

**REPRODUCTIVE BEHAVIOUR OF THE
DECORATED CRICKET, GRYLLODES SUPPLICANS
(ORTHOPTERA: GRYLLOIDAE): CALLING SCHEDULES,
SPATIAL DISTRIBUTION, AND MATING**

by

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(With 4 Figures)
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Introduction

Male crickets (Orthoptera: Gryllidae) compete for females through direct physical aggression (ALEXANDER, 1961; BURK, 1983; BOAKE, 1984; DIXON & CADE, 1986) and acoustic signalling behaviour (ALEXANDER, 1975; CADE, 1979a). Females respond phonotactically to the calling songs of conspecific males by walking or flying to them (WALKER, 1957; ZARETSKY, 1972; ULAGARAJ & WALKER, 1973; PAUL, 1976; POPOV & SHUVALOV, 1977; CADE, 1979a; FORREST, 1980; SAKALUK, 1982). Mating is accomplished when a male successfully transfers the sperm-containing ampulla or spermatophore, which remains outside the female's body following the mating (ALEXANDER & OTTE, 1967). Often, the female subsequently consumes the evacuated spermatophore (ALEXANDER & OTTEN, 1967; LOHER & RENCE, 1978; SAKALUK & CADE, 1980, 1983).

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The success of a male cricket in obtaining mates depends on when he calls and on where he positions himself relative to the location of other singing males. Males should call from locations at which they are likely to encounter females. One obvious possibility is for males to signal from sites at which there are resources important to females (food, oviposition sites, *etc.*). The benefits derived from this strategy depend on the spatial distribution of resources (EMLEN & ORING, 1977); if resources are abundant and scattered throughout the habitat, it may not be profitable for a male to call from these locations. Instead, if females compare different males before selecting a mate, the optimal location for a singing male may be next to other calling males (*i.e.* lek-breeding behaviour in acoustical insects, ALEXANDER, 1975). This apparently is the case for crickets; a variety of studies have demonstrated a significant spatial aggregation of males in areas within which there is no obvious clumping of resources (CAMPBELL & CLARKE, 1971; CADE, 1979a, 1981; CAMPBELL & SHIPP, 1979; CADE & OTTE, 1982).

Additionally, males should call only when receptive females are available (WALKER, 1983a). However, this simple rule should be subject to the energetic constraints on singing (PRESTWICH & WALKER, 1981), the activity of acoustically orienting predators (WALKER, 1964; CADE, 1975, 1984; CADE & WYATT, 1984; SAKALUK & BELWOOD, 1984), the influence of temperature (ALEXANDER & MERAL, 1967), and the potential for aggression from other males (CADE, 1979a). The temporal availability of females should, in turn, be determined by when females mature, temperature, predators, and the time required by females to perform other relevant biological activities (WALKER, 1983a).

WALKER (1983a) suggested that the temporal availability of females generally would peak in the 1-2 hrs following sunset because: 1) visual predators would select against female activity during the day, 2) the temperature at night would be optimal (warmest) earlier in the evening, and 3) females maturing during the day would first become available at sunset and mate early on in the night. Based on this analysis, WALKER (1983a) concluded that male calling likewise should peak in the same 1-2 hr period. However, calling periods of crickets generally extend past the time at which calling theoretically is expected to cease (ALEXANDER, 1960; WALKER, 1983a). WALKER (1983a) explained this anomaly by introducing the concept of the extended 'spree'; males call longer than expected because females utilize calling durations to choose among potential mates (*i.e.* females do not mate as soon as they become available but rather, monitor male calling for some time before copulating).

An alternative explanation that would account for extended periods of male calling, is that females make themselves available to other males later in the night, subsequent to earlier matings. If females: 1) mate more than once, 2) experience only a brief refractory period after mating, and 3) leave their mates some time after copulation, then males that call past the initial mating period should benefit in terms of additional matings. This explanation presumes that some benefits accrue to females through extra matings with other males. In this regard, SAKALUK & CADE (1980, 1983) suggested that female crickets, by mating repeatedly, might gain nutritional benefits through the consumption of additional spermatophores. This may be of particular relevance to the cricket species investigated here; male *Grylloides supplicans* transfer a spermatophore that includes a large gelatinous portion (spermatophylax), devoid of sperm, that is removed and eaten by the female after mating (ALEXANDER & OTTE, 1967a; SAKALUK, 1984). In katydids (Orthoptera: Tettigoniidae), the consumption of additional spermatophylaxes results in a significant increase in the size and number of eggs produced by the female (GWYNNE, 1984). While it would be convenient for a female to obtain these nutritional benefits from the same male, this would depend on the time required by her mate to produce new spermatophores (reviewed by SAKALUK, 1985). Additional benefits females could obtain by mating more than once include correcting for matings that do not result in successful insemination (LOHER & RENCE, 1978), and replacing the sperm of inferior mates with that of superior genotypes (WALKER, 1980).

It is clear, therefore, that our understanding of calling schedules and spatial distributions in crickets requires detailed information on the parameters of mating of males and females. Important parameters include: 1) mating frequencies, 2) intercopulatory intervals, 3) durations of copulations, and 4) the fate of spermatophores. Few studies have related calling patterns and spatial distributions to the sexual behaviour of individuals, but notable exceptions include CADE (1979a), WALKER (1980, 1983b), and EVANS (1983). Here I examine the adaptive significance of the temporal and spatial patterning of sexual activity in the decorated cricket, *Grylloides supplicans*. I do so by providing: 1) data on the calling schedules and spatial distribution of males in a natural population, 2) information on the site fidelity and locomotor activity of marked individuals in an outdoor enclosure, and 3) detailed observations on the sexual behaviour of individuals in the laboratory.

Methods

A. Field studies.

Calling schedules and nearest-neighbour distances of male *G. supplicans* were investigated at the University of Florida, Gainesville, in May/June 1981. The study site was an irregular-shaped area surrounding the Florida State Museum, and included a small parking lot, large courtyard, split terrace, and a sidewalk. The site was about 4140 m², and was bounded by other buildings. The study area was not uniformly illuminated, with some sections dimly lit by streetlights or by lights from within the building. On a typical night, temperatures ranged from 22°C at 2200 hr to 17°C at 0630 hr.

