



A simulation model of the effects of frequency dependence, density dependence and parasitoid flies on the fitness of male field crickets

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Abstract

There is substantial variation in the strategies animals use to obtain mates. In crickets, males may call to attract females or use a non-calling, or satellite, strategy and intercept females attracted to the calls of other males. Calling males are subject to attack by an acoustically orienting parasitoid fly and, after being parasitized, males die in 7–10 days. We used a simulation model to determine how frequency dependence, population density, and parasitoid flies affect the mating success of calling and non-calling males. The simulation demonstrated that calling males have higher mating success than satellite males under most conditions, and the fitness of both strategies increases with population density. Frequency-dependent selection did not have strong effects on calling or satellite male fitness. However, if parasitoid flies were present, satellite males had similar or higher mating success than calling males. These results demonstrate that the risk of parasitism strongly influences the fitness of calling and satellite males and likely contributes to the continued coexistence of alternative reproductive behavior in crickets.

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1. Introduction

Reproductive strategies can be quite different across species and it is common for there to be variation in the strategies a particular sex uses to obtain mates (Taborsky, 1994; Henson and Warner, 1997; Brockmann, 2001). Traditionally, the existence of these alternative strategies is explained through frequency-dependent selection or condition dependence. Frequency-dependent selection results in the

fitness of a particular strategy being dependent on the frequency of that strategy in the population (Maynard-Smith, 1982). Condition dependence results in changes in an individual's behavior as a function of their size, body condition or environmental conditions (Gross, 1996). Although usually treated as separate mechanisms, it is becoming increasingly clear that both condition and frequency dependence simultaneously influence the fitness of alternative strategies (Gross and Repka, 1998).

In some crickets, males use two different strategies to obtain mates. They can signal acoustically (call) to attract females or be silent and search for or intercept females (satellite behavior Cade, 1979a). The amount of time that a male spends calling or silent is heritable

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in *Gryllus texensis* (Cade, 1981a) and the relative fitness of calling or satellite behavior depends on population density and the operational sex ratio. At low densities or when sex ratios are male-biased, males generally call more and there is selection for calling behavior (French and Cade, 1989; Hissman, 1990; Cade and Cade, 1992; Souroukis and Cade, 1993). In a previous simulation model, Rowell and Cade (1993) demonstrated that satellite males had the same or greater encounter rates with females as calling males when the sex ratio was female-biased and the population was at high density. These studies suggest that fluctuations in population density and the operational sex ratio contribute to the continued coexistence of calling and satellite behavior in field crickets.

In some species of field crickets male calling song attracts parasitoid flies, *Ormia ochracea*, as well as females (Cade, 1975; Walker, 1993; Zuk et al., 1993; Wagner, 1996). After locating a cricket based on its calling song, the parasitoid fly deposits a larva that burrows into the host and emerges 7–10 days later, killing the host. Flies exhibit selection on reproductive behavior through preferences for certain calling song characteristics (Wagner, 1996; Gray and Cade, 1999; Zuk et al., 2001) and on the amount of calling behavior exhibited (Cade and Wyatt, 1984; Zuk et al., 1993; Bertram, 2002). In particular, the presence or absence of flies is hypothesized to be a factor influencing the evolution and maintenance of calling and satellite behavior in crickets (Cade, 1975, 1979a, 1981a). Here we present the results of a computer simulation of alternative reproductive behavior in the field cricket, *G. texensis*, to test this hypothesis. Our model examines the relative impacts of changes in population density, the frequency of calling males, and the presence or absence of parasitoid flies on the fitness of calling and satellite males.

2. Materials and methods

2.1. Basic model information

This simulation model was developed using R software, an open source package for statistical computing (Ihaka and Gentleman, 1996; Ripley, 2001). The model is a substantial modification of an earlier model which was used to examine the influence of population

density, sex ratio, and frequency dependence on the female encounter rates of calling and satellite males (Rowell and Cade, 1993). The code for the model is available from the corresponding author upon request. We created a 10×10 cell grid in which crickets were able to move into any surrounding cell. The grid resembles outdoor enclosures used in field studies (Cade and Cade, 1992). Movement was limited to cells inside the grid and if an animal moved outside this grid the movement was cancelled (see Rowell and Cade, 1993). In the model, simulated male crickets were either callers or satellites throughout each simulation run. Although there is a continuous distribution of time spent calling (Cade, 1981a; Cade and Wyatt, 1984), we chose to treat males as silent or calling because these represent discrete ways to obtain mates. In addition, this makes the results of this model comparable to Rowell and Cade (1993). In the beginning of each simulation, satellite males and females were distributed randomly among grid cells. Calling males were also distributed randomly among grid cells, but with the condition that calling males were at least one empty cell apart from each other. This is similar to observed spacing patterns (Cade, 1981b).

