

# Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer*

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**Abstract.** Mating behaviour of male field crickets, *Gryllus integer*, was studied during 10-h observation periods at night and early morning in a large outdoor enclosure placed in the natural habitat. Duration of nightly calling, amount of searching, and mating frequency were determined over 113 nights for 93 and 111 males at high and low density, respectively. Male body weight was also determined. Males called significantly more and searched less at low density. In the low-density population, body weight and calling duration were positively correlated, whereas searching was inversely correlated with both calling and body weight. Mating frequency was positively correlated with calling duration and inversely correlated with searching at low density. Mating frequency did not vary with body weight at either density. There were no significant correlations at high density. Directional selection was estimated using covariance analysis as the total selection ( $s'$ ) on calling, searching, and weight (including selection on correlated traits). Partial regression coefficients ( $\beta'$ ) were used to estimate selection directly on each trait alone. Total selection favoured calling and opposed searching at low density. There was no selection on body weight at low density and there was no selection on any of the observed traits at high density. Data are discussed in terms of density-dependent fluctuations in male mating success and maintenance of phenotypic and genetic variation.

Male field crickets call and attract mates, silently search for females in the vicinity of calling males, and fight for access to calling sites and females. Song intensity, type of song, duration of singing, time of calling, amount of searching and body size (a correlate of fighting behaviour) are important in male–male competition and female choice (Alexander 1975; Otte 1977; Walker 1980). Many factors probably contribute to variation in male mating behaviour, but population density is thought to be a major variable. As density increases the following changes should characterize field cricket mating behaviour: calling sites become limited; the cost of defending calling sites increases; the frequency of encounters between satellite males and females increases; and the proportion of matings resulting from non-calling, searching behaviour increases (Alexander 1961, 1968). There are few data available to test these predictions on density-dependent changes in mating behaviour in field populations. Fluctuations in selection with population density may be important in the maintenance of additive genetic variation underlying sexual behaviour in crickets and other species

(Cade 1981a, 1984a). We report on observations intended to measure variations in male mating success with body size, the amount of calling and searching behaviour in the field cricket, *Gryllus integer*, at high and low population densities in a field arena placed in the natural habitat of this species. Local population density fluctuates greatly over a short period of time in this species, and density-dependent variation in sexual selection may be responsible, in part, for maintaining additive genetic variation underlying male fitness traits (Cade 1981a, 1984a).

## METHODS

We conducted this study at various times between April and August 1983–1989 (except 1984) at the Brackenridge Field Laboratory, Austin, Texas, a location where *G. integer* commonly occurs. (This species has been routinely referred to as *G. integer*, but this designation may be incorrect; Weissman et al. 1980; Smith & Cade 1987.)

### Field Arena

Observations were carried out in an outdoor arena measuring 13.5 × 13.5 × 1.2 m enclosed by concrete walls. The arena contained a variety of native grasses that were mowed to a low level to make crickets more visible. This habitat is characteristic of *G. integer*. The arena was divided into 25 quadrats each measuring approximately 2.7 × 2.7 m. A shelter was placed in the centre of each quadrat and consisted of a hole (15 × 15 cm) partially covered with a piece of concrete (20 × 20 cm). Shelters were also placed at the midpoint of the side of a quadrat that was adjacent to a wall. There was a total of 42 shelters. Orchard net was suspended above the arena to prevent entry by birds. The grassy areas outside the arena and adjacent arenas also contained *G. integer* males and females. The arena was, in effect, a 'window' on a larger *G. integer* aggregation.

### Collecting and Observing Crickets

We collected crickets in nearby areas or we broadcast tape recorded *G. integer* calling song (see Cade 1989 for details on song broadcasting) and attracted flying crickets to the arena. Crickets were weighed and marked with model airplane paint (Testor). Body weight is a very good predictor of overall body size in *G. integer* and other field crickets (Simmons 1986; McGowan & Cade, unpublished data). At the beginning of a series of several nights observations, we placed marked male and female *G. integer* in the centre of the arena several hours before the start of observations. In 1983 and 1985, we observed an average ( $\pm$ SE) of 22.4 ± 0.5 males and 21.3 ± 0.5 females in the enclosure. These values give a density of 0.12 males and 0.11 females per m<sup>2</sup>. In 1986–1989 there were an average ( $\pm$ SE) of 4.4 ± 0.2 males and 5.2 ± 0.3 females, or densities of 0.02 males and 0.03 females per m<sup>2</sup>. Crickets sometimes died or disappeared from the arena and flying crickets routinely landed in the arena probably in response to the calling of conspecific males. We constantly added *G. integer* to and removed them from the arena to maintain the intended density and to observe as many individuals as possible. Individuals in unmanipulated *G. integer* populations routinely fly into and later leave aggregations (Cade 1979b, 1989).

