

Simulation of alternative male reproductive behavior: calling and satellite behavior in field crickets

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ABSTRACT

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Male field crickets and other acoustically communicating insects call and attract females and silently intercept females attracted by the calling of other males, so-called satellite behavior. A simulation of field cricket, *Gryllus integer*, mating behavior suggests that population density and sex ratio changes during the breeding season are important factors determining mating success of calling and satellite males. Satellite mating success increased with the proportion of satellite males, but mating success of callers was independent of the proportion of calling males. Satellite male mating success was greatest in high density populations with extremely female-biased sex ratios. Calling males also mated more often under most population densities, various populations differing in the proportion of callers and in sex ratios. Calling male mating advantage decayed exponentially, however, with increasing population density. Variation in male *G. integer* reproductive behavior has previously been associated with fluctuating population densities in empirical studies on laboratory and field populations. The simulation suggests that variation in male mating success with the operational sex ratio also contributes to the continuing existence of alternative male reproductive behavior. Predictions derived from the simulation can be tested in actual populations of *G. integer* and other species.

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INTRODUCTION

Many animal species have males that have very different mating behavior (for examples see Van Rhijn, 1973; Howard, 1978; Cade, 1979a; Fairchild, 1984; Greenfield and Shelly, 1985). Alternative mating behavior often involves some territorial males attracting females by signalling visually or acoustically while non-signalling males search for females in the territories of other males. Non-territorial males are often termed satellite or parasitic males and various factors contribute to the occurrence of alternative male behavior in a population (Cade, 1981a). High density in field cricket mating aggregations, for example, results in some males adopting satellite behavior (Alexander, 1961, 1975; French and Cade, 1989; Cade and Cade, 1992). Genetic models have shown frequency dependent selection where the reproductive success of a given behavior decreases as it becomes more common in the population (Gadgil, 1972; Gadgil and Taylor, 1975; O'Donald, 1978; Rubenstein, 1980). Also, variations in sex ratios in mating aggregations may give rise to different levels of male-male competition and thus affect the success of alternative male behavioral patterns (Waltz, 1982; Waltz and Wolf, 1984; Hoglund, 1989).

Population density, sex ratio and frequency dependent selection contributed to variations in male reproductive success in a computer graphical simulation by Fairchild (1984). This previous study did not, however, address the relative contributions of density, sex ratio and the proportion of males with different strategies. We here present results from a computer graphical simulation on alternative mating behavior in field crickets, *Gryllus integer* Scudder, a species found in central Texas which has been widely studied in laboratory and field experiments. This simulation assesses the relative importance of population density, sex ratio, and the frequency of male behavior in maintaining alternative forms of behavior in a population. The simulation results are compared with empirical data from *G. integer* and predictions are made that are now being tested in *G. integer*.

Alternative male reproductive behavior in field crickets

G. integer is found in grassy areas in central Texas where males call in spatial aggregations and the song attracts conspecific females for mating. The song also repels other calling males to a distance of at least 1 m. Flying *G. integer* are attracted to calling song and land nearby. Satellite males are also routinely observed and they walk or remain motionless in the general area, sometimes within a few centimeters of a calling male. Satellite males court and mate with females attracted by the calling of other males.

Calling behavior is a continuously distributed trait across individual *G. integer* males and some individuals call very much whereas others do not call. Many males perform both calling and satellite behavior during a night. Although the duration of calling is continuously distributed, calling and satellite behavior represent discrete ways of acquiring mates. Calling behavior is much more common in low density populations, usually in the spring and early summer. During the late summer and early fall, however, local densities may reach very high levels and the frequency of satellite behavior increases greatly. Calling occurs throughout the night in *G. integer*, but is much more common at sunrise when most matings also occur. There is no variation in nightly calling duration with age in sexually mature males, and there is additive genetic variation underlying the amount of calling in *G. integer* (Cade, 1979a, b, 1981b, c; Cade and Wyatt, 1984; French and Cade, 1987; Cade and Cade, 1992).

