines* are standard deviations of the means. *Bars* above **A** and **B** as in Fig. 4. *Inset* indicates the position of the recording devices (*open circles*) among occupied burrows (all other symbols) in area B. For further details see text

no significant difference between male and female timing (*U* test, $P > 0.05$). Figure 4B shows the total number of crickets found in the trench during the daytime. Fifteen males and 3 females were found in the trench at the start of daily routine surveys (4:00 to 7:30 a.m.). Since we did not observe any walking crickets between 4:00 and 7:30 a.m. it seems safe to conclude that these animals fell into the trench at night. Assuming that our conclusion is correct, more males than females migrated during the night.

Diel pattern of the male calling song

The calling activity of 12 selected males of the population was investigated continuously. Since most males migrate, we had to cage those males. As a consequence they could not mate. Figure 5 shows the diel pattern of the calling activity of 4 of the 12 males.

Male 5-1 was predominantly day-active at the start of the actogram and then changed to predominant night activity. With increasing age its activity

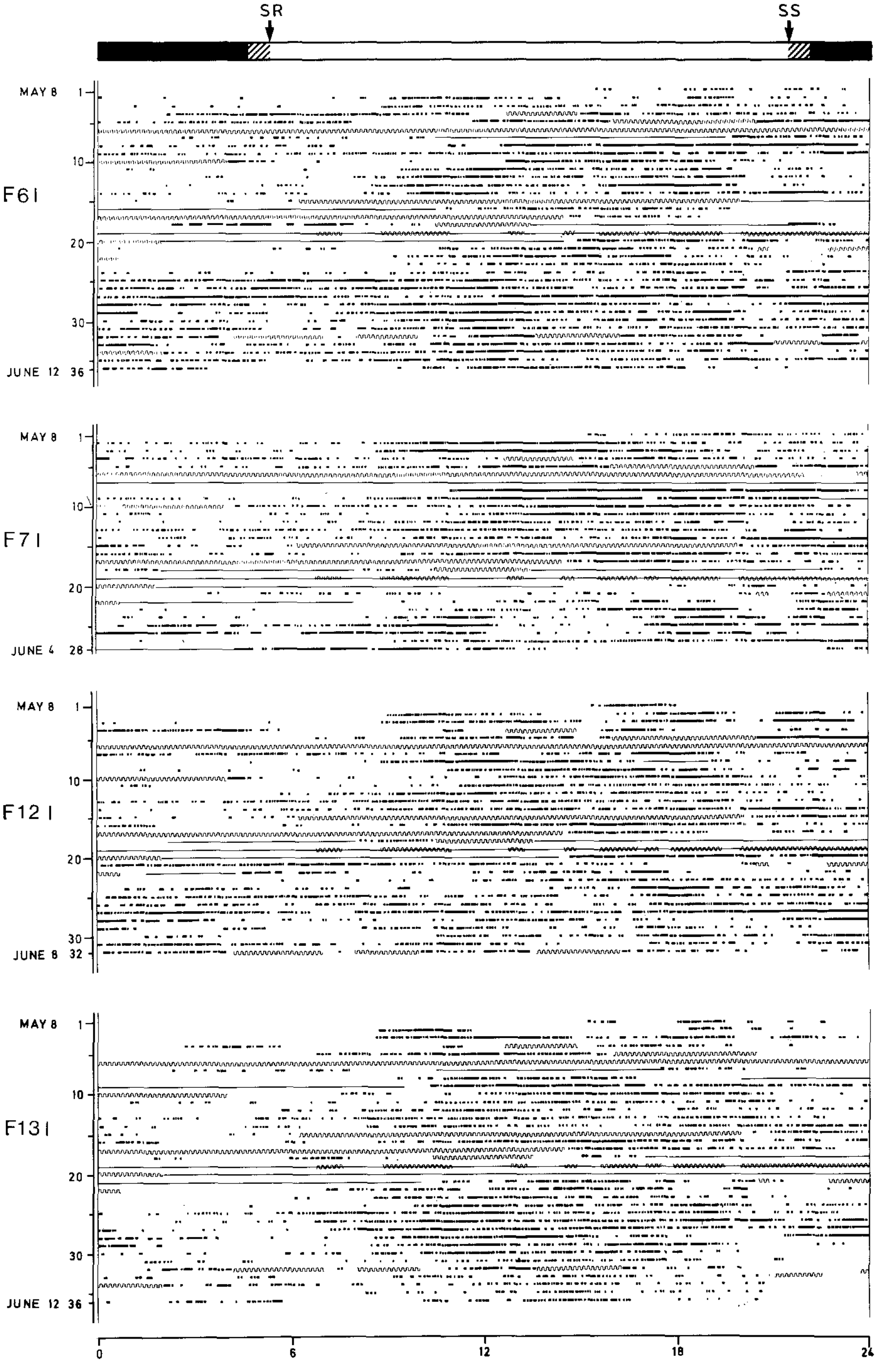

Fig. 7. Event recorder displays of the locomotor activity of 4 females between 8 May and 12 June. All symbols as in Fig. 5. For further details see text

moved into the light period. During the last 4 days before it died its calling activity was weak and again restricted to the light period. *Male 8-II* was initially active both day and night, but later had its main calling activity during the night. *Male M9-I* was mainly day-active and male *M11-I* more night-active. All males showed periods of low activity, during which longer periods of silence were interrupted by calling bouts in the range of some minutes up to more than 1 h. These bouts do not recur at the same time on successive days. In all 4 actograms a gap in calling activity before dusk can be discerned.

