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***Short Communication***

# The Influence of Rearing and Monitoring Environment on Temporal Mate Signaling Patterns in the Field Cricket, *Gryllus texensis*

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**KEY WORDS:** cricket; *Gryllus texensis*; monitoring environment; rearing environment; calling song.

## INTRODUCTION

The logistics of conducting research in the natural environment often precludes people from carrying out fieldwork. Researchers are, therefore, frequently restricted to rearing animals and performing experiments in the laboratory and making the assumption that the results are reflective of those that would have been obtained in a field setting. Two critically important research topics in animal behavior are thus (1) establishing whether experimental results obtained in a laboratory are relevant to those obtained in the field and (2) ascertaining what the environmental contribution is to behavioral development. Although these two topics have received some attention, the subjects of such investigations have most often been vertebrates, even though evidence exists that insects exhibit behavioral phenotypic plasticity dependent on the monitoring and/or rearing environment. For example, in desert seed harvester ants, multiple foundress colonies outlive single foundress colonies in the laboratory but not in the field (Pfennig, 1995). Moreover, light regimes during rearing affect courtship behavior in *Drosophila melanogaster* (Barth *et al.*, 1997). The effects of monitoring and rearing environment on insect mating behavior are of special interest because, due to their small body size, researchers often raise and test large numbers in the laboratory but are

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precluded from conducting the fieldwork necessary to determine the validity of the assumption that the results are reflective of the natural environment.

Crickets display quantifiable mating behaviors in both the field and the laboratory, making them ideal candidates for investigating the effects of monitoring and rearing environment on mating behavior. Males typically solicit a mate by rubbing their raised forewings together to emit an acoustic signal known as "calling song." Because calling song functions as a long-range acoustic advertisement of the caller's sexual readiness, its perception is the initial point of contact between reproductive partners (Alexander, 1961). Several calling song parameters are known to influence female mate choice positively, including the total amount of time spent calling throughout the night (Cade and Cade, 1992), average number of pulses per trill (Gray and Cade, 1999b), and shorter intercall intervals (Wagner *et al.*, 1995).

Acoustic mating displays have a strong heritable component (Cade, 1981; Crnokrak and Roff, 1998b; Gray and Cade, 1999a, b; Simmons, 1987). High heritability is often equated with reduced phenotypic plasticity (Schlichting and Pigliucci, 1998). While this might suggest that cricket acoustic mating displays will be influenced minimally by monitoring and rearing environment, investigations reveal conflicting results. Laboratory experiments with the striped ground cricket (*Allonemobius fasciatus*) indicate that rearing temperature contributes significantly to variation in chirp rate (Olvido and Mousseau, 1995). In the Texas field cricket, however, Gray and Cade (1999a) found that rearing temperature did not significantly influence the number of pulses per trill. Walker (2000) showed similar negative results for the pulse rate of *G. texensis* when raised under different temperature and photoperiod conditions but attributed the negative result to small sample sizes. With a larger sample size, he found a significant effect in *G. rubens*.

The Texas field cricket (*Gryllus texensis*) is an ideal organism to investigate whether monitoring and/or rearing environment influences mate signaling behavior. Both field-captured and laboratory-reared crickets have been used to investigate mating song variation, yet few studies have investigated whether rearing environment may influence this variation. Further, even though several studies have been published on mate signaling behavior using field-monitored as well as laboratory-monitored individuals (Bertram, 2000; Cade, 1981, 1991; Cade and Cade, 1992; Cade and Wyatt, 1984; French and Cade, 1987; Gray and Cade, 1999a, b), little information exists on whether experimental results obtained in a laboratory are relevant to those obtained in the field.

My research focuses on two temporal characteristics of *Gryllus texensis* mating song. The first, the amount of time spent calling (TSC) per 24-h period, is highly variable among males (Cade, 1991; Cade and Wyatt, 1984). Some males never call, others signal for a few minutes to a few hours a night, while

others produce mating calls for up to 10 h or more in an evening (Bertram, 1999). My second characteristic of mate signaling (Bertram and Johnson, 1998) is temporal calling pattern (TCP). TCP is a family of parameters that depict how males partition their calls throughout the night (Bertram and Johnson, 1998). Using an electronic apparatus I built to monitor TSC and TCP, I can easily categorize males into (1) early-evening callers, (2) all-night callers, (3) early-morning callers, or (4) noncallers (Bertram and Johnson, 1998). TSC and TCP parameters are repeatable (Bertram, 2000).

