

The effects of temperature and age on calling song in a field cricket with a complex calling song, *Teleogryllus oceanicus* (Orthoptera: Gryllidae)

Sean E. Walker and William H. Cade

Abstract: We examined the effects of temperature and age on calling song in the field cricket *Teleogryllus oceanicus*. *Teleogryllus oceanicus* has a complex calling song made up of two different kinds of chirp, long and short. The long chirp is made up of three to eight single pulses of sound and the short chirp consists of several paired pulses. The properties of *T. oceanicus* calling song did not vary with age, but almost every property of the song varied with temperature. Pulse duration, interpulse interval, and pulse rate in both the long and the short chirp varied with temperature. The number of pulses in the long chirp, number of chirps in the short chirp, chirp rate in the short chirp, duration of the long chirp, carrier frequency of both the short and long chirps, and total song duration were also affected by temperature. The duration of the short chirp and the degree of frequency modulation were the only characteristics that did not vary with temperature. Temperature does not affect the properties of the long and short chirps in the same manner. The long chirp decreases in duration with temperature and has fewer pulses, while the short chirp stays the same in duration and contains a higher number of chirps. These data demonstrate that temperature influences calling-song parameters in a field cricket with a complex calling song.

Résumé : On trouvera ici une étude des effets de la température et de l'âge sur le chant d'appel du grillon des champs *Teleogryllus oceanicus*. L'insecte émet un chant d'appel complexe formé de deux types de trilles, l'un long, l'autre court. Le trille long consiste en trois à huit pulsations sonores séparées et le trille court de plusieurs pulsations en paires. Les propriétés du chant d'appel ne varient pas en fonction de l'âge, mais presque toutes les autres caractéristiques du chant changent selon la température. La durée d'une pulsation, l'intervalle entre les pulsations et le taux de pulsations changent avec la température, tant dans les trilles longs que courts. La température affecte aussi le nombre de pulsations dans le trille long, le nombre de pépiements dans le trille court, le taux de pépiement dans le trille court, la durée du trille long, la fréquence porteuse des trilles longs et courts et la durée totale du chant. La durée du trille court et l'importance de la modulation de fréquence sont les seules caractéristiques indépendantes de la température. La température n'affecte pas les caractéristiques des trilles longs et courts de la même façon. La durée du trille long diminue avec la température et le nombre de pulsations est réduit, mais le trille court maintient la même durée et le nombre de pépiements augmente. Nos données montrent que la température influence les caractéristiques du chant chez un grillon des champs qui possède un chant d'appel complexe.

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Introduction

In many species of cricket, males produce a calling song that attracts females (Boake 1983; Loher and Dambach 1989; Otte 1992). This song is generally species-specific (Hoy et al. 1982; Doherty and Storz 1992; Gray and Cade 2000) and in some species, certain elements of calling song

are preferred by females (e.g., Wagner 1996; Simmons et al. 2001). Songs are made up of repetitive pulses of sound and males produce a single pulse by closing their forewings (for details see Bennet-Clark 1989). Many properties of these songs vary with temperature (Souroukis et al. 1992; Martin et al. 2000), genetics (e.g., Web and Roff 1992; Gray and Cade 1999; Roff et al. 1999), rearing environment (Walker 2000), age (Simmons and Zuk 1992), geography (Zuk et al. 2001), or infestation with parasitoids that use acoustic cues to locate hosts (Zuk et al. 1993).

Temperature affects numerous aspects of calling song. In particular, the temporal properties, i.e., pulse duration, interpulse interval, and pulse rate, change with temperature. The effects of temperature on the temporal properties of calling song have been noted in several subfamilies of cricket (e.g., Walker 1962a). The pulse rate increases in a linear fashion with temperature (Doherty and Huber 1983; Souroukis et al. 1992; Toms 1992). Increases in temperature

