Fine-scale temperature effects on cricket calling song

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Abstract: The effects of temperature on the structure of cricket calling song were examined in the trilling field cricket *Gryllus integer.* A repeated-measures design was used to assess the effects of temperature and individual differences among males simultaneously. Temperature affected most aspects of calling song, specifically pulse length, interpulse length, peak frequency, trill length, intertrill length, and pulse duty cycle. Unaffected by temperature were the number of pulses per trill, the proportion of pulses missed within a trill, and the trill duty cycle. After controlling for temperature, significant individual differences among crickets were found in peak frequency, number of pulses per trill, trill length, and intertrill interval. Both the environmental and individual, that is, possibly genetic, influences on calling song may influence sexual communication in this species.

Résumé : Nous avons étudié les effets de la température sur la structure des cris d'appel chez le Grillon des champs *Gryllus integer.* Nous avons utilisé un protocole de mesures répétées pour évaluer les effets de la température et les différences individuelles simultanément. La température affecte les cris d'appel sous plusieurs aspects, longueur des pulsations, intervalles entre les pulsations, fréquence maximale, longueur des trilles, intervalles entre les trilles et coefficient d'utilisation des pulsations. Certains aspects des cris ne sont pas affectés par la température, notamment le nombre de pulsations par trille, la proportion des pulsations ratées dans un trille et le coefficient d'utilisation des trilles. En contrôlant les effets de la température, il est possible de mettre en évidence les différences entre individus, différences dans la fréquence maximale, dans le nombre de pulsations par trille, dans la longueur des trilles et dans la longueur des intervalles entre les trilles. Des influences environnementales et individuelles, peut-être de nature génétique, peuvent affecter la communication sexuelle chez cette espèce.

[Traduit par la Rédaction]

Introduction

Male crickets produce calling song to attract receptive females for mating (Boake 1983; Loher and Dambach 1989). Calling song is species-specific, allowing females to identify calling males reliably (Walker 1957; Ulagaraj and Walker 1975; Oldfield 1980; Doherty and Callos 1991; Doherty and Storz 1992). Although a major function of calling song is species recognition, females of some species show preferences for certain song variants within the species normal range of variation (Simmons 1988; Wagner et al. 1995; Brown et al. 1996; Wagner 1996; Gray 1997; Hedrick and Weber 1998; Gray and Cade 1999*a*, 1999*b*). Given the importance of calling song to male reproductive success, factors affecting song have been of interest to researchers for some time (Walker 1962*a*). Of the many factors investigated, temperature has been by far the most important, although genetic effects have been found (Webb and Roff 1992; Olvido and Mousseau 1995; Mousseau and Howard 1998; Gray and Cade 1999*a*; Roff et al. 1999), as have nontemperature-related environmental effects (Whitesell and Walker 1978; Olvido and Mousseau 1995; Walker 1998; Wagner and Hoback 1999).

Calling song is composed of repeated pulses of sound grouped into chirps or trills. Each pulse of sound is produced by the closing stroke of the modified forewings. When the wings close, a "scraper" on the upper surface of the lower wing engages a "file" composed of teeth on the lower surface of the upper wing. Passage of the scraper along the file causes the wings to vibrate at a characteristic frequency, resulting in the relatively pure tone characteristic of cricket calling song (Bennett-Clark 1989, but see Simmons and Ritchie 1996 for frequency modulation).

Temperature predominantly affects the rate of pulse repetition. Pulse rate increases with temperature in a linear manner (Walker 1962*a*, 1975; Doherty and Huber 1983; Souroukis et al. 1992; Toms 1992). The increase in pulse rate may be partially due to a decrease in pulse (wing closure) or interpulse (wing opening) length. Whether an increased rate of wing opening or closing, or a combination of both, is the primary cause of increased pulse rates at higher temperatures is unclear, although most evidence indicates that the pulse length changes less than the interpulse length (Doherty and Huber 1983; Koch et al. 1988). Given that pulse rate increases with temperature, several other aspects of calling song may be affected. The frequency of the song may be expected to increase with temperature, because the faster closing stroke of the wing implies a faster passage of the scraper across the file. Indeed, in tree crickets (Oecanthinae), frequency has been shown to increase with temperature, often by several kilohertz (Walker 1962*a*, 1962*b*, 1963). In field crickets (Gryllinae), the effects of temperature on frequency are much less certain (Bennett-Clark 1989), with several

Received July 15, 1999. Accepted November 25, 1999.