Studies in large outdoor enclosures on *G. integer* and on the related species *G. veletis* and *G. pennsylvanicus* have measured relative male mating frequency and intensity of sexual selection at varying densities. At high densities male mating success does not vary with calling or searching behavior. At low densities, however, male mating frequency is correlated with the amount of time that males spend calling in *G. pennsylvanicus* and *G. integer* (French and Cade, 1989; Cade and Cade, 1992). Density-dependent variations in selection by male mating success may be responsible, in part, for maintaining genetic variation in male calling duration in *G. integer*.

METHODOLOGY

A simulation analysis was developed in Macintosh Pascal that predicts mating success of calling and satellite males over a range of population densities, sex ratios and proportions of callers. To examine the effects of population density and proportion of male strategies on mating success, the simulation was run a total of 54 times under six conditions of varying proportions of callers and nine population densities while holding sex ratio constant at 50/50. Similarly, to examine the effects of population density and sex ratio, 45 simulation runs were completed using five sex ratios and nine population densities while holding the proportion of callers at 0.5. The mating arena was simulated as a two-dimensional 10×10 quadrat grid (Fig. 1) with individuals capable of moving in four directions (up, down, left, right) and leaving or entering a shelter within each quadrat. This grid resembles the outdoor enclosures used in field studies (French and Cade, 1987, 1989; Cade, 1989; Cade and Cade, 1992). Individual males continuously displayed either calling or satellite behavior for the duration of the

C ^F	C	C	C	C ^C	C	C	C	C	C
C	C	C	C	C ^F	C	C	C	C	C
C	C	C ^C	C ^F	C	C ^C	C	C	C	C
C ^S	C	C	C	C ^S	C	C ^F	C	C	C
C ^F	C ^C	C	C ^S	C	C	C ^F	C	C	C
C	C	C	C ^F	C	C	C	C	C ^F	C
C	C	C	C	C	C	C	C	C	C
C	C	C	C ^S	C	C	C	C	C	C
C	C	C	C	C	C	C	C	C	C
C	C ^C	C	C	C	C ^F	C	C	C	C

Fig. 1. Simulated field cricket mating arena with input parameters of population density = 0.2, proportion of calling males = 0.5, sex ratio = 50/50. C denotes calling males, S, satellite males and F, females. Each quadrat contains one shelter.

simulation run (C and S in Fig. 1). Figure 2 shows a flow diagram of the computer algorithm and illustrates the measurement of average numbers of mate encounters and average numbers of male-male encounters for calling and satellite males, respectively.

At the beginning of each simulation run, females and satellite males were distributed randomly in individual quadrats over the mating arena while calling males are distributed with a minimum nearest neighbor distance of one quadrat. Movement rules in the simulated mating arena involved the calling males remaining stationary and females orienting towards nearest calling males in a step-wise fashion. In real populations male crickets remain stationary while calling and some females show positive phonotaxis. The movement of satellite males in the simulation was random within the mating arena. Although male *G. integer* orient to calling males over long distances, many males in the short distances involved in actual mating arenas walk in apparently random directions with respect to calling males. A random walk was therefore used for simulated satellite males since it represents a first approximation as the simplest possible movement rule and requires no additional assumptions about male movement. With each successive move, females and satellite males have a 0.50 chance of foregoing movement to a new quadrat in order to move into or remain at a shelter of the current quadrat.