2.2. Rules for movement, parasitism and mortality

Calling males are stationary when calling, and thus do not move during the simulation. Satellite males moved randomly one cell in any direction and had a fixed probability of moving per iteration of the model. The probability of moving per iteration for satellite males was 0.5. At a larger spatial scale (2000–10,000 m²) males exhibit phonotaxis towards males that are calling resulting in a clumped distribution of calling and satellite males (Cade, 1979a, 1981b). However, at the spatial scale represented by the model (100 m²), movement of satellite males relative to calling males is random (Rowell and Cade, 1993). As in the previous study, these rules are an approximation and require us to make few assumptions about the way satellite males move. In addition, this results in a similar amount of movement when compared to individuals monitored in enclosures (Cade and Cade, 1992). If satellite males moved into a cell occupied by a calling male, then they always moved during the next iteration of the model. This results in satellite males never occupying the same cell as

a calling male for more than one iteration but does allow them to occupy adjacent cells.

Females also moved one cell in any direction with a fixed probability per iteration which was set at 0.5. A female could move randomly or exhibit positive phonotaxis towards the nearest calling male by moving one cell in that direction. Females always moved towards calling males unless there were no calling males alive, in which case they moved randomly one cell in any direction. Lastly, if a female had recently encountered a male, that female moved randomly one cell in any direction for a period of 3 days. This is consistent with empirical data that show mated females are not as phonotactic as unmated females (Koudele et al., 1987; Prosser et al., 1997; Lickman et al., 1998) and females in the presence of males exhibit reduced phonotactic responses compared to females deprived of males (Cade, 1979b).

Parasitoid flies were also incorporated into the model. In the beginning of the simulation, flies were randomly positioned in the grid. Flies always exhibited positive phonotaxis towards calling males and always moved one cell towards a calling male per iteration. When a fly was in the same cell as a calling male, the calling male became parasitized and the male died 5 days after the encounter. Flies did not parasitize satellite males or females in the model. In *G. texensis* there is a low rate of parasitism in satellite males and no parasitized females have been found (Cade, 1979a, 1984). During this period males could still attract females. Although this is shorter than the duration required to kill a male cricket, infected males exhibit reduced calling and reproductive behavior after 3–4 days (Cade, 1984; Adamo et al., 1995; Kolluru et al., 2002).

Longevity of unparasitized males and females was based on a fixed probability per iteration (males = 0.00125, females = 0.001) that resulted in similar mean survival times as those measured in the lab (Gray and Cade, 2000). This resulted in females, on average, living for 33 days and males for 28 days.

In all experiments, the model was run for 50 days with 20 iterations per day, resulting in 1000 total iterations. For all experiments, five simulation runs were completed and the average from the individuals in each simulation was used as a replicate in all statistical analyses. The resulting data included the average lifespan of calling males, satellite males and females,

the average lifetime number of female encounters of satellite and calling males, and the number of parasitized males. An encounter is defined as two individuals occupying the same cell. If a female encountered a calling and satellite male in the same cell, we assumed a preference for the calling male and it was scored as an encounter for the calling male not for the satellite male. While an encounter between a male and female in the field does not necessarily result in mating, male mating success is related to the number of female encounters (Rowell and Cade, 1993). All simulations were run on a personal computer with a 500 MHz Intel Celeron processor running Windows 98 and R version 1.4.1.

2.3. Experiment 1: frequency and density dependence

To examine how the frequency of calling males in the population and total cricket density influenced the lifetime number of female encounters for both calling and satellite males, we varied the total cricket density (ranged from 0.08 to 0.64 crickets/cell) and the proportion of calling males (0.25–0.75), while holding the sex ratio constant (1:1). It should be noted here that because females and males die, density and sex ratio vary as the simulation runs. Because the data were counts and were not normally distributed, we used Poisson regression to examine the effects of density and the proportion of calling males on lifetime number of female encounters for both calling and satellite males. Poisson regression is a generalized linear model with a log link and Poisson error distribution. This approach is essentially linear regression using the correct link and distributional assumptions for count data and results in a model that is on the scale of the original data without transformation (McCullagh and Nelder, 1989). Because the relationship between lifetime number of female encounters, density, and the proportion of calling males was non-linear, we included quadratic terms in each model. To avoid problems with multicollinearity, density and the proportion of calling males were expressed as deviations from their respective means (Neter et al., 1990). In addition, this makes the intercept interpretable as the mean number of female encounters at the average density and average proportion of calling males used in the analysis.

