

Variation and Repeatability of Calling Behavior in Crickets Subject to a Phonotactic Parasitoid Fly

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Male Teleogryllus oceanicus (Orthoptera: Gryllidae) produce a conspicuous calling song to attract females. In some populations, the song also attracts the phonotactic parasitoid fly Ormia ochracea (Diptera: Tachinidae). I examined the factors affecting calling song by characterizing the calling behavior of caged crickets from an area where the fly occurs. Calling activity (proportion of time spent calling) was repeatable and a significant predictor of female attraction. However, calling activity in the parasitized population was lower than in an unparasitized Moorea population (Orsak, 1988), suggesting a compromise between high activity to attract females and low activity to avoid flies. Calling activity peaked simultaneously with fly searching, so crickets did not shift to calling when the fly is less active. Males harboring larvae did not call less than unparasitized males; however, a more controlled study of the effects of parasitization on calling behavior is needed to evaluate this result. The results are discussed in the context of other studies of the evolutionary consequences of sexual and natural selection on cricket calling behavior.

KEY WORDS: crickets; acoustic signals; calling duration; calling activity; calling patterns; phonotactic parasitoids; repeatability; Orthoptera; Gryllidae; *Teleogryllus*; *Ormia*.

INTRODUCTION

Male field crickets produce a conspicuous, long-range calling song to attract females for mating. However, the song may also attract acoustically-orienting natural enemies (Zuk and Kolluru, 1998). Therefore, both sexual selection and natural selection by eavesdropping enemies can shape the evolution of cricket

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calling song (Bailey, 1991; Burk, 1982; Sakaluk, 1990). A unique opportunity to examine the consequences of these selective forces occurs in the field cricket *Teleogryllus oceanicus* Le Guillou, which is native to Australia and has been introduced into Hawaii (Otte and Alexander, 1983; Kevan, 1990). In some parts of its range *T. oceanicus* calling song attracts the phonotactic parasitoid fly, *Ormia ochracea* (Bigot), which was also introduced into Hawaii but which does not occur in other *T. oceanicus* populations (Zuk *et al.*, 1993). Because parasitization is always fatal for the host, the fly is expected to be an important selective agent (Zuk *et al.*, 1993; Simmons and Zuk, 1994; Murray and Cade, 1995). Zuk *et al.* (1993) showed that parasitized *T. oceanicus* populations differ from unparasitized populations in several aspects of the calling song, including nightly calling patterns. Their results warrant a closer examination of the variation in *T. oceanicus* calling behavior under natural conditions and of the relationship among calling behavior, female attraction, and presence of the parasitoid.

Calling activity (proportion of time spent calling per night) is an important measure of cricket calling behavior. Calling in *T. oceanicus* and other field crickets is energetically expensive compared to resting and is therefore unlikely to be sustained all night by all males (Prestwich, 1994; Hoback and Wagner, 1997). Males with high calling activity are therefore expected to be at an advantage in mating, either because females choose males that are able to sustain high levels of calling (Walker, 1983) or, more plausibly, because males that call a lot are more likely to be calling when a searching female passes by (Zuk and Simmons, 1997). The female may then evaluate male quality based on song structure elements such as pulse rate, frequency, and intensity (Pollack and Hoy, 1981; Doolan and Pollack, 1985). In either case, nightly calling activity is expected to be a predictor of female attraction, a relationship which has not always been straightforward to demonstrate in previous studies (Vaughan, 1995; Zuk and Simmons, 1997).

For calling activity to be a reliable indicator of male performance, it must be repeatable, varying among males but remaining relatively consistent within males (Boake, 1989). Repeatability is important not only because it gives an indication of individual male stereotypy (Boake, 1989), but also because it sets an upper limit to heritability (Falconer, 1989). Cade (1981) and Hedrick (1988) showed that nightly calling duration and bout lengths, respectively, are heritable (and therefore repeatable) in *Gryllus*. However, they both conducted laboratory studies that may have reduced environment-induced variation that is important in the context of mate choice in the wild (Boake, 1989).

In addition to calling activity levels, nightly calling patterns may have important consequences for male reproductive success (Walker, 1983). For example, males should reach a peak in calling activity at the same time during the night that receptive females reach a peak in searching activity (Walker,

1983). For nocturnal species in areas with uniformly favorable temperatures, Walker (1983) predicted that the optimal pattern is a peak in calling at dusk, when females that became available that day are searching for mates, and a subsequent sharp decline in calling activity for the remainder of the night. Orsak (1988) and Loher and Orsak (1985) tested Walker's model in an unparasitized *T. oceanicus* population in Moorea, French Polynesia. They determined calling activity levels and showed that males peak in calling at both dusk and dawn. Because the evolution of both calling activity and calling patterns may be influenced by the parasitoid fly (French and Cade, 1987; Zuk *et al.*, 1993; Cade *et al.*, 1996), I conducted experiments similar to those of Orsak (1988) and Loher and Orsak (1985), to compare the parasitized, Hawaii population of *T. oceanicus* with the unparasitized, Moorea population.

In this paper, I examine variation in calling activity (proportion of time spent calling) and patterns of calling in the Hawaiian *T. oceanicus* by addressing the following questions: (1) What is the variation within and among males in calling activity? and Is calling activity repeatable over a period of several days in the laboratory and field? (2) Does calling activity predict female cricket attraction? (3) Does the Hawaii cricket population call less or have different calling patterns than the unparasitized population studied by Orsak (1988) in Moorea? (4) Do Hawaii males avoid the parasitoid fly by calling when the fly is not active? and (5) Within the parasitized population, do males harboring parasitoid larvae differ in calling activity from unparasitized males?

