

Female mating frequency increases with temperature in two cricket species, *Grylloides sigillatus* and *Acheta domesticus* (Orthoptera: Gryllidae)

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Abstract: Although the effect of temperature on calling song of male crickets has been widely studied, its influence on female mating behaviour remains largely unexplored. We examined the effect of varying temperature on female mating frequency in two cricket species (*Grylloides sigillatus* (F. Walker, 1869) (= *Grylloides supplicans* (F. Walker, 1859)) and *Acheta domesticus* L., 1758) by providing females with multiple mating partners and recording the number of matings over 72 h intervals using time-lapse video recording. Female mating frequency increased with temperature in both species, but increased more steeply in *A. domesticus* than in *G. sigillatus*. Temperature accounted for approximately 50% of the variation in female mating frequency. These results suggest that the threshold for mating in females is temperature dependent, such that at lower temperatures only certain males are able to elicit the female mounting response required for successful mating. If temperature affects female selectivity, then male mating success in different seasons may vary, with a wider range of males gaining the opportunity to copulate at warmer times of the year. Consequently, the intensity of sexual selection may vary seasonally.

Résumé : Bien que les effets de la température sur les appels des grillons mâles aient été bien étudiés, son influence sur le comportement reproducteur de la femelle reste en grande partie inexplorée. Nous avons examiné l'effet de températures variables sur la fréquence des accouplements des femelles de deux espèces de grillons (*Grylloides sigillatus* (F. Walker, 1869) (= *Grylloides supplicans* (F. Walker, 1859)) et *Acheta domesticus* L., 1758) en procurant aux femelles des partenaires d'accouplement multiples et en comptabilisant le nombre des accouplements sur des intervalles de 72 heures à l'aide d'enregistrements vidéo à temps échelonné. La fréquence des accouplements des femelles augmente en fonction directe de la température chez les deux espèces, mais de façon plus marquée chez *A. domesticus* que chez *G. sigillatus*. La température explique environ 50 % de la variation de la fréquence des accouplements chez les femelles. Ces résultats indiquent que le seuil pour l'accouplement chez les femelles est dépendant de la température, ce qui a pour résultat qu'à température plus basse, seuls certains mâles réussissent à provoquer chez les femelles le réflexe de saillie requis pour un accouplement réussi. Si la température affecte la sélectivité des femelles, le succès de l'accouplement chez les mâles peut donc varier d'une saison à une autre, puisqu'une plus grande gamme de mâles peut avoir accès à la copulation avec les femelles durant les périodes plus chaudes de l'année. En conséquence, l'importance de la sélection sexuelle peut varier au fil des saisons.

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Introduction

Insects are ectothermic; hence, their body temperature is greatly influenced by the temperature of their immediate surroundings. Because most metabolic processes are temperature dependent, many aspects of insect reproduction are affected by temperature, including those related to mating behaviour (Willmer 1991). Although the influence of temperature on a wide array of male mating behaviours has been documented, including sexual signalling (Ritchie et al. 1995; Hill 1998), alternative mate-finding tactics (Merckx

and Van Dyck 2005), territorial behaviour (Stutt and Willmer 1998; Ide 2002; but see Takeuchi 2006), and the frequency of homosexual mountings (Switzer et al. 2004), its effect on female mating behaviour remains largely unstudied. Indeed, aside from well-documented effects on female egg production and oviposition (Chapman 1982), little else is known of the role of temperature in mediating female reproductive decisions.

In crickets, metabolic rate is highly correlated with ambient temperature (Nespolo et al. 2003), and not surprisingly,

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a number of studies have shown significant effects of temperature on the most conspicuous aspect of mate acquisition in crickets, male acoustical signalling (e.g., Souroukis et al. 1992; Ciceran et al. 1994; Martin et al. 2000; Hedrick et al. 2002; Walker and Cade 2003). Although temperature undoubtedly influences male mating success through its effect on male calling, it seems likely that female mating behaviour is also directly affected by temperature; however, the fitness consequences to females remain largely unexplored. A growing body of evidence suggests that female crickets derive direct material benefits (Ivy et al. 1999; Wagner et al. 2001; Shoemaker et al. 2006) or indirect genetic benefits (Tregenza and Wedell 1998, 2002; Fedorka and Mousseau 2002; Sakaluk et al. 2002; Ivy and Sakaluk 2005) by mating multiply with the same or different males. Hence, if female mating frequency is affected by temperature, the total fitness benefits gained by females through matings over a particular interval should also vary in accordance with this environmental parameter. Moreover, if female receptivity varies with temperature, this would necessarily impose constraints on the mating success of males that could influence the intensity of sexual selection.