2.4. Experiment 2: parasitoid flies

We examined the effects of parasitoid flies on the lifetime number of encounters with females of calling and satellite males by varying the density of flies (0, 1, 2, or 8 flies in the simulation) and crickets

(ranged from 0.08 to 0.64 crickets/cell) while holding the proportion of calling males (0.5) and sex ratio (1:1) constant. Lifetime number of female encounters was modeled in the same manner as in the previously described experiment for both calling and satellite males. To measure the impact of parasitoid

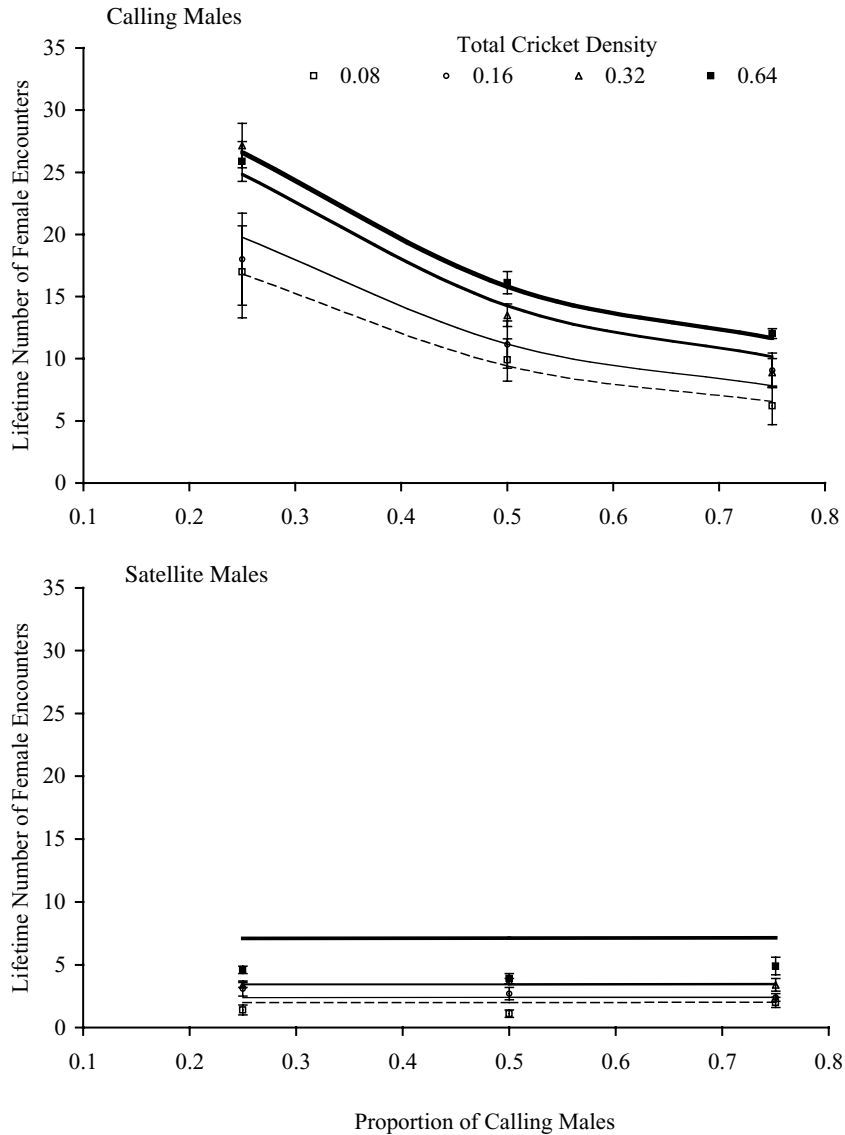


Fig. 1. The average number of female encounters over the lifetime of both calling and satellite males varying total cricket density (crickets/cell) and the proportion of calling males in the population. For all data the operational sex ratio is 1:1. Lines are predicted values based on a polynomial Poisson regression. Line thickness corresponds to the number of crickets in the simulation. The thickest line corresponds to the highest density (0.64 crickets/cell) and each successive thinner line a lower density. The dashed thin line corresponds to the lowest density (0.08 crickets/cell). Data are shown as the mean of five replicate simulations \pm 1 S.E.

flies on lifespan in both calling and satellite males, we compared the average lifespan of males using a three-factor ANOVA in which cricket density, fly density and male strategy were factors.