MATERIALS AND METHODS

I conducted experiments in Hilo, Hawaii, during July and August 1997. *T. oceanicus* adults were collected from the grounds of the University of Hawaii—Hilo campus a few days before the start of each experiment. All crickets were maintained under the natural light:dark schedule (approximately 13:11) and kept on an ad libitum diet of dry cat food and water.

Calling Behavior in the Laboratory

I first investigated calling behavior in the laboratory to minimize disturbance from environmental factors known to influence calling (Loher and Orsak, 1985; Orsak, 1988) and to observe males continuously. The experiment was conducted under ambient temperature (26–28°C) and light levels, using males caught 2 to 10 days prior to the start of observations. These males were not experimentally infested with parasitoids, and their parasitization status was not known prior to the experiment. Each of the 11 males was housed for the duration of the experiment in an individual screen cage (diameter, 6.4 cm; height, 10 cm) with a piece of egg carton for cover. Cages were arranged on the floor surrounding

me such that each cage was separated from all neighbors and myself by at least 0.7 m. I simultaneously observed all males and scored calling activity by listening and recording start and stop times. To minimize disturbance, I did not walk past the cages unless absolutely necessary. Although males sometimes called from under the egg-carton cover, calling males usually sat on top of or next to the cover. Therefore, I obtained visual confirmation of calling (wings raised and vibrating) whenever possible. Observations were conducted from either 1830 to 0030 or 0030 to 0630 for a total of eight sessions (=4 full nights of observation), with one exception of a 2-h gap in the seventh session. To prevent desiccation and ant infestation, all cages were removed to a shaded area during daylight hours and then returned to the same positions in the laboratory during the night.

Calling Behavior in the Field

I used a different group of wild-caught males to examine calling behavior in the field. These males were not experimentally infested with parasitoids, and their parasitization status was not known prior to the experiment. The study was conducted on the grounds of the Hilo campus in the same location from which the crickets were collected. Air temperatures ranged from 21 to 25°C during the course of each night. Sunset was at approximately 1900 and sunrise was at 0600. Occasional light rainfall did not appear to affect calling activity. Although moonlight can suppress calling (Loher and Orsak, 1985; Orsak, 1988), this experiment was probably not affected because it was begun 4 days after the new moon and completed 4 days before the full moon. The experiment was conducted over 8 consecutive nights, during which I observed 25 males each night. However, because several males died and were replaced during the course of the experiment, a total of 39 males was observed. Of these, 21 were observed for all 8 nights and no male was observed for fewer than 2 consecutive nights.

A pilot study conducted in 1995 in which I flagged and observed uncaged males was only marginally successful because males moved among burrows, making it impossible to keep track of the behavior of individual males. Therefore, the males in this experiment were housed individually in the cages described above. Each cage was placed on a 30 × 30-cm ceramic tile coated with Tanglefoot. This prevented ant infestation and allowed me to capture crickets and flies attracted to each male. Cages were arranged in a 10 × 12-m grid such that each tile was separated from all others by 2 m. Five randomly chosen tiles coated with Tanglefoot but without a cage served as controls to assess incidental capture of crickets and flies.

Because Hawaiian *T. oceanicus* do not call during the day (Zuk *et al.*, 1993; G. R. Kolluru, personal observation), observations began at 1830 each night and ended at 0530, at which time all caged and most uncaged males in the area had stopped calling. Cages were arranged on the tiles every evening at least 1 h

prior to observations and removed again in the morning, to prevent death of the crickets in the intense daytime heat. Each male was placed on the same tile each night. Observations were conducted in the manner of Loher and Orsak (1985) and other studies of cricket calling behavior (Walker and Whitesell, 1982; Lee and Loher, 1993). I censused males for calling every 10 min beginning at 1830 and ending at 0530, for a total of 68 censuses per night. Whenever possible, I obtained visual confirmation of calling by looking for raised wings. During each census, I examined tiles for attracted male or female crickets; flies were too small to detect without disturbing calling crickets. Although my walking sometimes caused calling males to stop briefly, they always resumed after I had passed. Each morning the tiles were examined for any flies captured during the night. All flies, crickets, and debris were removed from the tiles each morning. At the end of each experiment all males were frozen and pronotum width was measured to the nearest 0.1 mm using dial calipers. Males were dissected at 40× magnification to look for parasitoid larvae.

As part of another experiment, I determined the activity patterns of the parasitoid fly in June 1998 on the same lawn where the field calling experiment was conducted. I generated *T. oceanicus* calling songs by digitizing a natural pulse from a calling male recorded in the field and using Canary 1.2 software (Charif *et al.*, 1995). The synthesized songs were broadcast for 28 consecutive nights at two traps. Each trap consisted of five 30 × 30-cm ceramic tiles coated with sticky Tanglefoot placed on top of and around a Radio Shack Mini Amplified Speaker situated on a center tile. Each speaker was connected to a Sony Professional Walkman. Broadcasts began at 1900 (approximately 15 min before sunset) and ended between 2200 and 1230, depending on whether heavy rainfall threatened the equipment. All songs were broadcast at 80–90 dB at 30 cm.

Data Analysis

I calculated the following calling variables. (1) Proportion of censuses calling (number of censuses during which calling was heard/total number of censuses per night): I created this variable for the laboratory data by scoring which males would have been heard calling at 10-min censuses if I had collected the data every 10 min instead of continuously. (2) Number of bouts of calling. Because long-term calling patterns were the focus of the study, I scored calling bouts to the nearest minute. Therefore, only singing or silence for 1 min or more was scored. In the field experiment, a bout ended when there was no calling for one or more censuses. (3) Length of longest bout (time in minutes of the longest bout per night). (4) Calling duration (total time in minutes that each male called per night.) I assumed that if a male was heard calling at two consecutive censuses, then he also called for the 10 min between those two censuses. Results from the laboratory experiment, in which I observed the males

continuously, supported the assumption that males often call for bouts as long as or longer than 10 min.

