Alternative Reproductive Tactics Arising from a Continuous Behavioral Trait: Callers versus Satellites in Field Crickets

John T. Rotenberry,1,* Elizabeth Swanger,2 and Marlene Zuk2

1. College of Biological Sciences, University of Minnesota, St. Paul, Minnesota 55108; 2. Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108

Submitted September 4, 2014; Accepted December 5, 2014; Electronically published February 26, 2015


Abstract: Alternative reproductive tactics may arise when natural enemies use sexual signals to locate the signaler. In field crickets, elevated costs to male calling due to acoustically orienting parasitoid flies create opportunity for an alternative tactic, satellite behavior, where noncalling males intercept females attracted to callers. Although the caller-satellite system in crickets that risk detection by parasitoids resembles distinct behavioral phenotypes, a male’s propensity to behave as caller or satellite can be a continuously variable trait over several temporal scales, and an individual may pursue alternate tactics at different times. We modeled a caller-satellite-parasitoid system as a spatially explicit interaction among male and female crickets using individual-based simulation. Males varied in their propensity to call versus behave as a satellite from one night to the next. We varied mortality, density, sex ratio, and female mating behavior, and recorded lifetime number of mates as a function of a male’s probability of calling (vs. acting as a satellite) along a gradient in parasitism risk. Frequently, the optimal behavior switched abruptly from being pure caller (call every night) to pure satellite (never call) as parasitism rate increased. However, mixed strategies prevailed even with high parasitism risk under conditions of higher background mortality rate, decreasing density, increasing female-biased sex ratio, and increasing female choosiness. In natural populations, high parasitoid pressure alone would be unlikely to yield fixation of pure satellite behavior.

Keywords: alternative reproductive tactics, field crickets, individual-based simulation, parasitoids, satellite behavior.

Introduction

How are alternative phenotypes created and maintained within populations? Many animal species exhibit alternative reproductive tactics, discontinuous behavioral and other traits that represent two or more alternative ways of achieving reproductive success (Oliveira et al. 2008). Alternative reproductive or mating tactics evolve in the context of intraspecific and intrasexual reproductive competition when there is fitness to be gained by pursuing divergent tactics. An individual may pursue different tactics through time (alternating among them on timescales ranging from seconds to most of a lifetime), or one alternative may be fixed for life (Oliveira et al. 2008). The phenotypic discontinuity that characterizes alternatives can arise on both a monomorphic or polymorphic genetic background. In the former case, this discontinuity usually arises by differential expression of a condition-dependent trait (Emlen 2008); in the latter, it may be maintained by disruptive or frequency-dependent selection (Tompkins 1999).

One common class of alternative reproductive tactics involves differing expression of a sexually attractive signal (see Brockmann and Taborsky 2008 for a recent review). Under sexual selection, sexually attractive signals usually evolve such that they become both costly to the signaler (usually male) and conspicuous to the receiver (usually female; Andersson 1994). However, as a signal becomes more costly, the signaler becomes increasingly vulnerable to exploitation by an individual that employs an alternative tactic that avoids use of the signal (Taborsky 1998). Moreover, as a signal becomes more conspicuous, it becomes increasingly susceptible to “eavesdropping” by unintended recipients that exploit the signal to their own benefit, often with some additional associated cost to the signaler (Zuk and Kolluru 1998; Peake 2005). Eavesdroppers may be of either the same species or a different species from the signaler, but in either case, the increased costs to the signaler expand the opportunity for selection favoring an alternative mating tactic (Gonçalves et al. 2008).

Acoustically orienting parasites and predators provide excellent examples of interceptive eavesdropping, or using a signal to locate host or prey (Peake 2005). One particularly well-studied example of this phenomenon involves the parasitoid tachinid fly Ornria (formerly Euphasiapteryx) ochracea and a number of grylline crickets that serve as its host (Cade 1975; Walker and Wineriter 1991).
The larvae burrow into the cricket, consume fat, muscle, and organ tissues during a development period of around 7–10 days, and then emerge to pupate in the soil (Cade 1975; Walker and Wineriter 1991; Adamo and Hoy 1995). Infested males may continue to call for a few days post-parasitization, but their tendency to do so wanes after a few days, and they die upon larval fly emergence (Cade 1984; Kolluru et al. 2002). Thus, although calling in the absence of an acoustically orienting parasitoid may carry some cost compared to not calling (e.g., increased energy expenditure; Prestwich 1994), calling in the parasitoid’s presence can drive up a male’s costs (paid in the currency of reduced longevity) substantially. These higher costs have indeed provided an opportunity for exploitation by an alternative mating tactic. Cade (1975, 1980) observed that some male field crickets (Gryllus texensis [formerly Gryllus integer]; Cade and Otte 2000) in populations subject to parasitoid Ormia did not call but instead were seen in the vicinity of callers. Cade (1975) called such males satellites and suggested that they were intercepting females as they moved toward callers, thereby avoiding parasitization. The trade-offs are evident: callers are far more likely than satellites to attract females (and hence more likely to mate) but bear the cost of elevated mortality associated with calling and attracting a fly, whereas satellites trade reduced mortality (and hence acquire increased longevity) for reduced female encounter rates.

Although the caller-satellite system in field crickets under risk of fly parasitization represents a set of distinct behavioral phenotypes that qualify as alternative reproductive tactics (Brockman 2008; Taborsky et al. 2008), it is important to recognize that in many species a male cricket’s propensity to behave as a caller or satellite is not a discrete, fixed trait but instead may be continuously variable over multiple temporal scales. Laboratory and field investigations of calling behavior in several species of Gryllus and Teleogryllus demonstrate variation in the amount of time calling among individuals within a night, among individuals within a population, and in the same individual across nights (Cade 1981b, 1991; Cade and Wyatt 1984; Loher and Örsak 1985; Bertram and Johnson 1998; Kolluru 1999). Moreover, although environmental attributes such as temperature or population density may influence whether or how long a cricket calls during any night, several studies have demonstrated that the duration of nightly calling may have a genetic component (Cade 1981a; Hedrick 1988; Bertram 2002; but see Bertram et al. 2007). And finally, the abundance of phono-tactic parasitoids, and the resulting rate or intensity of parasitism, can be highly variable within as well as between populations and seasons (Walker and Winewriter 1991). Thus, we observe a continuously variable trait (propensity to call) overlaid on a continuously variable selection gradient (parasitization risk), potentially giving rise to a dichotomous behavioral response.