To establish whether experimental results obtained in a laboratory are relevant to those obtained in the field, I compared the mating songs of field-captured male *G. texensis* monitored in a natural field setting with those monitored in a laboratory setting. To provide data about the environmental contribution to behavioral development of the temporal parameters of mate signaling, I compared the calling song of field-captured males monitored in a laboratory setting with laboratory-reared males monitored in a laboratory setting.

## METHODS

*Rearing Environments.* To determine the influence of rearing environment on male temporal signaling patterns, males were reared in the laboratory ($N = 167$) or captured as adults in the field ($N = 48$) and their mating signals were monitored. Individuals were reared in the laboratory by first collecting several hundred adult crickets from bright streetlight aggregations at a driving range that is surrounded by large grassy fields in the outskirts of Austin, Texas, in the autumn of 1996 and 1997. Immediately after capture, individuals mated freely and females oviposited in containers with moist sand. The containers were transported back to the laboratory at the Life Sciences Complex of Arizona State University in Tempe.

Offspring of the field-captured males were reared in laboratory stock populations, housed in an environmental chamber for one or two generations under a 12:12-h light:dark (L:D) cycle at a temperature of $\sim 28^{\circ}$C. To minimize the influence of a communal rearing environment on male temporal signaling components, $\sim$1 week prior to adulthood males were housed individually in clear glass containers with a food and water source. They were checked daily for full wing development indicative of their final moult and maturity. Laboratory-reared males were no younger than 7 days and no older than 20 days post-final molt during signal monitoring. The laboratory did not have any windows, and thus the transition between light and dark was abrupt for both sunrise and sunset.

The field-captured adult males monitored in a laboratory setting were collected in the autumn of 2000 from streetlight aggregations, located at the

same driving range in the outskirts of Austin from which the parental population of the laboratory-reared individuals was collected. These field-captured adults were housed together in clear plastic containers with food and a water source, in natural light conditions, for at least 3 days postcapture. They were flown from Austin to Tempe and transferred to a different laboratory than was used for the laboratory-reared/monitored crickets. They were housed individually in clear glass containers with a food and water source. Male mating signals were then monitored. The laboratory had several large windows, and thus there was a natural transition between light and dark at both sunset and sunrise. The air temperature remained virtually constant at ~28°C. All monitoring was completed within 1 week of capture in the field.

*Monitoring Environment.* To determine the influence of monitoring environment on male temporal signaling patterns, the mating signals of the field-captured adult males that were monitored in the laboratory in Tempe were compared to the mating signals of field-captured adult males that were monitored in a natural setting in Austin ($N = 363$).

The field-captured males that were monitored in a natural setting were collected in the autumn of 1998 and 1999 at the same driving range in the outskirts of Austin from which the field-captured laboratory-monitored males were collected in the autumn of 2000. For the first 12–36 h field-captured males were housed together in clear plastic containers with food and a water source, under natural light conditions at the Brackenridge Field Laboratory in Austin. Immediately prior to monitoring the temporal patterns of the mating signals in the field, males were transferred to individual 1-liter containers with food and water. Each plastic container had four side panels cut from it and wire screen glued in place to allow adequate air ventilation. Plastic containers were each placed in a shallow Styrofoam container filled with a water "moat" to ensure that imported fire-ant pests (*Solenopsis invicta*) could not attack the crickets. Plastic containers were placed in a large grassy field, separated from each other by a distance of two meters, in the fashion of a grid. The temporal components of male mating signals were monitored electronically.

*Monitoring Apparatus.* TSC and the family of TCP parameters were monitored using an electronic device that recorded each male's signaling/nonsignaling behavior, six times per second, from 1800 to 1000 h (Bertram, 2000; Bertram and Johnson, 1998). This sampling rate ensured continuous courtship information, as cricket trills consist of a series of short calls ($N = 686$; $X \pm \text{SD} = 450.3 \pm 7.96$ ms; range, 98–1770 ms) interspersed with silent intercall intervals [$N = 686$; $164 \pm 2.75$ ms; range, 23–563 ms; S. Bertram and P. Montoya, unpublished data]. To ensure microphone accuracy, two microphones were hung in each container. The outputs of each container's microphones were strongly correlated (Bertram and Johnson, 1998) and were

averaged for all results. Each male in every environment was monitored for a minimum of 3 nights; each male's data were averaged over all nights he was monitored.

