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; Bennett 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; Bennett-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...
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 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 \( \mu \)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 (±1°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-m\(^2\) area around each crack was photographed. Photographic slides of male cracks and the surrounding 1-m\(^2\) 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