Previous simulation modeling has treated the two mating tactics as discrete and fixed. Walker and Cade (2003) showed that in the absence of parasitoid flies, the number of females encountered during a male’s lifetime (their measure of fitness) went up for both callers and satellites, as population density increased but was always higher for callers than for satellites under no-fly conditions. They observed no frequency dependence; satellites did not encounter more females per capita than callers, even when satellites constituted 90% of the simulated population. Thus, absent flies, satellite behavior should disappear from a population. Introducing flies modified the outcome dramatically. Although the density effect remained the same (number of female encounters increased as cricket density increased), per-male encounter rates decreased for callers as fly density increased, whereas they increased for satellites. At relatively low fly density, female encounter rates for satellites began to exceed that of callers, with the gap increasing as fly abundance increased in their simulations, indicating very strong selection for satellite behavior.

But as noted above, individual field crickets often do not follow a fixed strategy of being either a caller or satellite. Thus, a more realistic approach than modeling a mixture of animals that are either always callers or always satellites is to model a population of individuals that has some propensity for satellite behavior and examine the response of that variable to selection. Clearly, variation in the risk of parasitization creates a selection gradient, and along this gradient we might expect to see variation in the fitness of crickets with different propensities for satellite behavior. Moreover, we might expect to see variable environmental conditions influence the outcome. Here we use individual-based modeling to ask, How does selection, in the form of likelihood of parasitization when calling, affect the evolution of satellite behavior when we treat it as a trait that is continuously variable over at least some temporal scale? Does selection on variation in a continuous trait lead to relatively discrete alternative tactics? How do additional environmental conditions (e.g., sex ratio, population density, background mortality rate) influence the propensity for either type of behavior? Variation in components of female mating behavior, such as propensity to approach calling males and to mate with males encountered, may also influence the costs and benefits of calling, thereby affecting the relative fitness of alternative behaviors. For example, if females are extremely choosy and reluctant to mate, then a male accrues little additional benefit from calling while continuing to bear any costs associated with attracting eavesdroppers. How does variation in female choosiness or mating behavior affect the fitness of alternative male mating tactics under variable risk of parasitization?
Thus, we seek to identify the optimal behavior (in terms of the probability of pursuing a calling or satellite tactic) that maximizes fitness under various combinations of these environmental and behavioral conditions. Our objectives are twofold: (1) to extend the approach of Walker and Cade (2003) to include additional components of cricket behavior, particularly female choosiness at two different stages in the mate selection process; and (2) to shift from a dichotomous perspective of satellite versus calling behavior toward a more realistic continuous one (Andersson 1994; Shuster and Wade 2003). Of the various temporal scales over which the pattern of male calling may vary, we choose to focus on between nights (e.g., Rowell and Cade 1993; Walker and Cade 2003). If an attracted female moves into his patch, she may mate with him with some probability or reject him and seek other mates. However, in a night during which he calls, he also has a specified risk of being parasitized; variation in this nightly probability of parasitization if calling represents the selection gradient. If he becomes parasitized, he continues to follow male behavioral rules in subsequent nights, but he is removed from the population after the third night postparasitization. Callers do not occupy adjacent patches.

Females are phonotactic; during a particular time interval, a female is attracted (with some probability) to calling males that she hears but may encounter satellites as well. A female mates with whomever she encounters with some probability, which is the same whether he was encountered as a caller or as a satellite. If she decides not to mate with whomever she has encountered, she moves on. If she does mate, she is done for the evening: she no longer responds to calls, he also has a specified risk of being parasitized; variation in this nightly probability of parasitization if calling represents the selection gradient. If he becomes parasitized, he continues to follow male behavioral rules in subsequent nights, but he is removed from the population after the third night postparasitization. Callers do not occupy adjacent patches.

Females are phonotactic; during a particular time interval, a female is attracted (with some probability) to calling males that she hears but may encounter satellites as well. A female mates with whomever she encounters with some probability, which is the same whether he was encountered as a caller or as a satellite. If she decides not to mate with whomever she has encountered, she moves on. If she does mate, she is done for the evening: she no longer responds to calls, he also has a specified risk of being parasitized; variation in this nightly probability of parasitization if calling represents the selection gradient. If he becomes parasitized, he continues to follow male behavioral rules in subsequent nights, but he is removed from the population after the third night postparasitization. Callers do not occupy adjacent patches.

Methods

The Model

We modeled the caller-satellite-parasitoid system as a time-dependent, spatially explicit interaction among male and female crickets. We used the individual-based modeling environment provide by NetLogo (Wilensky 1999), which is particularly well suited for exploring the connection between the microlevel behavior of individuals and the macrolevel patterns that emerge from the interaction of many individuals. We employed a spatially explicit approach because satellite behavior, at least in crickets, is inherently a spatially explicit process.

We followed the general approach of Walker and Cade (2003; see also Rowell and Cade 1993) in structuring time: individual behavior (calling, moving, encountering other individuals, mating) takes place throughout a “night,” and at the end of the night the demographic consequences (deaths, emergences of replacement adults) are reckoned. In NetLogo, program steps advance in “ticks”; individuals perform a behavior during each tick. Each individual also occupies a “patch” in the landscape and can move among patches. We parameterized our simulations based on our own field investigations of Teleogryllus oceanicus in the Hawaiian Islands, where it is parasitized by Ormia ochracea (Zuk et al. 1993; Simmons and Zuk 1994; Kolluru et al. 1999; M. Zuk et al., unpublished data) as well as those used by Walker and Cade (2003) based on extensive studies of Gryllus texensis, also parasitized by O. ochracea.