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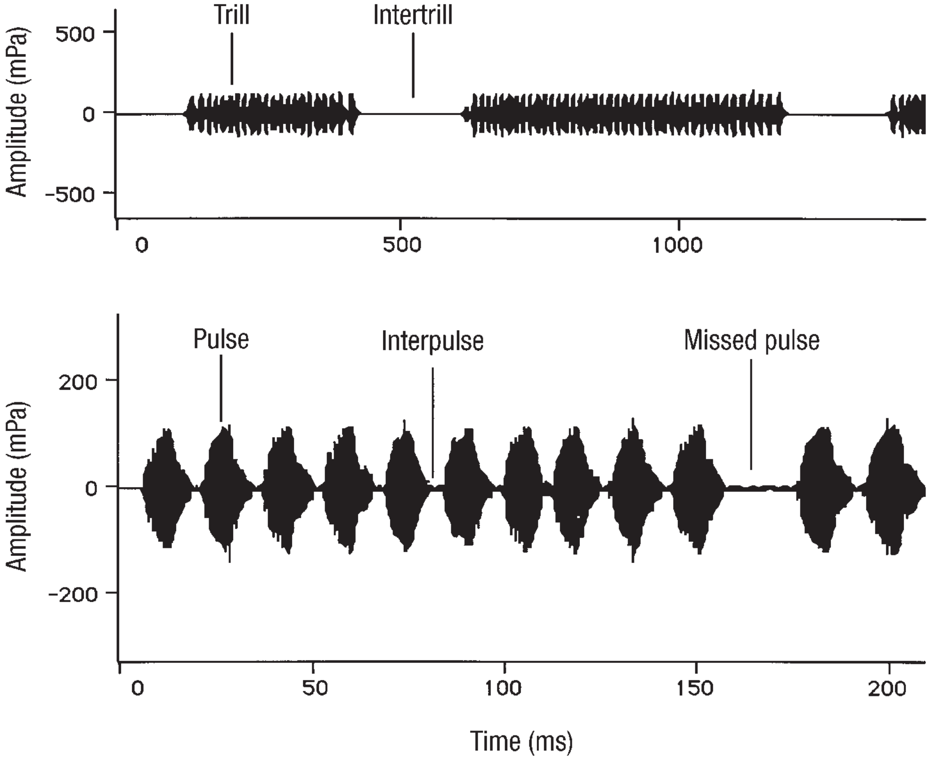
Fig. 1. The calling song of *Gryllus integer.* Labels indicate song characters measured in this study. The top panel shows the trill structure as amplitude versus time, whereas the bottom panel shows the pulses comprising a single trill, also as amplitude versus time.



studies having reached different conclusions (Doherty 1985; Pires and Hoy 1992*a*; Van Wyk and Ferguson 1995). In *Gryllus rubens*, Walker (1962*a*) noted that the effect of temperature on frequency was masked by differences among males and was only apparent by examining song changes within males.

Another aspect of calling song possibly affected by temperature is the number of pulses per unit of song. In chirping species, which typically have low variation in the number of pulses per chirp, temperature appears to have no effect (Doherty and Huber 1983; Ciceran et al. 1994; Van Wyk and Ferguson 1995). In trilling species, however, a temperature effect could arise due to the indirect effect of an increased pulse rate. As the number of pulses produced in a given amount of time is higher at higher temperatures, the number of pulses per trill will increase if song is produced for a fixed-time interval, that is, if crickets trill for a fixed amount of time per trill, then the number of pulses per trill will increase with temperature. Alternatively, crickets may trill for a fixed number of pulses per trill, requiring the amount of time per trill to decrease at higher temperatures. Whether the neural central pattern generator of trilling crickets measures the length of a trill in units of pulses per trill or in units of time will determine whether or not the number of pulses per trill increases with temperature. This also is currently unknown but of considerable interest; in *G. integer*, the number of pulses per trill is important in a female's choice of mates, with females preferring an average number of pulses per trill (Gray and Cade 1999*a*, 1999*b*).