Male *G. supplicans* usually located their burrows in the fine gravel that filled the narrow spaces separating concrete courtyard stones, or the abundant cracks in curbs and sidewalks. Occasionally they called from under garbage bins, in the drains of storm sewers, or beneath temporary shelters such as fallen leaves and candy wrappers. This habitat is not unusual for this species; *G. supplicans* occurs circumglobally in tropical regions where it normally is associated with human habitation (KHAN, 1954; BHOWMIK, 1972; AHMAD & SIDDIQUI, 1983; VICKERY & KEVAN, 1983; THOMAS, 1985).

Each night of the study (n = 12; May 8-12, 20-23, 26; June 8, 9), I located the burrows/sites of all calling males. The site at which a cricket called was marked with a dab of fluorescent paint so that it could be readily relocated with a portable UV light. Occasionally, males called from locations from which they could not be observed directly (*e.g.* some males called from behind a metal flashing that was fastened at the bottom of an outside wall). When this occurred, I marked the spot at which the calling was loudest. The entire study area was systematically surveyed at different times throughout the night (1900 hrs-0700 hrs); thus, for each hourly interval, it was possible to determine the number of males calling in the study area as a percentage of the night's total. The following day, the distance between the site at which a male called and that of his nearest neighbour, was measured for all males.

The calling intensity of five different males was recorded at various times throughout the night (four were measured on the same night, the fifth was measured on another night). Measurements were made with a Bruel and Kjaer impulse precision sound level meter Type 2204 (A weighting), fitted with a half-inch microphone (4165) that was held 2 cm directly above the burrow of the calling male.

B. Outdoor arena.

Studies were conducted in a large outdoor arena (12.5 × 12.5 m) at Brock University, St. Catharines, Ontario, to examine sexual differences in the site fidelity and movement of *G. supplicans*. The arena was enclosed by a galvanized steel wall (1 m), secured to a chain link fence (2 m). Chicken wire was suspended over the top of the enclosure to deter birds from entering the arena. The area enclosed by the fence was covered with grass, excepting a 20-cm strip along the inside edge where sand and gravel had been tamped in at the bottom of the wall.

The arena was divided into 25 quadrats, each 2.5 × 2.5 m. In preliminary studies, crickets invariably walked to the wall regardless of where they had been released in the arena, and spent virtually all of their time in the 16 outside quadrats. As such, the 16 outside quadrats defined the study area for this investigation.

Twenty wooden shelters were placed against the inside wall of the arena, and distributed randomly over the 16 quadrats; no quadrat contained more than three shelters. Each shelter consisted of a block of wood (15 × 15 × 2 cm) whose underside contained a t-shaped hollow. Each arm of the 't' was 1 cm deep × 2 cm wide and extended to the edge of the shelter, thus enabling crickets to crawl easily beneath the shelter.

In total, 11 adult males and 10 adult females (collected as late-instar nymphs) were released into the arena. The quadrat into which a cricket was released was determined using a random numbers table. Data collection took place from 21 July to 2 August 1981,

inclusive. Because of different release dates and the loss of some individuals, the number of males in the arena varied from 7-10 over the course of the study period ($\bar{X} = 9.2/\text{day}$); the number of females varied from 5-7 ($\bar{X} = 6.6/\text{day}$).

Crickets were marked with fluorescent paint on their hind femora so that they could be located readily with a portable UV light. They also each were marked on the pronotum with a number (or letter) to permit individual identification. Each night of the study, a systematic search of the arena was conducted once every hr for eight consecutive hrs, beginning at 2130 hrs. The quadrat and shelter location for each cricket were recorded at all sampling intervals. The edge of each shelter was slowly raised and carefully lowered to minimize the disturbance to any crickets beneath the shelter. If a cricket was exposed rather than beneath a shelter, the distance from the nearest marker (shelter or quadrat boundary) was estimated. Thus it was possible to determine the linear distance that a cricket moved in successive sampling periods. If a cricket could not be found during a given survey, a '?' was entered for that individual. Additionally, data were recorded only for individuals who had been in the arena for at least 24 hrs.

Calling activity of males was recorded at each sampling period. The raising of a shelter invariably caused a male to cease calling. However, because a male's wings remained elevated in the calling position, it was possible to determine the identity of a caller when two or more males were beneath the same shelter.

C. Laboratory.

Laboratory studies were conducted to determine the parameters of mating behaviour and ontogeny of reproduction in *G. supplicans*. Crickets used in laboratory studies were first-generation descendants of crickets collected at Florida in July, 1981. They were housed in glass terraria and provided with ample food (Purina™ cat chow) and water in test tubes plugged with cotton wicks. The surface area of each terrarium was increased by the addition of several egg cartons. Eggs were obtained by allowing adult females to oviposit in trays containing a layer of moistened vermiculite. Late instar individuals of each sex were removed and held separately, thus ensuring their virginity upon the imaginal ecdysis. Adult crickets were considered 1 day old on the day they were found to have molted. All crickets were maintained at $28 \pm 2^\circ\text{C}$ and 30% relative humidity, on a 12 h light : 12 h dark photoperiod.

Fifteen one-day-old virgin adult males and 15 one-day-old virgin adult females each were placed in individually marked, plastic margarine tubs (2 L), covered with screened lids. These individuals hereafter are referred to as 'experimental' crickets. Cat chow and two petri dishes (5.5 cm) containing fine-grade vermiculite were placed into each of the 30 containers. The vermiculite was moistened daily and served as an oviposition substrate. Two randomly selected adults, opposite in sex to the experimental cricket, were introduced into each container on each night of the study (4 hrs into the dark portion of the photoperiod). These introductions were staggered by a few minutes to enable observation of matings occurring immediately after contact between a male and a female. The mating behaviour of experimental crickets was monitored continuously for four hrs. Introduced crickets were removed immediately after the 4-hr observation period.

The mating frequency of experimental crickets was recorded for 20 consecutive nights. The following parameters were recorded for each mating: 1) its temporal occurrence, 2) its duration, and 3) the fate of the spermatophore.

Experimental crickets were kept in their respective containers, subsequent to the 20-day study period, until they died. Adult longevity was recorded for each cricket. Offspring emerging from oviposition dishes in the containers of experimental females were aspirated and counted daily. Ovaries of females were removed after they died, and unfertilized eggs remaining in the ovaries were counted. Any unhatched eggs remaining in the oviposition dishes also were counted.