Crickets move across the landscape and interact with other crickets based on particular rules. These rules describe the events and movements that occur during each tick throughout a 50 × 50 grid of patches; for convenience, we model only nighttime hours, where 240 ticks (equivalent to 3 min each) = 1 12-h night. Each patch is functionally equivalent to a 1 × 1-m square, and a moving cricket can traverse one square per tick. Edges of the landscape are hard, and a moving cricket that encounters an edge is deflected back onto the landscape.
vivors age one night; and summary statistics are collected. Ticks are reset to zero, a male decides whether to be a caller or satellite, and a new night begins.

We begin a simulation run with an initial cohort of a specified total number of individuals and sex ratio. All males have the same nightly probability of behaving as a satellite, although each male decides each night independently of the others. As each individual male from the original cohort dies, we record his age, the number of females he has encountered, the number of females he mated with, and whether he was parasitized. When the last male of the original cohort dies, the simulation run ends and we average these variables over all males of the cohort. Our measure of fitness is the average lifetime number of females mated. To account for the stochastic nature of sex and death in the model, we perform 10 independent runs for each combination of input variables examined.

Although similar in many respects, our approach differs in three important ways from that of Walker and Cade (2003). First, dead individuals are replaced in kind (males by males, females by females) to maintain constant density and sex ratio. Otherwise, the actual density toward the end of a simulation can become a small fraction of the nominal density, particularly at higher background mortality rates or strongly biased sex ratios, with potentially important effects on spatially dependent processes such as encounter rates. Second, satellite males do not continually wander randomly but instead are attracted to males they hear calling. Phonotaxis of male *Gryllus* and *Teleogryllus* toward conspecific callers has been well documented and is one of the principal mechanisms producing clumped aggregations of calling males (Cade 1981b; Tinghitella et al. 2009; Jang 2011; McCarthy et al. 2013). Third, a simulation ends when the last male of the original cohort dies, rather than running for a fixed duration. Thus, all males over which we average lifetime statistics have lived a complete life; we do not collect data from noncohort males as many of these have not yet died and thus would yield biased lifetime data.

### The Simulations

Our objective is to examine how variation in the nightly probability of following a satellite tactic interacts with the risk of parasitization to affect fitness under a variety of environmental conditions. The simulation experiments involved independent sets of manipulations of population density, sex ratio, background death rate, female phonotaxis, and female propensity for mating with an encountered male (table 1). For every set of simulations, we vary the nightly probability that a male following a caller strategy that night will be parasitized from 0 (i.e., no flies) to 0.4 (which can result in more than 80% of the males in a cohort being parasitized) in increments of 0.05 and cross that with the nightly probability that a male will behave as a satellite from 0 (yielding a population of all callers) to 1.0 (a population of all satellites) in increments of 0.1. We take as an arbitrary baseline a set of simulations with a total number of crickets (population density) of 50; a sex ratio of 50:50 females to males (F:M); a background nightly mortality rate of 0.045 (which yields a theoretical life span of about 22 days, consistent with an average age of 9–13 days observed for *Gryllus* and *Teleogryllus*; Simmons and Zuk 1994; Murray and Cade 1995; Gray 2013); a female phonotaxis, or the probability of moving toward a calling male, of 0.5; and a probability of a female mating with an encountered male of 0.6 (e.g., Tinghitella and Zuk 2009 for *Teleogryllus*). We subsequently vary each of these five parameters (density, sex ratio, background death rate, female phonotaxis, and female mating probability) independently to encompass a realistic range of values for each (table 1).

Following Rowell and Cade (1993) and Walker and Cade (2003), we varied density (total number = 25, 50, 100, and 200) and, independently, sex ratio (F:M = 40:60, 50:50, 60:40, 70:30, 80:20, and 90:10). We also varied background mortality rate (nightly probability of dying of 0.025–0.075 in steps of 0.010), female phonotaxis.
(probability of moving toward a male heard of 0.3, 0.5, and 0.7), and female mating behavior (probability of a female mating with an encountered male of 0.2–0.8 in steps of 0.2; table 1). In all simulations reported here, we left fixed male and female auditory radii (number of patches over which a calling male could be detected of 20).

The Analysis

We used locally weighted scatterplot smoothing (LOWESS; Cleveland and Devlin 1988) to empirically describe fitness (lifetime number of females mated) as a function of nightly probability of being parasitized if calling (the selection gradient) versus propensity for satellite behavior. LOWESS creates a nonparametric surface by computing small-scale, locally weighted regressions at points uniformly scattered over an output data set (fig. 1). This allowed us to describe a fitness surface without resorting to parametric functions of the independent variables, functions that may be poorly defined (Mitchell-Olds and Shaw 1987; Schluter 1988). We created surfaces with a resolution of 30 × 30 equally scaled intervals using a tricubic weighting function for a locally linear estimate based on sampling a radius encompassing 10% of the total data using SigmaPlot 12.5 (Systat Software 2013). We empirically determined the value of the nightly probability of being a satellite that maximized fitness at each value of parasitization rate for each of the 30 intervals (see “Baseline” section below). We then plotted this fitness-maximizing propensity for satellite behavior as a function of parasitization rate to generate a graph of the optimal behavioral phenotype along the selection gradient (see “Baseline”).

As supplemental material (available online), we provide (1) the annotated NetLogo code and (2) a flowchart of the simulation program. Data underlying all analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.dp4qg (Rotenberry et al. 2015).

Results

Baseline

We describe in detail results from the baseline experiment (1) to provide an example of how we display, analyze, and interpret the output and (2) to provide a benchmark for comparing output across the simulation experiments, since many of the fitness surfaces generated have similar shapes. Each of the five principal manipulations (variation in density, sex ratio, background death rate, phonotaxis, and female propensity for mating) included one set of runs at baseline values (table 1). Here we present the baseline results from the density experiment (fig. 1).

