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Temperature preferences of male field crickets (*Gryllus integer*) alter their mating calls

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Abstract Temperature affects the mating displays of many ectothermic animals, yet almost no information exists on the temperature preferences of ectotherms while they are displaying for mates. This study investigated the preferences of displaying male field crickets (*Gryllus integer*) for microhabitats of different temperatures. *G. integer* males attract sexually receptive females by calling from cracks in the ground. We collected data from the field on the temperature of male calling sites (cracks in the ground), on the amount of herbaceous cover (which affects crack temperature) surrounding calling sites, and on the temporal properties of male calls at different temperatures. Laboratory experiments demonstrated that males prefer warmer sites and confirmed that temperature influences mating calls. We conclude that males of this ectothermic species prefer to call for mates from warmer sites, and that microhabitat choice on the basis of temperature affects their mating calls, and potentially their reproductive success.

Keywords Calling · *Gryllus* · Mating displays · Temperature · Temperature preferences

Introduction

Temperature is an important determinant of activity for many animals, especially for ectotherms (Riechert and Tracy 1975; Huey and Slatkin 1976; May 1979; Bennet 1980; Dunham et al. 1989; Huey et al 1989; Huey 1991). In particular, temperature often influences mating activity. Within the range of temperatures normally experienced by a species, warmer temperatures tend to increase mating activity, whereas cooler temperatures depress it (Bligh et al. 1976; Navas 1996a; Simmons and Marti 1992; Munro 1990; Hoffmann 1985a, 1985b; Gillet et al. 1995). Temperature determines the mating strategies adopted by different individuals in a digger wasp (Larsson 1989), whereas in many other species, mating displays are dramatically affected by ambient temperature. For example, temperature changes the cadence of head-bobbing displays in iguanid lizards (Phillips 1995), and both the rate (Liu and Haynes 1994) and nightly duration (Webster and Yin 1997) of pheromone emission by moths. Similarly, in crickets, frogs and a variety of other organisms including spiders, fireflies and electric fish, the temporal properties of advertising signals change with temperature (Edmunds 1963; Enger and Szabo 1968; Walker 1975; Carlson et al. 1976; Prestwich and Walker 1981; Pires and Hoy 1992a, 1992b; Gerhardt 1994; Shimizu and Barth 1996; Silva et al. 1999; Martin et al. 2000; Ritchie et al. 2001). These signals often encode species-specificity via their temporal patterning (Walker 1957; Walker 1962; Bentley and Hoy 1972; Bennet-Clark 1989; Gerhardt 1994; Doherty and Callos 1991; Doherty and Storz 1992). Therefore, temperature-induced changes in the properties of mating signals raise the interesting question of how the responding sex recognizes a species-specific signal when the signal changes with temperature. Previous work demonstrates that in many acoustically advertising species such as crickets and frogs, the responding sex's song preferences also change with temperature. The result is that responders at the same temperature as the displayer

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can recognize the displayer's call (e.g., Walker 1962; Gerhardt 1994). This phenomenon has been called "temperature coupling" (Pires and Hoy 1992a, 1992b; Gerhardt 1978; Ritchie et al. 2001).

The influence of temperature on the mating displays of ectotherms, particularly those with "temperature coupling", suggests that these animals should be sensitive to differences in temperature when they are choosing a location from which to display for mates. Although some studies have documented the temperatures at which these animals call (e.g., Navas 1996a, 1996b; Walker 1980; Souroukis et al. 1992; Ciceran et al. 1994), virtually none have demonstrated the choice of particular temperatures by ectotherms that are engaged in mating displays. Here, we describe choice of warmer calling sites by male field crickets (*Gryllus integer*) and demonstrate that warmer temperatures modify their mating calls.

The study system

In the cricket *G. integer*, males call from cracks in the ground to attract sexually receptive females, and females travel above-ground to search for males in their calling sites. Females enter the male's crack to mate with the male, and leave it after mating. The male's call is a rapid trill (produced by rubbing the wings together), and males vary individually in the durations of uninterrupted trilling (hereafter referred to as calling bout lengths; Hedrick 1986). Previous work demonstrated that females prefer calls with longer bout lengths (Hedrick 1986), and that bout length is a heritable trait in males (Hedrick 1988). Females also show preferences for fine-scale aspects of male calls, e.g., syllable period, chirp pause, and syllable number (Fig. 1, Hedrick and Weber 1998). Although studies of several closely related species (*Gryllus* spp.) have shown that temperature affects the temporal properties of song (Martin et al. 2000; Ciceran et al. 1994; Souroukis et al. 1992; Pires and Hoy 1992a, 1992b; Walker 1962, 1975; Koch et al. 1988), the effects of temperature on the calling song of *G. integer* have not previously been studied.