Data from all experiments were analysed with a Hewlett-Packard statistical analysis package, and in accordance with ZAR (1984). All values are means \pm S.E.

Results

A. Field studies.

The number of male *G. supplicans* calling in the study area ranged from 18-38 ($\bar{X} = 25.2 \pm 1.7$). Fig. 1 shows a cumulative frequency distribution of the nearest-neighbour distances of all calling males. The majority of males (59%, 130/221) called within 4 m of their nearest calling neighbour; some males ($n = 9$) were found within as little as 40-50 cm of each other.

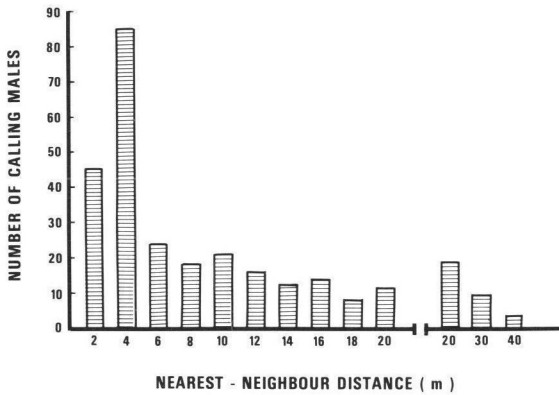


Fig. 1. Frequency distribution of the distances separating nearest calling *Grylloides supplicans* in a field population, cumulated over 12 nights.

Fig. 2 shows the average number of males that called (as a % of the night's total) at various times throughout the night. Shortly after sunset, the number of calling males increased sharply and, thereafter, decreased only marginally throughout most of the night. About two and one-half hrs before dawn, there was a rapid decrease in the number of calling males such that shortly after sunrise, no males were heard calling.

The calling intensity of males, measured at various times throughout the night, is shown in Fig. 3. The calling intensity of individual males was not constant over the course of the night. The calling intensity of four of the five males appeared to diminish slightly towards dawn. The fifth male exhibited a steady decrease in calling intensity over the course of the night, but showed a sudden increase two hrs before sunrise.

Additional observations indicated that males remained at the same sites over successive nights. For example, of the 18 sites first marked on May 8, calling was recorded at 14 of them the next night, at 9 of them

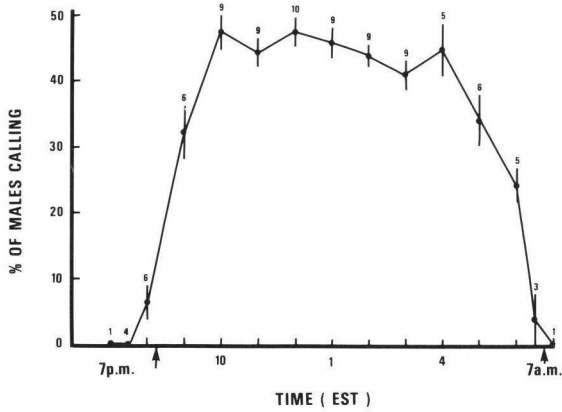


Fig. 2. Temporal pattern of calling in a field population of *G. supplicans*. The number of calling males is shown as the mean percent of the night's total (\pm SE). Sample sizes are shown above the means, and represent the number of nights each hourly interval was sampled. Arrows beneath the X-axis indicate sunset and sunrise, respectively.

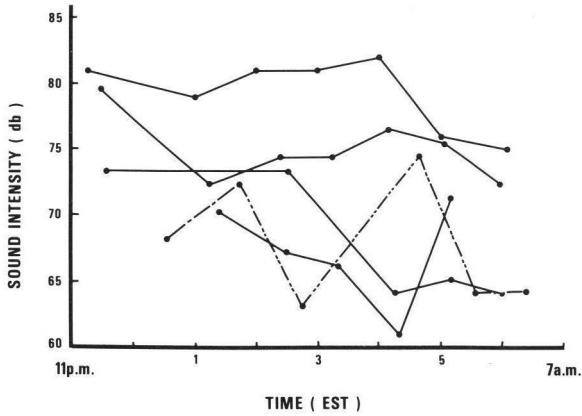


Fig. 3. Changes in the calling intensity of individual *G. supplicans* over the course of the night. The dashed line represents a male that was monitored on a different night from the other 4 males (solid lines).

on May 12, and at 7 of them on May 21 (13 days later). However, because individual males were not marked, it was not possible to determine if it was always the *same* male that called from a marked site. Thus, site fidelity of males was examined more rigorously in a later experiment (see section below).

B. Outdoor arena.

The site fidelity and hourly and nightly movements of individual *G. sup-plicans* are shown in Table 1. Only crickets that were in the arena for at least eight days were included in the calculations. For within-night comparisons: 1) the distance moved (m) per hr is the sum of the distances over which an animal moved in consecutive sampling periods, divided by the total number of consecutive sampling periods, 2) the site fidelity index is the number of times an individual was found in the same location as the previous sampling period, divided by the total number of consecutive sampling periods (a site fidelity index of 1.0 indicates that the probability of finding an individual in the same location one hr later is 1.0), and 3) the percent of time spent under shelters is the percent of the total number of sampling periods an individual was found beneath a shelter. Note that for the first two measures, 'consecutive' sampling periods do not include the last sampling period of one night and the first sampling period of the next; only data from within-night consecutive sampling periods are included in the analysis.

The mean distance moved (m) per hour was significantly greater for females than for males (ANOVA, $F = 20.1$, $p < 0.002$). Thus, females moved further than males, on the average, from where they were located one hr earlier. The mean site fidelity index of males was significantly higher than that of females ($F = 47.6$, $p < 0.001$; arc-sin \sqrt{X} transformed to normally distributed data); males were more likely than females to be found in the same location from one hr to the next. Also, males spent significantly more time under shelters than did females ($F = 53.2$, $p < 0.001$; arc-sin transformed).

For between-night comparisons: 1) the distance moved (m) per night is the sum of the distances over which an individual moved in consecutive nights, divided by the total number of consecutive nights that the individual spent in the arena and 2) the site fidelity index is the number of times an individual was found at the same site it occupied the previous night, divided by the total number of consecutive nights. Since crickets moved at least some distance over the course of a night, it was necessary to determine what constituted an individual's 'site' for a particular evening. I used the following criterion: the location (*i.e.* shelter) at which a cricket most often was found in the eight sampling periods over the course of a night was considered its primary site for that night; if there was a tie in the number of sampling periods spent at two or more locations, the one last occupied was considered the primary site.