The edges were informative and made sense. With no parasites (fig. 1, edge A; fig. 2A), reproductive success declined (not necessarily linearly) with increasing propensity for satellite behavior due to decreased encounter rates; calling is clearly important in attracting females in this simu-
lated system. With high parasites, however (fig. 1, edge B; fig. 2A), success increased with increasing probability of satellite behavior, although it was always less than success in the no-parasite case. In a population of all callers (fig. 1, edge C; fig. 2B), fitness declined rapidly (nonlinearly) as soon as parasites were introduced, whereas a population of satellites (fig. 1, edge D; fig. 2B) remained largely unaffected by their introduction. The fitness surface is warped, as it must be as we move from an ascending edge (B) to a descending edge (A) along the parasitization rate dimension and simultaneously from a descending edge (C) to a flat edge (D) along the satellite behavior dimension. This complexity provided the rationale for describing the surface using LOWESS rather than attempting to fit a mathematical function. By a conventional criterion, the fitted LOWESS surface captured variation in the raw output well, with an $r^2 = 0.754$ and a slope (regressing raw simulated output on values predicted from the surface) of $b = 1.01$ (figs. A1, A2). Residual deviation was greatest at higher values of females mated, which also tended to have higher variances.

For the baseline, the optimal strategy for a male cricket with respect to propensity for satellite behavior is approximately a step function (fig. 3): below a parasitization rate

![Figure 2: A, Average male fitness at different propensities for satellite behavior in populations with high versus no parasitism. B, Average male fitness at different parasitization rates for populations with all callers versus all satellites. Results from baseline simulation. Lines A–D are taken from edges of the fitted surface in figure 1.](image)

![Figure 3: Propensity for satellite behavior that maximizes the number of females mated for differing probabilities of parasitization. The bold line across the surface denotes the probability of satellite behavior that yields the maximum number of females mated for each value of probability of parasitization. Results are from the baseline simulation (fig. 1).](image)
of 0.1 (nearly probability of becoming parasitized if calling), always (or nearly so) behave as a caller, whereas above that rate, always behave as a satellite. Thus, in this particular simulation, essentially no level of parasitization exists at which a mixed strategy (some nights as a caller, some nights as a satellite) is optimal. At low risk of parasitization, the cost of not singing outweighed the risk of a shorter life, whereas above a threshold, the value of those trade-offs was reversed. Note, however, that selection is somewhat relaxed (i.e., the fitness surface is relatively flatter) at parasitization rates on either side of the steep transition, suggesting that the exact location of the transition with respect to parasitization rate is somewhat fuzzy.

This result from examining continuous variation in the target behavior is, in this case, similar to that from previous analyses treating behavior as discontinuous, that is, comparing the fitness of a population of all callers to one of all satellites (fig. 2B; Walker and Cade 2003). The fitness lines cross at a parasitization rate of 0.1, implying that a caller tactic is optimal below that value and that a satellite tactic is optimal above it.

**Background Mortality Rate**

As background mortality rate increases, the number of females mated declines in direct association with decreased life span (fig. 4A, 4B). More importantly, the surfaces flatten out as parasitoid-independent mortality increases, indicating a less intense selection gradient associated with parasitism. This arises because the additional mortality associated with calling in the presence of parasitoids becomes an increasingly smaller proportion of total mortality, which affects callers and noncallers alike.

In an all-caller population, male reproductive success drops dramatically as soon as parasites come into the picture, but at higher background mortality rates, the lifetime number of females mated flattens out and the curves converge (fig. 4C). Satellites, on the other hand, show no effect of parasitism (the highest linear \( r^2 \) is only 0.01), and average reproductive success simply declines with increasing background mortality (fig. 4D).

In the absence of parasites, increasing propensity for satellite behavior was associated with decreasing reproductive success, and the principal effect of increasing background mortality was simply to reduce the elevation of that relationship (fig. 4E). Under conditions of high parasitism, fitness differences associated with any propensity for calling behavior declined rapidly and essentially flattened out and converged across mortalities as probability of satellite behavior decreased below about 0.5 (fig. 4F).

Variation in background death rate strongly influences the shapes of the fitness maximization curves (fig. 5). As background mortality rate increases, there is a shift between a step function versus more continuous variation in the probability of satellite behavior that maximizes fitness as parasitization rate increases. For at least the three highest mortality rates, there is a stretch of parasitization rate over which a mixed strategy is favored over all calling or all satellite.

**Density**

Variation in population density strongly influences the number of females mated, generating several complex fitness surfaces (fig. 6A, 6B). The most apparent result is that increasing density lifts the fitness surface due to increased encounter rates. Density, parasitization rate, and satellite behavior all interact, as the shape of the surface changes considerably as density increases. The effects on all-satellite and all-caller populations are also as expected (fig. 6C, 6D). Caller reproductive success drops rapidly as soon as parasitoids are introduced, although the curves maintain their spacing (more crickets translates into more encounters, which translates into more matings) and have the same general shape (fig. 6C). Satellites show no effect of parasitism (the highest linear \( r^2 \) is only 0.001; fig. 6D), and reproductive success increases with increasing density.

In the absence of parasitoids, reproductive success declines monotonically at the two lowest densities as the propensity for satellite behavior increases; thus, at lower densities, males that call on fewer nights experience an increasing penalty in the form of lower female encounter rates (fig. 6E). At the two highest densities, however, the decline does not continue but instead begins to rise at higher levels of satellite propensity. In general, the number of females mated rises with density due to increased rates of encounter, with or without parasitoids, as observed by Walker and Cade (2003). However, at the highest densities and when most males are behaving as satellites most nights (probability of satellite behavior is >0.8), the relatively rare calling males begin to experience a reduction in mating success, as females attracted to them are more likely to be intercepted by satellites that are also attracted to the same vicinity. Under high parasitization pressure, fitness rises with increasing propensity for satellite behavior, and this increase accelerates at the highest values (fig. 6F). Viewed alternatively, under high risk of parasitization, any increase in the number of nights spent calling results in a rapid decrease in fitness, and this is exacerbated at higher densities (consistent with Walker and Cade 2003).