Here we test the hypothesis that temperature influences female mating frequency in two cricket species (*Grylodes sigillatus* (F. Walker, 1869) (= *Grylodes supplicans* (F. Walker, 1859)) and *Acheta domesticus* L., 1758) by providing females with multiple mating partners and recording the number of matings over 72 h intervals using time-lapse video recording. Based on the correlation between metabolic rate and temperature, we predicted that female mating frequency would increase with increasing temperature. In crickets, copulation is completed with the transfer of a spermatophore, a discrete sperm-containing vessel that remains attached outside the female's body after mating (Zuk and Simmons 1997). Hence, matings are easily scored because the spermatophore remains readily visible at the base of a female's ovipositor in video playbacks. The spermatophore consists of a simple sperm-containing ampulla in *A. domesticus*, whereas the ampulla in *G. sigillatus* is accompanied by a gelatinous, non-sperm-containing mass (the spermatophylax) that the female detaches from the ampulla immediately after mating and consumes (Sakaluk 1984, 1987). The spermatophylax functions to keep the female preoccupied during the time it takes the ampulla to be emptied of sperm (Sakaluk 1984, 1985, 2000).

Materials and methods

Experimental *G. sigillatus* were the descendants of approximately 500 adults collected in Las Cruces, New Mexico, in May 2001. Crickets were maintained in a large, panmictic population of approximately 5000 individuals to prevent inbreeding and the depletion of genetic variation. Experimental *A. domesticus* were obtained from a commercial supplier (Fluker Farms®, Baton Rouge, Louisiana), whose rearing practices also promote the maintenance of genetic variation (see Fleischman and Sakaluk 2004). Because experiments examining the influence of temperature on female mating frequency were conducted on the two species at different times and using somewhat different protocols, methods used for each species are described separately below.

Grylodes sigillatus

Adult crickets were maintained in 55 L plastic bins provisioned with Flukers® cricket chow, water supplied in 40 mL plastic tissue culture flasks plugged with cotton dental rolls, and egg cartons to provide shelter and to increase surface area for rearing nymphs. Moistened peat moss contained in small plastic cups was provided as an oviposition substrate and also served as a source of additional water. Late-instar nymphs were separated by sex and reared to adulthood in an incubator at 31 °C on a 16 h light : 8 h dark photoperiod.

Nymphs were checked daily and, once they had undergone their adult moult, females were separated and placed in individually labelled storage containers to ensure their virginity. Newly moulted males were also maintained in separate containers, and each held with a non-virgin female taken from the stock colonies until 24 h prior to mating trials to ensure their sexual experience. Only crickets of an adult age of 9–14 days were used in mating trials.

Mating behaviour of adult crickets was recorded over a 72 h period using a Panasonic CCTV camera (WV-BP330) equipped with a vari-focal lens (Computar TG4Z2813FCS) and connected to a JVC digital video recorder (VR-510U). Trials were conducted in a VWR environmentally controlled chamber (model 2015) that was maintained on a 16 h light : 8 h dark photoperiod. Mating trials were conducted at each of six temperatures: 21.9, 24.8, 26.0, 28.1, 30.1, and 32.5 °C (these were the actual temperatures recorded within the unit using an Omega data logger (OM-60), rather than the temperature values shown on the digital display of the chamber). Crickets were randomly assigned to the prescribed temperature regimes and used only once in experimental trials.