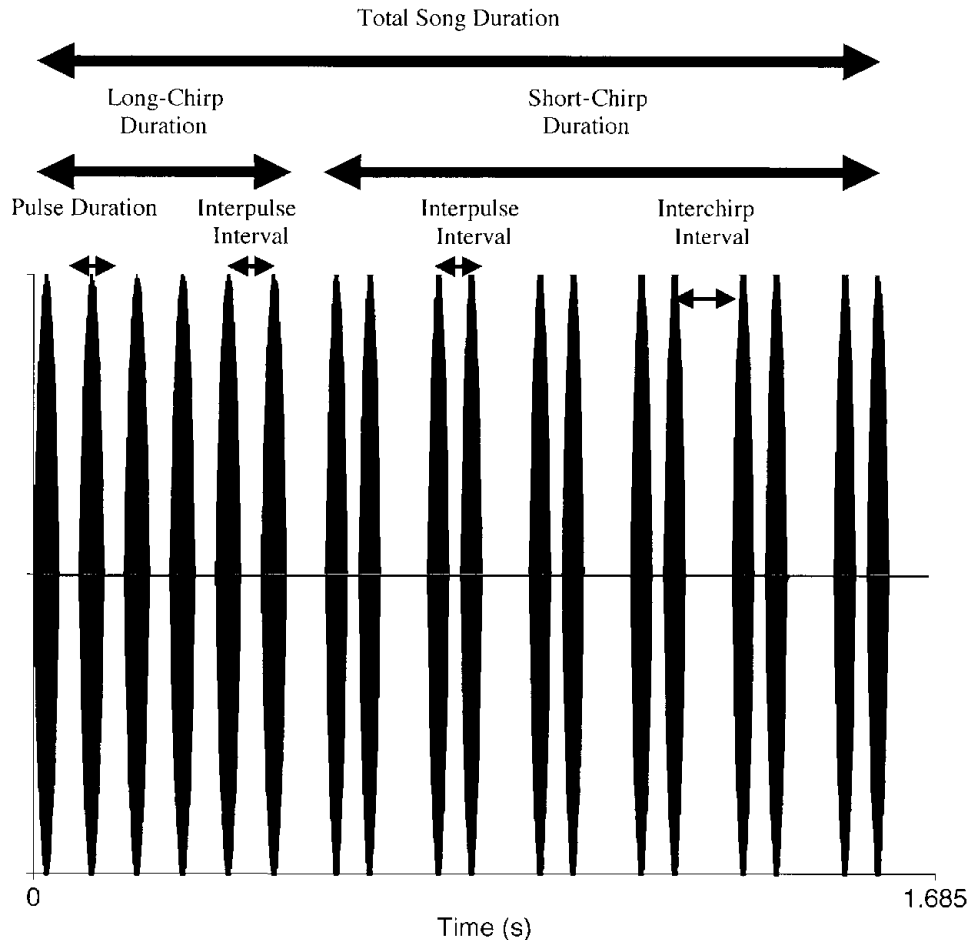
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S.E. Walker^{1,2} and W.H. Cade. Department of Biological Sciences, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada.

¹Corresponding author (e-mail: swalker@fullerton.edu).

²Present address: Department of Biological Science, California State University, 800 North State College Boulevard, Fullerton, CA 92834-6850, U.S.A.

Fig. 1. Wave form of the calling song of *Teleogryllus oceanicus*, illustrating the long- and short-chirp sections of the song and the characteristics that we measured. Pulse duration was the same in both the short- and long-chirp sections and is only shown for the long chirp.



decrease the duration of the pulse and the interpulse interval. These properties are limited by the rate at which the cricket closes and opens its wings (Bennet-Clark 1989; Martin et al. 2000). The frequency of sound produced by crickets generally increases with temperature (Walker 1962a, 1962b, 1963; Van Wyk and Ferguson 1995; Martin et al. 2000). However, not all studies have demonstrated this (Doherty 1985; Doherty and Callos 1991). In particular, carrier frequency is strongly dependent on temperature in tree crickets (Oecanthinae) but is only slightly influenced by temperature in field crickets (Gryllinae, Walker 1962a). These results suggest that temperature may not affect the calling song of all crickets in the same way.

Here we examine changes in the calling song of *Teleogryllus oceanicus* (Le Guillou, 1841) as a function of temperature. *Teleogryllus oceanicus* is an Australian species with a wide geographic range that includes several Pacific islands, and it has been introduced into the Hawaiian Islands (Kevan 1990; Otte 1990). It is an interesting species to study, for numerous reasons. The calling song of *T. oceanicus* consists of two distinct types of chirp (Fig. 1): a trill-like section of three to eight single pulses called the long chirp, which is followed by a number of short chirps each consisting of two pulses (Otte 1992; Zuk et al. 1993, 2001). Although the ef-

fects of temperature on the calling songs of crickets have been investigated, only species with simple songs have been studied (e.g., chirping species (Doherty 1985) or trilling species (Doherty and Callos 1991; Martin et al. 2000)). There are no data showing how temperature influences the calling song of a species with a complex song.