*Quantifying Temporal Signaling Behavior.* TSC was quantified using the number of hours called per night. The TCP family was described using three parameters: start time, stop time, and mean time. Start time was the time that a male was first observed to call within the night. Stop time was the last time a male was observed to call within the night. Mean time was calculated as the normalized mean of the indicator function of time (Bertram, 1999, 2000). Data presented represent average start time, mean time, stop time, and TSC for each male. Using the TSC and TCP parameters, I categorized each male as either (1) an early-evening caller—a signaler (TSC $>$ 0) with start and stop times prior to 0200 h; (2) an all-night caller—a signaler with a start time before 0200 h and a stop time after 0200 h; (3) an early-morning caller—a signaler with a start and stop time after 0200 h; or (4) a noncaller—a male that was never observed signaling (TSC $=$ 0).

*Statistical Analyses.* I use $P < 0.05$ to indicate statistically significant differences and provide exact probabilities. To test the hypotheses that rearing environment and/or monitoring environment influenced average TSC and start time, mean time, and stop time, I used an ANOVA. Only signaling males (TSC $>$ 0 h) were included in the analysis for start time, mean time, and stop time. To determine if the number of signaling versus nonsignaling males differed between environments, while accounting for the different population sizes, I used a log-linear analysis. To determine if the proportions of all-night callers and early-morning callers differed between environments, I used a contingency table.

## RESULTS

*Effect of Rearing Environment.* The population reared and monitored in the laboratory had significantly more signalers (64%) than the population that was captured as adults in the field and then monitored in the laboratory (42%) (Table I; $\chi^2 = 14.23$, $P = 0.0002$, df $= 3$). The laboratory-reared population also spent more time calling than the field-captured population when all males (both signalers and noncallers) were included in the analysis (Table I, Fig. 1; $F = 4.92$, $P = 0.028$, df $= 213$). When only the signalers were included in the analysis, TSC did not differ between the two populations (Table I; $F = 0.588$, $P = 0.445$, df $= 120$).

Rearing environment also influenced male TCP. There were significantly more all-night callers (79%) and fewer early-morning callers (15%) in the laboratory-reared population than the field-captured population (40 and

**Table I.** Comparison of Time Spent Calling (TSC) and Temporal Calling Patterns for Males Reared and Monitored in the Laboratory and Males Captured as Adults in the Field and Then Monitored in Either the Laboratory or the Natural Environment

| | Field captured, field monitored | Field captured, laboratory monitored | Laboratory reared, laboratory monitored |
|---|---|---|---|
| Total monitored | 363 | 48 | 167 |
| TSC (h), all males | $0.42\ (0.05)^{A,*}$ | $0.58\ (0.21)^{A}$ | $1.35\ (0.17)^{B}$ |
| % silent males[a] | $55^{A}$ | $58^{A}$ | $36^{B}$ |
| % signaling males[b] | $45^{A}$ | $42^{A}$ | $64^{B}$ |
| TSC, signaling males | $1.02\ (0.11)^{A}$ | $1.65\ (0.51)^{A,B}$ | $2.14\ (0.25)^{B}$ |
| % early-evening callers[c] | $4^{A}$ | $5^{A}$ | $6^{A}$ |
| % all-night callers[d] | $40^{A}$ | $40^{A}$ | $79^{B}$ |
| % early-morning callers[e] | $56^{A}$ | $55^{A}$ | $15^{B}$ |
| Start time[f] | $9.22\ (0.33)^{A}$ | $9.62\ (1.16)^{A}$ | $4.61\ (0.31)^{B}$ |
| Mean time[f] | $11.66\ (0.25)^{A}$ | $11.42\ (0.85)^{A}$ | $8.82\ (0.24)^{B}$ |
| Stop time[f] | $13.73\ (0.17)^{A}$ | $13.68\ (0.76)^{A}$ | $13.04\ (0.23)^{A}$ |