Experimental crickets were held at their prescribed temperature in the environmental chamber for 24 h prior to mating trials to allow them to acclimate to experimental conditions. While the choice of a 24 h acclimation period was arbitrary, studies on other species have shown that insects can acclimate quite rapidly (i.e., within an hour or two) to modest changes in temperature of the kind imposed in this study (Shreve et al. 2004). Matings were staged in a Plexiglas® observation chamber that was divided into four equal compartments, each containing one virgin female and three sexually experienced males. Mating activity in all four mating compartments was monitored simultaneously using the recording system. Each compartment was equipped with a small cup filled with moistened peat, to serve as an oviposition substrate and a source of water, and wedged in one corner of the chamber with a dental cotton roll to ensure that the experimental subjects were never hidden from view of the camera. Several pellets of Purina® cat chow were placed into each chamber as food.

We established two replicates of the four mating groups at each prescribed temperature, yielding a total sample size of 48 females (8 females per temperature). Within each set of replicates, the order in which crickets experienced the temperature treatments was randomized. Upon review of video recordings, we determined the number of matings for each female (mounts resulting in successful transfer of spermatophore) and the time at which these matings occurred.

Acheta domesticus

Crickets were purchased as nymphs and maintained according to the same procedures used for *G. sigillatus*, except that they were maintained on a 12 h light : 12 h dark photoperiod at 28 °C. Male and female nymphs were reared separately to ensure their virginity upon eclosion.

Newly emerged adult female crickets were housed together in groups of 6–8 in plastic shoe boxes (10.5 cm × 7.5 cm × 3 cm) and provisioned with food and water. Newly emerged adult males were housed in shoe boxes in groups of 13–17 with a similar number of non-experimental adult females to ensure their sexual experience prior to mating trials. Adult crickets used in experimental trials were 7–9 days of age. Twenty-four hours prior to mating trials, non-experimental females were removed from male containers to allow males sufficient time to replenish spent spermatophores.

Mating behaviour of adult crickets was recorded over a 72 h period using a Panasonic CCTV camera (WV-PB310) equipped with a vari-focal lens (Panasonic WV-LZ80/2) and connected to a Panasonic time-lapse video recorder (AG-6740). Trials were conducted in a VWR environmentally controlled chamber (model 2015) maintained on a 12 h light : 12 h dark photoperiod. Mating trials were conducted at each of five temperatures and in the following randomly determined sequence: 32, 22, 27, 25, and 29 °C (as indicated by the digital display of the chamber).

Experimental crickets were held at their prescribed temperature in the environmental chamber for 24 h prior to mating trials to allow them to acclimate to the experimental conditions. Matings were staged in the same observation chambers, provisioned in the same manner, as in *G. sigillatus* trials. Unlike *G. sigillatus*, however, there was no replication of mating groups within temperatures. Thus, we determined the mating frequency of a total of 20 *A. domesticus* females (4 females recorded at each temperature). As before, we determined the number of matings for each female and the time at which these matings occurred.

Statistical analysis

For data on mating frequency of female *G. sigillatus*, we employed a mixed-model nested ANOVA with temperature as the fixed effect and replicate as the random effect nested within temperature, using PROC MIXED in SAS® (SAS Institute Inc. 2004). As a follow up to this analysis, we used linear regression to visualize the manner in which mating frequency scaled with temperature and to allow direct comparison with the results for *A. domesticus*.

Because of the absence of replication within temperature for *A. domesticus*, we employed linear regression to examine the influence of temperature on female mating frequency. Although the use of a single environmental chamber necessitated that we monitor multiple females at the same time, we treated these observations as independent because the results of the *G. sigillatus* analysis revealed the absence of any random effect of the replicate.

Results

In two cases, one of the three males assigned as mates to a female *G. sigillatus* died during the 72 h observation pe-

riod; these two females, one recorded at 24.8 °C and the other at 32.5 °C, were omitted from further analysis. Mixed-model nested ANOVA revealed a significant effect of temperature on female mating frequency in *G. sigillatus* (type III test of fixed effects, $F_{[5,6]} = 6.41$, $p = 0.021$). To assess the magnitude of the random effect (replicate), we ran PROC MIXED twice, with and without the random effect, and calculated a likelihood ratio χ^2 probability using the protocol recommended in SAS® (SAS Institute Inc. 2004). The random effect was not significant ($p = 0.29$). Regression of female mating frequency on temperature revealed that female mating frequency increased in a strongly linear fashion with increasing temperature ($r^2 = 0.51$, $F_{[1,44]} = 46.1$, $p < 0.0001$). Over the approximately 10 °C range in temperature imposed on *G. sigillatus* in this study, the frequency of female mating nearly tripled (Fig. 1a).