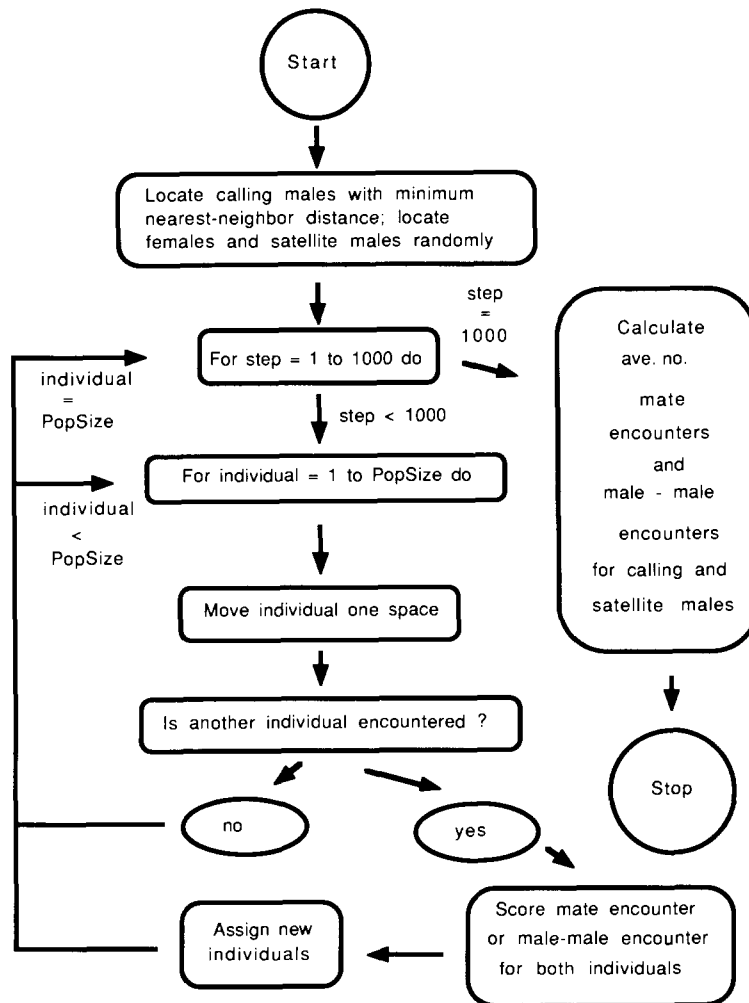


Fig. 2. Flow chart of field cricket mating system simulation. Program scores average number of mate encounters and average number of male-male encounters for calling and satellite males. Each simulation runs for 1000 steps where one step is defined as the movement or attempt to move by all satellite males and females in the population.

Mating success was measured directly from simulated mate-encounter frequencies. A mate-encounter occurred when a male and a female occupied the same quadrat and were both outside of or within a shelter. Each mate encounter was assumed to result in a mating. Mate encounters do not always result in matings in real populations of *G. integer*, but male mating success is correlated with the number of male-female interactions (Cade, unpublished). A male-male encounter occurred when two males occupied

the same quadrat and are both inside or outside of a shelter. After an encounter with another individual, a female or male cricket of the same strategy was randomly assigned to empty quadrats as in the start of the simulation. These were essentially new crickets that were assigned to the arena following encounters since the simulation was not intended to measure long-term mating frequency and agonistic behavior. The simulation runs for a duration of 1000 steps where each step is the movement or attempt to move by every movable individual in the population (Fig. 2). The edges of the mating arena restrict satellite male movement in that a randomly chosen direction leading to a step beyond the edge of the mating arena cancels the move. The decision to use movement-limiting boundaries in the simulation rather than treat the mating arena as an infinite field was based on the notion that edges or boundaries exist for the mating areas of most lek forming animals, including field crickets (Cade, 1981b). Also, the use of boundaries mimics the experimental arena thus permitting a direct comparison with previous field studies. Input parameters of the simulation