TABLE 1. Site fidelity and hourly and nightly movement of individual *G. supplicans* in an outdoor arena

| | Males | | | | | | | | | | | | $\bar{X} \pm \text{S.E.}$ |
|--|-------|------|------|------|------|------|------|------|------|------|--|--|---------------------------|
| | N | A | T | V | D | F | 2 | 1 | X | M | | | |
| <i>Within night</i> | | | | | | | | | | | | | |
| \bar{X} distance moved (m) in successive periods | 0.46 | 0.27 | 0.27 | 0.54 | 0.20 | 0.32 | 0.15 | 0.17 | 0.31 | 1.17 | | | 0.39 \pm 0.09 |
| site fidelity index | 0.77 | 0.88 | 0.89 | 0.76 | 0.90 | 0.73 | 0.94 | 0.87 | 0.87 | 0.67 | | | 0.83 \pm 0.03 |
| % of time under shelter | 96.9 | 95.8 | 95.8 | 95.8 | 99.0 | 84.8 | 97.5 | 96.9 | 95.3 | 95.2 | | | 95.3 \pm 1.20 |
| <i>Between night</i> | | | | | | | | | | | | | |
| \bar{X} distance moved (m) in successive nights | 0.46 | 0.56 | 0.86 | 1.20 | 0.56 | 0.62 | 1.89 | 0.32 | 0.00 | 0.83 | | | 0.73 \pm 0.16 |
| site fidelity index | 0.58 | 0.73 | 0.82 | 0.82 | 0.73 | 0.91 | 0.89 | 0.71 | 1.00 | 0.86 | | | 0.80 \pm 0.04 |
| nights spent in arena | 12 | 12 | 12 | 12 | 12 | 12 | 10 | 8 | 8 | 8 | | | 10.6 \pm 0.60 |
| longest interval at same site (nights) | 3 | 5 | 5 | 6 | 8 | 8 | 8 | 2 | 7 | 6 | | | 5.80 \pm 0.66 |
| <i>Females</i> | | | | | | | | | | | | | |
| K | 2 | 0 | N | 3 | L | | | | | | | | $\bar{X} \pm \text{S.E.}$ |
| <i>Within night</i> | | | | | | | | | | | | | |
| \bar{X} distance moved (m) in successive periods | 0.93 | 0.98 | 0.72 | 1.38 | 1.95 | 2.02 | | | | | | | 1.33 \pm 0.22 |
| site fidelity index | 0.59 | 0.52 | 0.45 | 0.35 | 0.32 | 0.19 | | | | | | | 0.40 \pm 0.06 |
| % of time under shelter | 78.4 | 76.2 | 82.8 | 76.1 | 62.4 | 56.4 | | | | | | | 72.1 \pm 4.19 |
| <i>Between night</i> | | | | | | | | | | | | | |
| \bar{X} distance moved (m) in successive nights | 1.78 | 0.89 | 1.16 | 3.07 | 3.12 | 4.42 | | | | | | | 2.41 \pm 0.55 |
| site fidelity index | 0.50 | 0.70 | 0.25 | 0.10 | 0.40 | 0.20 | | | | | | | 0.36 \pm 0.09 |
| nights spent in arena | 13 | 11 | 8 | 11 | 11 | 8 | | | | | | | 10.3 \pm 0.80 |
| longest interval at same site (nights) | 4 | 6 | 1 | 1 | 2 | 1 | | | | | | | 2.50 \pm 0.85 |

The mean distance moved (m) per night was significantly greater for females than for males ($F = 13.7$, $p < 0.002$; $\log(X+1)$ transformed to normally distributed data). Thus females moved significantly further than males, away from sites occupied previous nights. The site fidelity index also was significantly higher for males than for females ($F = 22.3$, $p < 0.001$; $\text{arc-sin } \sqrt{X}$ transformed); males were more likely to remain in the same location in consecutive nights than were females.

To compare the calling behaviour of individual males, I chose for analysis the longest period of consecutive nights during which the same ten males (Table 1) together were present in the arena. This was a period of six consecutive nights comprised of 48 sampling periods (eight sampling periods per night). Seven females also were present in the arena for four of these nights, and six females were present the remaining two evenings.

The number of sampling periods during which a male called was used as an indicator of the total time spent calling by a male. Calling times of individual males varied widely ($\bar{X} = 11.5 \pm 3.2$ hrs, range = 0-27 hrs), but the number of different females encountered by individual males beneath shelters did not differ substantially ($\bar{X} = 2.9 \pm 0.3$ females, range = 2-5). Although there was considerable variation in the proportion of sampling periods that a male was found beneath a shelter with one or more females ($\bar{X} = 14.5 \pm 2.9$ hrs, range = 5-30 hrs), there was no significant correlation between this measure of a male's mating opportunities, and the time he spent calling ($r = -0.13$; $F = 1.30$, $p > 0.05$). However, the relationship between individual calling and consequent mating opportunities could be obscured by any tendency of males to aggregate under shelters with other males; thus, a non-calling male could increase his mating opportunities simply by locating next to a calling male beneath a shelter, and thereby gaining access to phonotactic females (*i.e.* satellite males- CADE, 1975, 1979a). On the average, male *G. supplicans* were found under shelters with at least one other male in 2/3 of all sampling periods ($\bar{X} = 32.0 \pm 4.3$ hrs, range = 8-48 hrs). Males tended to restrict their associations to the same partner; males 'T' and 'A' were found together in 47/48 sampling periods, 'X' and 'M' in 29/48, '2' and 'F' in 26/48, and 'D' and 'N' in 25/48 sampling periods. The first three pairs consisted of a calling male (calling time: 15-27 hrs) associated with a non-caller (calling time: 0-2 hrs). In the fourth pair, both males called for about the same length of time, 21 hrs and 22 hrs, respectively.