Despite the fairly large number of studies in the literature on the effects of temperature, several questions remain unanswered, particularly with reference to (*i*) trilling species (the number of pulses per trill), (*ii*) peak frequency in field crickets (as opposed to tree crickets), and (*iii*) the importance of individual variation among crickets. The goals of this study were, therefore, to examine the effects of temperature on numerous aspects of calling song in a trilling field cricket, while assessing variation among males.

Methods

Crickets

Nymphal *G. integer* were reared from stock obtained from Austin, Texas, U.S.A., in plastic bins (33.8 × 31.2 × 15.6 cm) with a mesh-covered hole in the lid. The bins were maintained at 28°C and 13 h light : 11 h dark. Contained within the bins were egg cartons for shelter, moistened vermiculite to aid in moulting, cotton-plugged water vials, and cat food. Newly emerged adults were removed from the bins daily and weighed to the nearest 1 mg; they were then placed individually in 500-mL plastic containers and provided with food, water, and shelter, as described above.

Song recording

Two recording methods were used. The first method used soundproof boxes of plywood lined with ceiling tiles. The temperature could be raised using an electric heating pad placed in the bottom of the chamber. Cooling was via two air tubes. Outside the chamber, compressed air was run through tubing in an ice bath; inside the chamber, these air tubes terminated in aquarium "air-stones" that diffused the air. A 2.6 cm thick layer of foam padding over the air-stones helped to ensure an even temperature distribution. A test cricket was placed in the chamber while still within its original isolation container with its screen lid. A second isolation container within the chamber held a freshly killed cricket to be used as a temperature reference. Each reference cricket was within 10% of the mass of its paired test cricket. A thermocouple probe was

Table 1. *F* statistics and significance levels for tests of male age, nonlinear effects of temperature (T^2), and heterogeneity of slopes (individual (ID) × *T* (°C)).

	Male age		T^2		ID × T	
Song variable	$F_{[1,35]}$	P	$F_{[1,34]}$	P	$F_{[18,17]}$	P
Pulse rate	3.21	ns	1.45	ns	3.80	<0.01
Pulse length	0.05	ns	0.67	ns	2.03	ns
Interpulse length	3.26	ns	2.60	ns	0.88	ns
Pulse duty cycle	5.04	<0.05	0.00	ns	0.75	ns
Peak frequency	0.94	ns	3.43	ns[a]	2.03	ns
Pulses per trill	0.04	ns	0.26	ns	1.25	ns
Trill length	0.86	ns	1.89	ns	0.99	ns
Intertrill interval	0.66	ns	2.57	ns	1.63	ns
Trill duty cycle	0.12	ns	0.04	ns	1.28	ns
Missed pulses	2.14	ns	0.87	ns	0.73	ns

Note: ns, $P > 0.05$.
[a] $0.05 < P < 0.01$.

inserted into the thorax of the reference cricket. Once the test cricket began calling, the air hoses were turned off and the temperature at the time of calling was recorded. The temperature within the box was then increased gradually, and subsequent recordings were taken once the higher temperature stabilized.

The second method of collecting data involved placing the isolated males in a temperature-controlled room. Males were recorded by placing a microphone directly on the screened lid of their container. This method allowed for much more efficient data collection. The temperature of the room was measured using a thermocouple probe placed in the room. The temperature of the room was altered once a number of males had been recorded, and no recordings were made for 12 h following the adjustment of the ambient temperature. A temperature reference cricket was not used, as previous work has demonstrated that ambient temperature is a very strong predictor of cricket body temperature and that calling does not appreciably raise body temperature above ambient temperature. In *Gryllus bimaculatus*, a chirping species, the mean difference was less than 1°C (Toms et al. 1993); in trilling species, such as *G. integer*, this difference may be expected to be slightly higher.