Calling sites (cracks) of male *G. integer* are surrounded with varying degrees of herbaceous cover, which may affect calling site temperature. Cover also

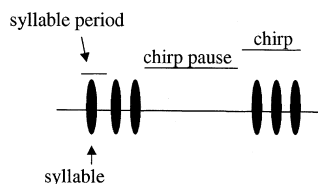


Fig. 1 *Gryllus integer* song. The diagram represents two chirps, each with three syllables, and shows the *syllable period*, consisting of the syllable plus the time interval until the next syllable in a chirp; the *chirp*, consisting of three syllables; and the *chirp pause* (i.e., the time interval between consecutive chirps). Calling bouts are made up of long trains of chirps. Syllables are delivered at a rate of approximately one syllable per 14 ms at 25°C

affects female choice of mates, presumably because it reduces the perceived risk of predation (Hedrick and Dill 1993). Although females prefer long-bout calls to short-bout calls, they also prefer to move through cover, and when cover is present, they make tradeoffs in their mating decisions, sometimes choosing short-bout calls in cover over long-bout calls in the open (Hedrick and Dill 1993). These results suggest that males with short bouts (whose calls are less attractive to females) might be able to gain matings by calling from areas with more cover. Nonetheless, in the field, cover itself is likely to affect crack temperatures.

Accordingly, in this study we present data on the temperatures of male calling sites (cracks) in the field, the effects of cover on crack temperatures, and the associations between crack temperature, cover and male calling bout length. We also demonstrate preferences for warmer versus cooler cracks by males in the laboratory. Finally, we describe changes in male song with temperature, which may affect female choice of mates.

Materials and methods

Field studies

Data were collected in the field during July–September 1991 and 1992 in Davis, California. Male calling sites ($n = 106$) were located by listening for males during peak calling times for males, between 2100 and 2400 hours. Once the male was calling continuously, we measured the sound pressure level of his song in decibels (re 20 μ Pa, "fast" mode) using a Simpson (886-2) sound level meter and microphone at a distance of 1 m from his crack. His song was then recorded for 5–10 min using a Sony Professional Walkman and Sony ECM-series microphone. Immediately after recording the male's song, we measured the calling site temperature ($\pm 1^\circ\text{C}$) using a digital thermometer placed 6 cm into the male's crack, and the air temperature using the same thermometer held 10 cm above the ground. All calling sites were marked with colored tape and a number to facilitate relocation the next day, when sites were mapped and a 1-m² area around each crack was photographed. Photographic slides of male cracks and the surrounding 1-m² area (calling site) were later projected onto a digitizing tablet, and the area of each patch of cover on the calling site was measured using Sigma Scan (Jandel Scientific, San Raphael, Calif., USA). These areas were then added together to calculate the total area of cover for each calling site. Cover on these sites consisted of low grasses and herbs (1–2 cm high); in many cases, cracks were surrounded by bare ground. Although males were not marked, we minimized the probability of resampling individual males by recording from each crack no more than once every 3 days. Available evidence suggests that the tenure of individual males at cracks is less than three days (A.V. Hedrick, personal observation). Tape recordings were later analyzed (see below) to yield data on syllable number, syllable period, chirp pause, and the number of calling bouts per 5 min of calling. As in our prior work (Hedrick 1986, 1988), a bout was defined as a period of calling containing no pause longer than 0.1 s. Complete data were not available for all 106 calling sites, so sample sizes for most statistical analyses ranged from 94 to 106. Syllable number, syllable period and chirp pause were analyzed for only a subset of the males ($n = 20$ for syllable number and syllable period; $n = 19$ for chirp pause).

Laboratory experiments on temperature preferences

To determine whether *G. integer* prefers warmer cracks to cooler cracks, we conducted choice experiments in the laboratory. For

these experiments, an electric soil warming cable (Gro-Quick, 5200 series) was placed on one side of an aquarium (62 cm×32 cm×42 cm high), and the aquarium was filled to a depth of 10 cm with a layer of clean sand. When connected to a power source, this cable warmed the sand sufficiently over a 2-h period to create at least a 2°C difference in temperature between the two sides of the aquarium. Artificial cracks (14.5 cm long×3.5 cm high×1 cm wide) were constructed from cardboard, and were open at the top and bottom. Two identical cracks were placed inside the aquarium, one on the side with the heating cable, and the other on the unheated side. The cracks were separated by 15 cm of sand. We used mercury thermometers to monitor the temperature at the bottom of each crack prior to each trial, and removed them before the start of the trial. Ambient air temperature was also recorded at the beginning and end of each trial.