3. Results

3.1. Experiment 1: density and frequency dependence

The average number of female encounters dependent on male strategy, density, and the proportion of calling males are in Fig. 1 and the results of the regression analyses for calling and satellite males are in Table 1. The number of female encounters increased with density for both calling and satellite males. Also, the number of female encounters by calling males declined in non-linear fashion as the proportion of calling males increased in the population. However, changes

in the proportion of calling males did not influence the number of females encountered by satellite males.

3.2. Experiment 2: density and parasitoid flies

The average number of lifetime encounters with females for calling and satellite males dependent on cricket density and fly density are in Fig. 2 and the regression models for calling and satellite males are in Table 2. The number of female encounters increased with density in both calling and satellite males, but calling male fitness declined in an exponential fashion as fly density increased. However, satellite male fitness increased in a hyperbolic fashion as fly density increased. Calling male lifespan was significantly reduced when flies were present (Table 3, Fig. 3) and the number of parasitized males increased with cricket density and the number of flies present in the model (Fig. 4).

Table 1

Results of Poisson regression relating lifetime number of female encounters to density and proportion of calling males for both satellite and calling males

Parameter	Callers	<i>P</i> -value (parameter = 0)	Satellites	<i>P</i> -value (parameter = 0)
Intercept (β_0)	2.63 (0.078)	<0.0001	1.192 (0.17)	<0.0001
Density (β_1)	1.23 (0.23)	<0.0001	2.26 (0.54)	0.0001
Proportion of calling males (β_2)	-1.79 (0.18)	<0.0001	0.013 (0.38)	0.9728
(Density) ² (β_3)	-2.52 (1.06)	0.0220	-0.46 (2.37)	0.0556
(Proportion of calling males) ² (β_4)	1.72 (1.23)	0.1674	1.59 (2.55)	0.5369
Density \times proportion of calling males (β_5)	0.42 (0.78)	0.5959	0.152 (1.63)	0.9262

The regression equation takes the form: number of female encounters = $\exp_{(0+1 \times \text{DENS} + 2 \times \text{PC} + 3 \times \text{DENS}^2 + 4 \times \text{PC}^2 + 5 \times \text{PC} \times \text{DENS})}$, where DENS is the centered density, PC is the centered proportion of calling males, DENS² and PC² are the squared proportion of calling and β_0 is the intercept and the other β_0 parameters relate the variable they are multiplied by to the number of female encounters. Regression estimates, their standard errors (in parenthesis), and *P*-values are presented for all terms.

Table 2

Results of Poisson regression of lifetime number of female encounters on density and number of parasitoid flies for both satellite and calling males

Parameter	Callers	<i>P</i> -value (parameter = 0)	Satellites	<i>P</i> -value (parameter = 0)
Intercept (β_0)	1.34 (0.12)	<0.0001	2.25 (0.12)	<0.0001
Density (β_1)	1.32 (0.32)	<0.0001	2.41 (0.35)	<0.0001
Fly density (β_2)	-29.78 (2.87)	<0.0001	21.8 (3.98)	<0.0001
(Density) ² (β_3)	-1.40 (1.38)	0.3128	-6.16 (1.49)	<0.0001
(Number of flies) ² (β_4)	493.87 (89.90)	<0.0001	-378.2 (109.1)	0.0009
Density \times number of flies (β_5)	-11.06 (8.17)	0.1797	7.24 (6.49)	0.2685

The regression equation takes the form: female encounters = $\exp_{(0+1 \times \text{DENS} + 2 \times \text{FD} + 3 \times \text{DENS}^2 + 4 \times \text{FD}^2 + 5 \times \text{FD} \times \text{DENS})}$, where DENS is the centered density, FD is the centered fly density, β_0 is the intercept and the other β parameters relate the variable they are multiplied by to the number of female encounters. Regression estimates, their standard errors (in parenthesis), and *P*-values are presented for all terms.