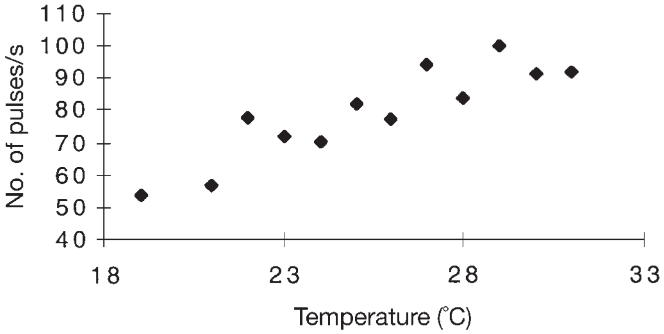
Song analysis

Calling song was analyzed using bioacoustic software (Canary 1.2.4) with a 22.05-kHz sample rate and 8-bit resolution; spectrogram analysis settings were 341.95-Hz filter bandwidth and 256-point Fast Fourier Transform (FFT) size, with Hanning window function. The song components (see Fig. 1) measured were number of pulses per trill, number of missed pulses per trill, peak frequency (from spectrogram, not shown in Fig. 1), trill and intertrill lengths (to 1 ms), and pulse and interpulse lengths (to 140 µs). The numbers of pulses and missed pulses were counted visually; all other song components were measured using the built in “measurement panel” options of the software. For each recording, 10 trills were analyzed and the average value used in analysis. Pulse duty cycle was calculated as pulse length/(pulse length + interpulse length) and trill duty cycle was calculated as trill length/(trill length + intertrill length).

Data analysis

We used analysis of covariance to test for effects of temperature and for differences among males. Preliminary analyses screened for effects of male age and nonlinear temperature effects, and checked the assumptions of ANCOVA, including homogeneity of slopes (Sokal and Rohlf 1981, p. 510). Pulse and trill duty cycles and the proportion of missed pulses were transformed by the arcsine of the square root; all other analyses were conducted on untransformed data. All significance levels are two-tailed.

Fig. 2. Pulse rate versus temperature. Each point represents the average pulse rate at a given temperature, corrected for differences among crickets. Pulse rate was calculated from the mean pulse length and the mean interpulse length at a given temperature, as pulse rate = 1/(mean pulse length + mean interpulse length).



Results

In total, 17 crickets were recorded 3 times each and a further 2 crickets were recorded twice each ($N = 55$ recordings). Males ranged from 9 to 56 days of age (mean ± SD = 34 ± 11 days) and from 0.263 to 0.468 g (mean ± SD = 0.376 ± 0.057 g). Results of the preliminary analyses are presented in Table 1. Male age did not significantly affect any of the song variables except for a possible effect on the pulse duty cycle ($P < 0.03$; see Table 1, male age). None of the song variables showed nonlinear effects of temperature (T^2; Table 1), although the results for peak frequency were suggestive ($P < 0.07$). Following these analyses, the assumptions of the ANCOVA were tested. For all song variables except pulse rate, there was no significant interaction between the individual (ID) and the covariate (ID × *T* interaction; Table 1). Thus, with the exception of pulse rate, the assumptions of the ANCOVA were justified.

As pulse rate violated the assumptions of ANCOVA, the model could not be applied directly. Instead, pulse rate was calculated from the mean pulse length at a given temperature and the mean interpulse length at a given temperature, corrected for differences among individuals. These means pro-

Fig. 3. Trill length versus temperature. Each point is the average trill length at a given temperature, corrected for differences among crickets.

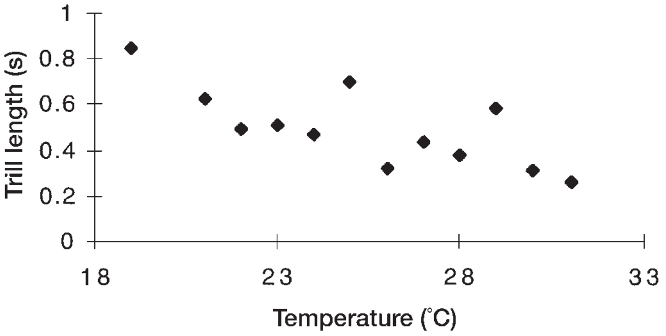


Table 2. Results of the analysis of covariance; for each song variable, model r^2 and F statistics and significance levels for effects of individual crickets (ID) and effects of temperature (T (°C)) are given.