Figure 6A presents the mean calling time in minutes per hour for three of the males shown in Fig. 5, averaged over all days a particular male was recorded. The data were calculated from the actograms (see Methods). The figure shows distinct activity peaks (U test, $0.01 < P < 0.05$), for each of the three males but at different times of the natural light-dark cycle. Of the 12 males whose calling activity was recorded over at least 7 days, 6 were predominantly night-active, 4 were day-and-night-active, and 2 were predominantly day-active. A typical feature of the pattern of the night-active males is that their block of night activity started 2–3 h before sunset (Fig. 5, M8-II and M11-I, and Fig. 6A). Male 5-I was the only male with a conspicuous and consistent change of its diurnal activity pattern during the time of recording. On the basis of its average pattern it was defined as day-and-night-active.

There were differences not only in the diel calling pattern of different males, but also in the amount of calling per day. Of the 12 males recorded, the weakest singer called for 329 min on its most active day, and its average call rate over the 7 days recorded was 238 min per day. The strongest singer called for 980 min on its most active day, and its average call rate over the 21 days recorded was 635 min per day (M11-I). One male (M1-I) was recorded for 40 days with a daily average of 497 min and a maximum of 871 min. Predominant day-callers had the lowest calling activity. All 6 night-callers were among the males with the highest calling activity (M11-I and M1-I). Since all males whose calling activity was investigated had to be caged (see Methods), we could not determine whether males with different calling durations attracted different numbers of females and/or males.

Diel pattern of female locomotory activity

Figures 6B and 7 show that female locomotory activity occurred mostly during the light phase of the natural light-dark cycle. As for male calling, the activity was lowest between 6:00 and 10:00 a.m. and during the late dark phase starting around midnight (Fig. 7). Periods of low motor activity were interrupted by short activity bouts. Some females displayed high activity throughout the night on some days but not on others (F6-I and F12-I, 25–29 May). As for male calling, there was no compensatory increase in activity after periods of rain. Note that locomotory activity of female F12-I in Fig. 6B shows a significant depression ($P < 0.05$) before dusk. This depression was evident for 4 of 7 females recorded.