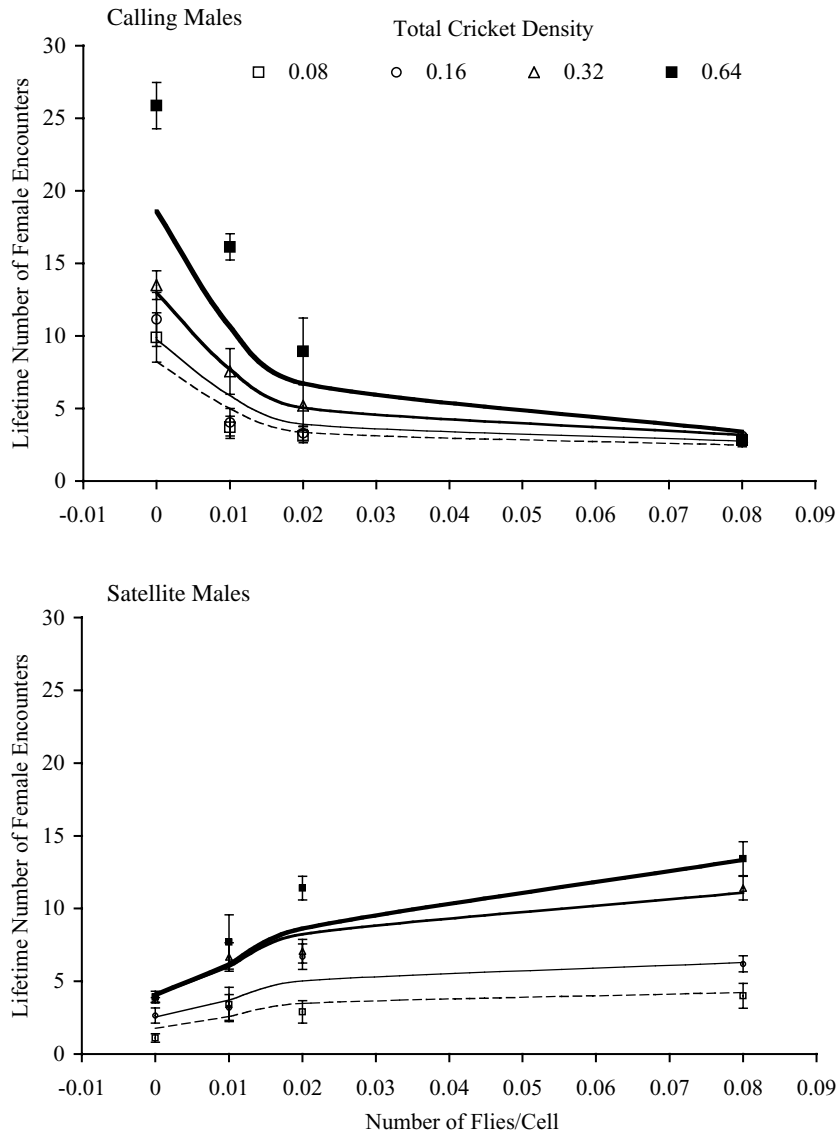


Fig. 2. The average number of female encounters over the lifetime of both calling and satellite males varying total cricket density and the number of parasitoid flies in the simulation. For all data the operational sex ratio is 1:1. Lines are predicted values based on a polynomial Poisson regression. The thickest line corresponds to the highest density (0.64 crickets/cell) and each successive thinner line a lower density. The dashed thin line corresponds to the lowest density (0.08 crickets/cell). Data are shown as the mean of five replicate simulations ± 1 S.E.

4. Discussion

Frequency dependence is hypothesized to be an important mechanism maintaining alternative strategies or phenotypes (Brockmann, 2001). When examining only changes in the proportion of calling males and

density, our model demonstrates frequency-dependent selection acting on calling males but not satellite males. The number of encounters a calling male has with females declined as the proportion of calling males increased. However, there was no change in the number of females encountered by satellite

Table 3

Results of three-factor ANOVA on the lifespan of satellite and calling males under different densities and differing numbers of parasitoid flies

Source	Type III sum of squares	d.f.	Mean square	F	P
Density	398.613	3	132.871	2.994	0.033
Number of flies	3039.9	3	1013.3	22.8	<0.001
Male strategy	10305.8	1	10305.8	232.2	<0.001
Density × number of flies	875.1	9	97.2	2.19	0.027
Density × male strategy	176.5	3	58.8	1.33	0.267
Number of flies × male strategy	4251.6	3	1417.2	31.9	<0.001
Density × number of flies × male strategy	520.1	9	57.78	1.302	0.242
Error	5680.6	128	44.38		
Total	25248.2	159			