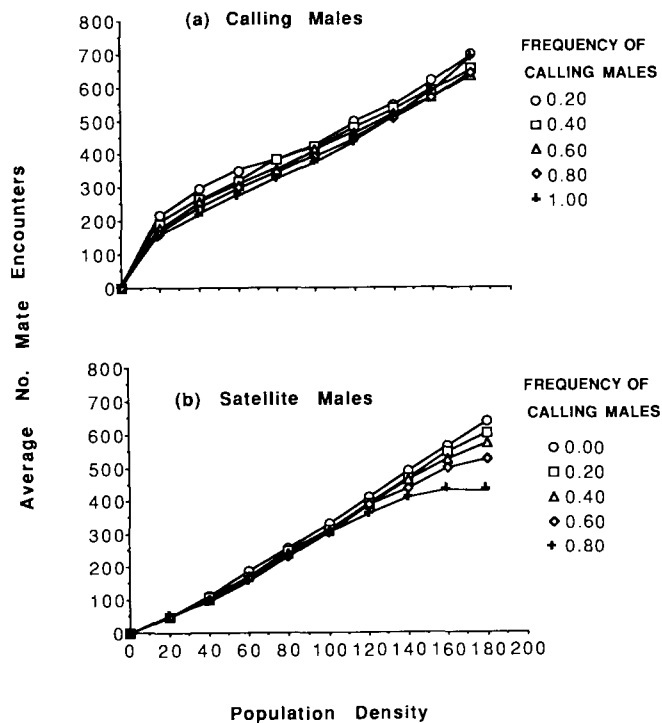


Fig. 3. Average number of mate encounters by males using (a) calling and (b) satellite strategies at varying proportions of calling males with increasing population density at a constant sex ratio of 50/50.

TABLE 1

Regressions of mate encounter on density at varying calling male frequencies

Strategy	Proportion of calling males ^a				Slope ^b	Elevation
	0.20	0.40	0.60	0.80		
Caller						
Slope ± SE	3.3 ± 0.3	3.2 ± 0.2	3.1 ± 0.2	3.2 ± 0.2	0.129	1.89
Y-intercept	107	96	88	73.5		
Satellite						
Slope ± SE	3.5 ± 0.1	3.3 ± 0.1	3.1 ± 0.1	2.6 ± 0.2	13.7 ^e	
Y-intercept	-20.9	-19.4	-11.9	9.4		
Slope ^c	0.714	0.413	0.00	2.44 ^d		
Elevation ^c	6.21 ^c	6.77 ^e	6.73 ^c			

^a Simulated populations with 50/50 sex ratio.^b *F*-statistic for multiple comparisons among slopes and elevations.^c Student's *t*-test for comparison of two slopes or elevations.^d Significantly different, $0.05 > P > 0.01$.^e Significantly different, $P < 0.001$.

include: population density (range: 20–180 individuals per 100 quadrats); proportion of calling males (range: 0.00–1.00); and sex ratio (number of females to males, range: 10/90–90/10).

RESULTS

Frequency of alternative mating strategies

Figure 3 shows the proportion of calling males and population density and their relative contribution towards mate encounters for calling males and satellite males while holding sex ratio constant at 50/50. Mate encounters increased linearly for both calling and satellite males, however calling males experienced an initial sharp increase at the lower population densities (Fig. 3a). In contrast, mate encounters for satellite males increased steadily from initially low values to those approaching calling males (Fig. 3b). A set of linear regressions of mate encounters on population density showed no significant differences either between slopes or line elevations of calling males in populations of varying strategy frequencies (Table 1). (The linear model was appropriate in most cases with the exception of the highest frequency of calling males in Fig. 3b where a better model is a third order polynomial, $Y = 5.332 + 1.344X + 0.03X^2 - 0.0001X^3$, $R^2 = 0.9$.) The

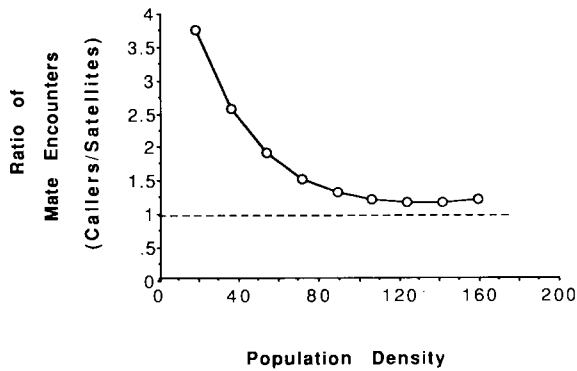


Fig. 4. The ratio of mate encounters by calling males to mate encounters by satellite males with increasing population density at a constant sex ratio of 50/50 and at a proportion of calling males of 0.5.