I also examined the behaviour of six females (Table 1) present in the arena during this 6-day portion of the study period. Females were found

under shelters which contained at least one male in 20.3 ± 1.6 sampling periods (range = 16-26). The mean fidelity index of females for those sampling periods during which they were located with males was 0.69 ± 0.06 ; this was significantly greater than the mean site fidelity index of these same females when male presence was not taken into account (see Table 1; paired t test, $t = 4.68$, $p < 0.005$). Thus, the probability of a female changing locations in consecutive sampling periods was significantly reduced when she was with a male. Nonetheless, females often relocated to a shelter containing a different male(s), after leaving the shelter occupied by another male(s) earlier in the evening; I recorded 11 such changes during the 6-night period, occurring at anytime from 0030 hrs to 0430 hrs within a night.

C. Laboratory results.

Experimental females.

Mating frequency.

Females mated for the first time at the average age of 1.9 ± 0.2 days (range = 1-3 days). They mated 22.1 ± 1.4 times over the 20-day experimental period (total = 332, range = 15-33); successful copulations lasted 109.6 ± 3.3 sec ($n = 201$, range = 30-230 sec). Frequently, a female mounted a male and he extruded the spermatophore, but the spermatophore was retained by the male after the female dismounted. The frequency of these aborted matings was 4.8 ± 3.2 (total = 72, range = 1-14), lasting 104.9 ± 10.3 sec (range = 6-450 sec). Thus, 17.8% of all instances in which females mounted males resulted in aborted matings; the rest (82.2%) ended with the successful transfer of the spermatophore. In 13 cases (18% of all aborted matings), an aborted mating occurred while the sperm ampulla from a previous mating was still attached to the female. In three of these cases, the female removed the ampulla of the previous mating immediately after the aborted mating.

There were 3.7 ± 0.5 days (range = 0-7 days) when females did not mate, 10.5 ± 0.7 days (range = 7-15 days) when they mated once, and 5.7 ± 0.9 days when they mated twice (range = 0-13 days). Only once did a female mate more than twice in a day (*i.e.* within the 4-hr observation period); on that occasion the female mated three times. When females mated twice within the 4-hr observation period ($n = 87$), the first of the two matings occurred 17.2 ± 2.4 min (range = <1-146 min) into the observation period. Females remated 89.3 ± 5.7 min (range = 12-210 min) after the initial mating.

Fate of the spermatophore.

The fate of the spermatophore was observed in 297 matings. Females used their mouthparts to detach the spermatophylax from the sperm ampulla in 295 of these matings; this usually occurred within 5 sec of the female dismounting the male (90% of all matings). The female fully consumed the spermatophylax after removing it and subsequently removed and ate the sperm ampulla in 143 matings (48%). This was the most common sequence of events following the dismounting of the male. Complete consumption of the spermatophylax took 39.8 ± 0.7 min (range = 6-120 min). Removal of the sperm ampulla usually occurred a few minutes later (< 7 min); the data on the relationship between the time at which the spermatophylax was fully consumed, and the time at which the sperm ampulla was removed, are in SAKALUK (1984). Often the female only partially ate the spermatophylax, dropping the remaining portion before subsequently removing the sperm ampulla (85 matings, 29%). Females dropped the remaining portion of the spermatophylax 10.5 ± 2.0 min after mating (< 1 min- 104 min). The sperm ampulla was removed usually within a few minutes of dropping the remaining portion of the spermatophylax; the data on the temporal relationship are in SAKALUK (1984).

In 39 matings (13%), the spermatophylax and sperm ampulla were removed simultaneously by the female (*i.e.* the spermatophylax failed to detach from the ampulla such that the entire spermatophore was removed). In the majority of such cases ($n = 29$), this occurred immediately after the female dismounted the male. The ampulla was dislodged against the substrate, rather than eaten, in an additional 16 matings (5%). This occurred before ($n = 9$) or after ($n = 7$) the spermatophylax was fully consumed. Two matings were characterized by unique events. In one, an ampulla attached to a female was dislodged as a result of her engaging in a subsequent mating (*i.e.* the ampulla was dislodged by the thrusting actions of the second male). In the other mating, the male transferred a spermatophore consisting solely of the sperm ampulla; it was removed by the female 21 min after mating.

Theft of the spermatophore.

There were 12 instances in which a portion of the spermatophore was appropriated by an individual to whom the spermatophore had not been originally transferred. On five of these occasions, a male detached a portion of the spermatophylax extruding from the mouth of a mated female,

and consumed it. The female finished consuming the portion of the spermatophylax that she had retained, and subsequently removed the sperm ampulla. I do not know which of the two males was the 'thief', the female's mate or the unmated male. On another occasion, I observed a male remove the extruded spermatophylax of a male engaged in a mating; the copulating male successfully transferred the sperm ampulla, but it was removed and eaten by the female 47 sec after dismounting the male. Six of the 12 instances of spermatophore 'theft' involved the sperm ampulla. In these cases, the male approached the mated female from the rear and, with his mouthparts, removed the attached ampulla and ate it. This occurred 21.0 ± 4.4 min after mating (range = 12-41 min), before the time required for the complete evacuation of sperm (50 min; see SAKALUK, 1984). The identity of the male also was unknown in these cases. Additional examples of spermatophore 'theft' are described in the section on experimental males.

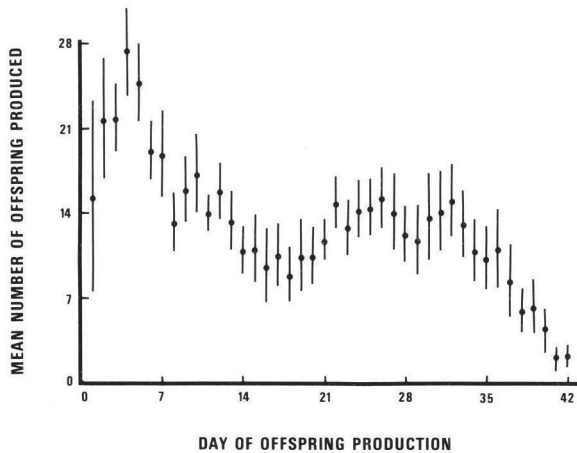


Fig. 4. The average number of offspring produced each day (\pm SE) by female *G. supplicans*.

Female reproduction.

The average number of offspring produced daily by females is shown in Fig. 4. Day 1 of offspring production refers to the first day that offspring emerged in the oviposition containers. Offspring first hatched 29.3 ± 0.4 days after the female's first mating ($n = 15$; range = 27-33 days). Daily offspring production peaked on the fourth day (27.5 ± 3.9 offspring per

female), although a secondary peak occurred on the 26th day of offspring production (15.3 ± 2.6 offspring per female). The mean duration over which offspring hatched was 42.6 ± 2.6 days (range = 26-62 days).