At the start of the trial, a male cricket was transported from its cage to the aquarium using a small plastic vial, and placed in the center of the aquarium, equidistant from the two cracks. We observed the male for the next 2 h, recording the time spent in each of the cracks. We defined the time to enter the crack as the time at which the animal's entire body entered the crack, and time to leave the crack as the time at which the animal's entire body emerged from the crack. We measured the temperature of each crack at the end of the trial. To minimize pheromone cues, the sand was stirred and new cracks were constructed for each trial.

Crickets were randomly chosen offspring of field-caught mothers from Davis, California. We tested 16 different males. Before trials, crickets were reared and maintained singly at 24°C, on a 12:12 h light-dark cycle, and continuously provided with commercial chick starter and water. Ambient temperature during the trials was 24.1±0.7°C. Warm and cold temperatures were significantly different during trials (mean warm temperature=27.0±0.9°C, mean cold temperature=24.0±1.2°C, $t=-9.554$, $df=15$, $P<0.001$), and warm cracks averaged 3.04±0.32°C higher temperature than cold cracks.

Temperature effects on male song

Temperature effects on male song were examined using both tape recordings of male songs made in the field, and recordings of males singing in a controlled laboratory setting. Laboratory males were first-generation offspring of mothers caught in Davis, California in 1995. The males were spatially and acoustically isolated from all conspecifics during recording, and recordings were made using a Marantz stereo recorder and Audio-Technica AT815A microphone during peak calling times for laboratory males, approx. 2–4 h after the onset of dark. Room temperature was monitored continuously during the recordings. Each of ten males was recorded twice, once at a high (26±1°C) and once at a low (22±1.5°C) temperature.

To examine temperature effects on song in the field, we analyzed field recordings of 20 different males made in Davis, California during July–September 1992, at crack temperatures of 17–28°C. Each recording represented a single male calling in the field at a single temperature. The sound pressure level of each male's song (dB re 20 µPa, "fast" mode) was measured using a Simpson sound level meter and microphone (model 886-2) at a distance of 1 m from the cricket's crack.

Field recordings were analyzed using Superscope 1.27, and laboratory recordings were analyzed using SoundEdit (v. 2.05). The following aspects of male calls were measured using at least 12 chirps per male (field) and 10 chirps per male (lab): syllable number, syllable period, chirp pause (Fig. 1). As an estimate of calling bout length, we measured the number of calling bouts per 5 min calling (field only; a bout was defined as a period of calling containing no pause longer than 0.1 s). Data that fit a normal distribution were analyzed using linear regression and t -tests. Decibel levels were converted to absolute sound pressure levels before calculating means and standard deviations. All other data were analyzed using non-parametric analyses (Fisher's Exact Test, Wilcoxon Signed Rank Test, Spearman Rank Correlation, Kendall Rank Correlation).

Results

Field studies

Crack temperatures recorded at 103 calling sites during July–September ranged from 17.0 to 29.0°C (mean±SE=24.3±0.2; Fig. 2). Crack temperatures exceeded the air temperature by a mean of 5.4±0.2°C ($n=103$). This difference between the crack and air temperature was affected by the amount of cover surrounding the crack, as was absolute crack temperature. Sites with more cover were generally cooler than those with less cover (linear regression, crack temperature versus cover, cover log-transformed, $r^2=0.07$, $t=-2.68$, $n=103$, $P<0.01$) and showed greater disparities from the air temperature ($r^2=0.05$, $t=2.40$, $n=103$, $P<0.02$) than sites with less cover. Crack temperature was correlated with the loudness of male calling song, with males at warmer cracks singing more loudly than males at cooler cracks (Fig. 3, Spearman Correlation=0.266, $n=100$, $P<0.01$). The mean sound intensity of male calling song at a distance of 1 m from the male's crack was 60.5±0.3 dB ($n=104$, range 50–66 dB). Crack temperature was not correlated with the number of bouts per min of calling ($n=97$, Kendall rank correlation=-0.03, $P=0.661$), nor with syllable number ($r^2=0.07$, $t=1.16$, $n=20$, $P=0.26$), but it did affect syllable period (Fig. 4A, $r^2=0.58$, $t=-5.02$, $n=20$, $P<0.001$) and the length of the pause between chirps (Fig. 4B, $r^2=0.29$, $t=-2.62$, $n=19$, $P<0.02$). Both the syllable period and the chirp pause became shorter at warmer temperatures.