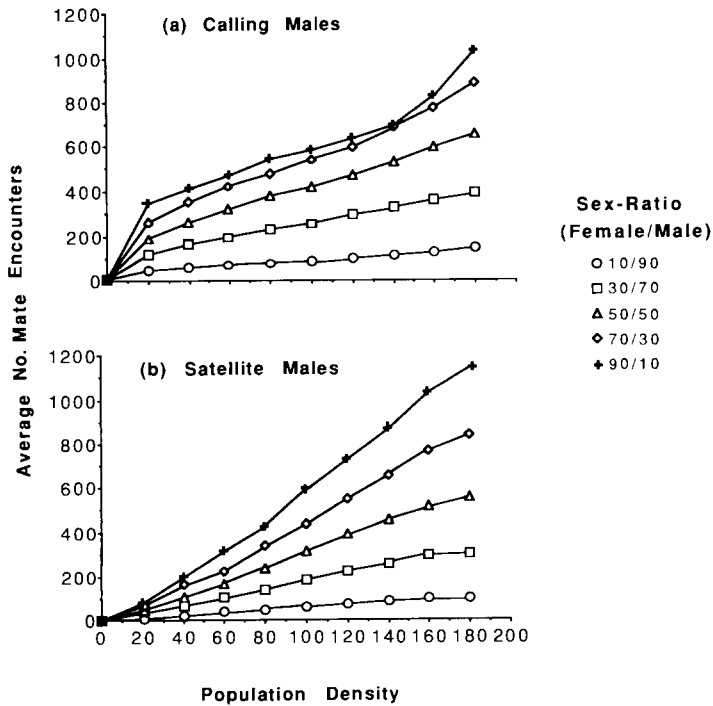


Fig. 5. Average number of mate encounters by males using (a) calling and (b) satellite strategies at varying sex ratios with increasing population density at a constant proportion of calling males of 0.5.

slopes of regressions of mate encounter of satellite males on population density showed highly significant differences among populations of varying proportions of satellite males. Satellite males showed lower mate encounters in populations having low proportions of satellite males and higher values in populations having higher proportions of satellite males. In comparing populations consisting of 20, 40, and 60% calling males, pair-wise comparisons of caller and satellite regression slope values (Table 1) indicated no significant differences in mate encounter rates with respect to increasing population density. There was a difference between strategies, however, when satellite males were rare (caller male frequency, 0.8). Males using the calling strategy in the simulation generally encountered females at higher rates than satellite males as shown by the elevations of the regression lines (Table 1). But this advantage decayed exponentially with increasing population density (Fig. 4).

Sex ratio

Figure 5 gives the relationship between mate encounters and population density in several simulated populations of varying sex-ratios while holding the proportion of callers constant at 0.5. Males of either strategy encountered lower numbers of females in populations with male-biased sex ratios and higher numbers of females in populations with female-biased sex

TABLE 2
Regressions of mate encounter on density at varying sex ratios

Strategy	Sex ratio (females/males) ^a					Slope ^b
	10/90	30/70	50/50	70/30	90/10	
Caller						
Slope ± SE	0.7 ± 0.04	1.9 ± 0.1	3.2 ± 0.2	4.2 ± 0.3	4.4 ± 0.5	29.8 ^c
Y-intercept	16.4	54.9	91.2	121.2	151.9	
Satellite						
Slope ± SE	0.5 ± 0.03	1.8 ± 0.1	3.2 ± 0.1	4.9 ± 0.1	6.6 ± 0.2	613.6 ^c
Y-intercept	0.7	-2.4	-13.9	-36.0	-54.7	
Slope ^c	3.93 ^d	0.701	0.00	2.09	4.34 ^e	
Elevation ^c	8.35 ^e	7.58 ^e	4.43 ^e			

^a Simulated populations with calling male proportion of 0.5.

^b *F*-statistic for multiple comparisons among slopes.

^c Student's *t*-test for comparison of two slopes or elevations.

^d Significantly different, $0.01 > P > 0.001$.

^e Significantly different, $P < 0.001$.