		ID		T	
Song variable	r^2	$F_{[18,35]}$	P	$F_{[1,35]}$	P
Pulse length	0.62	1.46	ns	30.02	<0.0001
Interpulse length	0.83	0.96	ns	114.98	<0.0001
Pulse duty cycle	0.62	1.32	ns	21.31	<0.0001
Peak frequency	0.82	7.28	<0.0001	42.20	<0.0001
Pulses per trill	0.64	3.38	<0.001	1.61	ns
Trill length	0.75	3.54	<0.001	40.80	<0.0001
Intertrill interval	0.69	2.03	<0.05	36.24	<0.0001
Trill duty cycle	0.47	1.65	ns	1.17	ns
Missed pulses	0.35	1.01	ns	0.55	ns

Note: ns, $P > 0.05$.

Fig. 4. Length of intertrill interval versus temperature. Each point is the average length of the intertrill interval at a given temperature, corrected for differences among crickets.

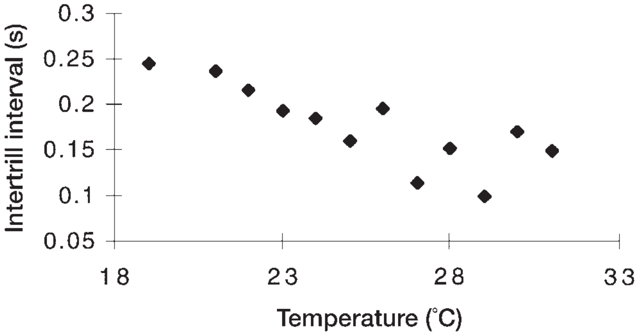
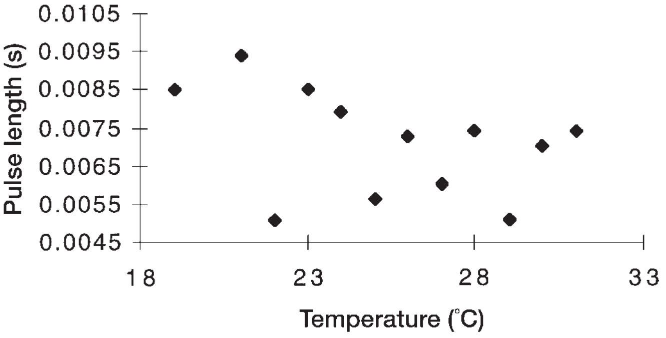


Fig. 5. Pulse length versus temperature. Each point is the average pulse length at a given temperature, corrected for differences among crickets.



vided corrected pulse rates, as: pulse rate = 1/(pulse length + interpulse length). Figure 2 shows these corrected pulse rates versus temperature. The regression of pulse rate on temperature was highly significant, with pulse rate increasing by about 3.5 pulses per degree increase in temperature ($r^2 = 0.87$, $t = 18.581$, $P < 0.0001$). Although the ANCOVA indicated that there was significant heterogeneity of slopes (see above), the average of the slopes from separate regressions for each male was in good agreement with this indirect estimate (mean slope ± SE = 3.41 ± 0.30; with mean slope = 0, $t = 11.36$; $N = 19$; $P < 0.0001$).

As all other song variables met the assumptions of the ANCOVA, the effects of differences among individuals and the effects of temperature were tested. These results are presented in Table 2. There were consistent differences between individual crickets in peak frequency, the number of pulses per trill, trill length, and intertrill length. Pulse length, interpulse length, pulse duty cycle, trill duty cycle, and the proportion of missed pulses showed no consistent differences among crickets. Temperature affected most aspects of song (Table 2; Figs. 3–8): trill length ($P < 0.0001$; Fig. 3), intertrill interval ($P < 0.0001$; Fig. 4), pulse length ($P < 0.0001$; Fig. 5), interpulse length ($P < 0.0001$; Fig. 6), pulse duty cycle ($P < 0.0001$; Fig. 7), and peak frequency ($P < 0.0001$; Fig. 8). Temperature did not have a significant effect on the number of pulses per trill, the trill duty cycle, or the proportion of missed pulses. For the song components that did show significant differences among males (pulses per trill, trill length, intertrill interval, and peak frequency), we tested if the least-squares means for each male (corrected for temperature) were correlated with either male mass or male age. No significant relationships were found ($N = 19$, $P > 0.1$ in all cases).

Pulse length predicted peak frequency (Fig. 9). The relationship was found to be significantly nonlinear (model $r^2 = 0.85$, pulse length $t = 4.90$, $P < 0.0001$, (pulse length)^2 $t = -6.51$, $P < 0.0001$).