The number of calling bouts per 5 min of calling ranged from 4 to 276 with a mean of 75.9±5.89 ($n=101$, Fig. 5). Because our prior experiments in the laboratory showed that females make tradeoffs in their mating

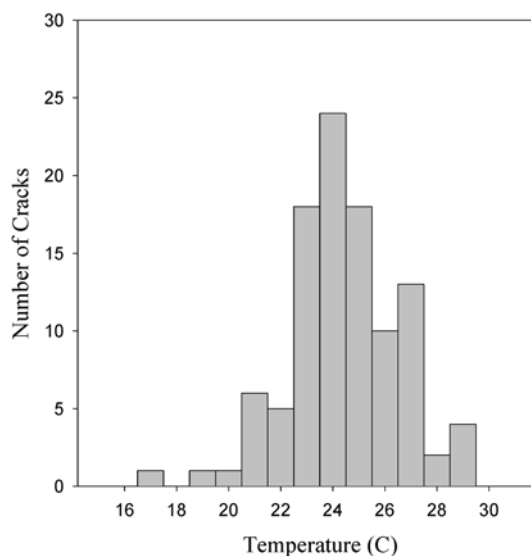


Fig. 2 Temperature (°C) of cracks used by calling *G. integer* in the field ($n=103$)

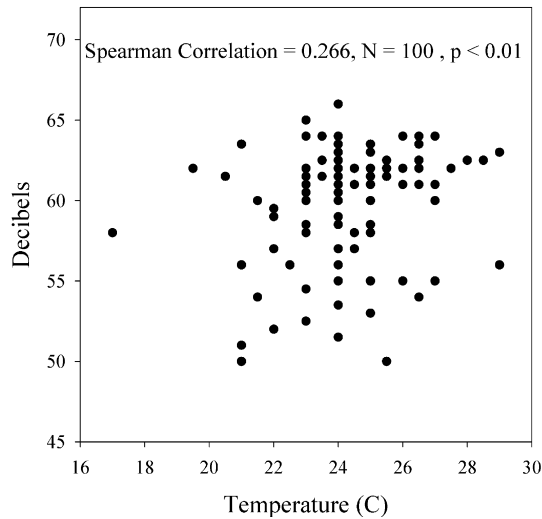
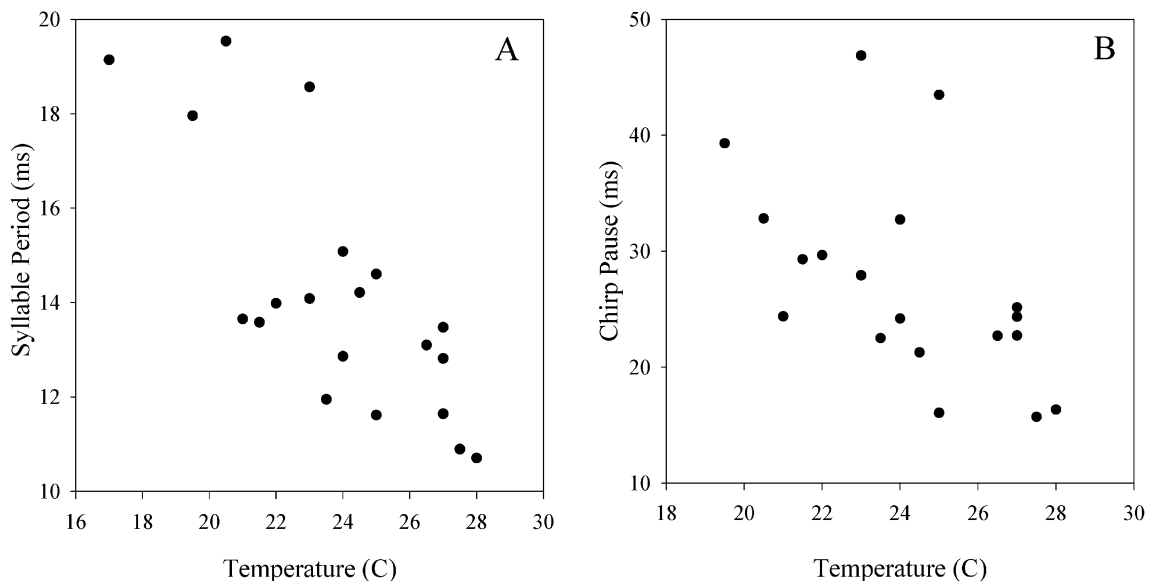


Fig. 3 Sound intensity (dB) of male calling song versus the temperature ($^{\circ}\text{C}$) of a male's crack

decisions between perceived predation risk (the amount of cover surrounding male calling sites) and male calling bout lengths, we also examined the relationship between cover and male calling bout length, measured as the number of bouts in 5 min. Cover on male sites ranged from 1.6 to 10,000 cm^2 (mean \pm SE = 2494.09 ± 286.14 cm^2 , median = 1255.80, $n = 106$; Fig. 6). Males with the shortest bout lengths (> 150 bouts in 5 min; 13 of 100 males) were found exclusively in sites with low cover ($< 3,000$ cm^2 of cover per 1 m^2 area surrounding the male's crack), whereas the remaining males were situated in both these and sites with more cover (3,000–10,000 cm^2 ; Table 1; Fisher's Exact $P = 0.019$, $n = 100$ males). Bout length and loudness were significantly and positively correlated, even when temperature was held

Fig. 4 Effects of temperature ($^{\circ}\text{C}$) on **A** syllable period ($n = 20$ males) and **B** chirp pause ($n = 19$ males) in the field



constant (partial Kendall correlation = 0.128, $n = 94$, $P < 0.05$). Note that although cover might be expected to decrease sound intensity through attenuation of sound, in this study we found no correlation between cover and sound intensity.

