



# The 'hot male' hypothesis: do female crickets prefer males with increased body temperature in mate choice scenarios?

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Insects have been extensively used as model systems to study mating preferences based on variation in acoustic signals. In many species, females perform phonotaxis towards attractive, long-range acoustic signals produced by males, whereas the final mating decision is based on an assessment of additional, multimodal, close-range cues. The production of acoustic signals is costly, because invested energy is inefficiently converted into acoustic power. Here, we investigated whether heat released as a by-product during song generation might serve as an additional cue during mate choice decisions. Males that broadcast highly energetic calling songs increased their thoracic temperature considerably above ambient temperatures. The use of this additional cue would turn the acoustic signal into an inherently bimodal one, indirectly indicating the quality of the sender. To test this hot male hypothesis, we performed trackball and Y-maze experiments with *Anurogryllus muticus*. For comparison, additional trackball experiments were conducted with *Gryllus bimaculatus* females. In all paradigms, females of both species showed no evidence of a preference for hot males and, therefore, we conclude that increases in thoracic temperature do not seem to play a role as a multimodal component in mate choice decisions in *A. muticus*.

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Acoustic signals, the most dominant secondary sexual traits known in orthopteran insects, have been widely used as a model system for behavioural and neuronal studies related to male–male competition and female choice, as well as to sound production and hearing (Gerhardt & Huber, 2002; Hedwig, 2006; Huber, Moore, & Loher, 1989). Calling songs primarily serve as long-range communication signals for mate attraction. In an ideal scenario, a receptive female phonotactically approaches a calling male by either walking or flying, often travelling over considerable distances (Alexander, 1961). Acoustic signals are informative for the female receiver, because they contain information about the senders' species (Gray & Cade, 2000; Zuk, Rebar, & Scott, 2008), sex, age (Verburtg, Ferreira, & Ferguson, 2011) or even quality (Rantala & Kortet, 2003; Scheuber, Jacot, & Brinkhof, 2004; Simmons & Ritchie, 1996; Simmons, Tinghitella, & Zuk, 2010, 2005; Stange & Ronacher, 2012), and allow individuals to discriminate between conspecifics (Gerhardt & Huber, 2002; Zuk & Simmons, 1997).

Crickets produce species-specific calling songs by rubbing a file-like structure that is usually located on the right wing against a line of sclerotized teeth located on the other wing (Bennet-Clark, 1989; Gerhardt & Huber, 2002; Montealegre-Z, Jonsson, & Robert, 2011; Otte, 1992). With every wing closure, a sinusoidal tone emerges. In particular, ensiferans (crickets and katydids) show an enormous variation in their calling songs with respect to the time spent signalling (Hartley & Stephen, 1989; Heath & Josephson, 1970), carrier frequency, pulse rate and song duty cycle. Song structures can be distinguished between chirping species, which produce groups of sound pulses that exhibit a relatively low-duty cycle in discrete sequences once or twice a second, and trilling species, which produce continuous trains of pulses that result in high-duty cycles (Gerhardt & Huber, 2002).

The muscles necessary for the wing movements are located in the thorax; depending on the song patterns, their activation can cause an increase in the surface temperature of singing males. Previous studies have described such body temperature increases in singing insects (Heath & Josephson, 1970; Heller, 1986; Prestwich, 1994), but Erregger et al. (2017) recently identified and summarized the relationship between song feature combinations

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associated with temperature increases and the energy invested in song production. Only cricket and katydid males that produce loud, continuous calling songs with high pulse rates and high effective calling rates (=the product of pulse rate and chirp/trill duty cycle) increase their thoracic temperatures considerably above ambient temperature (Erregger et al., 2017).

Calling song differences also lead to differences in the costs associated with song production (energy: Gillooly & Ophir, 2010; parasites: Lehmann & Lehmann, 2006). Indeed, the efficiency of sound production is low, since only some of the muscular energy used for calling is translated into the acoustic energy of the call (Forrest, 1991). Sound efficiency is measured by comparing the amount of energy used during calling and the amount of sound power that must be expended to ultimately produce audible sound. The empirical data reported for insects indicate that the efficiency of sound production ranges only between one and a few per cent (Kavanagh, 1987; Prestwich, 1994). Based on these data, the major part of the energy (up to 99%) invested in a calling song is lost (i.e. lost through frictional force and heat; Ryan, 1988; Erregger et al., 2017). If the energetic cost of sound production is high, it is expected to be limited by the physiological capacity of the male, particularly as he produces the repeated, long-lasting elements of acoustic displays (Kotiaho et al., 1998; Mappes, Alatalo, Kotiaho, & Parri, 1996). Thus, sound signals become additionally informative for females during mate choice scenarios, indicating that only individuals in good condition can expend the energy required for calling (Irschick & Garland, 2001; Zahavi, 1975). Indeed, results of behavioural studies have shown that females of some cricket species prefer calling songs with longer pulse durations and shorter interpulse intervals, or chirp intervals, which are characterized by their high chirp/trill duty cycle (Gerhardt & Huber, 2002; Blankers, Hennig, & Gray, 2015; Hennig, Blankers, & Gray, 2016).