Male crickets were observed for at least 2 nights, but usually for a longer period ( $\bar{X} \pm$ SE = 5.2 ± 0.6 and 4.3 ± 0.7 nights at low and high densities,

respectively). We observed crickets for a continuous series of 4–12 nights for totals of 49 and 64 nights at high and low densities, respectively. The months and numbers of nights in each series that we observed crickets were as follows: April–May 1983, 5 and 7 nights; May 1983, 6 and 5 nights; July 1983, 7 nights; July 1985, 10 nights; August 1985, 9 nights; April 1986, 4 nights; August 1986, 10 nights; June 1987, 10 nights; August 1987, 10 nights; May 1988, 5 nights; June 1988, 9 nights; June–July 1989, 4 nights and 12 nights. There was no replacement sampling because we included individual male and female *G. integer* in one series of observations only. The overall availability of *G. integer* in the Austin area can be estimated from the numbers of long winged, flying crickets that landed in the arena. These data demonstrate that cricket abundance was roughly equivalent during the times we carried out the high- and low-density observations (Cade 1989, unpublished data).

We performed observations from approximately 1.5–2 h after sunset to 3 h after sunrise, 2200–0800 hours local time, the period when *G. integer* is most active (Cade 1979a; French & Cade 1987). We wore headlights and used them very briefly in the dark to identify and determine the locations of individual males and females, and to determine if a spermatophore was attached to a female. There did not appear to be any effect of the light on crickets because we heard crickets continue calling or producing the songs characteristic of fighting or mating after the light was turned off. Walking crickets also continued their movement without any apparent change in speed or direction when the lights were turned on.

We conducted a complete survey of the arena at the beginning of the observation period and every hour thereafter. To avoid disturbing the crickets, we very carefully and slowly walked in the arena and marked the locations of individual male and female *G. integer* on a map of the arena. The amount of movement in the arena by individual *G. integer* was later calculated from maps as the minimum distance that a male or female moved from its location the previous hour. Movement from a previous location was assumed to reflect the amount of searching behaviour for females, but male movements from one location to another in the arena may also represent a search for signalling sites, food or other resources in addition to females. It is also possible that males walking in the arena were displaced by other males. In any case, our method of

measuring movement is probably an underestimate of total movement (French & Cade 1989), but the data provide a relative estimate of searching behaviour by males (Souroukis & Cade, unpublished data).

At 5-min intervals we noted the presence or absence of calling by individual male *G. integer* in known locations. If calling was heard from a location where a male had not been previously observed, we identified the male by walking to that place and carefully lifting the shelter. More than one male was occasionally present in a shelter from which calling was heard. In this situation we lifted the shelter and identified the male with his wings raised as the caller. Most crickets were not disturbed when we lifted the shelter and many continued calling. Crickets that stopped calling when the shelter was raised almost always started calling within a few seconds. We calculated the total time that males called each hour from the number of 5-min calling-interval scores by individual males. Cricket calling is usually delivered in a continuous fashion, and this method of interval scoring provides a reliable estimate of total calling time per hour for individual males (Cade & Cade, unpublished data).

We recorded a mating when we found a female with an attached spermatophore during the hourly surveys. Once we found a male–female pair, we observed them several times during the hour to ensure that we recorded any mating activity. We also observed recently mated females at intervals of 15–30 min to determine if the spermatophore was still present. It was possible for us in this way to identify rematings by the same female. If there was only one male with a mated female, we assigned the mating to that male. In a few cases where two or more males were in the same shelter with a female that had recently mated, we assigned the mating to the male that was next to and guarding the female. Matings were considered equivalent in this study, although sperm competition occurs in *G. integer* (Backus & Cade 1986).