Figure 7 summarizes the patterns described above. Interestingly, although there is more variation at lower values of probability of parasitization (associated with higher values of females mated; see above), at the lowest density, it is clear that there is a range of parasitization rates where a more mixed strategy prevails. However, as density increases,
Figure 4: Average male fitness as a function of parasitization rate and propensity for satellite behavior at different background mortality rates (m). A, B, Two different perspectives of the same fitness surface. For clarity, only three of five fitness surfaces are shown. C, D, Average male fitness at different parasitization rates for populations with all callers (C) versus all satellites (D) at different background mortality rates. Lines are the edges of the locally weighted scatterplot smoothing (LOWESS)-fitted surfaces in figure 4A, 4B at probabilities of satellite behavior equal to 0 and 1. E, F, Average male fitness at different propensities for satellite behavior at different background mortality rates under no (E) and high (F) rates of parasitism. Lines are the edges of the LOWESS-fitted surfaces in figure 4A, 4B, at probabilities of parasitization equal to 0 and 0.4. Raw simulation output is omitted for clarity.
we see a transition to a step function, a rapid shift from favoring a full caller (or mixed-strategy, predominantly caller) to a pure satellite strategy. And, as noted above, at even higher densities, fitness is maximized by a pure satellite strategy, even with no or very few parasitoids.

**Sex Ratio**

Increasing the proportion of females elevates the fitness surface, consistent with Walker and Cade (2003; fig. 8A, 8B). Moreover, the interaction between risk of parasitism and probability of satellite behavior on fitness is enhanced as F:M sex ratios increase (i.e., the surface becomes steeper and less linear overall). The effects on all-satellite and all-caller populations (fig. 8C, 8D) are similar to those for density. Caller reproductive success drops rapidly as soon as parasitoids are introduced, although the curves maintain their spacing and have the same general shape (fig. 8C). Satellites show little effect of parasitism (fig. 8D) and reproductive success increases slightly with increasing female bias in the population.

Note that, without parasites and at the highest female-biased sex ratio (F:M = 90:10), increasing satellite behavior from zero to low levels (~0.25) increases females mated, but beyond the low level, reproductive success begins to decline as it otherwise does for all less-biased sex ratios (fig. 8E). This was somewhat unexpected but probably results from spatial constraints. With a density of 50 crickets, this sex ratio yields 5 males; at a probability of calling of 25% or less (i.e., probability of satellite behavior of >0.25), there is likely at best only a single male calling per night, which means every cricket in the field goes to the same place, enhancing every male’s encounter rate. With less female bias, multiple callers are more likely. Under high predation pressure, females mated increases with increasing number of females available in the population, but females mated does not vary with satellite propensity given any particular sex ratio, except for showing a slight decline under the most biased simulations for males that are predominantly satellites (fig. 8F).

The fitness maximizer curves show substantial variation (fig. 9). At less female-biased sex ratios, we see the step function that indicates a rapid transition from mostly calling to mostly satellite behavior as the risk of parasitization increases beyond a critical point, whereas a mixed strategy is favored in the two most strongly female-dominated simulations regardless of the parasitization rate. We did not expect that in populations where females strongly outnumber males, retaining calling (and for a large proportion of nights) would be the best strategy under high risk of predation. Indeed, we expected that, similar to Rowell and Cade (1993) and our own density simulations, more females would generally translate into more matings for satellites, an outcome that normally appears enhanced under parasitoid pressure. That is clearly not the case here and, as noted above, is likely reflective of spatial constraints and the very small number
Figure 6: Average male fitness as a function of parasitization rate and propensity for satellite behavior at different densities (N). A, B, Two different perspectives of the same set of fitness surfaces. C, D, Average male fitness at different parasitization rates for populations with all callers (C) versus all satellites (D) at different densities. Lines are the edges of the locally weighted scatterplot smoothing (LOWESS)-fitted surfaces in figure 6A, 6B at probabilities of satellite behavior equal to 0 and 1. E, F, Average male fitness at different propensities for satellite behavior in populations at different densities with no (E) versus high (F) parasitization rates. Lines are the edges of the LOWESS-fitted surfaces in figure 6A, 6B at probabilities of parasitization equal to 0 and 0.4. Raw simulation output is omitted for clarity.
of males in a population at these sex ratios. However, such strongly biased sex ratios likely rarely occur naturally.

Female Mating Behavior—Phonotaxis

Changing the level of phonotaxis (the probability that a female would approach a male she heard calling) changed male mating success in the expected way, with females mated increasing with increasing phonotaxis (fig. 10A, 10B).

The effects on all-satellite and all-caller populations were consistent with previous results; success of callers declined nonlinearly with increasing parasitism rate, whereas satellites were unaffected (fig. 10C, 10D). Moreover, since satellites do not interact with females in the context of females being attracted to their calling, we observed no difference among them with respect to phonotaxis probability.

Probability of satellite behavior interacts with female phonotaxis to influence reproductive success (i.e., the lines are not parallel) under both high and no parasitoid conditions (fig. 10E, 10F), but overall, fitness declines with increasing satellite behavior in the absence of parasites and increases in their presence, albeit relatively more slowly in the latter case.

As we go from baseline phonotaxis (p = .5) to decreased responsiveness (p = .3), the transition from all caller to all satellite occurs at a lower probability of parasitization; calling while at risk to flies when few females are answering is clearly not an optimal tactic (fig. 11). Alternatively, having an increased response by females to calls (p = .7) selects for continuing to call even as risk increases (although call with lesser nightly probability).

Female Mating Behavior—Propensity to Mate

Not surprisingly, as females become less choosy (i.e., more apt to mate with a male they encounter), the average number of females mated rises (fig. 12A, 12B). The effects on all-satellite and all-caller populations are as expected: callers demonstrate nonlinear declines as parasitization rates increase, offset in the appropriate sequence (choosier females lead to fewer matings; fig. 12C); on the other hand, satellites show essentially no variation as the probability of parasitization changes and fitnesses associated with decreasing female choosiness are stacked in the appropriate sequence (fig. 12D).