[a] Silent males were never observed to signal.
[b] Signaling males called for at least 1 night.
[c] Early-evening callers finished signaling by 0200 h. 0200 h was used as a cutoff point, as 95% of parasitoids are observed between sunset and 0200 h.
[d] All-night callers started calling before 0200 h and stopped calling after 0200 h.
[e] Early-morning callers completed calling between 0200 h and monitoring cessation.
[f] Number of hours after sunset (field monitoring) or lights out (laboratory monitoring).
[*] Superscripts A and B indicate significant differences within a row. Populations with the same superscript are not significantly different, populations with different superscripts are significantly different at the level of $P = 0.05$.

55%, respectively) (Table I; Pearson $\chi^2 = 35.634$, $P < 0.001$, df $= 1$). Further, laboratory-reared males had significantly earlier start (Fig. 2) and mean (Fig. 3) times than field-captured males (start time, $F = 32.635$, $P < 0.001$, df $= 126$, $R^2 = 0.206$; mean time, $F = 15.382$, $P < 0.001$, df $= 126$, $R^2 = 0.109$). Male stop times did not differ between the two populations (stop time, $F = 1.004$, $P = 0.318$, df $= 126$).

*Effect of Monitoring Environment.* Monitoring environment did not appear to influence the temporal components of male mating signals. The proportion of signalers versus noncallers did not differ between the field-captured population that was monitored in the laboratory (42% signalers) and the population that was monitored in the field (45% signalers) (Table I; $\chi^2 = 1.78$, $P = 0.1828$, df $= 3$). These two populations had similar TSCs when all males (both signalers and noncallers) were included in the analysis (Fig. 1, Table I; $F = 1.14$, $P = 0.286$, df $= 408$), as well as when only the signalers were included in the analysis (Table I; $F = 3.079$, $P = 0.081$, df $= 179$). Male start time (Fig. 2), mean time (Fig. 3), and stop time also did not differ between the field-captured males monitored in the laboratory and those monitored in their natural environment (start time, $F = 0.148$,

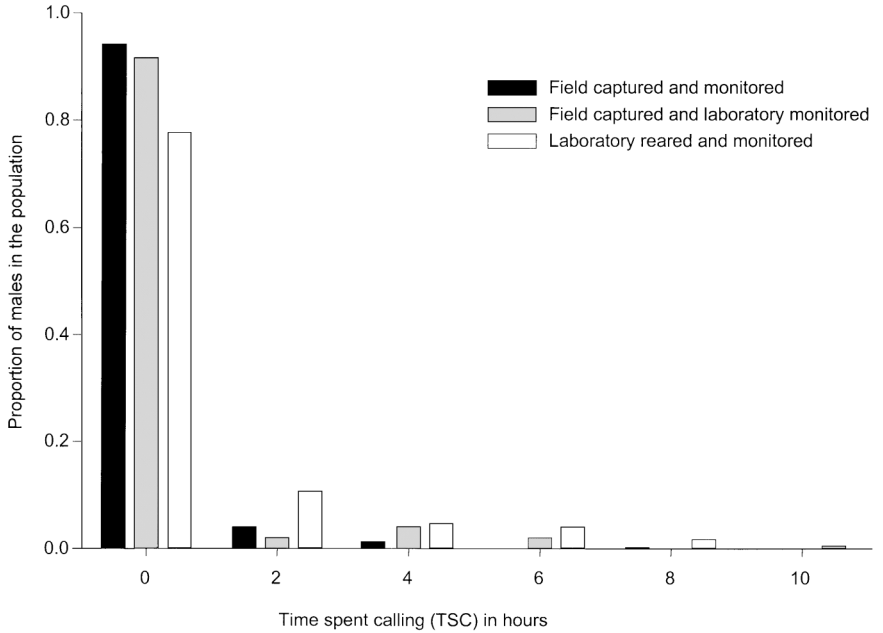


**Fig. 1.** Average time spent calling (TSC) of all males reared and monitored in the laboratory ($N = 167$), as well as males captured as adults in the field and then monitored in either the laboratory ($N = 48$) or the natural environment ($N = 363$). Populations are presented as the proportion of males calling, in 2-h blocks of time.