#### Data Analysis

There were 93 and 111 males included in the analysis at high and low densities. For statistical comparisons, the means per night of searching distance, duration of calling and number of matings for each male were calculated. Data from observations at the same density were combined and In-

transformed to meet assumptions of parametric tests. We calculated sample means from individual means for each density and used *t*-tests to determine differences between high- and low-density populations. One-tailed probabilities were calculated for data on calling and searching because calling duration should decrease and movement increase with increased density (Alexander 1975). Two-tailed probabilities were calculated for comparisons of male body weights and mating frequencies at low and high density.

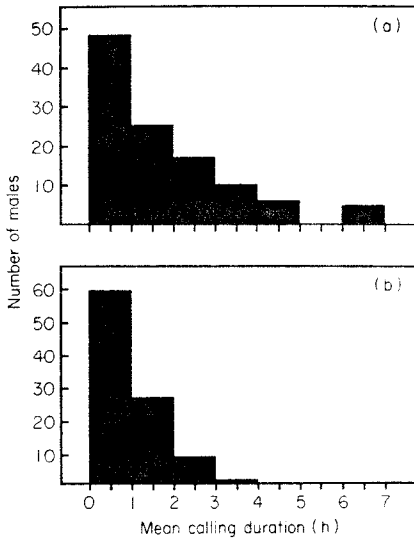
The standardized selection differential ( $s'$ ) was used to estimate the total intensity of directional selection on a trait and was calculated as the covariance between relative mating success and the standardized variables of calling, searching and weight. Correlation coefficients were used to estimate significance levels. Total selection includes selection directly on the trait as well as indirect pressures by way of selection on correlated traits. Variables were standardized to have means of 0 and variances of 1. We estimated selection directly on a trait (excluding selection on correlated traits) as the standardized selection gradient or partial regression coefficients ( $\beta'$ ) of mating frequency on the standardized variables. Multiple correlation coefficients ( $R^2$ ) were determined (Price 1970; Lande & Arnold 1983). Significance levels for  $\beta'$  and  $R^2$  were determined with *t*-tests and ANOVAs, respectively (Zar 1984). Mating frequencies were standardized to have means of 1, but were not transformed to natural logarithms, thus not affecting variation in this measure of fitness (Lande & Arnold 1983).

## RESULTS

Calling durations per night by individual males averaged ( $\pm$ SE)  $1.7 \pm 0.2$  h and  $0.8 \pm 0.1$  h at low and high density, respectively (Fig 1a, b). Males called significantly more in the low-density populations ( $t = 3.5$ ,  $df = 202$ ,  $P < 0.0002$ , one-tailed).

Average ( $\pm$ SE) distances moved per night by individual males were  $12.2 \pm 1.0$  m and  $18.1 \pm 0.7$  m at low and at high density, respectively (Fig. 2a, b). Males moved significantly greater distances at high density ( $t = -6.1$ ,  $df = 202$ ,  $P = 0.0001$ , one-tailed).

The average ( $\pm$ SE) weights of males in the low- and high-density populations were  $599 \pm 10$  mg and  $605 \pm 11$  mg, respectively. There was no significant difference between male weights at the two densities ( $t = 0.3$ ,  $df = 202$ ,  $P = 0.7$ , two-tailed).

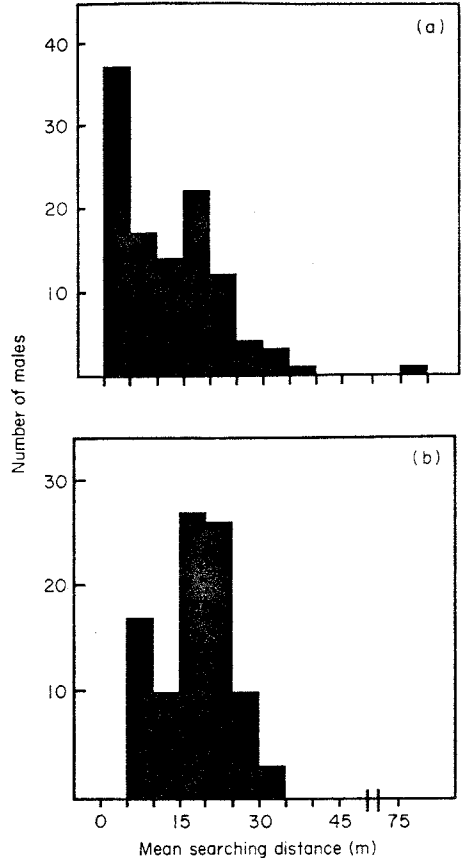


**Figure 1.** The distribution of average calling times per night by individual *G. integer* males in (a) low-density and (b) high-density populations as determined from 5-min interval scores of calling.