I did not include average bout lengths in the analysis because the males varied enough in the number of bouts they produced that an average length would be misleading. Instead, I calculated nightly calling activity according to Orsak (1988) to allow comparison to his results:

calling activity (per night)

$$= \frac{\text{No. of individual inspections during which calling was heard}}{(\text{No. of males observed}) (\text{No. of hours of observation})}$$

In the present study I observed 25 males for 11 h per night. The result is a number between 0 and 6 which indicates the average calling activity of the population per night. The highest value would be obtained if each male called continuously all night, and the lowest value would be obtained if no males sang. Values less than 1 indicate that, on average, each male called less than once per hour (Orsak, 1988). I determined the goodness of fit of the distribution of calling activity to a normal distribution using the Wilk–Shapiro test (SAS Institute, 1990).

Comparisons of calling variables of parasitized and unparasitized males were conducted using repeated-measures multivariate ANOVA (SAS Institute, 1990, p. 988). Only those males for whom I had 3 consecutive nights of observations were used in the analysis. I determined correlations among variables and the relationship between calling variables and number of females attracted by using correlation and multiple regression analyses (SAS Institute, 1990). The semipartial correlation coefficient for pronotum width was calculated after Hatcher and Stepanski (1994). Repeatabilities of calling variables were calculated according to Lessels and Boag (1987):

$$r = s_A^2 / (s^2 + s_A^2)$$

where s_A^2 is the among-males variance component and s^2 is the within-male variance component. Standard errors were computed according to Becker (1984).

RESULTS

The distribution of calling activities in the field was skewed toward low levels of calling, and several males remained silent for the duration of the experiment (Fig. 1). This skew resulted in a significant departure from a normal distribution (Wilk–Shapiro test; $W = 0.7442$, $P < 0.0001$). There was considerable variation in calling activity in the laboratory and field, as indicated by the large

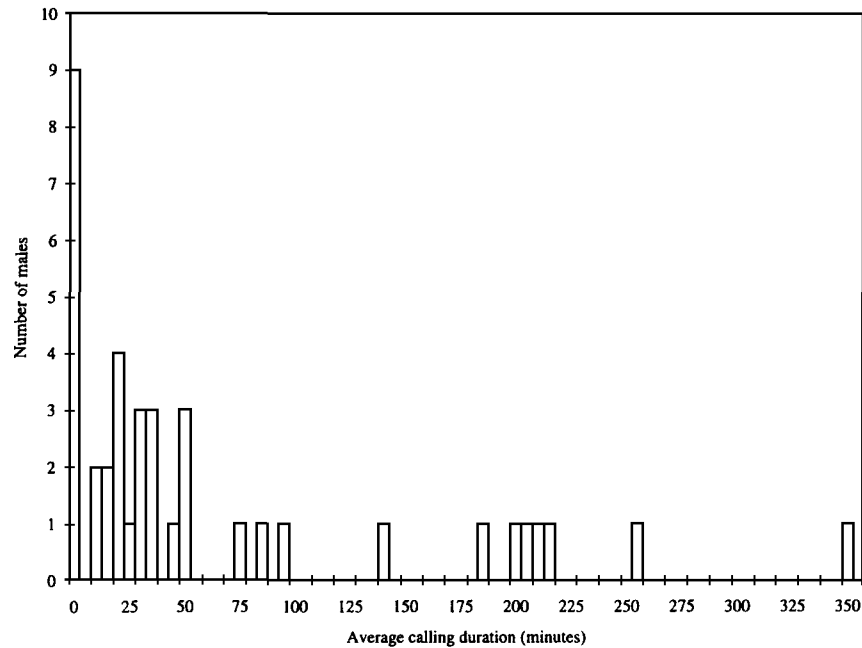


Fig. 1. Average nightly calling duration in minutes from the field experiment on calling patterns of *T. oceanicus*. Males in the 0 column are potentially pursuing a "silent" strategy.

coefficients of variation (Table I). Within-male coefficients of variation are not shown but were equally large. Despite the high degree of variation, all of the measures of calling activity in the field were repeatable, showing significantly more variation among than within males (Table I). Repeatabilities from the laboratory study and from parasitized males in the field study were lower than those from unparasitized males in the field due to smaller sample sizes.

Body size (pronotum width) could not be measured on all individuals because 13 of the 39 males were lost to ants before being measured. Pronotum width was not significantly correlated with any of the calling behavior variables. Multiple regression revealed that pronotum width was not a significant predictor of number of females attracted. The semipartial correlation coefficient (a measure of the percentage of variance in number of females attracted accounted for by pronotum width after excluding the variance accounted for by the other predictors) was not significant (semipartial $r = 0.05$, $df = 1,20$, $F = 5.87$, $P > 0.05$). Therefore, to retain the larger sample size of 39 males, I performed multiple regression analysis excluding pronotum width.