$P = 0.701$, df = 179; mean time, $F = 0.091$, $P = 0.763$, df = 179; stop time, $F = 0.008$, $P = 0.929$, df = 179). Finally, the populations had similar percentages of males that were categorized as early-morning callers, all-night callers, and early-morning callers (Table I; Pearson $\chi^2 = 0.004$, $P = 0.951$, df = 1).

## DISCUSSION

The temporal calling parameters (TSC and TCP) produced by the Texas field cricket do not appear to be influenced by monitoring environment. Males signaled in the field as well as in the naturally lighted laboratory, and monitoring environment did not influence how much time males spent calling or how they apportioned their calls throughout the night. This indicates great promise for results produced by experimentation using songs produced by *G. texensis* captured as adults in the field.

The population of first-generation crickets that were reared and monitored in the laboratory produced different calling songs from the populations

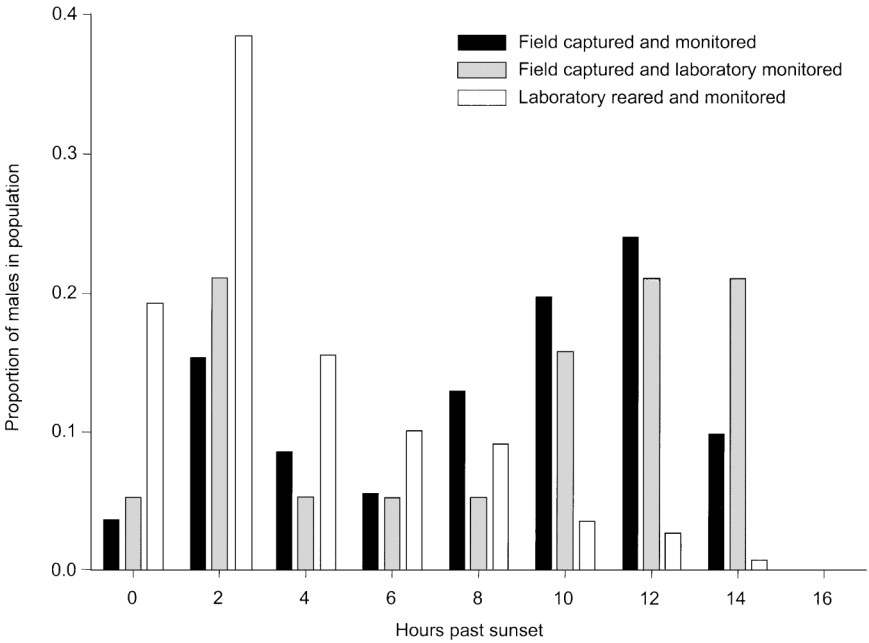


**Fig. 2.** Average male start time (time first observed signaling) of all males reared and monitored in the laboratory ($N = 167$), as well as males captured as adults in the field and then monitored in either the laboratory ($N = 48$) or the natural environment ($N = 363$). Populations are presented as the proportion of males initiating their calling behavior, in 2-h blocks of time, where the blocks of time represent the number of hours after sunset (field monitoring) or lights-out (laboratory monitoring).

of field-captured males that were monitored in either the laboratory or the field. The laboratory-reared population had a significantly higher percentage of callers. Further, its average start time was at least 4 h earlier, average mean time almost 3 h earlier, proportion of all-night callers much higher, and proportion of early-morning callers much lower than those observed in field-captured populations.

Differences in calling song between laboratory-reared and field-captured populations are likely not due to age differences. Although very young (<7 days post-final molt) and very old (>20 days post-final molt) crickets call less often than 7- to 20-day-old males (Bertram, 2000), both populations were in the 7- to 20-day age range when they were monitored. The laboratory-reared crickets were of known age, and field-captured crickets are typically 8–18 days of age at capture, it being very unusual to find an adult cricket younger than 7 days or older than 20 days post-final molt (Murray and Cade, 1995).