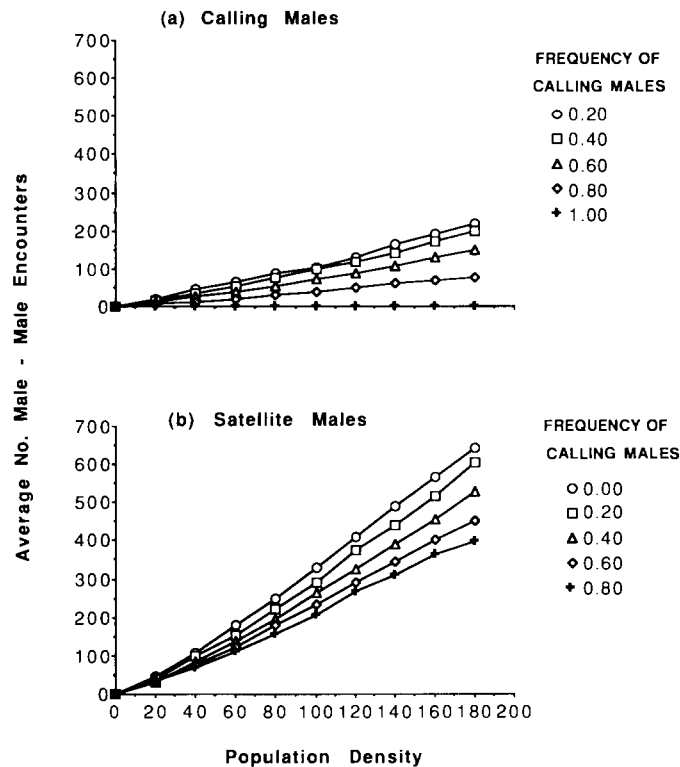


Fig. 6. Average number of male-male encounters for (a) calling and (b) satellite males in populations of varying proportions of callers with increasing population density at a constant sex ratio of 50/50.

ratios. The rate of increase in mate-encounter frequency as indicated by the slope of mate encounter over population density also increased significantly in populations with more female-biased sex ratios (Table 2). (The linear model was appropriate in most cases except for calling males under conditions of the most female biased sex ratio where a third order polynomial was a better model, $Y = 34.391 + 14.34X - 0.14X^2 + 0.001X^3$, $R^2 = 0.9$.) Satellite males experienced significantly higher levels of mate encounters than calling males in simulated populations with highly female-biased sex ratios, particularly at high population densities (Fig. 5b and Table 2). These were the only conditions under which satellite males were more successful at encountering females than calling males.

Male-male interactions

Figures 6 and 7 give results of male-male encounter frequencies for calling and satellite males in simulated populations of varying proportions