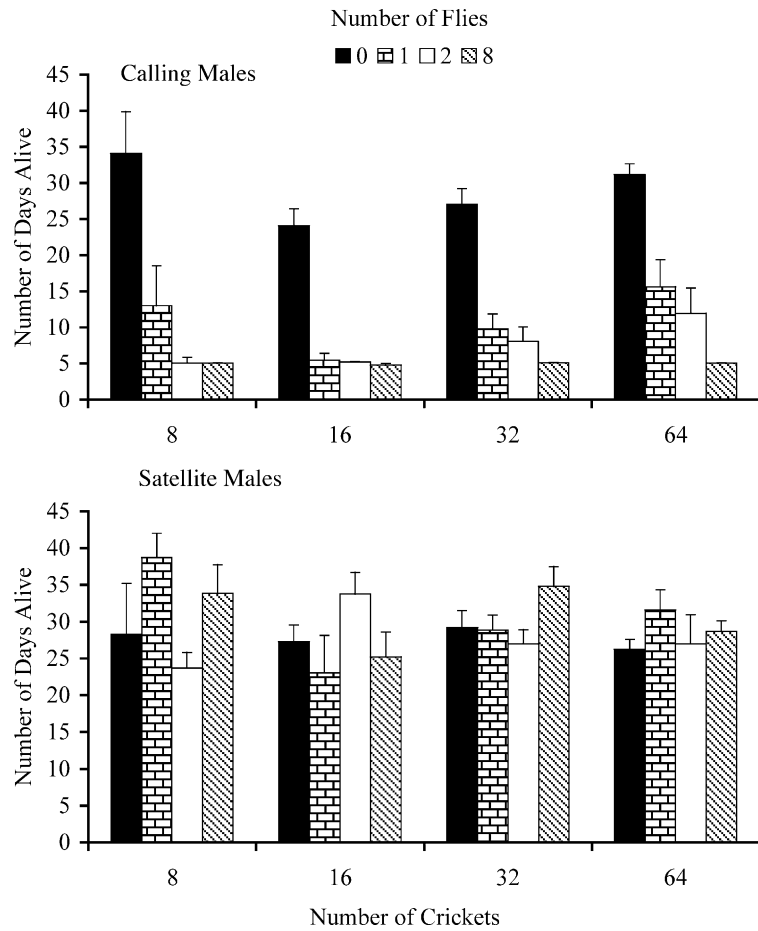


Fig. 3. The average lifespan of both calling and satellite males varying density and the number of parasitoid flies. Adding parasitoid flies results in a significant reduction in calling male life span compared to satellite males or to calling males under conditions with no parasitoid flies. Data are shown as the mean of five replicate simulations ± 1 S.E.

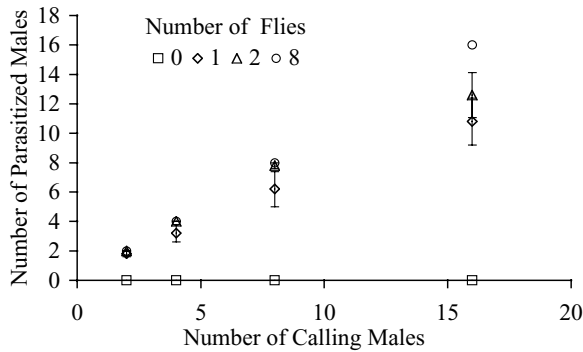


Fig. 4. The number of calling males parasitized by flies as a function of density and number of flies. Data are shown as the mean of five replicate simulations ± 1 S.E.

males. Although the number of females a calling male encounters declines as their frequency increases in the population, calling males always encounter a greater number of females than do satellite males. This suggests that, under the simulation conditions used here, there is no stable frequency at which both calling and satellite males would have equal fitness and frequency dependence alone would not result in the coexistence of these two alternative strategies.