I used multiple regression to regress the number of females captured on the linear combination of proportion of censuses calling, number of bouts, and

Table I. Intermale Coefficients of Variation and Repeatabilities of Calling Behavior Variables from the Laboratory and Field Studies of Calling Behavior Patterns in *T. oceanicus*: Data Are for 4 Nights (Laboratory Experiment) and 2–8 Nights (Field Experiment)

Variable	Intermale coefficient of variation (%)	Repeatability \pm SE
Laboratory ($n = 11$ males)		
Proportion of censuses calling	58.24	0.176 \pm 0.163
Number of bouts	48.38	0.055 \pm 0.142
Length of longest bout	56.21	0.100 \pm 0.151
Calling duration	54.73	0.109 \pm 0.153
Field		
Unparasitized males ($n = 28$)		
Proportion of censuses calling	143.37	0.394 \pm 0.090**
Number of bouts	97.92	0.324 \pm 0.089**
Length of longest bout	134.49	0.358 \pm 0.090**
Parasitized males ($n = 11$)		
Proportion of censuses calling	115.41	0.287 \pm 0.133**
Number of bouts	103.66	0.347 \pm 0.138**
Length of longest bout	112.50	0.239 \pm 0.127*

* $P < 0.01$ (F ratio).

** $P = 0.0001$

length of longest bout. The equation containing these three variables accounted for 43% of the variance in the number of females captured ($df = 3,35$, $F = 8.86$, $P = 0.0002$). Because all of the calling activity variables were highly correlated ($r > 0.75$, $P = 0.001$), no one variable accounted for a significant amount of the variance in number of females captured. Instead, all measures of calling activity together formed a significant model predicting female attraction.

Calling patterns in the field experiment generally agree with pilot data from uncaged males (Fig. 2). Males in the laboratory experiment called later into the morning than males in the field experiment, and the peak calling activity occurred later in the laboratory than in the field (Fig. 3). Not surprisingly, the distribution of females captured in the field experiment corresponds to male calling activity (Fig. 3). Data on number of flies attracted are not shown because only 12 flies were captured during the entire experiment. Control tiles did not capture any flies or crickets.

A comparison of calling activity scored as a number between 0 and 6 reveals that the Hawaii males in the field experiment called significantly less than Orsak's (1988) unparasitized population of *T. oceanicus* (population without flies, $n = 7$ nights, mean = 1.68; population with flies, $n = 8$ nights, mean = 0.87; t test, $t = 2.35$, $P = 0.035$) (Fig. 4). Although the dusk calling peak in the field data coincides with peaks in Orsak's (1988) and other studies of *T. oceanicus* (Loher and Orsak, 1985; Zuk *et al.*, 1993), the distribution of averaged calling activity (Fig. 3) shows no pronounced dawn peak as in those studies. However, exami-

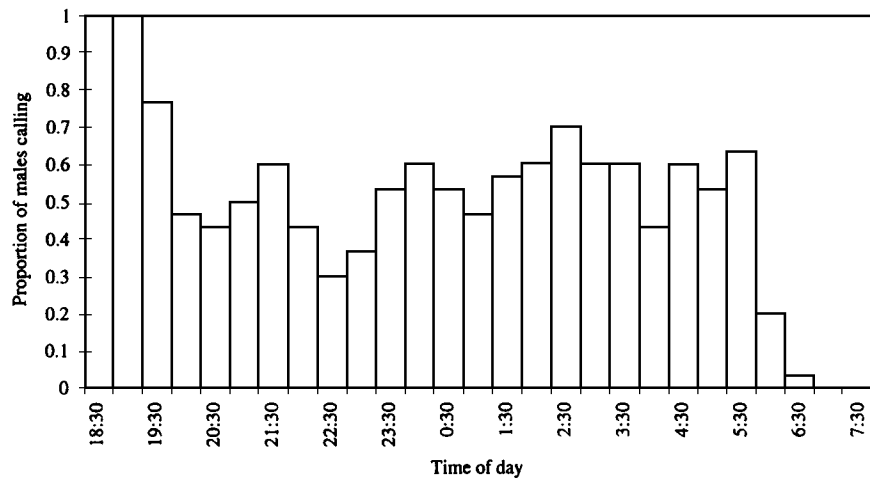


Fig. 2. Calling activity (proportion of males calling) from a pilot field experiment conducted in 1995 using uncaged, flagged males. Data are from three partial nights of observation. Sunset was at approximately 1800 and sunrise was at 0600.

nation of individual male distributions revealed that three males show both dusk and dawn peaks combined with a lower than average calling activity (Fig. 5). A plot of the cumulative number of males calling at each observation is similar to Orsak's (1988) caged population in showing a sharp increase in the number of new males calling at dusk, with a subsequent plateau after dusk. In both data sets there is only a slight increase at dawn, suggesting that almost all males that called had already done so by dawn (Orsak, 1988).

Broadcasts of synthesized song attracted 342 flies. The peak capture of flies coincided almost exactly with the peak in calling activity (Fig. 6), suggesting that males do not alter the timing of calling activity to avoid the fly. Although I did not systematically look for flies at dawn, one day's worth of song broadcasts in 1997 caught no flies between 0330 and dawn, supporting previous studies showing that fly activity is lower at dawn than at dusk (French and Cade, 1987; Cade *et al.*, 1996). Control traps consisting of Tanglefoot-coated tiles but with no song did not capture any flies.