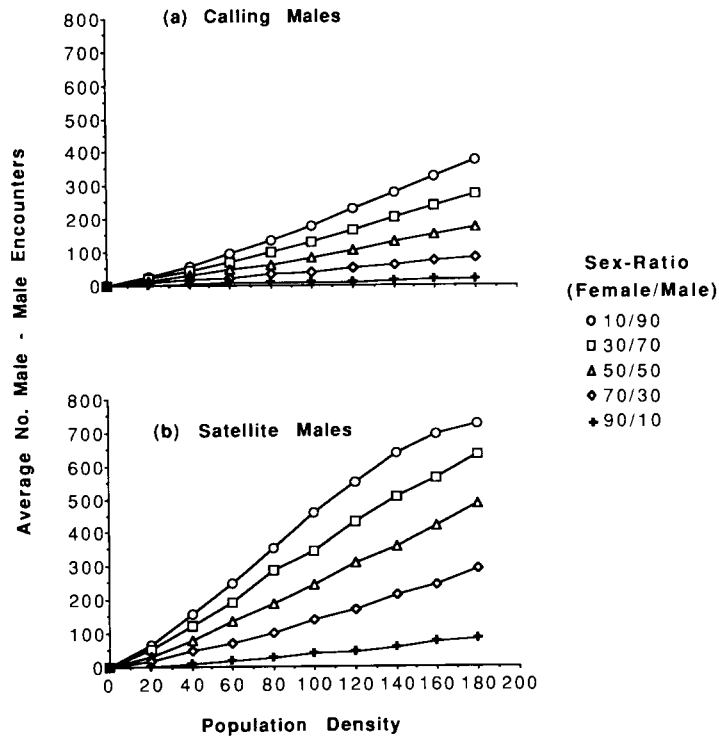


Fig. 7. Average number of male-male encounters for (a) calling and (b) satellite males in populations of varying sex ratios with increasing population density at a constant proportion of callers of 0.5.

of calling males and sex ratios, respectively. When sex ratio was held constant at 50/50, both calling and satellite males had significantly lower rates of male-male encounters with respect to population density in populations containing mostly calling males (Table 3). Calling males experienced lower levels of male-male encounter rates across all populations of varying proportions of callers than did satellite males (Fig. 6 and Table 3). Similarly, in comparisons of simulated populations of varying sex ratios (holding the proportion of calling males constant at 0.5), calling males showed significantly lower male-male interactions than satellite males across all sex ratios (Table 4). Significantly lower levels of male-male encounters were found for both satellite and calling males in populations with female-biased sex ratios (Fig. 7 and Table 4).

DISCUSSION

Matings resulting from male calling and female attraction should decline relative to satellite male matings with increased population density in

TABLE 3

Regressions of male-male encounters on density at varying proportions of calling male frequencies

Strategy	Proportion of calling males ^a				Slope ^b
	0.20	0.40	0.60	0.80	
Caller					
Slope ± SE	1.2 ± 0.03	1.1 ± 0.03	0.8 ± 0.03	0.5 ± 0.02	109.9 ^d
Y-intercept	-5.5	-9.1	-8.3	-4.5	
Satellite					
Slope ± SE	3.4 ± 0.1	3.0 ± 0.1	2.6 ± 0.1	2.3 ± 0.1	41.1 ^d
Y-intercept	-31.4	-28.7	-20	-16.5	
Slope ^c	21.2 ^d	7.84 ^d	28.6 ^d	29.4 ^d	

^a Simulated populations with 50/50 sex ratio.

^b *F*-statistic for multiple comparisons among slopes.

^c Student's *t*-test for comparison of two slopes.

^d Significantly different, *P* < 0.001.

acoustically communicating insects (Alexander, 1961, 1975; Otte, 1977). The present simulation supports this prediction. Satellite and calling male mating success increased with increasing population density. Calling male mating frequency declined exponentially with increasing population den-

TABLE 4

Regression analysis of male-male encounters on density at varying sex ratios

Strategy	Sex ratio (females/males) ^a					Slope ^b
	10/90	30/70	50/50	70/30	90/10	
Caller						
Slope ± SE	2.1 ± 0.1	1.6 ± 0.05	1.0 ± 0.03	0.5 ± 0.01	0.1 ± 0.01	382.9 ^d
Y-intercept	-21.4	-14.4	-8.3	-2.4	0.3	
Satellite						
Slope ± SE	4.4 ± 0.2	3.6 ± 0.1	2.7 ± 0.1	1.6 ± 0.1	0.5 ± 0.03	324.1 ^d
Y-intercept	-2.0	-13.9	-22.6	-17.0	-8.5	
Slope ^c	13.6 ^d	26.3 ^d	24.6 ^d	17.2 ^d	7.17 ^d	

^a Simulated populations with calling male proportion of 0.5.

^b *F*-statistic for multiple comparisons among slopes.

^c Student's *t*-test for comparison of two slopes.

^d Significantly different, *P* < 0.001.

sity, however, relative to that of satellite males. These simulation results are similar to data from field studies on *G. integer*, *G. pennsylvanicus* and *G. campestris* where calling behavior resulted in significantly more matings than satellite behavior at low population densities (French and Cade, 1989; Hissman, 1990; Cade and Cade, 1992).