The edges describing females mated as a function of probability of satellite behavior at high versus no parasitization, however, show disproportional changes: without parasitoids, the number of matings declines with increasing satellite behavior (fig. 12E); at high parasitism rates, satellites do proportionally better as female choosiness declines (fig. 12F). This interaction between female probability of mating and male propensity for satellite behavior is somewhat unexpected, as females do not differentiate
Figure 8: Average male fitness as a function of parasitization rate and propensity for satellite behavior at different sex ratios. A, B, Two different perspectives of the same fitness surface. For clarity, only four of six ratios simulated are shown. C, D, Average male fitness at different parasitization rates for populations with all callers (C) versus all satellites (D) at different sex ratios. Lines are the edges of the locally weighted scatterplot smoothing (LOWESS)-fitted surfaces in figure 8A, 8B at probabilities of satellite behavior equal to 0 and 1. E, F, Average male fitness at different propensities for satellite behavior in populations with different female to male (F:M) sex ratios with no (E) versus high (F) parasites. Lines are the edges of the LOWESS-fitted surfaces in figure 8A, 8B at probabilities of parasitization equal to 0 and 0.4. Raw simulation output is omitted for clarity.
between a caller and a satellite—mating probability is the same for each.

The fitness maximizer curves showed an abrupt change in behavior, from a step function at lower choosiness (i.e., higher probability of mating with an encountered male) to favoring a mixed strategy over a broad range of parasitization rates at higher levels of female choosiness (fig. 13). This is perhaps even more unexpected than the disproportionality noted above (and does not appear to stem from that). Instead, it seems to be similar to a low-density effect; although actual female density does not change, effective female density (from the standpoint of a male trying to attract a mate) is lower (compare the line for $c = 0.2$ in fig. 13 with the line for $N = 25$ in fig. 7). Note that while treating calling–satellite as a lifetime continuum revealed this pattern (fig. 12E, 12F), the pattern was otherwise opaque to treating the alternative behaviors as fixed (fig. 12C, 12D), which showed very little interaction.

**Discussion**

Modeling a caller-satellite-parasitoid system by treating calling versus satellite behaviors as a trait that is continuously variable over a cricket’s lifetime rather than as discrete, fixed alternative tactics provided greater insight into the dynamics of fitness associated with environmental variation. The fitness surfaces arising from the interaction between the nightly probability of behaving as a satellite with the probability of parasitization if calling were complex and nonlinear but yielded consistently interpretable results. To summarize: (1) Similar to Walker and Cade (2003), increasing density favors more satellite behavior, presumably by decreasing the cost of not attracting females with audible signals, which is achieved by increasing chance encounter rates. In addition, at higher densities, calling males may experience additional costs due to interception of attracted females by surrounding attracted satellites. (2) Unexpectedly, under highly female-biased sex ratios, spending most nights calling remains the optimal strategy even under high risk of parasitization. This appears to be a product of spatial constraints and the small number of males actually singing, leading to a local aggregation containing almost all males. (3) As background mortality rate increases, calling behavior is more likely to persist even in the face of increasing parasitization rates. This occurs because parasitoid-induced mortality of callers is a decreasing proportion of total mortality, reducing the relative difference between their death rates and those of noncallers. (4) As female phonotaxis decreases (i.e., females are less likely to approach a calling male she hears), calling behavior becomes increasingly less optimal. Sensibly, increasing calling while at risk of parasitization when females are reluctant to approach is not a sound tactic. (5) As female propensity to mate decreases, calling behavior is more likely to persist even under increasing risk of parasitization. This, too, was unexpected and likely represents what is
Figure 10: Average male fitness as a function of parasitization rate and propensity for satellite behavior at different probabilities of female phonotaxis ($p$). A, B, Two different perspectives of the same fitness surface. C, D, Average male fitness at different parasitization rates for populations with all callers (C) versus all satellites (D) at different levels of female phonotaxis. Lines are the edges of the locally weighted scatterplot smoothing (LOWESS)-fitted surfaces in figure 10A, 10B at probabilities of satellite behavior equal to 0 and 1. E, F, Average male fitness at different propensities for satellite behavior for populations with no (E) versus high (F) parasitization rates at different levels of female phonotaxis. Lines are the edges of the LOWESS-fitted surfaces in figure 10A, 10B at probabilities of parasitization equal to 0 and 0.4.

Raw simulation output is omitted for clarity.
functionally a low-density (i.e., few females available for mating) effect.

As we manipulate female choosiness, we are essentially modeling variation in attractiveness of males (although female tendency to be choosy can vary independently of that as well; Gray 1999). We know that calling song attributes influence the likelihood of a male attracting a female (Zuk and Simmons 1997), and once a female encounters him, qualities of his courtship song and other male traits influence whether she actually mates with him (Tregenza et al. 2006). Although we do not specifically manipulate any particular one of these attributes in the model, we do examine their potential effects along a parasitoid risk gradient. For example, consider female phonotaxis (fig. 11). If some element of a male’s calling song (e.g., pulse rate) influences its attractiveness to females, as parasitization rate increases, a male with a more attractive song (high $p$) should continue to sing at least some nights well past the point where those with less attractive songs should cease altogether. In contrast, males that are less attractive up close (i.e., low $c$, probability of female mating with an encountered male; fig. 13) should still persist in calling even at very high rates of parasitization well after more acceptable males should have switched to a pure satellite strategy. We presume that this represents a need to enhance encounter rates to offset the higher rejection rates.

One salient feature of our results is that despite having a continuous trait (nightly probability of pursuing a calling vs. satellite tactic) distributed along a uniform selection gradient (variation in the nightly probability of becoming parasitized if calling), we frequently observed a threshold-type outcome: the optimal behavior of pure (or nearly so) calling at lower rates of parasitization suddenly switched to an optimum of pure satellite behavior at higher rates of parasitization. This abrupt shift in the favored phenotype along an otherwise smoothly varying selection gradient is both theoretically predicted (Haldane 1948; Levins 1968; May et al. 1975) and observed experimentally (Endler 1973) and in nature (Handford and Nottebohm 1976; Millar 1983; Cameron et al. 2013). This phenomenon is frequently discussed in the context of phenotypic differentiation along geographical clines (Endler 1977), but the underlying process is the same as we observed.