Comparison of female and male activity

Although male calling activity (Fig. 8B) and female locomotion (Fig. 8A) cannot be compared quantitatively, several points can be deduced. First, comparison of the standard deviations indicate that the diel locomotory pattern of the 7 females is less variable than the diel calling patterns of the 12 males (U test, $P < 0.001$). However, a comparison of the motor patterns of the 7 females (Friedman test) shows that they are significantly different from each other ($P \ll 0.01$). Of the 7 females recorded 4 are day-active and 3 are day-and-night-active but with a strong tendency to a day-active pattern, i.e. the amount of day-activity was

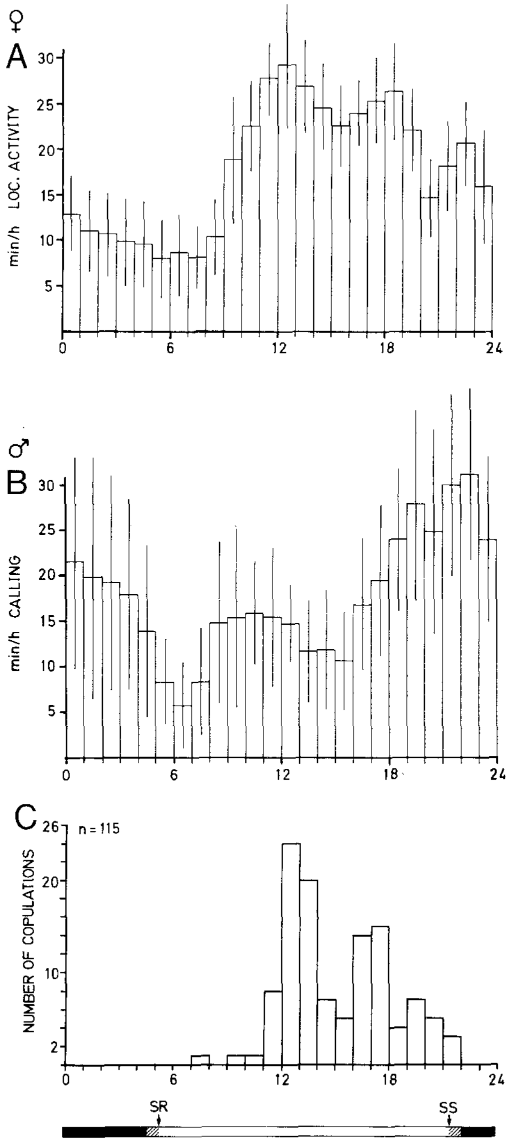

Fig. 8. **A** Sum of the mean locomotory activity per hour of the 7 females. **B** The mean calling activity per hour of 12 males, recorded by the automatic devices. **C** The distribution of copulations observed between 8 May and 28 June ($n = 115$). *Vertical lines* in **A** and **B** are standard deviations of the means. *Bar* below **C** as in Figs. 4–7. For further details see text

Table 1. Number of copulations of selected females and distances between burrows where individuals remated

No. of female	Date	No. of burrow	Copulation +/−[a]	Distance in m[b]	No. of male
42	5/10	B3	−		
	5/11	B70	+	0.3	208
157	5/ 8	A161	+		2
	5/ 9	A156	+	5.45	180
190	5/14	B48	−		
	5/15	B113	−	2.5	
	5/16	B13	+	2.75	192
219	5/14	B121	+		202
	5/21	C23	+	10.6	[c]
	5/30	C21	+	6.8	234
242	5/18	D111	+		208
	5/20	C50	−	46.5	
243	5/18	C50	−		[d]
	5/21	C50	+		208
	5/29	C23	+	3.2	48
	5/30	C23	+		48
	6/ 4	C22	+	0.95	215
	6/ 6	C57	+	6.15	82
	6/ 7	C23	+	6.85	297
	6/11	C22	+	0.95	224
	6/13	C50	+	2.85	377
	6/16	C21	+	3.8	48
	6/24	C50	−	3.8	
276	5/30	B128	+		192
	6/24	C21	+	10.9	48
341	6/ 7	C17	−		
	6/13	C21	+	4	48
	6/17	C17	−	4	
	6/23	C57	−	2.85	
	6/24	C21	+	1.2	48