In three cases, one of the three males assigned as mates to a female *A. domesticus* or the female herself died within the 72 h observation period; these three females, recorded at 25, 27, and 32 °C, respectively, were omitted from further analysis. Regression of female mating frequency on temperature revealed that female mating frequency increased in a strongly linear fashion with increasing temperature ($r^2 = 0.56$; $F_{[1,44]} = 19.0$, $p < 0.001$). Over the 10 °C range in temperature imposed on *A. domesticus* in this study, female mating frequency of female mating tripled (Fig. 1b).

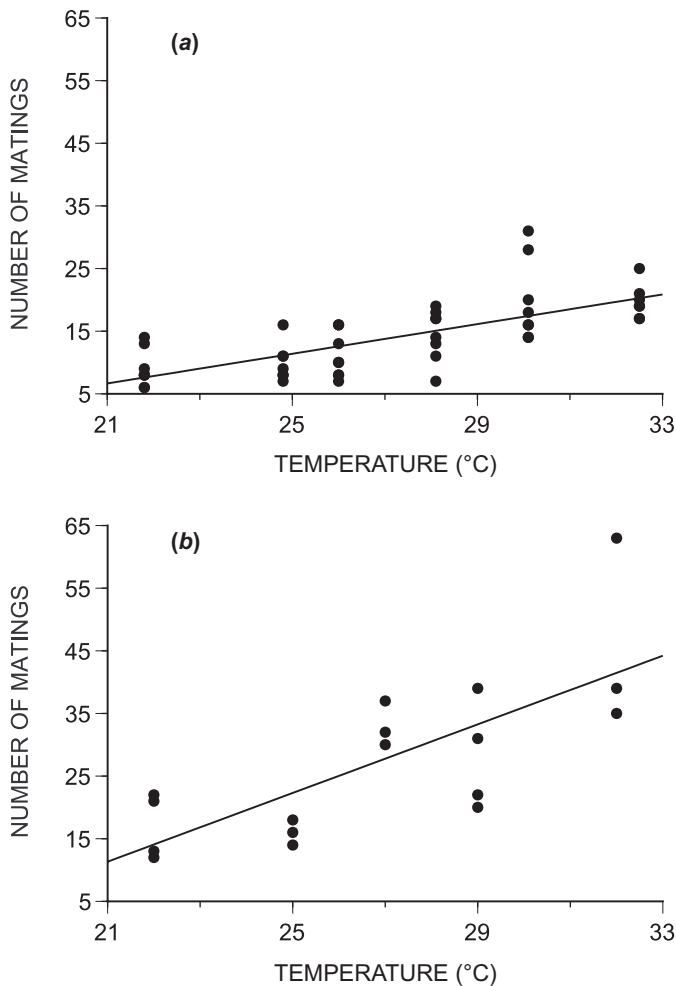
The mating frequency of *A. domesticus* females at any given temperature was nearly double that of *G. sigillatus* (compare Figs. 1a and 1b). Also, female mating frequency increased more quickly with temperature in *A. domesticus* ($b = 2.74 \pm 0.63$ (mean \pm SE)) than in *G. sigillatus* ($b = 1.20 \pm 0.18$; Student's *t* test, $t_{[59]} = 3.27$, $p < 0.002$).

Discussion

The results of our study show that temperature can have a profound influence on female mating behaviour, accounting for over 50% of the variation in female mating frequency. Although the effect of temperature on the propensity of females to mate could conceivably have as great or greater impact on male mating success as does the effect of temperature on male signalling behaviour, environmental influences on female mating behaviour have, until this study, been largely ignored (but see Hedrick and Dill 1993).