The mean number of eggs laid by females over their entire life was 713.4 ± 73.3 (range = 133-1078 eggs). The mean number of offspring that hatched was 567.7 ± 59.5 (range = 131-935 offspring), representing a mean fertility of $82.9 \pm 3.2\%$.

Adult females lived 79.5 ± 5.4 days in the laboratory (range = 49-129 days). The mean number of unfertilized eggs retained in their ovaries when they died was 10.7 ± 5.1 (range = 0-56 eggs).

Experimental males.

Mating frequency.

Males first mated at an average age of 7.7 ± 0.4 days (range = 6-11 days), and were significantly older than females at their first mating ($F = 154.9$, $p < 0.001$). The average mating frequency of males was 10.9 ± 0.6 (total = 163, range = 5-14), significantly less than that of females ($F = 57.8$, $p < 0.001$). Matings lasted 119.2 ± 6.2 sec ($n = 90$, range = 30-395 sec). Males never mated more than once in a single observation period. Matings occurred 27.0 ± 3.6 min (range = <1-207 min) into the observation period.

The mean number of aborted matings was 0.9 ± 0.3 (total = 13, range = 0-3), lasting 106.2 ± 32 sec (range = 28-435 sec). Thus, 7.4% of all mountings resulted in aborted matings. Aborted matings never occurred after a male had successfully mated.

The mean longevity of males, after the imaginal ecdysis, was 91.7 ± 6.1 days (range = 57-138 days); this did not differ significantly from that of females ($F = 2.23$, $p > 0.05$).

Fate of the spermatophore.

Females removed the spermatophylax with their mouthparts in 128 matings, and did so usually within 5 sec of dismounting the male (92% of all matings). The spermatophylax was fully consumed, and the ampulla subsequently removed and eaten, in 75 matings (58%). The mean feeding-phase duration was 40.9 ± 2.1 min (range = 6-101 min); ampulla removal occurred 10.4 ± 1.3 min later. In 59% of such cases, the ampulla was removed in 7 min or less after consumption of the spermatophylax. In 20 matings (15%), the spermatophylax was only partially eaten, and the remaining portion subsequently was discarded. This remaining por-

tion was dropped by the female 5.0 ± 1.7 min after mating (range = <1-34 min); ampulla removal occurred 13.7 ± 3.6 min later (range = 1-60 min). The spermatophylax was dropped in two additional matings, but it adhered to the prothoracic leg of the female where she resumed feeding on it.

The spermatophylax and sperm ampulla were removed simultaneously in 9 (7%) matings. As was the case with experimental females, this usually occurred immediately after the female dismounted the male. In 6 matings (5%), the ampulla was dislodged by one of the female's metathoracic legs before the spermatophylax was fully consumed.

Theft of the spermatophore.

There were 17 cases in which a mated female was robbed of at least a portion of the spermatophore by her mate ($n = 3$) or the unmated female ($n = 14$). Unmated females engaged in spermatophore theft significantly more often than males ($\chi^2 = 5.88$, $p < 0.025$). In nine of these 17 cases, the entire spermatophylax ($n = 6$) or a piece of it ($n = 3$) was pulled from the mouth of the mated female by her mate ($n = 3$), or by the unmated female ($n = 6$). Theft of the entire spermatophylax occurred 5.0 ± 2.8 min after mating (range = <1-17 min); the mated female removed the attached ampulla 5.0 ± 1.0 min later (range = 2-8 min). There was also one unsuccessful attempt by an unmated female to grasp the spermatophylax from the mouth of a mated female. On that occasion, the two females engaged in a 'tug-of-war' over the spermatophylax, with the mated female successfully retaining possession of it.

The ampulla attached to a mated female was removed by an unmated female on four occasions. This occurred 12.0 ± 4.9 min after mating (range = 4-21). In another instance, the entire spermatophore was stolen by an unmated female before the mated female had removed the spermatophylax. In the remaining three cases of spermatophore theft, an unmated female fed on or removed the spermatophylax while it was still attached at the base of the victim's ovipositor. A female's mate never removed any portion of the spermatophore while it was still attached at the base of her ovipositor.

Discussion

Calling of male *G. supplicans* peaked shortly after sunset, decreased slowly throughout most of the night, and ceased at about dawn. This pattern

of calling activity corresponds to that considered typical of crickets (WALKER, 1983a), and apparently reflects the temporal availability of female *G. supplicans*. The average probability of a female changing locations from one hour to the next was greater than 50%; there was no apparent change in this probability over the course of the night. Females were significantly more likely than males to change locations, both within and between nights. Additionally, the locomotor activity of females, as indicated by the average distance an individual was displaced each hour of the night (and between nights), was significantly greater than that of males. Movement of females was depressed upon encountering males; nonetheless, female *G. supplicans* often relocated to different males later in the night, as also was observed in the cricket, *Teleogryllus commodus* (EVANS, 1983). The reduction of movement in females, following contact with males, may have been due to a reduction in the phonotactic response of females after mating (MORRIS *et al.*, 1975; CADE, 1979b; LOHER, 1981) or to mate guarding by males (ALEXANDER & OTTE, 1967; LOHER & RENCE, 1978). Mate guarding behaviour also occurs in *G. supplicans* (pers. obs.), but its function is unclear. In any event, male *G. supplicans* that call throughout the night increase their opportunities for mating, because females clearly are active throughout the night.

The diversity in patterns of calling, in other cricket species for which there are empirical data, reflects some of the factors affecting the temporal availability of females (WALKER, 1983a). Female mole crickets, *Scapteriscus aetetus* and *S. vicinus*, fly during the early hours of the evening when predator pressure is reduced, and also when temperatures are still above the threshold for flight activity; males call only during this portion of the night (FORREST, 1980, 1983a). In Puerto Rican mole crickets, *S. didactylus* and *S. imitatus*, flight of females is not limited by temperature and males call throughout the scotophase (FORREST, 1983b). Male short-tailed crickets, *Anurogryllus arboreus* and *A. celerinictus*, also restrict their calling to within the first 2 hours after sunset (WALKER, 1973, 1980). In this case, selection apparently has acted on females to increase the number of potential mates by responding only within this narrow time window, and thereby forcing males to call synchronously within the interval (WALKER, 1983a). In contrast, male *A. muticus* in Panamanian populations begin calling shortly after sunset and continue calling for the next 11 hrs; walking or flying females are available throughout the night (WALKER & WHITESELL, 1981).