[a] Copulations (−): particular females which were found alone in a burrow without carrying a spermatophore

[b] Distances between burrows are calculated as straight lines between the burrows where a female had been found

[c] Female 219 carried a spermatophore but was found alone in burrow C23

[d] Female 243 approached a pair and was chased away by the male

Note that also particular males copulated frequently. Male 208 migrated 47.2 m between burrow B70 (11 May) and D111 (18 May). It was refound on 21 May in burrow C50, 44.5 m away from burrow D111

53.5%–58.4% (for pattern definition, see Methods). Thus, in spite of the general impression that female activity is higher during the daytime, there are individual differences in the motor patterns of the females. Second, both female locomotion and male calling display a significant peak around noon. Third, female locomotion shows a small peak at 10:00–11:00 p.m. when calling reaches its highest level of the 24-h cycle. Fourth, as would be expected from the actograms (Fig. 7) female locomotion shows a depression just before sunset.

Copulations

Copulating pairs were located almost exclusively by the male courtship song. The courtship song is distinctly different from the calling song, and is performed by males after physical contact with an approaching female (Gerhardt 1913). In only one case did we find a female carrying a spermatophore without finding the male (see Table 1, female 219). There are two significant peaks of copulation (Fig. 8C), one after noon and a smaller peak between 4:00 and 6:00 p.m. There is a sharp decline towards dusk. In the early morning, very few copulations were observed. This is consistent with the observation that during the night and the early morning very few migrating females were found (Fig. 4). No courtship song was heard on the three nights where we checked for copulations (see Methods). Thus, we assume that few if any copulations took place during the night in our study population. This is supported by the observation that 96% of all copulations occurred at temperatures above 16° C. Only 5 of the 115 copulations observed during the day took place at below 16° C. During our observation period the temperature dropped at dusk until 11:00 p.m., from an average of about 16.5° C to 13.5° C. After 2:00 a.m. the temperature was usually below 10.5° C until 7:00 a.m.

Individual females were observed to copulate up to nine times (Table 1). Female 243 moved within a small area of plot C between 18 May and 24 June. She visited three burrows more than once for matings but remated only once with the same male (M48) in one of these burrows (C23) because males also changed burrows frequently and mated several times (see Table 1, male 48). The majority of other females did not seem to have moved large distances, (females 42, 190, 243, 341). Female 242 is one of the females which were observed to have moved over long distances.

All 115 burrows in front of which a copulating pair was observed were rechecked for 3 consecutive days. Of the 115 pairs only 14 stayed together for 1 day and 8 pairs for 2 days. In most cases the female could not be found subsequently in the burrow where a sexual interaction had taken place (91 out of 115); 38 of the 115 males had also moved within the first day. Table 1 shows one example where a male copulated with two females within 2 h (male 48 with females 276 and 341 on 24 June).

Not all copulations occurred in front of a male burrow. Seven copulations were observed in front of a burrow occupied by a female on that particular day. One male was observed to copulate on three successive days with the same female, at a time when he had no burrows of his own (24–26 June: very near the end of the mating season). This male moved around in a sparsely populated part of the fertilized meadow north of area B and called continuously.

Comparison of female and male activity and copulations

Pairwise comparisons between the mean locomotory activity of females (Fig. 8A), mean calling activity of the males (Fig. 8B) and the distribution of the observed copulations (Fig. 8C) in the time window between 7:00 a.m. and 10:00 p.m. reveal a significant correlation between female locomotion and copulations (Spearman rank test, $P < 0.01$). No significant correlation ($P > 0.1$) was found between female locomotion and male calling; nor between male calling and copulations.