Laboratory experiments

In our laboratory tests of temperature preference, males spent significantly more time in warmer cracks than in cooler cracks (mean \pm SE = 76.2 ± 9.98 min warm, 20.8 ± 10.6 cold; Wilcoxon signed ranks test, $T = 187$, $n = 16$, $P = 0.004$). Experiments on the effects of warm ($26.0 \pm 1.0^{\circ}\text{C}$) versus cool ($22.0 \pm 1.5^{\circ}\text{C}$) temperatures on the songs of individual males revealed that both syllable period and chirp pause were shorter at the warmer temperatures than at cooler temperatures (syllable period, mean warm duration = 12.8 ± 0.4 ms, mean cold duration = 14.9 ± 0.2 ms, paired t -test, $n = 10$, $t = 4.57$, $P = 0.001$; chirp period, mean warm duration = 33.3 ± 2.6 ms, mean cold duration = 50.1 ± 3.3 ms, paired t -test, $t = 3.81$, $P = 0.004$). Syllable number was not affected by temperature.

Discussion

In the field, the cracks inhabited by calling male *G. integer* had mean temperatures of 24.3 ± 0.2 , exceeding the ambient air temperature by a mean of 5.4°C . Our laboratory experiments clearly demonstrate that males prefer warmer cracks, at least within the temperature range (21 – 28°C) used in our laboratory experiments. When offered a choice of cracks at two temperatures, males spent significantly more time in the warmer crack. Both in the field and in the laboratory, crickets singing at higher temperatures shortened their syllable periods and chirp pauses, but did not change syllable number.

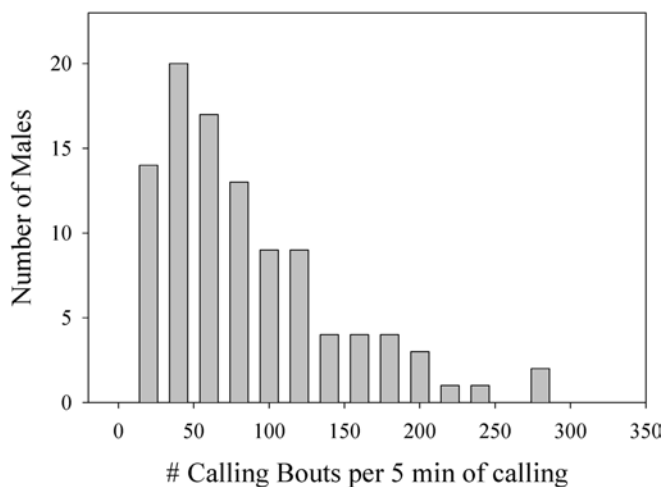


Fig. 5 Number of calling bouts per 5 min of calling for males in the field ($n = 101$)

The latter results are similar to those from other species of *Gryllus* in which higher temperature has been shown to increase song rate (*G. firmus*, *G. bimaculatus*, *G. rubens*, *G. campestris*, *G. texensis*; Pires and Hoy 1992a; Doherty 1985; Walker 1962; Koch et al. 1988; Martin et al. 2000). Previous work (Hedrick and Weber 1998) conducted at 25°C on female preferences and male calls in *G. integer* indicated that females prefer slightly longer syllable periods (20 ms) and chirp pauses (36 ms) than those produced by conspecific males calling at 25°C (syllable period = 14.0 ± 0.2 ms, chirp pause = 30.4 ± 5.0 ms, $n = 20$ males). However, females search for males above-ground, and are unlikely to find males that are at the same temperature as themselves in the field (unless the locomotory activity of running towards males significantly increases the females' thoracic temperatures). Rather, males in cracks are probably warmer than females at the surface, so females must often be attracted to males who are calling at a warmer temperature than themselves. This suggests that any "temperature coupling" in this species between the songs of males and the preferences of females must be relatively permissive. As in a number of other species (Ritchie et al. 2001), the microclimates of calling males and acoustically orienting females are probably often different.