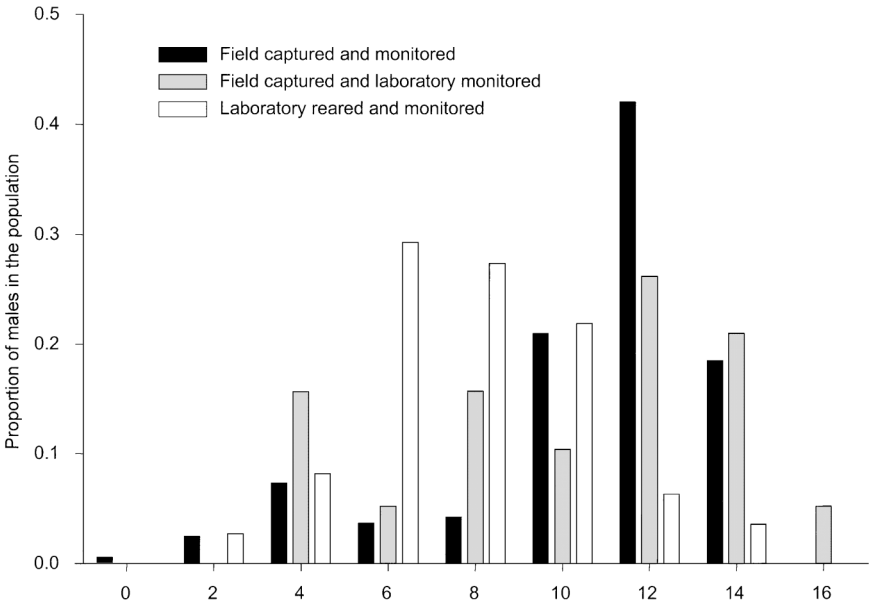


**Fig. 3.** Average mean calling time (the normalized mean of the indicator function of time) of all males reared and monitored in the laboratory ($N = 167$), as well as males captured as adults in the field and then monitored in either the laboratory ($N = 48$) or the natural environment ($N = 363$). Populations are presented as the proportion of males with mean calling time in 2-h blocks of time, where the blocks of time represent the number of hours after sunset (field monitoring) or lights-out (laboratory monitoring).

Calling song differences between laboratory-reared and field-captured individuals may be rooted in differences in the rearing environment and/or the selective regimes to which the populations were exposed. There are at least two possible ways in which rearing environment might influence the temporal components of male mating signals. First, laboratory-reared individuals were fed an unlimited amount of nutritious food and therefore may be in better overall condition than field-captured individuals, allowing them to sing for longer periods of time. Time spent calling depends on the food supply in the wing-dimorphic sand cricket, *G. firmus. Gryllus firmus* adult males fed ad libitum water with severely restricted food supplies had significantly reduced daily and lifetime mean and median TSC compared to control crickets (Crnokrak and Roff, 1998a). If food is limited in the *G. texensis* field populations, field-captured males may exhibit reduced TSC over individuals reared under laboratory conditions.

Second, there is indirect evidence that changes in the lighting cycle may influence calling behavior in crickets. In the common house cricket, *Acheta*

*domesticus*, males monitored in a 0:24 (L:D) cycle called more often than males monitored in a 12:12 (L:D) cycle (Shaw *et al.*, 1995). Further, field experiments on *G. texensis* show changes in TCP correlated with a scotophase increase. Males captured and monitored in spring (14:10 L:D) called most often after 0200 h (70% of calls), while males captured and monitored in fall (12:12 L:D) distributed their calls evenly throughout the night (Bertram, 1999).

Differences in the selective regime experienced by field-captured males compared with selection experienced by laboratory-reared males may also explain the observed dissimilarities between the population's TSC and its TCP. Field-captured males were collected in the fall, when its parasitoid *Ormia ochracea* is most abundant. As *O. ochracea* locates its cricket hosts using their acoustic mating signals (Cade, 1975), is most prevalent between sunset and 0200 h (Cade, 1989), and causes host death within 1 week, the parasitoid may have culled both the callers with elevated TSC and the early-evening callers from the population prior to my field collections. Loss of early-evening callers and individuals with high TSC would explain the shift toward the reduced calling and later calling times observed in the field-captured populations compared to the laboratory-reared population.

Overall, this study should serve to caution researchers not to assume that the behavior of laboratory-reared animals is virtually identical to that of animals in the field.

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