Predation

Many adult crickets fall prey to lizards. Most of them were caught in front of their burrows (5 of 7 observed kills). In one case a lizard waiting in front of a male burrow snapped off a hind leg of a male cricket when it appeared at its burrow entrance abdomen first. In addition, nearly 30% of the 384 marked crickets were injured, mainly on the tarsi and cerci, and in some cases complete hind legs were lost. Of these injuries 70% were to males. After the start of the calling period, magpies (*Pica pica*), carrion crows (*Corvus corone corone*) and starlings (*Sturnus vulgaris*) frequently visited the study area. All these birds are known to feed on crickets.

Discussion

The main results of our investigation are: (1) that the timing of female locomotory activity and of the male calling song do not overlap to the extent expected from laboratory experiments on *Teleogryllus commodus* (Loher 1972, 1979a); (2) that no significant correlation was found between male calling and copulations; and (3) that the timing of female locomotory activity and the distribution of the copulations show a significant correlation.

Male calling and female walking have never previously been recorded automatically in the field. The actograms show that individual males call predominantly either during the night, during the day, or both day and night, similarly to those observed under artificial light-dark conditions (Honegger 1981), while females are all more or less day-active. The sum of male calling was highest early during the night throughout our observation period, as predicted by Walker (1983) as an optimal male strategy, and female locomotory activity was still relatively high during this period. Since no copulations were observed during this period, female locomotion would presumably not be a phonotactic response bringing the female into physical contact with a male, but instead would involve other activities (Walker 1983).

Particularly at the start of the reproductive period in May, night temperatures are below the temperatures at which copulations occur. Hence, there may be a constant environmental pressure for females to shift their sexual activities into the day. Other orthopterans shift their phonotactic activities to mid-afternoon during cold spells (Walker 1983).

In spite of low night temperatures, some night-active males called until sunrise (e.g. Fig. 6; males

M8-II and M11-I) although there are no receptive females available. *Gryllus campestris* males in the Caucasus have a morning peak and a night peak (5:30 p.m. to midnight) of calling (Popov 1975). The upper and lower temperatures in the Caucasus are more extreme than in our climate and suppress calling and locomotion equally. In Florida, *Gryllodes supplicans* males which call throughout the night increase their opportunity of mating because females are also active throughout the night (Sakaluk 1987).

Night-callers are not completely silent during the day. They call frequently in bouts often exceeding 1 h. In aggregated dense populations such as ours, with a mean distance of 146 cm between individuals at the time of the imaginal moult, these daytime calling bouts of night-callers would be sufficient to compete with day-callers and attract females (see Hedrick 1986). Walker (1983) suggested that females may keep track of a male for a period of time, and Caucasian *G. campestris* females and males were observed to approach burrows of males which were not calling at the time (Popov et al. 1974). Sakaluk and Belwood (1984) have shown that predators intercept *G. supplicans* females during their phonotactic response. If females approach males that are not at that time calling they avoid interception. Our data (p. 287) suggest that day-active predators may locate *G. campestris* males acoustically. Alexander (1961) proposed that in dense populations males and females should encounter each other by chance. We show that males can find a female (apparently by accident) and copulate with her (p. 286).

The male calling song attracts not only females but also other males. Males changed burrows both during the day and during the night (Fig. 4A, B) and sometimes males tried to force other males out of their burrows by attacking them. Night callers call quantitatively more than day callers, (calling and walking do not occur simultaneously); they would therefore attract more competitors. However, predominant night-calling may be a strategy to avoid day-active birds or lizards which are less efficient at night and day-calling may be as dangerous as moving.

Many females copulated more than once with different males in restricted areas. This is in agreement with observations on other cricket species (Sakaluk and Cade 1980; Simmons 1986; Sakaluk 1987). The majority of the females which had mated could not be found at the mating-burrow 1 day after a copulation. Thus, for a male the opportunity to mate with a female which it has attracted usually passes quickly and its only chance to attract another female is to keep singing. Our actograms in the laboratory and in the field show that males sing until shortly before they die.

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