The mechanism underlying this phenomenon is captured in Levins’s (1962, 1968) fitness set theory (see also Waltz and Wolf 1984). The differences between the fitnesses of a caller versus a satellite phenotype in environments with and without flies are relatively high, and there is no phenotype that does well both in the presence of flies and in the absence of flies. This results in an optimum strategy of a single phenotype that is specialized on one or the other environments, depending on the intensity of selection. Under conditions of no flies, calling has relatively higher fitness (the intensity of selection on satellites is high) and is selected for; as flies (or the probability of being parasitized by flies) increase, calling may still be favored, but at some critical point, satellite be-
Figure 12: Average male fitness as a function of parasitization rate and propensity for satellite behavior at different probabilities of mating with an encountered female (c). A, B, Two different perspectives of the same fitness surface. C, D, Average male fitness at different parasitization rates for populations with all callers (C) versus all satellites (D) at different levels of female choosiness. B, Average male fitness at different propensities for satellite behavior in populations with high versus no parasites at different levels of female choosiness. Lines are the edges of the locally weighted scatterplot smoothing (LOWESS)-fitted surfaces in figure 12A, 12B at probabilities of satellite behavior equal to 0 and 1. E, F, Average male fitness at different probabilities of satellite behavior for populations with no parasites (E) versus high parasitization rates (F) at different levels of female choosiness. Lines are the edges of the LOWESS-fitted surfaces in figure 12A, 12B at probabilities of parasitization equal to 0 and 0.4. Raw simulation output is omitted for clarity.
behavior has a higher fitness and the optimum strategy shifts completely. This yields the step function we frequently see (e.g., fig. 5). The point of inflection (where the transition occurs) depends on the difference in fitness between the two phenotypes in each of the environments. Pertaining to, for example, figure 7, we see that the transition from caller to satellite shifts to the left (i.e., with decreasing probability of parasitization) with increasing overall density. As noted, increasing density increases the relative fitness of satellites by decreasing the cost of not attracting females, which is achieved by increasing chance encounter rates. What leads to attenuation of the step function, that is, more smoothly clinal variation in optimal phenotype (e.g., fig. 5, mp 0.075)? Levins’s (1962, 1968) models predict a transition from an abrupt to a gradual change in favored phenotypes (given the same environmental gradient) as the difference in fitness between two phenotypes in the same environment becomes smaller. Again using the example of high background mortality (fig. 5, m = 0.075), we expect that the cost of calling and risking parasitization is only incrementally larger than the chances of dying anyway, thereby reducing the magnitude of the fitness difference between callers and satellites that otherwise exists when background mortality rates are lower.

Numerous studies examining the effect of acoustic parasitoids on cricket singing behavior have focused on a different timescale, variation among individuals in time spent calling within a night (Cade and Wyatt 1984; Kolluru 1999; Bertram 2002; Velez and Brockmann 2006; Beckers and Wagner 2012). Even in the absence of acoustic parasitoids, within-night variation across male crickets can be substantial (Loher and Orsak 1985; Cade 1991; Cade and Cade 1992). At this temporal scale, we might expect to see more clinal variation in optimal behavior (in this case, proportion of the night spent calling vs. rate of parasitization), as the fitness differences between calling a little and calling a little more (or calling a lot and calling a little less) are likely to be small across substantial variation in risk of parasitism (i.e., a convex fitness set). It is also the case that, in the field, not all callers call all of the night as they do in our simulations. Although low-effort calling presumably reduces the risk of parasitization in natural populations, it also reduces encounter rates with females. In addition, in our simulations, the addition of even a low risk of parasitization substantially depresses fitness compared to the absence of risk (fig. 1C). We expect, therefore, that introducing variation in effort among callers would likely yield fitness functions of the same shape (mostly stepped) but shifted to the right.

Our model is set up such that the selection gradient (increasing parasitoid pressure) is always pushing the optimal strategy in the direction of fewer nights calling and more nights behaving as a satellite, and this frequently results in an abrupt transition favoring a population consisting of pure satellites. However, pure satellite populations of crickets that normally call are rare; indeed, that natural cricket popula-
tions consist of mixtures of individuals with varying propensities for nightly calling inspired the form of our model. Under what conditions, then, is calling behavior likely to persist even in the presence of abundant parasites? (1) Decreasing density appears to retard the shift to an all-satellite strategy under increasing probability of parasitization (fig. 7). At the lowest density modeled, at least some nightly calling was optimal even at high parasitization rates, whereas at the high density, an all-satellite tactic was optimal with any parasite pressure. These results are consistent with those of Cade and his colleagues (Rowell and Cade 1993; Walker and Cade 2003). (2) An increasingly female-biased sex ratio is also associated with persistence of calling in the face of high parasitization rates. This is in contrast to Rowell and Cade (1993), who observed that the mating success of satellites surpassed that of callers at the highest sex ratios. In our case, we suspect that we are observing a male density effect because we held total population size constant. For example, a population of 50 individuals at a F:M ratio of 90:10, has only 5 males. Although the average number of females mated is highest at the highest F:M sex ratios (fig. 8), consistent with Cade and colleagues, at those ratios, the most successful of the few males present are those that spend the majority of their nights calling. It appears that with so few males, interception of females by satellites has little impact on callers. (3) Higher background mortality rates are also associated with persistence of calling, most likely due to a reduction in the proportional difference in overall mortality between steady callers versus satellite males. (4) Higher female phonotaxis (greater willingness to approach a calling male she hears) provides advantages to callers that render the behavior more likely to persist under increased parasitization risk. (5) Increasing female choosiness (decreasing willingness of a female to mate with an encountered male) selected for persistence in calling, a somewhat unexpected result given that females do not discriminate between an encountered caller or satellite in their propensity to mate. This, too, may be a low-density effect; although actual female density does not change across simulations in this experiment, the effective mating female density is lower. (Note that the line in fig. 13 for $c = 0.2$ is similar to that for $N = 25$ in fig. 7.)