Parasitized and unparasitized males in the field experiment did not differ significantly from each other in calling activity (repeated-measures MANOVA; $N = 18$ unparasitized, 9 parasitized males, $df = 3,23$, $F = 0.472$, $P = 0.705$) and did not differ significantly across nights ($N = 3$ nights; $df = 6,20$, $F = 2.051$, $P = 0.106$) (Table II). However, one-third of the males who remained silent throughout the experiment harbored parasitoid larvae, and 7 of the 11 parasitized males remained silent for the last 2 days of the experiment. Each of the parasitized

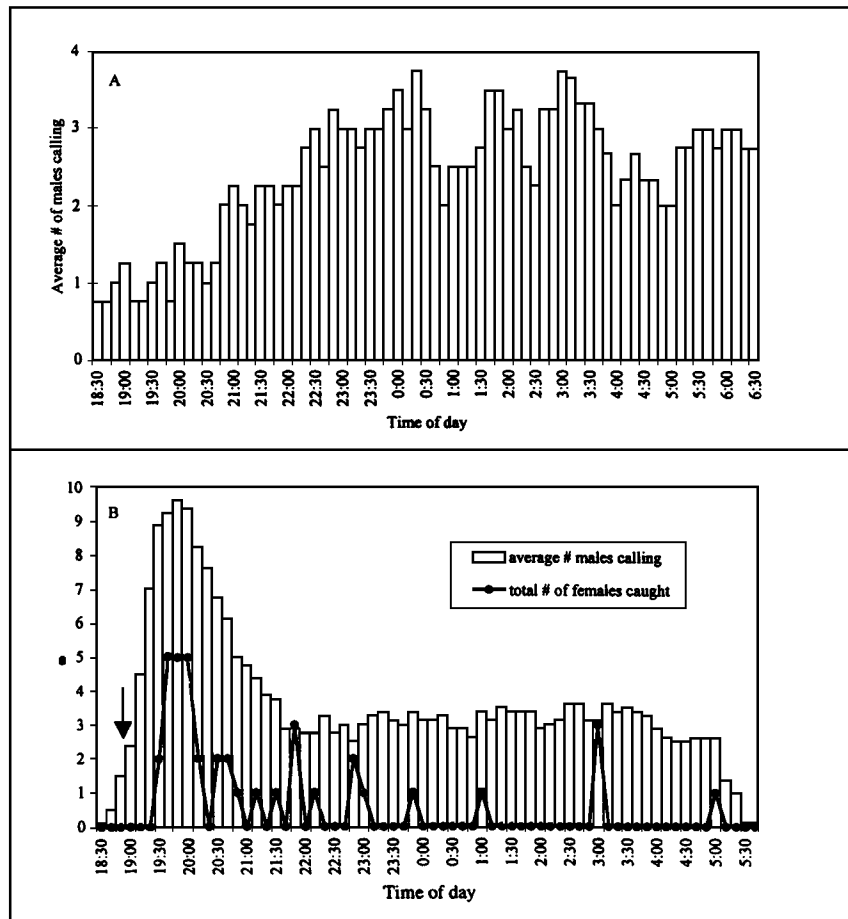


Fig. 3. Average calling activity across nights for wild-caught *T. oceanicus* males from the laboratory (A) and field (B) experiments. B also shows the total number of females captured in the field experiment. Data from parasitized and unparasitized males are combined. The arrow marks sunset. Sunrise was at approximately 0600.

males had one or two larvae, with the exception of one male that had five larvae. Only 1 of the 11 males in the laboratory experiment was parasitized, and his calling behavior did not appear to differ from that of the other males.

DISCUSSION

Calling activity in the Hawaii population of *T. oceanicus* was repeatable under natural conditions and was a significant predictor of female attraction,

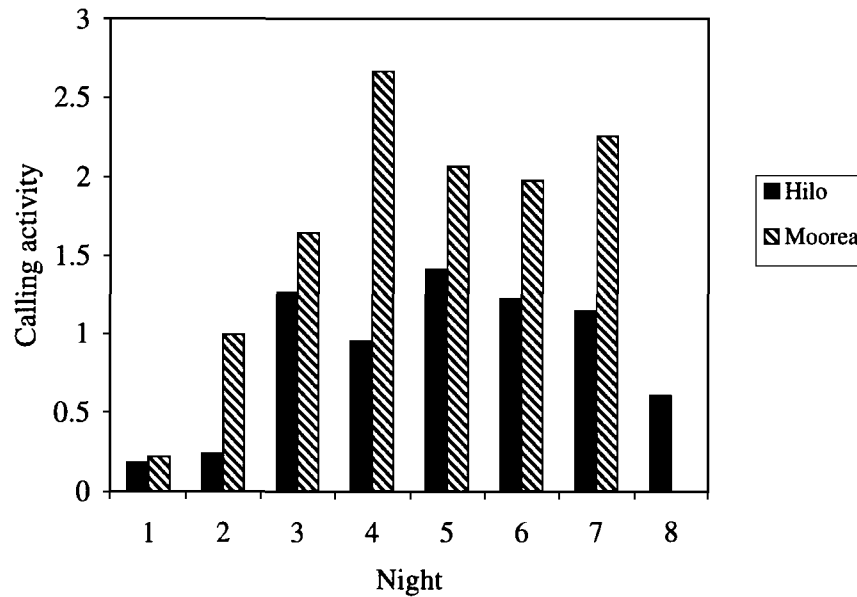


Fig. 4. Calling activity across nights for the Hilo, Hawaii, population (parasitoid fly present) and the Moorea, French Polynesia population (parasitoid fly absent). Moorea data are taken from Orsak (1988).

suggesting that there may be selection favoring high levels of calling. However, calling activity was significantly lower in this population than in the unparasitized Moorea population of the same species (Orsak, 1988). These results support previous, interspecific studies showing reduced calling in crickets subject to flies (Cade, 1991). The frequency distribution of calling in the Hawaii population was consistent with other species in which directional selection imposed by the fly has apparently resulted in some males remaining silent and intercepting females attracted to nearby calling males (Cade, 1984; French and Cade, 1989; Cade, 1991). These results suggest a compromise between sexual selection and natural selection in the Hawaii population. However, males did not peak in calling when flies were least active, as seen in other cricket species (Cade, 1979; Cade *et al.*, 1996). Instead, calling activity peaked at dusk, when fly searching activity also peaked (see also Cade *et al.*, 1996).