CADE (1979a) related the calling pattern of male field crickets, *Gryllus integer*, to selective factors acting directly on the males rather than to the

temporal availability of females. In his study, calling increased steadily from sunset and peaked at sunrise, dropping rapidly over the next 2 hours. A peak in calling activity just before dawn also was observed in the cricket *Teleogryllus oceanicus* (LOHER & ORSAK, 1985). CADE (1979a) attributed the morning peak to the recruitment of previously silent males, who are less likely to attract competitors while signalling at this time. The calling intensity of male *G. integer* also was reduced towards dawn, as was the case with *G. supplicans* in this study. CADE (1979a) suggested that the lowered intensity of calling might still be sufficient to attract nearby females, while reducing the risk from acoustically orienting predators.

Comparative data on the locomotor activity and site fidelity of females of other cricket species are few. In *Teleogryllus commodus*, female locomotor activity occurs entirely or mainly in the dark portion of a 12:12 LD photoperiod (LOHER, 1979a), and also is stimulated by male calling (LOHER, 1979b). BATE (1970) showed that the locomotor activity of female *Acheta domesticus* was greater than that of males, as measured by the number of circuits made by individual crickets in a glass cylinder. Additionally, CADE (1979a) showed that female *Gryllus integer* moved significantly longer distances than males in consecutive nights. In contrast, the site fidelity of female *T. commodus* was greater than that of males; 14/25 females remained at the same burrow for 3-4 days, whereas none of 30 males occupied burrows for more than 2 days (EVANS, 1983).

What benefits accrue to female *G. supplicans* by their continuous movement throughout the night? I suggest that females gain increased access to males, and thereby consume additional spermatophores that they otherwise would forego by remaining with the same mate. Females that consume spermatophores may acquire an important source of nutrition. In the katyid, *Requena verticalis*, protein contained in spermatophores ingested by females is incorporated into females' eggs (BOWEN *et al.*, 1984); the consumption of additional spermatophylaxes results in an increase in the size and number of eggs produced (GWYNNE, 1984).

An increased demand by female *G. supplicans* for additional spermatophores was evidenced by: 1) repeated mating, 2) frequent consumption of spermatophores, 3) brief intercopulatory intervals, and 4) the theft of spermatophores from mated females. It could be argued that some of these mating parameters were artifactual of confinement of crickets experimental containers. However, the composition of laboratory cricket groups corresponded to that of groups occurring in the outdoor enclosure (semi-natural environment); that is, it was not uncommon to find 1 female with 2 males beneath the same shelter or *vice versa*. Although females could not avoid males or escape from them in the

laboratory situation, the 4-h confinement period was not discordant with the time spent by females under shelters with males. Additionally, small aggregations of male and female crickets under rocks or within cracks in the soil, are not uncommon in field situations (CADE, 1980; EVANS, 1983).

Experimental females mated, on the average, 22 times in 20 nights, and consumed at least a portion of the spermatophore following these matings. However, females were permitted access to males only for 4 hr each night whereas continued access may have resulted in additional matings. The observed mating frequency further underestimates female receptivity, because female demand for matings clearly exceeded males' ability to supply spermatophores: experimental females often mated twice when 2 mature males were present, whereas experimental males never mated more than once when 2 receptive females were available. Male *G. supplicans* require an average interval of 3.25 hrs before they will mate again (SAKALUK, 1985). Here, the mean intercopulatory interval of females was about 90 min; females remated within as little as 12 min. Additionally, females often mounted males while the sperm ampulla from a previous mating was still attached.

The theft of spermatophores from mated females demonstrates that females solicit spermatophores for benefits other than genes (*i.e.* nutrition); to the best of my knowledge, spermatophore theft previously has not been reported for any insect. When a mated female was present with her mate and another female, theft of the spermatophore occurred significantly more often by the unmated female than by the male. Additionally, no portion of a mated female's spermatophore ever was removed by her mate while it was still attached at the base of her ovipositor, at least in the group for which the identity of crickets could be ascertained. This suggests that males recognize recent mates: the hypothesis could be tested by comparing rates of spermatophore theft by males confined with their own mates, or confined with females recently mated to other males. Males should be more willing to steal spermatophores from females other than their own mates.

Opportunistic feeding (BELL, 1980) occurs in other forms in insects. During copulation in the tree cricket, *Oecanthus nigricornis*, the female feeds on secretions from the male's metanotal gland; occasionally, a nearby female replaces a male's mate, and feeds on the secretions without copulating (BELL, 1980). In the flies, *Schistopterus moebiusi* and *Sepedon aenescens*, males produce a nuptial secretion (orally and anally, respectively) which is consumed by the female during copulation (FREIDBERG,

1981; BERG & VALLEY, 1985). Unpaired flies also may feed on the food mass with the mating female while her mate is otherwise preoccupied. In the primitive Orthopteran, *Cyphoderris strepitans* (Haglidae), females consume male hindwing material and the resulting flow of haemolymph during matings; occasionally, females engage in feeding but subsequently do not allow copulation to occur (DODSON *et al.*, 1983). Such exploitation of males by females may have selected for the evolution of the male's abdominal pinching organ (gin trap), which acts to hinder the female from pulling away from the male during mating (MORRIS, 1979). In scorpionflies, *Hylobittacus apicalis*, males must provide females with nuptial prey items before females will mate; some males adopt female postures and behaviours to steal the prey items of successful hunters (THORNHILL, 1979).

In addition to the acquisition of matings, other biological needs may compel nocturnal movement by females. For example, females may move around in order to disperse their eggs in space and, incidentally, increase the availability of females to males. Oviposition by female *G. supplicans* begins approximately 1 week after their final molt (KHAN, 1954; GHOURI & MCFARLANE, 1958), and continues for about 42 days on the average (GHOURI & MCFARLANE, 1958; this study). During this period, the female must deposit about 700 eggs. Continuous observation of female *G. supplicans* in the laboratory showed that oviposition usually occurred in the evening, and that each bout of oviposition lasted from 2-4 hrs (SHARMA, 1976).