Discussion

Neither male age nor male mass affected song structure, with the exception of a possible effect on pulse duty cycle. Several previous studies have also found no effect of male age on calling song structure in house and field crickets (Souroukis et al. 1992; Ciceran et al. 1994; Gray 1997; Gray and Cade 1999*a*). However, older male *G. bimaculatus* were found to produce more variable pulse rates than younger males (Simmons and Zuk 1992) and a study of a katydid found that male song changed with age, owing to wear of the stridulatory apparatus (Ritchie et al. 1995). Indicators of male age in song are relevant to sexual communication, as several studies have shown that female crickets prefer older males as mates (Zuk 1987; Simmons and Zuk 1992; reviewed in Zuk and Simmons 1997). We are hesitant to attribute biological significance to the pulse duty cycle – age

Fig. 6. Interpulse length versus temperature. Each point is the average interpulse length at a given temperature, corrected for differences among crickets.

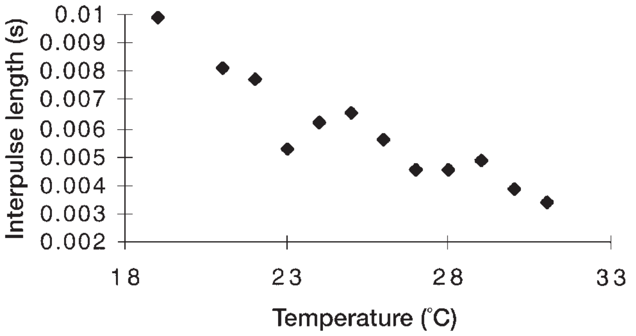


Fig. 7. Pulse duty cycle versus temperature. Each point is the average pulse duty cycle at a given temperature, corrected for differences among crickets.

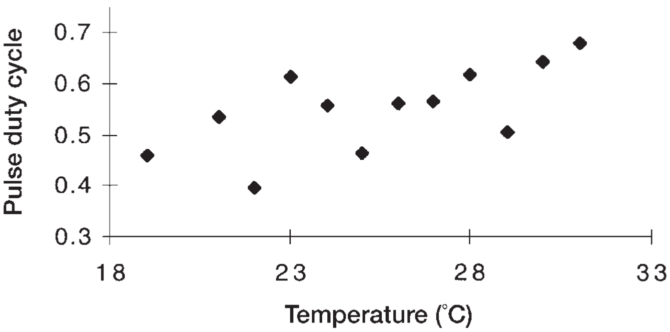


Fig. 8. Peak frequency versus temperature. Each point is the average peak frequency at a given temperature, corrected for differences among crickets.

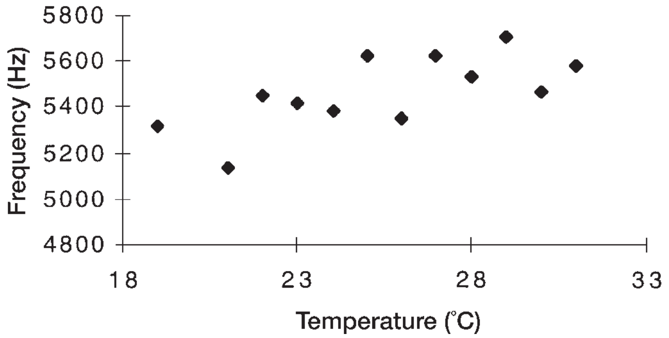
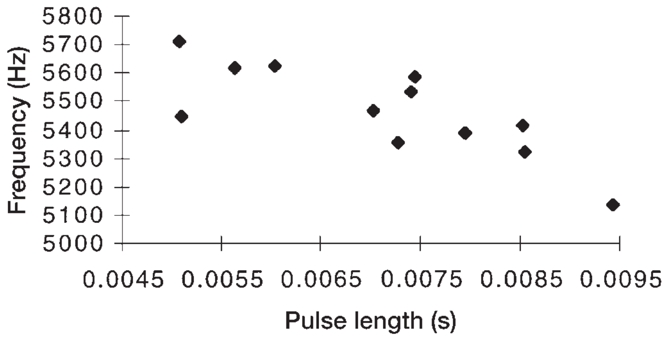


Fig. 9. Average pulse length versus average peak frequency, corrected for differences among crickets. The relationship is significantly curvilinear.



relationship found here for two reasons. First, because of the experimental design, there was a slight tendency for recordings at higher temperatures to be made following recordings at lower temperatures and, thus, male age and recording temperature were somewhat confounded (Spearman's rank correlation, $r_s = 0.24$, $N = 55$, $P < 0.07$). Secondly, the result is not strongly significant ($P < 0.03$) and would not remain significant following Bonferoni correction for multiple tests. Further experimentation is required to resolve this.