Number of matings by individual males per night averaged ( $\pm$  SE)  $0.8 \pm 0.1$  and  $0.7 \pm 0.1$  at low and at high density, respectively (Fig. 3a, b). The difference was not significant ( $t=1.1$ ,  $df=202$ ,  $P=0.2$ , two-tailed). Variance of individual mating success is one indication of the opportunity for selection. These values for the low- and high-density populations were very similar, 0.5 and 0.4, respectively.

There was an inverse and significant correlation between calling duration and distance moved in the enclosure at low density ( $r=-0.38$ ,  $P<0.001$ ), but there was no significant relationship at high density ( $r=-0.7$ ,  $P>0.05$ ). Body weight and distance moved were inversely and significantly correlated at low density ( $r=-0.23$ ,  $P<0.005$ ), but there was no significant relationship at high density ( $r=-0.05$ ,  $P>0.05$ ). Body weight and calling duration were positively correlated at low density ( $r=0.3$ ,  $P<0.001$ ), but there was no significant relationship at high density ( $r=0.02$ ,  $P>0.05$ ).

There was a positive and significant correlation between mating success and calling duration at low density ( $r=0.32$ ,  $P<0.001$ ), but there was no significant relationship at high density ( $r=0.05$ ,  $P>0.05$ ). Mating success and distance moved in the enclosure were significantly and negatively correlated at low density ( $r=-0.18$ ,  $P<0.02$ ), but there was no significant relationship at high density



**Figure 2.** The distribution of average distance moved per night by individual *G. integer* males in (a) low-density and (b) high-density populations.

( $r=0.07$ ,  $P>0.05$ ). Body weight was not significantly correlated with mating frequency at low density ( $r=0.07$ ,  $P>0.05$ ) or high density ( $r=0.03$ ,  $P>0.05$ ).

Selection intensities are presented in Table I. At low density there was significant total selection ( $s'$ ) in favour of calling and against searching (correlation coefficients were used to determine significance values of  $s'$ ) and significant direct selection ( $\beta'$ ) in favour of calling ( $t=2.8$ ,  $df=107$ ,  $P=0.005$ ). Direct selection on searching and on body weight was not significant at low density ( $t=0.7$ ,  $df=107$ ,  $P=0.4$ , and  $t=0.3$ ,  $df=107$ ,  $P=0.7$ , respectively). The multiple correlation coefficient at low density was small but statistically significant ( $F=4.1$ ,  $df=3$ ,  $107$ ,  $P<0.05$ ). Total selection on calling, searching and body weight was not significant at high density (see correlation coefficients) and direct

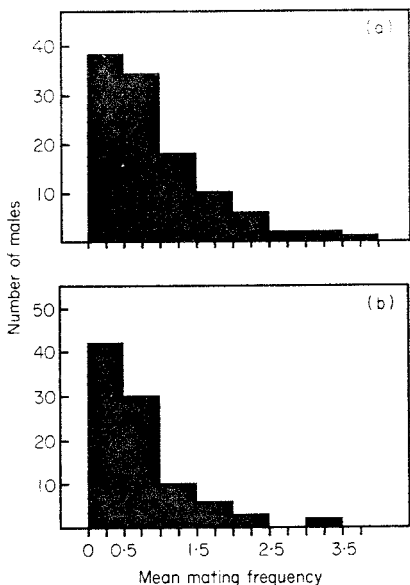


Figure 3. The distribution of average number of matings per night by individual *G. integer* males in (a) low-density and (b) high-density populations

selection on these traits at this density was also not significant (calling:  $t=0.2$ ,  $df=89$ ,  $P=0.8$ ; searching:  $t=0.04$ ,  $df=89$ ,  $P=0.6$ ; body weight:  $t=0.2$ ,  $df=89$ ,  $P=0.8$ ). The multiple correlation coefficient at high density was not significant ( $F=0.1$ ,  $df=3, 89$ ,  $P=0.9$ ).