Bout length, a heritable trait that females of this population use to discriminate among potential mates, was unaffected by temperature in the field. Bout length and loudness were positively correlated, even with

Table 1 Association between bout lengths of males and the total area of cover on their calling sites. Short bouts: > 150 bouts/5 min; long bouts: < 150 bouts/5 min; low cover: < 3000 cm² of cover per m²; high cover: > 3000 cm² of cover per m². Fisher's Exact $P = 0.019$ ($n = 100$ males)

	Short bouts	Long bouts
Low cover	13	61
High cover	0	26

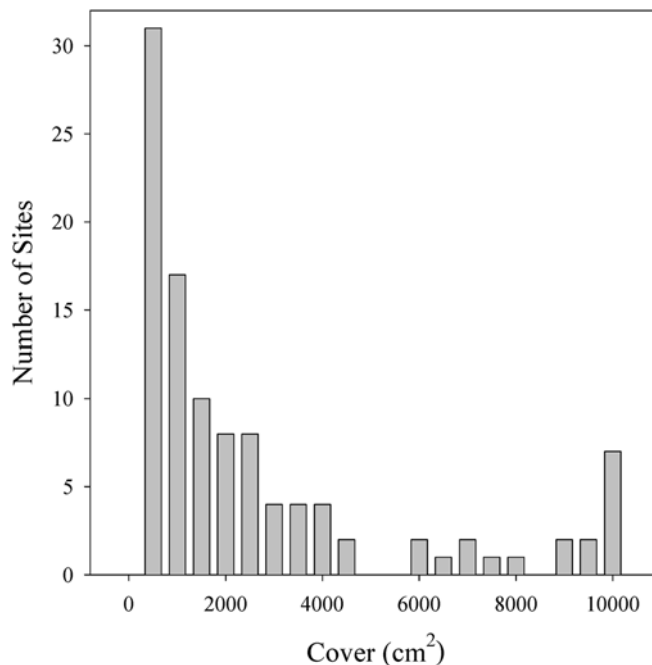


Fig. 6 Total area of herbaceous cover surrounding male calling sites ($n = 106$)

temperature held constant; this correlation between bout length and loudness was also seen when field-caught males were recorded in the lab (A.V. Hedrick, personal observation). Additionally, loudness was correlated with temperature even with bout length held constant: males in warmer cracks in the field sang significantly more loudly. Calling efficiency may increase with temperature (Heath and Josephson 1970; Prestwich and Walker 1981; Walker 1975), allowing warm males to increase the power of their wing strokes, resulting in higher sound pressure levels (louder songs). However, it is also possible that inherently louder males competed more successfully for the warmer cracks. Laboratory experiments on the effect of temperature on sound pressure levels (loudness) in a controlled environment are necessary to distinguish between these alternative explanations.

Crack temperature was strongly affected by the amount of cover over the crack; cracks with more cover were cooler. Although females have strong mating preferences for males with longer calling bouts, in the laboratory they also prefer to move through cover versus open space (Hedrick and Dill 1993), sometimes choosing a less attractive call in cover over a more attractive call in the open. Cover around a site presumably reduces the perceived risk of predation on that site, making it more attractive to females. However, it is not clear how females value cover in the field, where cover results in colder temperatures (as we have shown here); if females also prefer warmer temperatures, then cover may be less important to searching females than temperature. In this study, males with the shortest calling bout lengths were found exclusively at sites with low cover. This implies that males with very short bouts do

not “compensate” for their unattractive calls by choosing safer sites with more cover. Rather, they appear to choose less safe sites, perhaps because they prefer higher crack temperatures. Note that if females also prefer warmer temperatures, this strategy may improve the mating success of less attractive males.

In summary, the cracks inhabited by male *G. integer* are warmer than ambient air temperature, and males prefer warmer cracks. Warmer temperatures alter some elements of male song (syllable period and chirp pause) and may make it energetically more efficient to call loudly. Crack temperature does not seem to affect calling bout lengths of males, a trait used by females in mate choice. Although cover over a male’s crack presumably decreases the perceived risk of predation, it also lowers the temperature of the crack. Therefore males may have to make tradeoffs between safety (more cover) and temperature when choosing a crack from which to advertise.

Thermoregulation by microhabitat choice has been observed in numerous ectothermic organisms (e.g., snakes, Huey et al. 1989; lizards, Bauwens et al. 1996; butterflies, Kingsolver 1983, Pivnick and McNeil 1986; spiders, Henschel et al. 1992; ants, Porter and Tschinkel 1993). Its function has been variously described as a means to optimize predator escape (Bennet 1980), aid in food capture (Ayers and Shine 1997), increase the development rate of eggs or larvae (Porter and Tschinkel 1993), or reduce competition with heterospecifics (reviewed in Huey and Slatkin 1976; Dunham et al. 1989; Huey 1991), among others. In a few organisms (e.g., dragonflies, May 1977; butterflies, Pivnick and McNeil 1986) thermoregulation is thought to enhance mate-searching abilities of males by enabling sustained flight. However, virtually no previous studies have linked thermoregulation by microhabitat choice to mating displays or mating success (but see Larsson 1989, 1990; Larsson and Tengo 1989). The results of this study demonstrate that while they are breeding, ectotherms can choose microhabitats based on temperature preferences, and that this microhabitat choice may influence their mating behavior, including their mating displays. In these animals, thermoregulation by microhabitat choice can clearly influence reproductive success.