Zuk *et al.*'s (1993) comparison of calling patterns among parasitized and unparasitized *T. oceanicus* populations revealed that Hawaii males start and stop calling more abruptly than Moorea males. They suggested that the difference was due to selection by the parasitoid on Hawaii males to restrict calling to darkness. This study shows that the general levels of calling are also lower in Hawaii.

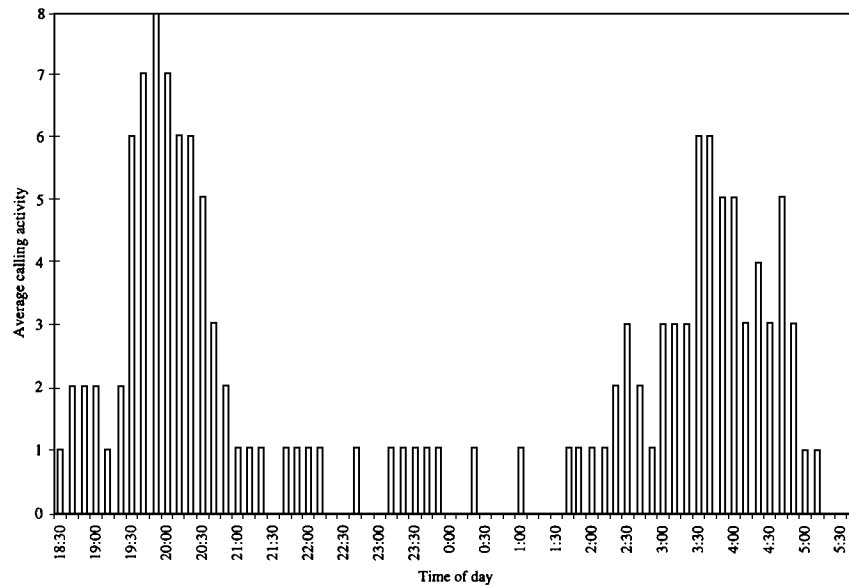


Fig. 5. Combined average calling activity for the three males from the field experiment who showed a dawn peak in calling activity. Sunset and sunrise are the same as in Fig. 3.

Although calling activity is highly heritable in other cricket species (Cade, 1981), it is also highly variable (Cade and Wyatt, 1984; Bertram and Johnson, 1998), due both to the presence of silent males in the sample and to strong environmental influences (Cade and Wyatt, 1984; Boake, 1989; Loher and Dambach, 1989; Shaw *et al.*, 1995). Therefore, the repeatability values are not as high as for some other traits used in courtship (Boake, 1989). However, the values fall within the range of repeatabilities (0.25 to 0.85) given by Boake (1989) for song traits in other acoustical insects.

Calling patterns in natural cricket populations are highly variable and often depart from Walker's (1983) predictions, due in part to the presence of natural enemies (Walker, 1983). *T. oceanicus* males that call at dusk have a greater chance of attracting females for mating (Orsak, 1988). However, they also have a greater chance of attracting flies, because, for reasons that are unclear, fly searching activity declines after dusk (Cade *et al.*, 1996). Therefore, males in parasitized populations are expected to peak in calling activity at dawn, to avoid flies searching at dusk (Cade, 1979; French and Cade, 1987). Other studies of calling activity in caged and uncaged *T. oceanicus*, including one conducted on the Hilo campus (Zuk *et al.*, 1993), show both dusk and dawn peaks (Loher and Orsak, 1985; Orsak, 1988; Vaughan, 1995). However, with the exception of three individuals, the males

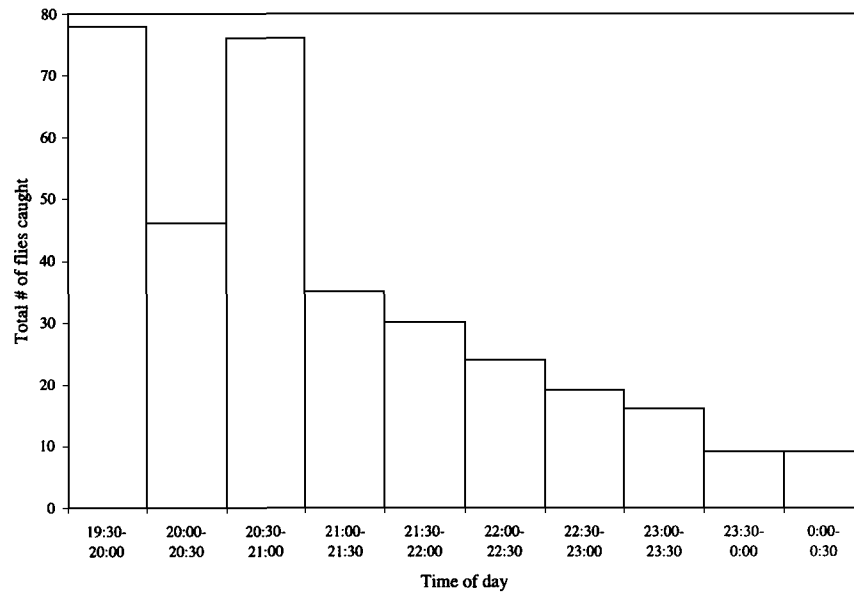


Fig. 6. Distribution of flies captured during field broadcasts of computer-synthesized *T. oceanicus* calling songs in 1998. Data are totals from 28 broadcast nights. Sunset and sunrise are the same as in Fig. 3.

in the present study conformed almost exactly to Walker's (1983) model: calling activity peaked at dusk and declined throughout the night. There are several possible explanations for the relative absence of a dawn peak in calling.