## DISCUSSION

Field crickets call and defend territories in spatial aggregations (Cade 1981b; Campbell 1990). As density increases, the cost of defending territories should increase and males should adopt non-calling, satellite behaviour (Alexander 1975; Otte 1977; Cade 1979a). Our data support this prediction. Male *G. integer* decreased the amount of calling and increased the amount searching at high density. Similar inverse relationships between calling and density were observed in laboratory populations of the cricket *G. bimaculatus* (Simmons 1986), in field populations of the grasshopper *Ligurotettix coquillettii* (Greenfield & Shelly 1985), in field populations of the cricket *G. campestris* (Hissmann 1990), and in earlier field studies on *G. integer* (Cade & Wyatt 1984).

The shape of the frequency distribution of nightly calling duration in field crickets may reflect

the type of selection acting on male acoustic signalling (Sakaluk 1990). Duration of nightly calling was skewed toward reduced calling in this study and in previous studies on this species (Cade & Wyatt 1984; Cade 1991). Male *G. integer* are parasitized by acoustically orienting flies, *Ormia ochracea* (Diptera: Tachinidae; formerly *Euphasiopteryx*), that deposit living larvae on calling crickets. Parasitized crickets die in about 7 days. Directional selection by flies may have resulted in reduced calling in *G. integer* (Cade 1975, 1984b).

Some male *G. integer* were not observed calling, but most males called and showed satellite behaviour. Calling and searching are continuously distributed patterns of behaviour, but are discrete ways of acquiring mates. In this context, calling and movement were inversely correlated in low-density population. Males always called from stationary positions. There was no relationship between calling and searching at high density, but male *G. integer* had greatly reduced calling durations at this density.

At low density large *G. integer* males called more and searched less than smaller competitors. Large males defeated small males in laboratory containers in *G. integer* (Dixon & Cade 1986), and Simmons (1986) found that large *G. bimaculatus* males called more and won aggressive encounters more often than small males in laboratory arenas. In the field arena used here, large males were probably able to defend and thus retain calling sites and, as a consequence, called for longer periods. Aggressive interactions were probably less frequent at high density, but we did not collect data on fighting behaviour to avoid disturbing the crickets. Aggression was reduced at higher densities in *G. bimaculatus* (Simmons 1986).

Mating success varied greatly between *G. integer* males at high and at low densities. Similar variation has been observed in *G. veletis* and *G. pennsylvanicus* (French & Cade 1989). Variation in male mating success should be a characteristic trait in species of field crickets with high levels of male-male competition (Walker 1980; Burk 1983). Low-density populations of *G. veletis* showed greater variance in male mating frequency than high-density populations, suggesting that the opportunity for selection was greatest at low density. No relationship was found, however, between variance in male mating frequency and density in *G. pennsylvanicus* (French & Cade 1989) or in this study. Different findings on *G. veletis* and on *G. integer* and *G. pennsylvanicus* may result from the natural history of

**Table 1.** The standardized selection differentials ( $s'$ ), selection gradients ( $\beta' \pm \text{SE}$ ) and multiple correlation coefficients for the variables of calling duration, distance moved (searching) and body weight for *G. integer* males at low density ( $N = 111$  males) and high density ( $N = 93$  males)

Density	Variable	$s'$	$\beta'$	SE	$R^2$
Low	Calling	0.31*	0.26*	0.09	0.1*
	Searching	-0.17*	-0.06	0.09	
	Weight	0.07	-0.02	0.09	
High	Calling	0.02	0.02	0.1	0.003
	Searching	0.02	0.04	0.1	
	Weight	-0.05	0.01	0.09	

\*Denotes statistically significant values. See text for description of tests and values.

these species. *Gryllus pennsylvanicus* and *G. integer* are common species with very dense populations. *Gryllus veletis* has much less dense populations (Alexander & Meral 1967; Cade 1979b, 1981b). High-density arena populations were probably studied at the extreme range of density for *G. veletis*, whereas *G. integer* and *G. pennsylvanicus* arena populations were well within the range of possible densities (Cade 1981b; French et al. 1986).

Insect calling behaviour is energetically expensive and represents mating effort (Prestwich & Walker 1981). Male mating frequency increased with calling duration in *G. bimaculatus* in the laboratory (Simmons 1988a) and in field populations in *L. coquilletti* (Greenfield & Shelly 1985). In high-density populations, calling should be less successful as searching males encounter females more often (Alexander 1975; Otte 1977; Cade 1979a). Data presented here on correlations between male mating frequency and calling and searching support this prediction. Male *G. integer* mating success was positively correlated with calling duration at low density, but not at high density. Searching behaviour, however, was never more successful than calling. Calling duration was also correlated with mating frequency in low-density populations of *G. pennsylvanicus* (French & Cade 1989). Similar relationships between calling, searching and mating success at varying population densities were demonstrated in field populations of *G. campestris* (Hissmann 1990).