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References

Ayers DY, Shine R (1997) Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Funct Ecol* 11:342–347

- Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard – the relative contributions of distinct behavioral mechanisms. *Ecology* 77:1818–1830
- Bennet AF (1980) The thermal dependence of lizard behaviour. *Anim Behav* 28:752–762
- Bennet-Clark HC (1989) Songs and the physics of sound production. In: Huber F, Moore TE, Loher W (eds) *Cricket behavior and neurobiology*. Cornell University Press, Ithaca, pp 227–261
- Bentley DR, Hoy RR (1972) Genetic control of the neuronal network generating cricket (*Teleogryllus*, *Gryllus*) song patterns. *Anim Behav* 20:478–492
- Bligh J, Cloudsley-Thompson JL, Macdonald AG (1976) *Environmental physiology of animals*. Blackwell, London
- Carlson AD, Copeland J, Raderman R, Bulloch AGM (1976) Role of interflash intervals in a firefly courtship (*Photinus macdermotti*). *Anim Behav* 24:786–792
- Ciceran M, Murray AM, Rowell G (1994). Natural variation in the temporal patterning of calling song structure in the field cricket *Gryllus pennsylvanicus*: effects of temperature, age, mass, time of day, and nearest neighbor. *Can J Zool* 72:38–42
- Doherty JA (1985) Temperature coupling and “trade-off” phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* de Geer (Gryllidae). *J Exp Biol* 114:17–35
- Doherty JA, Callos JD (1991) Acoustic communication in the trilling field cricket, *Gryllus rubens* (Orthoptera: Gryllidae). *J Insect Behav* 4:67–82
- Doherty JA, Storz MM (1992) Calling song and selective phonotaxis in the field crickets, *Gryllus firmus* and *G. pennsylvanicus* (Orthoptera: Gryllidae). *J Insect Behav* 5:555–569
- Dunham AE, Grant BW, Overall KL (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol Zool* 62:335–355
- Edmunds LN (1963) The relation between temperature and flashing intervals in adult male fireflies, *Photinus pyralis*. *Ann Entomol Soc Am* 56:716–718
- Enger PS, Szabo T (1968) Effect of temperature on the discharge rates of the electric organ of some gymnotids. *Comp Biochem Physiol* 27:625–627
- Gerhardt HC (1978) Temperature coupling in the vocal communication system of the gray tree frog, *Hyla versicolor*. *Science* 199:992–994
- Gerhardt HC (1994) The evolution of vocalization in frogs and toads. *Annu Rev Ecol Syst* 25:293–324
- Gillet C, Dubois JP, Bonnet S (1995) Influence of temperature and size of females on the timing of spawning of perch, *Perca fluviatilis*, in Lake Geneva from 1984–1993. *Environ Biol Fish* 42:355–363
- Heath JE, Josephson RK (1970) Body temperature and singing in the katydid *Neoconocephalus robustus* (Orthoptera, Tettigoniidae). *Biol Bull* 138:272–285
- Hedrick AV (1986) Female preferences for male calling bout duration in a field cricket. *Behav Ecol Sociobiol* 19:73–77
- Hedrick AV (1988) Female choice and the heritability of attractive male traits: an empirical study. *Am Nat* 132:267–276
- Hedrick AV, Dill L (1993) Mate choice by female crickets is influenced by predation risk. *Anim Behav* 46:193–196
- Hedrick AV, Weber T (1998) Variance in female responses to the fine structure of male song in the field cricket, *Gryllus integer*. *Behav Ecol* 9:582–591
- Henschel JR, Ward D, Lubin Y (1992) The importance of thermal factors for nest-site selection, web construction and behaviour of *Stegodyphus lineatus* (Aranea: Eresidae) in the Negev Desert. *J Therm Biol* 17:97–106
- Hoffmann KH (1985a) Metabolic and enzyme adaptation to temperature. In: Hoffmann KH (ed) *Environmental physiology and biochemistry of insects*. Springer, Berlin Heidelberg New York, pp 1–32
- Hoffmann KH (1985b) Environmental aspects of insect bioluminescence. In: Hoffmann KH (ed) *Environmental physiology and biochemistry of insects*. Springer, Berlin Heidelberg New York, pp 225–244

- Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 137:S91–S115
- Huey RB, Slatkin M (1976) Costs and benefits of lizard thermoregulation. *Q Rev Biol* 51:363–384
- Huey RB, Peterson CR, Arnold SJ, Porter WP (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944
- Kingsolver JG (1983) Ecological significance of flight activity in *Colias* butterflies: implications for reproductive strategy and population structure. *Ecology* 64:546–551
- Koch UT, Elliott CJH, Schaffner K-H, Kleindienst H-U (1988) The mechanics of stridulation of the cricket *Gryllus campestris*. *J Comp Physiol A* 162:213–223
- Larsson FK (1989) Temperature-induced alternative male mating tactics in a tropical digger wasp. *J Insect Behav* 2:849–852
- Larsson FK (1990) Temperature reverses size-dependent male mating success of a cerambycid beetle. *Funct Ecol* 4:85–90
- Larsson FK, Tengo J (1989) The effects of temperature and body size on the mating pattern of a gregariously nesting bee, *Colletes cunicularius* (Hymenoptera: Colletidae). *Ecol Entomol* 14:279–286
- Liu Y-B, Haynes KF (1994) Temporal and temperature-induced changes in emission rates and blend ratios of sex pheromone components in *Trichoplusia ni*. *J Insect Physiol* 40:341–346
- Martin SD, Gray DA, Cade WH (2000) Fine-scale temperature effects on cricket calling song. *Can J Zool* 78:706–712
- May ML (1977) Thermoregulation and reproductive activity in tropical dragonflies of the genus *Micrathyrina*. *Ecology* 58:787–798
- May ML (1979) Insect thermoregulation. *Ann Rev Entomol* 24:313–349
- Munro AD (1990) Tropical freshwater fish. In: Munro AD, Scott AP, Lam TJ (eds) Reproductive seasonality in teleosts: environmental influences. CRC Press, Boca Raton, FL, pp 145–239
- Navas CA (1996a) Thermal dependency of field locomotor and vocal performance of high-elevation anurans in the tropical Andes. *J Herpetol* 30:478–487
- Navas CA (1996b) The effect of temperature on the vocal activity of tropical anurans: a comparison of high and low-elevation species. *J Herpetol* 30:488–497
- Phillips JA (1995) Does cadence of *Iguana iguana* displays facilitate individual recognition? *Behav Ecol Sociobiol* 37:337–342
- Pires A, Hoy RR (1992a) Temperature coupling in cricket acoustic communication. 1. Field and laboratory studies of temperature effects on calling song production and recognition in *Gryllus firmus*. *J Comp Physiol A* 171:69–78
- Pires A, Hoy RR (1992b) Temperature coupling in cricket acoustic communication. 2. Localization of temperature effects on song production and recognition networks in *Gryllus firmus*. *J Comp Physiol A* 171:79–92
- Pivnick KA, McNeil JN (1986) Sexual differences in the thermoregulation of *Thymelicus lineola* adults (Lepidoptera: Hesperidae). *Ecology* 67:1024–1035
- Porter SD, Tschinkel WR (1993) Fire ant thermal preferences: behavioral control of growth and metabolism. *Behav Ecol Sociobiol* 32:321–329
- Prestwich KN, Walker TJ (1981) Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *J Comp Physiol* 143:199–212
- Riechert SE, Tracy CR (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology* 56:265–284
- Ritchie MG, Saarikettu M, Livingstone S, Hoikkala A (2001) Characterization of female preference functions for *Drosophila montana* courtship song and a test of the temperature coupling hypothesis. *Evolution* 55:721–727
- Shimizu I, Barth FG (1996) The effect of temperature on the temporal structure of the vibratory courtship signals of a spider (*Cupiennius salei* Keys). *J Comp Physiol A* 179:363–370
- Silva A, Quintana L, Galeano M, Errandonea P, Macadar O (1999) Water temperature sensitivity of EOD waveform in *Brachyhypopomus pinnicaudatus*. *J Comp Physiol A* 185:187–197
- Simmons AM, Marti OG (1992) Mating by the fall armyworm (Lepidoptera, Noctuidae) – frequency, duration, and effect of temperature. *Environ Entomol* 1992 21:371–375
- Souroukis K, Cade WH, Rowell G (1992) Factors that possibly influence variation in the calling song of field crickets – temperature, time and male size, age and wing morphology. *Can J Zool* 70:950–955
- Walker TJ (1957) Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. *Ann Entomol Soc Am* 50:626–636
- Walker TJ (1962) Factors responsible for intraspecific variation in the calling songs of crickets. *Evolution* 16:407–428
- Walker TJ (1975) Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*) and reanalysis of published data. *J Comp Physiol* 101:57–69
- Walker TJ (1980) Reproductive behavior and mating success of male short-tailed crickets: differences within and between demes. In: Hecht MK, Steere WC, Wallace B (eds) Evolutionary biology, vol 13. Plenum Press, New York, pp 219–260
- Webster RP, Yin C-M (1997) Effects of photoperiod and temperature on calling behaviour of the gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae). *Can Entomol* 129:843–854