Given the degree of variation in these demographic and behavioral attributes exhibited in natural populations (indeed, our parameter values were selected to mimic the range of these variables under natural conditions), our results suggest that even under very high parasitoid pressure, fixation of pure satellite behavior may not occur without additional considerations. There are two taciturn (noncalling) species of *Gryllus* that occur within the native range of *Ormia ochracea*, *Gryllus ovispositis* and *Gryllus cayensis* (Walker 1974, 2001), and both are sister taxa of calling species (Harrison and Bogdanowicz 1995). Neither produces the long-range calling song that attracts parasitoids (and females), although both give courtship songs in close proximity to females and give aggressive calls to other males. Because of the overlap between the adult period in these species and the peak activity period of *O. ochracea* in the fall where they co-occur in Florida, it has been inferred that loss of calling is a response to parasitoid pressure (Mangold 1978; Burk 1982). In addition, both species also tend to occur in dense, relatively sedentary populations (Walker 1974, 2001), conditions that our results imply will enhance the likelihood of complete loss of song. Nonetheless, although *O. ochracea* naturally parasitizes at least six species of *Gryllus* in North America (Lehmann 2003), sometimes at very high rates of infestation, no other populations are reported to be obligately silent. Similarly, although parasitization by *O. ochracea* is responsible for maintaining the obligately silent flatwing male phenotype in some populations of *Teleogryllus oceanicus* in Hawaii (Zuk et al. 2006), in no populations under study has that phenotype become fixed (M. Zuk et al., unpublished data).

Alternative reproductive tactic theory suggests that any tactic that bears costs can potentially be invaded by an alternative tactic with lower costs (Taborsky 1998). Thus, even in the absence of acoustically orienting predators and parasitoids, to the extent that regular calling in field crickets carries costs (due to, e.g., increased energetic expenditure), satellite behavior could potentially occur. However, although our model did not explicitly incorporate any nonpredation costs, we still see some instances where nonzero propensity for satellite behavior is optimal even in the absence of parasitoids. In the absence of parasites, averaging over all simulations yields an optimal phenotype of probability of satellite behavior of $≈ 0.2$ at a probability of parasitization of $0.0$. This is unexpected if calling were absolutely cost free and silence bore some cost (as it must). At least for some simulations, this is due to the relative flatness of the fitness surface; although we identify an absolute maximum fitness (and associated nightly probability of satellite behavior) for any value of probability of parasitization, it is often only marginally (and certainly not significantly) greater than surrounding values. However, it seems that in our model there may actually be a slight cost to calling in the absence of parasitoids associated with attracting satellites that may then intercept females bound for a caller. Such an interception effect certainly seems consistent with the density effects we observed. That Cade and colleagues did not note such an effect is likely because satellites wander randomly in their simulations, whereas they were phonotactically attracted to calling males in ours.

As did Walker and Cade (2003), we observed very high correlations between age (life span) and number of females encountered in each of our simulations. For example, in the density experiment, correlations between average age at death (i.e., life span) and the number of females...
encountered for each of the four densities were ≥0.98 for pure callers. In the same experiment, the correlations between females encountered and females mated for each of the four densities were all 0.99. Similar correlations among age, females encountered, and females mated (all $r \geq 0.97$) for pure callers were observed in the background mortality experiment as well. These correlations provide a foundation for organizing the relationships among the principal variables we investigated (fig. 14).

In the absence of acoustic parasites and satellite behavior, age or average life span is determined by the background mortality rate (fig. 14), which is a function of the ecological conditions where a population occurs. Age in turn determines the number of females a male encounters, and the number of encounters determines his numbers of mates. Encounter rates are determined by population density, sex ratio (which, in our simulations, controls female density), and degree of female phonotaxis, and the relation between encounters and matings is controlled by female mating propensity. By itself, parasitism acts to reduce male life span, with follow-on effects on mating as filtered by encounter rates. Noncalling satellite behavior mediates both survivorship (hence, longevity) in the face of parasitism and encounter rates, positive in the first case and negative in the second. Modulated by female mating propensity (often a function of the attractiveness of a male), this trade-off propagates through to the number of females mated, which then feeds back to influence the optimal phenotype.

To conclude, although the basic shape of the fitness surfaces was largely driven by parasitization rate (primarily a nonlinear effect), population demography (density, mortality rate, sex ratio), risk of parasitization, and female behavior, each had substantial effects on the optimal balance between nightly calling versus satellite behavior in male crickets. Although many simulated scenarios resulted in a step function where the optimal behavior rapidly switched from all caller to all satellite as the probability of parasitization increased, many others did not. As these demographic, environmental, and behavioral attributes fluctuate considerably in most natural populations, and because the fitness surfaces we observed often showed large areas with only weak selection gradients (i.e., they were relatively flat), substantial parasitization risk by itself is unlikely to produce an evolutionarily stable pure satellite strategy over the long term. Instead, such environmental variation suggests that cricket populations—and perhaps those of other acoustically signaling animals—are likely to continue to consist of mixtures of individuals that vary substantially in their propensity to call.

Acknowledgments

We thank A. Shaw for assistance with programming in NetLogo. Two anonymous reviewers provided comments that helped us considerably to clarify a previous version of this article. This work was supported by National Science Foundation Integrative Organismal Systems grants to M.Z.
Appendix

**Fit of Locally Weighted Scatterplot Smoothing Surface (LOWESS) to Output Data**

![Figure A1: Raw simulated output (10 replicates) and LOWESS-fitted surface baseline simulations.](image1)

![Figure A2: Raw simulated output (10 replicates) compared to values predicted by LOWESS-fitted surface (figs. 1, A1) baseline simulations.](image2)

**Literature Cited**


“The fruit and ornamental trees grown throughout the country are affected more or less by insects belonging to the Coccidae family, or as they are commonly known, bark-lice. The elm and maple are among the number...Comparatively few of the male-lice have as yet been discovered by entomologists, and it was with pleasure that the male of Leucanum acericortisiss Fitch was found during the summer of 1877.”