As found in previous studies (Walker 1962*a*, 1975; Souroukis et al. 1992; Ciceran et al. 1994; Toms 1992), pulse rate increased with temperature. The number of pulses per second increased by approximately 3.5 pulses/s for each centigrade degree change in temperature. However, the slopes of pulse rate on temperature varied among males. This was an unexpected finding, suggesting genetic or nontemperature-related environmental differences among crickets in response to temperature. Both genetic and environmental effects other than temperature are known to affect cricket song (reviewed above). Changes in pulse rate with temperature are unlikely to disrupt acoustic communication, because female responsiveness to male pulse rates changes similarly with temperature (Doherty 1985; Pires and Hoy 1992*a*, 1992*b*).

The increase in pulse rate is due to a decrease in both the pulse and interpulse lengths with temperature. Neither pulse length nor interpulse length showed effects due to differences among individual males. The interpulse length changed with temperature more than pulse length did (as evidenced by the pulse duty cycle). Temperature, therefore, affects the rate at which the wing opens to a greater extent than the rate at which the wing closes. These results suggest that wing closing and opening comprise two different mechanisms, either neural or mechanical, that respond differently to temperature. Conversely, temperature did not have a greater effect on trill length than on intertrill interval, suggesting the existence of similar regulatory mechanisms.

As suggested by Walker (1962*a*), the peak frequency of the calling song is dependent on temperature, as well as on individual differences among males. The effect is much weaker than in tree crickets (Oecanthinae) and could be obscured by differences among males. The frequency is determined by the rate of the closing wing stroke, as well as by wing mass and reverberation (see Simmons and Ritchie 1996): as the rate of wing closure increases, the tooth strike rate also increases, resulting in a higher peak frequency. In this study, the rate of wing closure was reflected in pulse length. The relationship between pulse length and frequency was shown to be nonlinear. The reason for this nonlinearity is unknown, but a possible explanation could be that, at very high temperatures, the decrease in pulse length is due partly to a faster closing stroke and partly to a decrease in the proportion of the file being struck by the scraper. The significant nonlinearity of the frequency – pulse length relationship suggests that the nearly significant ($P < 0.07$) nonlinear effect of temperature on frequency may reflect a true nonlinear effect.

The number of pulses per trill varied among males, but not with temperature. Variation among males in the number of pulses per trill, as found here, is consistent with previous work (Gray and Cade 1999*a*), which showed significant genetic differences in cricket song. The absence of a temperature effect on the number of pulses per trill is consistent with previous work that did not control for variation among males (Souroukis et al. 1992). Given that the number of pulses per trill does not vary with temperature and that pulse rate increases, the trill length must change with temperature. We found that the trill length did decrease with temperature, suggesting that crickets "measure" their trills in units of pulses, rather than in units of time. This consistency of male song across temperatures may enhance female mate selection.

There was no significant variation among males in the proportion of missed pulses per trill. As well, there was no effect of temperature on the proportion of missed pulses. These results contrast with the findings of Souroukis et al. (1992) that the proportion of missed pulses decreased with temperature in both the field and the laboratory. Whether missed pulses convey any information to females about the calling male is unclear (Wagner et al. 1995).

In summary, the effects of temperature on calling song are manifest in the fine structure of the song and are not restricted to pulse-rate changes. Both the proximate basis for pulse-rate increase and the proximate basis for temperature independence of the number of pulses per trill were identified.

Acknowledgements

We appreciate the thoughtful input of G. Pollack, M. Ritchie, and J.W.H. Ferguson. This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to W.H.C. (No. A6174) and by a Brock University Postdoctoral Fellowship to D.A.G. This work is derived from a portion of a thesis submitted by S.D.M. in partial fulfillment of the requirements for B.Sc. (Hons.) at Brock University.

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