Mating frequency was expected to increase with body size in *G. integer* since male weight was correlated with calling duration and calling results in more matings at low density. Body weight was not correlated with mating success, however, in this

study on *G. integer* or in *G. veletis* and *G. pennsylvanicus* (Zuk 1988; French & Cade 1989). Large male *G. bimaculatus* in the laboratory mated more often and had greater lifetime reproductive success than small males. Body size shows heritable variation in *G. bimaculatus* and large males are preferred by females who have increased fecundity and offspring fitness (Simmons 1986, 1988b). Specimens of *G. bimaculatus* are, however, generally larger than *G. integer* (Otte & Cade 1984) and large body size in *G. bimaculatus* may reflect selection on this trait that is absent or reduced in *G. integer*.

Correlations between mating frequency and calling, and searching and calling at low density, and the absence of any significant correlations at high density, suggest that selection intensities fluctuate with density. Standardized selection intensities and directional selection gradients showed that total selection ( $s'$ ) favoured calling and opposed searching at low density. Also, selection only on calling ( $\beta'$ ) was detected at low density, but there was no direct selection on searching. Absence of selection on searching alone indicates that the total selection on searching results from selection on correlated traits at low density. Searching and calling were inversely correlated in the low-density population, and some of the negative total selection on searching may be the result of direct and positive selection on calling. Estimates of  $s'$  and  $\beta'$  for calling at low density were very close thus suggesting that most selection on calling is direct and not on correlated traits. There was no selection on body weight at low or high density, and there was no selection on calling or searching at high density. Similar measures of selection intensity were observed for *G. pennsylvanicus* (French & Cade 1989).

Directional selection on traits important in competition between males and female choice should reduce additive genetic variation (Cade 1984a). Artificial selection experiments, however, demonstrate that calling duration in *G. integer* had a narrow sense heritability of approximately 0.5. Heritable variation is often associated with sexually selected traits, and Cade (1981a, 1984a) suggested that density-dependent selection in part maintains genetic variation in *G. integer*. Our results demonstrate that selection on male traits does vary with density and previous studies have shown that local *G. integer* densities fluctuate greatly. In a single field, for example, isolated calling males occur, but calling males also occur in aggregations that range from sparse to extremely dense. Long winged, flying individuals orient to and land near calling males, leading to large increases in density in a single night (Cade 1979a, b, 1981b). In this situation, calling in low-density populations would be selected for and searching selected against. Attraction of flying conspecific males would, however, quickly increase the density and result in lower or negligent selection pressures on acoustic signalling and searching behaviour. *Gryllus integer* is also much more common in the late summer and early fall, and it is therefore likely that selection on male traits varies with season.

In the low-density population, the multiple correlation coefficient was significant but low. Only a small amount of the variation in mating success results from selection on the variables studied here. Other factors probably influence male mating success in addition to these variables. Male song intensity and structure may also contribute to the variation in male mating success in *G. integer*. Previous experiments demonstrated that loud songs attract more females in *G. integer* and other crickets (Cade 1979a; Forrest 1983), and female *G. integer* use song structure to select mates (Hedrick 1986). Relative male age may also influence male mating success. Our study and previous observations on *G. veletis* and *G. pennsylvanicus* used each male for only a few nights and thus represented a cross-sectional approach. Variations in individual male longevity and other age-related selection was not considered. Calling in *G. integer* probably results in reduced survivorship from the attraction of *O. ochracea* (Cade 1975). Searching behaviour over a longer adult life may result in greater mating success than calling and the resulting decreased longevity. Zuk (1988) showed that

older males attracted more females in *G. veletis* and *G. pennsylvanicus*. Another source of variation in male mating success is gregarines, a common parasite in field crickets. No data are available on gregarines in *G. integer*, but gregarines reduce male longevity and fertility in other cricket species (Zuk 1987a, b).

Information is needed on the relationship between calling duration, longevity, age and mating success in *G. integer*. Data on selection intensities at varying sex ratios, at very low densities when males are isolated from neighbouring males and on frequency dependent selection are also required. These additional data will help determine the types of fluctuations in selection important in the maintenance of phenotypic and genetic variation underlying mating behaviour in *G. integer* and other species.

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