Female mating preferences have been well documented in a variety of cricket species (e.g., Hedrick and Weber 1998; Bateman et al. 2001; Olvido and Wagner 2004), including *A. domesticus* (Gray 1997, 1999; Head et al. 2005) and *G. sigillatus* (Sakaluk 1984, 1997; Sakaluk and Eggert 1996). Such preferences are an important source of sexual selection on males, conferring a mating advantage on larger or more dominant males (Gray 1997; Bateman et al. 2001; Savage et al. 2005) or those males in better condition (Ryder and Siva-Jothy 2000; Rantala and Kortet 2003; Scheuber et al. 2004). Although it is often implicitly assumed that females' preferences are static, the present study suggests that the threshold for mating in females is temperature dependent. It may be that, at lower temperatures, only certain males are able to elicit the female mounting response required for successful mating. If temperature affects female selectivity, then male mating success in different seasons may vary,

Fig. 1. Female mating frequency as a function of temperature in two cricket species: (a) *Gryllodes sigillatus* and (b) *Acheta domesticus*. Virgin females were confined with three conspecific males, and their mating behaviour recorded over 72 h observation periods.



with a wider range of males gaining the opportunity to copulate at warmer times of the year. Consequently, the intensity of sexual selection may vary seasonally. If this is true, field workers would be well advised to avoid making inferences about the strength or direction of selection based on surveys conducted at a single time of year or on a single population.

The calling-site preferences of male crickets may help mitigate the effect of temperature on female mating propensity. Hedrick et al. (2002) showed that male western stutter-trilling crickets (*Gryllus integer* Scudder, 1902) selectively seek out calling sites that are warmer and they concluded that such microhabitat preferences are adaptive because of the beneficial effect such sites have on the acoustic qualities of males' calls. However, the results of our study suggest an additional advantage: males that seek out warmer calling sites may increase their probability of mating once females have been attracted to their calling sites. A female cricket that has been attracted to a calling male may remain with that male for a period of several hours or even the entire night (Sakaluk 1987), a period that is probably sufficient to

allow the female to acclimate to the higher temperature of the male's calling site (see Shreve et al. 2004).

It must be acknowledged that the temperatures imposed on mating crickets in this study may also have influenced male, as well as female, behaviour. Thus, the decreased mating frequency of females at lower temperature could have been due to a reduction in female sexual receptivity, a reduction in male sexual motivation, or both. Indeed, it was to mitigate the potential effect of temperature on male mating effort that we confined experimental females with three males simultaneously. However, previous work in our laboratory suggests that the decreased mating frequency of females can be attributed primarily to the effect of temperature on female mating behaviour. As part of an earlier study designed to examine the influence of the availability of mates on female mating frequency, we monitored the mating behaviour of female *G. sigillatus* ($N = 20$), each confined with 5 males simultaneously (i.e., 2 more than in the present study) over a 5-day period at 28 °C. These females mated 4.16 ± 0.40 (mean \pm SE) times/day (R.R. Anderson and S.K. Sakaluk, unpublished data), which was actually lower than the mating rate of females held at 28.1 °C with 3 males in the present study (4.83 ± 0.48 matings/day). If female mating frequency was primarily a consequence of male mating effort, we would have expected that females presented with a greater number of males would have mated more frequently. It could be argued that the decreased female mating frequency associated with the higher density of males may have arisen as a result of increased interference with males' courtship attempts by the other males. However, we have never observed male *G. sigillatus* interfering with the courtship of rival males, and when more than one male is confined with a female, they invariably court the female simultaneously. Additionally, Sakaluk (1987) showed that the mating frequency of females confined with two males was significantly higher than that of females confined with a single male, not what we would expect if male interference routinely disrupted mating attempts. Thus, it would appear that the female mating rate observed in the present study is primarily a function of female mating decisions.

Although temperature influenced female mating frequency in both species, female mating frequency increased more steeply with temperature in *A. domesticus* than in *G. sigillatus*. Because metabolic rate in crickets is influenced by body mass (Nespolo et al. 2003), this difference may simply reflect differences in body size between the two species. Alternatively, natural selection may have favoured different metabolic pathways in the two species that function best at particular temperatures. In support of this possibility, recent work examining the functional significance of the enzyme isocitrate dehydrogenase in southern ground crickets (*Allo-nemobius socius* (Scudder, 1877)) has shown that the geographical distribution of alternative alleles at the *Idh-1* locus is tied to environmental variation in temperature, and that the genotype of individuals at this locus interacts with temperature in their effects on the egg-laying behaviour of females (Huestis and Marshall 2006). Whether similar genetic variation underlies variation in the effect of temperature on female mating behaviour in crickets remains to be determined.

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