For those species whose metabolic investments (as measured via their CO<sub>2</sub> production rate) and thoracic temperatures are strongly positively correlated, it is true that the more energy they invest in calling, the hotter they become (Erregger et al., 2017). Thus, the increase in thoracic temperature could indirectly reflect the energetic investment in song production. Depending on the song type, maximum increases in thoracic temperature of up to 15 °C above ambient temperature have been described (Erregger et al., 2017; Heath & Josephson, 1970; Heller, 1986; Stevens & Josephson, 1977). Some trilling species were found to increase their metabolic costs from 6- to 16-fold while singing over their resting metabolic state (Erregger et al., 2017; Prestwich & Walker, 1981).

Although acoustic signals are the most conspicuous communication signals in crickets and katydids, additional signals that are perceived in different sensory modalities have been shown to critically influence final mating decisions. After a female has successfully reached a singing male, attracted by long-range acoustic signals, close-range signals (e.g. courtship songs: Alexander, 1961; Zuk et al., 2008; vibrational and chemical signals: Kortet & Hedrick, 2005; Thomas & Simmons, 2009b) and tactile cues allow the receptive female to gain even more information about her potential mating partner. Some of these close-range cues include cuticular hydrocarbons, which are located on the cuticle of most terrestrial arthropods (Blomquist & Bagnères, 2010). These contain additional relevant information regarding pairing and mating (Andersson, 1994; Balakrishnan & Pollack, 1997; sex recognition: Leonard & Hedrick, 2009; Otte & Cade, 1976; Singer, 1998; Tregenza & Wedell, 1997; species recognition: Mullen, Mendelson, Schal, & Shaw, 2007; Leonard & Hedrick, 2009; kin recognition: Simmons, 1989, 1990; Thomas & Simmons, 2011; quality: Rantala & Kortet, 2003). Finck and Ronacher (2017), for example, demonstrated that chemical signals can act as a barrier to prevent hybridization in the grasshopper *Chorthippus biguttulus*.

To the best of our knowledge, this is the first study that has tested whether increases in thoracic temperature resulting from sound production are used as potential, multimodal, close-range signals during intraspecific communication. Females could evaluate this information through thermoreception, via thermosensitive receptor cells on their antennae (Nishikawa, Yokohari, & Ishibashi, 1985; Schneider & Römer, 2016), a hypothesis that has thus far been unexplored in the context of communication and mate choice. Preliminary recordings of the activity of sensory cells in these sensilla in a katydid species (trilling *Mecopoda* sp.) in which males also increase their thoracic temperature considerably while singing revealed that they are sensitive to temperature changes (Schneider, Kleineidam, Leitinger & Römer, n.d.). The sensitivity of thermoreceptors in this katydid is similar to that reported for other insects (e.g. *Rhodnius prolixus*: Zopf et al., 2014).

The hot male hypothesis predicts that females of ensiferan species in which males increase their thoracic temperature due to calling will be able to assess the quality of males at close range using this additional thermal cue for mate choice decisions. Therefore, the acoustic signal would be an inherently bimodal one, whereby the energy invested in sound production is not wasted but is reliably reflected in the elevated thoracic temperature of a male (Erregger et al., 2017). An additional advantage of thermal signals compared to acoustic ones is that they can be perceived and processed by receivers continuously; these signals do not fade away as soon as they are no longer produced and, with them, the information they contain about the sender. The thorax of a previously singing male stays 1–2 °C higher than ambient temperature even up to 10 min after the male has stopped signalling (Erregger et al., 2017). Thus, the males' elevated surface temperatures would still be perceivable and informative for arriving females. Furthermore, particularly in a sequential mate choice situation in which it is difficult for the receiver's sensory system to evaluate differences in the time dimension of the acoustic domain properly (Hartbauer & Römer, 2014; Hennig, Heller, & Clemens, 2014), additional thermal information could be highly informative. Moreover, insects often communicate in choruses that contain many conspecific and heterospecific signallers, which makes it more difficult to attribute relatively costly signals to certain sound sources distributed in space (Römer, 2013).

Along their phonotactic path towards singing males, females may encounter males that either sing or are silent. Some of these silent males represent satellite males, which attempt to intercept females on their way to singing males without incurring any of the personal costs associated with sound production (Cade, 1975; Zuk & Kolluru, 1998). Another advantage of the thermal cue is that it allows a female cricket in the field to distinguish between males that have been singing for a long period but stopped signalling before the female reached them, as they would still have an increased surface temperature, and mute satellite males that position themselves near singing males, but have (nearly) ambient body temperatures. Hence, perception of thermal cues could allow females to distinguish between males that embark on different signalling strategies, identify satellite males and enhance their own genetic benefits by avoiding mating with these 'cheating' males.

To test this hot male hypothesis and the role of thermal cues during mate choice, we performed behavioural experiments using two different paradigms with females of a trilling cricket species, *Anurogryllus muticus*, in which males produce loud, continuous song sequences with high pulse rates, high effective calling rates and high trill duty cycles. In *A. muticus*, song production causes an average increase in thoracic temperature of  $5.2 \pm 1.2$  °C above the ambient temperature (Erregger et al., 2017). As a comparison we used *Cryllus bimaculatus*, a chirping species for which no such

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