In contrast to females, male *G. supplicans* exhibited increased site fidelity and reduced locomotor activity in the arena. Additionally, males spent considerably more time under shelters than did females. By calling only when hidden and stationary, males probably reduce the possibility of detection by the various predators that orient acoustically to singing male Orthoptera (WALKER, 1964, 1979; CADE, 1975; MANGOLD, 1978; BELL, 1979; BURK, 1982; SAKALUK & BELWOOD, 1984). Silent female crickets are not automatically immune to the risks posed by these predators. Geckos that are attracted to male *G. supplicans* calling from within their burrows, may wait beside the inaccessible males and intercept phonotactically responsive female *G. supplicans* (SAKALUK & BELWOOD, 1984).

Male *G. supplicans* called in close proximity to other singing males, often within as little as 40 cm. One pair of males in the arena called from beneath the same shelter. This contrasts with the spatial distribution of calling *Gryllus integer*; in this species, males do not call within 1.2 m of

each other, even in high density populations (CADE, 1979a). Calling by a male within this limit often results in physical aggression from his neighbour (CADE, 1979a). Male *G. supplicans* possess an aggressive song (ALEXANDER, 1962) and also engage in some aspects of the fighting behaviour described by ALEXANDER (1961), but only after males have been isolated from females for at least a week (SAKALUK, per. obs.). In this study, males never were observed fighting. This lack of aggression by male *G. supplicans*, relative to that of other crickets, may be due to the higher level of investment by *G. supplicans* in their spermatophores (SAKALUK, 1985). As this investment increases, males are expected to compete less with other males, and become more selective of their mates (TRIVERS, 1972; GWYNNE, 1981).

Males also occurred beneath shelters with other calling males, but did not themselves call or did so at reduced levels. These males probably were 'satellites', silent males that locate next to calling males and intercept females orienting acoustically to the singing male (CADE, 1975, 1979a). Such males also save energy that otherwise would be lost in calling (PRESTWICH & WALKER, 1981). Satellite males occur in other crickets including *Gryllus integer* (CADE, 1975, 1979a), *Acanthogryllus fortipes* (CADE & OTTE, 1982), and *Gryllus pennsylvanicus* at high densities (CADE & WYATT, 1984).

This study supported WALKER's (1983a) prediction that calling of male crickets should be coincident with the temporal availability of females. There were, however, marked differences in the locomotor activity and site fidelity of males and females. These differences reflected the different sets of selective forces operating on the sexes. This study also revealed some of the mechanisms by which adaptive decision-making in one sex (e.g. timing and frequency of mating), can influence the evolution of spatial and temporal patterns of activity in the other: the adaptive significance of these patterns will be understood only when all such pathways of sexual feedback have been identified.

Summary

The temporal and spatial patterns of sexual activity in the cricket, *Gryllodes supplicans*, were examined. Calling by males in a natural population occurred throughout the night, reflecting the temporal availability of females. In an outdoor enclosure, females were significantly more likely than males to change locations from one hr to the next; the average probability of such a change by a female was 0.6, and this did not vary significantly over the course of a night. The locomotor activity of females, as indicated by the average distance an individual moved each hour (and between nights), also was significantly greater than that of males.

The greater mobility of females increased their access to additional males, and probably allowed them to consume more spermatophores (sperm-containing vessels transferred by males which remain outside females' bodies after mating) than they would otherwise obtain by remaining with the same mate. An increased demand by females for additional spermatophores was evidenced in the laboratory by repeated mating, frequent consumption of spermatophores, brief intercopulatory intervals, and the theft of spermatophores from mated females. Spermatophore theft demonstrates that females solicit spermatophores for benefits other than genes (*i.e.* nutrition), and has not previously been reported for any insect.

In contrast to females, males exhibited increased site fidelity and reduced locomotor activity in the enclosure. By calling only when hidden and stationary, males probably reduce the possibility of detection by acoustically orienting predators. Males also occurred beneath shelters with other calling males, but did not themselves call or did so at reduced levels. These males probably were 'satellites', silent males that locate next to calling males and intercept the phonotactically responding females.

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Zusammenfassung

Die zeitlichen und räumlichen Gewohnheiten der sexuellen Tätigkeit der Grille *Grylloides supplicans* wurden geprüft. In freier Natur signalisiert das nächtliche Rufen der Männchen das zeitweilige Vorhandensein der Weibchen. In einer Umzäunung draussen sind die Weibchen signifikant mehr als die Männchen dazu geneigt, die Stellen stundenweise zu ändern. Die durchschnittliche Wahrscheinlichkeit einer derartigen Veränderung vom Weibchen war 0.6 und das variierte nicht signifikant während der Nacht. Die Beweglichkeit der Weibchen, betreffs ihrer durchschnittlichen Entfernung pro Stunde und von Nacht zu Nacht, ist gleichfalls grösser als beim Männchen. Dieser Unterschied ist signifikant.

Die grössere Beweglichkeit der Weibchen erlaubt mehr Männchen den Zugang und ermöglicht somit einen zusätzlichen Spermatophorenverzehr der Weibchen. Diest ist mehr als sie erziehen würden, wären sie beim einem Männchen geblieben. (Spermatophore sind Spermaenthaltende Gefässe, die von Männchen übertragen werden und nach der Paarung ausserhalb des Körpers der Weibchen hängen bleiben.) Das steigende Verlangen der Weibchen nach mehr Spermatophoren wurde im Labor bewiesen durch mehrmalige Paarungen, häufigen Spermatophorenverzehr, kurze Pausen zwischen Paarungen und dem Diebstahl der Spermatophoren von gepaarten Weibchen. Der Spermatophorendiebstahl beweist dass die Weibchen Spermatophoren nicht nur für die Genen brauchen, sondern auch als Nahrung haben wollen. Dies wurde vorher noch nie über ein Insekt berichtet.

Im Gegensatz zu den Weibchen bleiben die Männchen mehr am Platz. Beim Rufen, wobei sie sich verstecken und stillstehen, scheinen die Männchen so die Möglichkeit der Entdeckung durch sich akustisch orientierende Raubtiere, zu vermindern. Männchen, die wenig oder nicht rufen wurden in unmittelbarer Nähe der rufenden Männchen gefunden. Dies sind wahrscheinlich Satelliten - stumme Männchen die sich neben rufende Männchen setzen und ihnen die Weibchen wegfangen.