The importance of frequency-dependent selection in the evolution of calling and satellite behavior is difficult to evaluate. Our results demonstrate frequency-dependent selection acting on calling males, but the effect on male fitness is fairly weak and satellite male fitness is not influenced by frequency dependence. Greenfield and Shelly (1985) found no evidence of frequency dependence in a field study of calling and silent grasshoppers. In addition, despite the plethora of species in which males exhibit alternative behaviors to obtain mates (Andersson, 1994; Henson and Warner, 1997), there are few species in which frequency-dependent selection has been documented (e.g. Bluegill sunfish Gross, 1991; side-blotched lizards Sinervo and Lively, 1996). Unlike many models examining alternative male strategies that assume frequency-dependent selection (Arak, 1988; Lucas and Howard, 1995; Lucas et al., 1996; Hugie and Lank, 1997; Alonzo and Warner, 2000), our model and Rowell and Cade (1993) examine the properties of the caller-satellite system based on interactions between individuals

and both suggest that frequency-dependent selection has a limited role. Rowell and Cade (1993) showed no frequency-dependent selection acting on calling males and positive frequency dependence for satellite males. The differences between our and Rowell and Cade's (1993) model can be explained by a number of factors. Rowell and Cade's (1993) model does not estimate long-term mating frequencies, whereas our model estimates the lifetime number of encounters a male cricket has with females. In addition, their model did not incorporate mortality or changes in female response to calling song as a function of encounters with males. Although their results are quantitatively different from ours, they also suggest that frequency dependence may only have a small effect on calling and satellite male fitness.

As cricket density increases the number of female encounters for both calling and satellite males also increases. However, the rate that female encounters increase with density for satellite males is approximately twice that of calling males. Although satellite male fitness increases more quickly, calling males still encounter more females when parasitoids are absent. A previous simulation model showed a similar pattern (Rowell and Cade, 1993). In addition, research on several cricket species indicates that selection favors calling only at low densities (Alexander, 1968; French and Cade, 1989; Hissman, 1990; Cade and Cade, 1992). These data suggest that, as in other systems, density-dependent effects on male fitness can have effects on the fitness of different behavioral strategies (Greenfield and Shelly, 1985; Radwan, 1993).

For alternative strategies to coexist, the two strategies should have equal fitness under some set of conditions (Brockmann, 2001). Our model shows that the number of females encountered by calling males decreases rapidly with increasing fly density while the number of females encountered by satellite males increases. The effect on calling males is quite substantial and results in calling males encountering the same number of females in the presence of one to two flies as satellite males and fewer at higher fly densities. Thus, the presence of parasitoid flies may result in equal fitness for calling and satellite males and could promote the coexistence of these two alternative phenotypes.

The primary mechanism for the changes in calling male fitness is a decrease in calling male lifespan. This is not surprising since our model reflects the fact that

O. ochracea impairs reproductive behaviors in 3–4 days following parasitism and kills male crickets in 7–10 days (Cade, 1979a, 1984; Adamo et al., 1995; Kolluru et al., 2002). Our results reflect patterns seen in the field. In species and populations not parasitized by *O. ochracea*, males live longer (Simmons and Zuk, 1994; Murray and Cade, 1995). These studies and our results suggest that *O. ochracea* can have dramatic effects on the fitness of male crickets by a reduction in their lifespan.

A number of studies have documented calling and silent males in species that are parasitized by *O. ochracea* (Cade and Wyatt, 1984; Walker and Wineriter, 1991; Zuk et al., 1993). Although not all studies suggest that not calling is an adaptive strategy to avoid parasitism (see Zuk et al., 1995), there is an overwhelming amount of evidence supporting this hypothesis. One way to avoid being located by an acoustically orienting parasitoid is to reduce the amount of time spent calling. Populations of *T. oceanicus* that are parasitized by *O. ochracea* do not call as much as populations that are not (Kolluru, 1999). Also, species that are not attacked by *O. ochracea* call more than *G. texensis*, which is attacked by the parasitoid (Cade and Wyatt, 1984; Cade, 1991). Several studies have shown that silent males are less likely to be attacked by *O. ochracea* than calling males (Cade, 1975, 1979a; Walker and Wineriter, 1991). Our results demonstrate that the presence of parasitoid flies reduces the number of females encountered by calling males, while satellite males encounter the same number of females or more females than calling males when fly density is high. Thus, satellite behavior would be an effective strategy to avoid flies and, when flies are present, satellite males will have similar or greater fitness than calling males.