First, caged males may not behave like free males because they do not mate during the night and so may not alter calling patterns accordingly (Orsak, 1988). This explanation is contradicted by the fact that Orsak (1988) and Vaughan

Table II. Average Values of Calling Behavior Variables for Laboratory and Field Males

Variable	Mean \pm SE		
	Laboratory	Field unparasitized	Field parasitized
Number of bouts	4.77 \pm 0.35	1.20 \pm 0.22	1.16 \pm 0.36
Length of longest bout (min)	66.36 \pm 8.95	40.64 \pm 10.33	41.25 \pm 13.99
Proportion of censuses calling	0.22 \pm 0.04	0.09 \pm 0.03	0.10 \pm 0.03
Calling duration (min)	138.57 \pm 12.29	63.66 \pm 17.25	66.68 \pm 23.20

(1995) found dawn peaks in their caged populations. Alternatively, it is possible that the dawn peak was absent because population densities were not high enough. French and Cade (1987) showed that the dawn peak was much more pronounced in high-density populations than in low-density populations, suggesting that increased competition for females at high densities favors dawn calling.

The more likely explanation for the absence of the dawn peak, however, has to do with the function of dawn calling. Dusk and dawn calling are controlled by two different circadian pacemakers in *T. commodus* and other species (e.g., Wiedenmann and Loher, 1984), so that individual males may specialize in dusk and dawn calling (Orsak, 1988). The sample of males I examined may have excluded dawn callers, either because I collected males at dusk and therefore largely missed dawn callers or because dawn callers are not prevalent in the population. Indeed, Cade (1979) suggested that dawn calling, which is lower in intensity than dusk calling, serves not to avoid flies but to remate with nearby females that had been attracted earlier in the night, while avoiding agonistic encounters with rival males.

The calling activity differences among parasitized and unparasitized populations support the idea that silent male crickets are pursuing the alternative reproductive strategy of remaining silent to avoid attracting parasitoid flies (Cade, 1979; Cade and Wyatt, 1984). Cade (1979, 1984) demonstrated that silent *Gryllus integer* males were indeed less likely to be parasitized than their singing neighbors. However, Zuk *et al.* (1995) show that some silent *T. oceanicus* males have a *higher* prevalence of larvae than calling males, suggesting that silence is a consequence of harboring fly larvae rather than a strategy to avoid flies. Given these and other data showing that parasitized acoustical insects call less (Cade, 1984; Lehmann and Heller, 1997), it is surprising that I did not find stronger effects of parasitization on calling activity. However, I am currently conducting laboratory experiments of calling activity which are controlled for male age and stage of parasitoid larvae. The results suggest that parasitized males do indeed call less than unparasitized conspecifics (G. R. Kolluru, unpublished data).

When examining variation in mating behavior it is important to understand the contribution of different selection pressures to the evolution of the behavior. Future studies of *T. oceanicus* calling behavior should therefore concentrate on the interaction between sexual selection by female crickets and natural selection by acoustically-orienting enemies. More work is needed to show both the proximate fitness effects of harboring parasitoid larvae and the ultimate consequences of evolving under potentially conflicting selection pressures.

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REFERENCES

- Becker, W. A. (1984). *Manual of Quantitative Genetics*, Academic Enterprises, Pullman, WA.
- Bertram, S., and Johnson, L. (1998). An electronic technique for monitoring the temporal aspects of acoustic signals of captive organisms. *Bioacoustics* **9**: 107–118.
- Boake, C. R. B. (1989). Repeatability: its role in evolutionary studies of mating behavior. *Evol. Ecol.* **3**: 173–182.
- Burk, T. (1982). Evolutionary significance of predation on sexually signalling males. *Fla. Entomol.* **65**: 90–104.
- Cade, W. (1979). The evolution of alternative male reproductive strategies in field crickets. In Blum, M. S., and Blum, N. A. (eds.), *Sexual Selection and Reproductive Competition*, Academic Press, New York, pp. 343–379.
- Cade, W. H. (1981). Alternative male strategies: genetic differences in crickets. *Science* **212**: 563–564.
- Cade, W. H. (1984a). Effects of fly parasitoids on nightly calling duration in field crickets. *Can. J. Zool.* **62**: 226–228.
- Cade, W. H. (1984b). Genetic variation underlying sexual behavior and reproduction. *Am. Zool.* **24**: 355–366.
- Cade, W. H. (1991). Inter- and intraspecific variation in nightly calling duration in field crickets, *Gryllus integer* and *G. rubens* (Orthoptera: Gryllidae). *J. Insect Behav.* **4**: 185–194.
- Cade, W. H., and Wyatt, D. R. (1984). Factors affecting calling behaviour in field crickets, *Teleogryllus* and *Gryllus* (age, weight, density, and parasites). *Behaviour* **88**: 61–75.
- Cade, W. H., Ciceran, M., and Murray, A.-M. (1996). Temporal patterns of parasitoid fly (*Ormia ochracea*) attraction to field cricket song (*Gryllus integer*). *Can. J. Zool.* **74**: 393–395.
- Charif, R. A., Mitchell, S., and Clark, C. W. (1995). *Canary 1.2 User's Manual*, Cornell Laboratory of Ornithology, Ithaca, NY.
- Doolan, J. M., and Pollack, G. S. (1985). Phonotactic specificity of the cricket *Teleogryllus oceanicus*: Intensity-dependent selectivity for temporal parameters of the stimulus. *J. Comp. Physiol. A* **157**: 223–233.
- Falconer, D. S. (1989). *Introduction to Quantitative Genetics*, Longman Scientific and Technical, London.
- French, B. W., and Cade, W. H. (1987). The timing of calling, movement, and mating in the field crickets *Gryllus veletis*, *G. pennsylvanicus*, and *G. integer*. *Behav. Ecol. Sociobiol.* **21**: 157–162.
- French, B. W., and Cade, W. H. (1989). Sexual selection at varying population densities in male field crickets, *Gryllus veletis* and *G. pennsylvanicus*. *J. Insect Behav.* **2**: 105–121.
- Hatcher, L., and Stepanski, E. J. (1994). *A Step-by-Step Approach to Using the SAS System for Univariate and Multivariate Statistics*, SAS Institute, Cary, NC.
- Hedrick, A. V. (1988). Female choice and the heritability of attractive male traits: an empirical study. *Am. Nat.* **132**: 267–276.
- Hoback, W. W., and Wagner, W. E., Jr. (1997). The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiol. Entomol.* **22**: 286–290.
- Kevan, D. K. McE. (1990). Introduced grasshoppers and crickets in Micronesia. *Bol. San. Veg. Plagas (Fuera de serie)* **20**: 105–123.