There was no evidence that the proportion of calling males influenced calling male mating success in this simulation. By contrast, mating success for satellite males was highly frequency dependent, showing the highest values when satellite males were most frequent in the population across all densities. That is, there was positive frequency dependence instead of the negative frequency dependence predicted by some models (Gadgil, 1972; Gadgil and Taylor, 1975; O'Donald, 1978; Rubenstein, 1980). No data are available from field studies on *G. integer* to test these hypotheses on frequency-dependent mating success. In the grasshopper *Ligurotettix coquilletti* there was no evidence for negative frequency-dependent mating success in field populations (Greenfield and Shelly, 1985).

Previous simulations and graphical models have indicated that the chances of calling and noncalling males obtaining mates is partly a function of sex ratio (Waltz, 1982; Fairchild, 1984). In general, populations with female-biased sex ratios should give rise to higher male mating success for males utilizing any mating behavior. In this simulation, an exception to the higher calling male-female encounter rates occurred in populations having extremely female-biased sex ratios. In those populations where females outnumbered males by a factor of nine, satellite males showed higher mating success than calling males (especially at high densities). There is some information on sex ratios in natural populations of field crickets (Veazey et al., 1976; Cade, 1979b, 1989), but these data do not show a biased sex ratio of the order of nine females to one male, the extreme levels at which satellites had higher mating success than calling males in this simulation.

Waltz (1982) developed a static threshold model to explain the persistence of satellite males in populations. Signalling males had physical access to all attracted females, but male ability to inseminate females declined as the number of females increased. Our model assumes that males can inseminate all females encountered, but the probability of calling males attracting females declines as satellite male-female encounters increase with increasing female population density. In real populations, however, male physiology limits cricket ability to inseminate females (Loher and Rence, 1978), an effect that may be enhanced in parasitized males (Zuk, 1987). Physiological limitations would enhance the sex ratio and density-dependent effects on mating success shown here.

Variations in population density and the resulting fluctuations in sexual

selection intensity may maintain additive genetic variation underlying *G. integer* calling (Cade, 1981c). Our simulation results indicate, however, that density-dependent selection alone is probably not responsible for maintaining calling and satellite behavior since calling males almost always encounter females more frequently than satellites. It is possible, however, that very high population densities and female-biased sex ratios may contribute to the maintenance of genetic variation for calling behavior.

In this simulation we assumed that longevity did not vary between calling and satellite males. In actual populations, however, calling males may have reduced survivorship due to parasitism by acoustically orienting parasitoid flies, *Ormia ochracea* (Diptera; Tachinidae; formerly *Euphasiopteryx*). Non-calling *G. integer* are rarely parasitized (Cade 1975). Reduced survivorship may be important in maintaining genetic variation for calling behavior in *G. integer*.

Male–male interactions may also contribute to the maintenance of alternative male behavior (Cade, 1979a). Male field cricket interactions are characterized by loud stridulation, biting, flaring of the mandibles and kicking with hind legs (Alexander, 1961; Dixon and Cade, 1986). The simulation results suggest that, by remaining stationary, calling males substantially reduce their chances of encountering other males. Calling males only encounter satellite males, whereas satellites encounter callers and other satellites. Male–male encounters should therefore be higher for satellite males. The costs of male encounters will depend, however, on whether agonistic behaviors result. Alexander (1961) predicted that male–male encounters increase with population density, but that the proportion of encounters that result in fighting behavior declines. Simmons (1986) found that male–male encounters increased with population density, but that the proportion of encounters resulting in aggression declined at high densities in the field cricket *G. bimaculatus*. Interactions between satellite males probably do not result in increased costs. Male–male interactions in field crickets may allow males to monopolize females and thus contribute to the maintenance of alternative mating behavior (Alexander, 1961).

This simulation confirmed, in part, empirical findings that population density is a major factor influencing male mating success in *G. integer* and other field crickets. The simulation also makes the following predictions that present and future field studies will examine: proportion of calling males does not influence mating success of callers, but is a factor influencing satellite male mating success; and sex ratio is a major factor influencing male mating success.

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