Most models of alternative male strategies have stressed the importance of frequency as well as condition dependence (e.g. Lucas and Howard, 1995; Lucas et al., 1996; Repka and Gross, 1995; Gross and Repka, 1998; Alonzo and Warner, 2000). Early theoretical work concentrated on how frequency-dependent selection results each strategy having equal fitness (Maynard-Smith, 1982). However, it is now clear that frequency dependence, condition dependence, or both can result in the coexistence of alternatives and these alternatives do not necessarily have to have equal fitness (Repka and Gross, 1995; Gross and Repka,

1998). Our model does not account for how changes in condition or state (energetic condition, body size, or age) could influence the optimal behavior of calling and satellite males. Using a stochastic dynamic game model Lucas et al. (1996) have shown that energetic state, predation risk, female arrival rate, and frequency-dependent selection influence the likelihood of exhibiting calling or satellite behavior. As in our model, risk of being killed impacts the fitness of calling and satellite males and when calling is risky (e.g. high predation or parasitism risk), satellite behavior is favored. Given that calling is energetically expensive in crickets (Prestwich and Walker, 1981; Hoback and Wagner, 1997) and there may (Bertram, 2000) or may not (Cade and Wyatt, 1984) be correlations between age, size and calling behavior in *G. texensis*, condition dependence could play a role in maintaining calling and satellite male strategies. However, interspecific comparisons and comparisons between populations show that species or populations that are parasitized by *O. ochracea* exhibit reduced calling behavior compared to species or populations that are not (Cade, 1991; Kolluru, 1999). These data suggest that parasitoid flies exhibit strong selection on reproductive behavior in crickets and our model suggests that this effect is large enough to result in the coexistence of calling and satellite strategies without frequency or condition dependence.

Our simulation results examine the interactions between cricket density and the frequency of calling males and cricket density and the density of parasitoid flies. Although both cricket density and frequency dependence impact which strategy encounters more females, neither has strong effects. However, flies have a very large effect on the fitness of calling and satellite males. Although the effects of frequency dependence and density are small, this does not suggest they are unimportant. Satellite behavior will be favored under conditions of high cricket density and high parasitism risk, but calling males will have higher success when crickets are at a low density, low parasitism risk and low frequency. If fly and cricket density are variable, this creates a situation in which selection will vary and calling males will be favored in some situations and satellites in others.

Fluctuating patterns of selection can clearly help to maintain variation in reproductive behavior and may result in the maintenance of alternative reproductive

behavior (Brockmann, 2001). It has been hypothesized that fluctuating selection as a consequence of variation in fly and cricket density helps to maintain variation in reproductive behaviors (Cade, 1975, 1979a; Bertram, 2002). Field studies have shown that fly density varies seasonally, spatially, and over the time course of a single night (Mangold, 1978; Cade et al., 1996). For instance, Zuk et al. (1995) have shown that fly abundance varies across the different islands in the Pacific. In addition, variation in the prevalence of *O. ochracea* is correlated with differences in reproductive behaviors across populations (e.g. Zuk et al., 1993; Rotenberg et al., 1996; Kolluru, 1999). Since the intensity of selection against calling behavior varies with fly density, the fitness of calling and satellite males will fluctuate. This is particularly well illustrated in *G. texensis* where generational changes in calling behavior reflect seasonal changes in cricket density and parasitism risk (Bertram, 2002). Parasitoid flies and crickets are at low density in the spring and calling behavior is selected for, but in the fall crickets and parasitoids are at high density and calling behavior is selected against. Bertram (2002) found shifts in the amount of time males of successive generations call that were consistent with this hypothesis. Thus, there is a pattern of fluctuating selection acting on male behaviour and based on our model it will likely help to maintain calling and satellite strategies in crickets (Cade, 1975, 1979a; Cade and Wyatt, 1984; Bertram, 2002).

It is becoming increasingly clear that predators and parasitoids influence the reproductive strategies and signals used by animals to attract mates (Zuk and Kolluru, 1998). Our model demonstrates that a number of factors influence the fitness of crickets possessing alternative strategies. We show that the fitness of calling and satellite males changes with cricket density, the proportion of calling males, and the presence or absence of parasitoid flies that attack and kill calling males. However, the strongest effects on calling and satellite male fitness were due to parasitoid flies. Although not considered here, female preferences for a certain strategy or changes in the operational sex ratio can impact the fitness of calling and satellite males (Souroukis and Cade, 1993; Alonzo and Warner, 2000). Thus, fluctuating selection pressures from changes in density, the presence or absence of parasitoid flies, changes in female preferences or frequency dependence could all potentially maintain

alternative strategies and genetic variation for these male reproductive strategies.

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