- Lee, H.-J., and Loher, W. (1993). The mating strategy of the male short-tailed cricket *Anurogryllus muticus* de Geer. *Ethology* **95**: 327–344.
- Lehmann, G., and Heller, K.-G. (1997). The influence of a parasitoid fly on males of southern European bushcrickets. Contributions to the XXV International Ethological Conference, Vienna, Austria, Blackwell Wissenschafts, Berlin.
- Lessels, C. M., and Boag, P. T. (1987). Unrepeatable repeatabilities: A common mistake. *Auk* **104**: 116–121.
- Loher, W., and Dambach, M. (1989). Reproductive behavior. In Huber, F., Moore, T. E., and Loher, W. (eds.), *Cricket Behavior and Neurobiology* Cornell University Press, Ithaca, NY, pp. 43–82.
- Loher, W., and Orsak, L. J. (1985). Circadian patterns of premating behavior in *Teleogryllus oceanicus* Le Guillou under laboratory and field conditions. *Behav. Ecol. Sociobiol.* **16**: 223–231.
- Murray, A.-M., and Cade, W. H. (1995). Differences in age structure among field cricket populations (Orthoptera: Gryllidae): Possible influence of a sex-biased parasitoid. *Can. J. Zool.* **73**: 1207–1213.
- Orsak, L. J. (1988). *Sexual Behavior in Teleogryllus Field Crickets (Orthoptera: Gryllidae): Elicitation in the Laboratory and in Nature*, Ph.D. thesis, University of California, Berkeley.
- Otte, D., and Alexander, R. D. (1983). The Australian crickets (Orthoptera: Gryllidae). *Acad. Nat. Sci. Philadelphia Monogr.* **22**.
- Pollack, G. S., and Hoy, R. (1981). Phonotaxis to individual rhythmic components of a complex cricket calling song. *J. Comp. Physiol.* **144**: 367–373.
- Prestwich, K. N. (1994). The energetics of acoustic signaling in anurans and insects. *Am. Zool.* **34**: 625–643.
- Sakaluk, S. K. (1990). Sexual selection and predation: Balancing reproductive and survival needs. In Evans, D. L., and Schmidt, J. O. (eds.), *Insect Defenses*, State University of New York, Albany, pp. 63–90.
- SAS Institute (1990). *SAS/STAT User's Guide, Version 6*, SAS Institute, Cary, NC.
- Shaw, K. C., Bitzer, R. J., Galliard, P. L., Troendle, M. A., and Shaffer, C. S. (1995). Effect of a strong, DC-induced magnetic field on circadian singing activity of the house cricket (Orthoptera: Gryllidae). *Ann. Entomol. Soc. Am.* **88**: 362–365.
- Simmons, L. W., and Zuk, M. (1994). Age structure of parasitized and unparasitized populations of the field cricket, *Teleogryllus oceanicus*. *Ethology* **98**: 333–340.
- Vaughan, L. J. (1995). *The Mating System of the Polynesian Field Cricket Teleogryllus oceanicus (LeGuillou)*, Ph.D. thesis, University of California, Berkeley.
- Walker, T. J. (1983). Diel patterns of calling in nocturnal Orthoptera. In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*, Westview Press, Boulder, CO, pp. 45–72.
- Walker, T. J., and Whitesell, J. J. (1982). Singing schedules and sites for a tropical burrowing cricket (*Anurogryllus muticus*). *Biotropica* **14**: 220–227.
- Wiedenmann, G., and Loher, W. (1984). Circadian control of singing in crickets: Two different pacemakers for early-evening and before-dawn activity. *J. Insect Physiol.* **30**: 145–151.
- Zuk, M., and Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**: 415–438.
- Zuk, M., and Simmons, L. W. (1997). Reproductive strategies of the crickets (Orthoptera: Gryllidae). In Choe, J. C., and Crespi, B. J. (eds.), *Mating Systems in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 89–109.
- Zuk, M., Simmons, L. W., and Cupp, L. (1993). Calling characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus*. *Behav. Ecol. Sociobiol.* **33**: 339–343.
- Zuk, M., Simmons, L. W., and Rotenberry, J. T. (1995). Acoustically-orienting parasitoids in calling and silent males of the field cricket *Teleogryllus oceanicus*. *Ecol. Entomol.* **20**: 380–383.