Materials and methods

Nymphal *T. oceanicus* were reared from stock in 84-L plastic trash cans under a 14 h light (L) : 10 h dark (D) cycle at 25 °C. The original stock for this culture is from Queensland, Australia, and has been in culture for more than 20 years. Egg cartons, moistened vermiculite, cotton-plugged water vials, and cat food were placed in each can. Newly emerged adults were removed daily. Single adults were placed in 500-mL plastic containers and provided with cat food, a cotton-plugged water vial, and an egg carton for shelter. After being put in individual containers, animals were placed in a temperature- and light-controlled room at 25 °C with a 14 h L : 10 h D cycle. However, the dark phase for this room occurred from 0900 until 1900. Prior to recording of songs, animals were moved into a room with the same light cycle at the appropriate test temperature (23, 25,

or 28 °C). Animals were given 24 h to acclimate to the new temperature and surroundings. We noted the number of days after adult molt of each individual recorded to examine the effects of age on the male calling song. Each male was recorded only once at a single temperature. Males were recorded from 1000 until 1800. Previous work with other species of *Teleogryllus* has demonstrated that males can vary the type of chirp (long or short) depending on the time of day (Otte and Cade 1983). During the time period that males were recorded, all males produced songs containing both the long and the short chirp. Singing males were recorded using a Linear X M51 measurement microphone (± 1 dB from 10 Hz to 40 kHz) and a Tascam DA-P1 digital audio tape recorder (44.1 kHz sampling rate, ± 1 dB from 20 Hz to 20 kHz). Males were recorded continuously singing for approximately 2 min, and 45-s sections of recorded song were digitized with a 44.1-kHz sampling rate and analyzed using Canary version 1.2.4 (Cornell Laboratory of Ornithology, Ithaca, N.Y.).

We chose to examine 13 different temporal aspects of the songs (Fig. 1). In the long-chirp portion of the song we measured the duration, number of pulses, pulse rate, pulse duration, and interpulse interval. In the short chirp we quantified the duration, number of chirps, chirp rate, pulse duration, interpulse interval, and interchirp interval. In addition, we measured the total song duration and the proportion of the song constituted by the long chirp. We also determined the carrier frequency of the long and short chirps using Fourier analysis (spectrogram-analysis settings were 21.56 Hz filter bandwidth and a 8192-point fast Fourier transform size with Hamming window function). The carrier frequency was determined by finding the frequency with the maximum intensity, based on a frequency by decibel plot from a sample consisting of a whole section of the long or short chirp (Bradbury and Vehrencamp 1998). In addition, we examined variation in sound-pulse frequency in both the long and the short chirp. In the same manner as above, we determined the carrier frequency of the first, middle, and last thirds of a randomly chosen pulse from the short and long chirps. This is similar to the procedure used by Prestwich et al. (2000) to examine frequency modulation in *Anurogryllus arboreus*. We made measurements of all song characteristics on six different segments of song recorded from each male.

The effects of temperature were evaluated in two different ways. We first used the means of the measurements for each male in a multivariate analysis of covariance (MANCOVA) to evaluate the effects of age and temperature. Secondly, the effects of temperature and among-male variation on male calling song parameters were examined using a mixed-model analysis of variance (ANOVA) with temperature as a fixed factor and male nested within temperature as a random factor. An ANOVA approach was chosen over an analysis using linear or quadratic regression because only three temperatures were used in the study. Since we analyzed 14 different characteristics, a Bonferroni adjustment was used to maintain an overall α level of 0.05. We analyzed frequency modulation separately from the other song characteristics using a mixed-model ANOVA with temperature, chirp type, and sample (first, middle, or last third) as factors. When needed, error mean squares were estimated using the Satterthwaite approximation (Neter et al. 1990). Means ob-

tained at different temperatures were compared by constructing contrasts that used the appropriate degrees of freedom and mean squared error based on the mixed model (Neter et al. 1990).

Results

We recorded a total of 24 males at three different temperatures. Seven males were recorded at 23 °C, 9 at 25 °C, and 8 at 30 °C. Males ranged in age from 4 to 23 days post adult molt (mean \pm SE = 11.3 \pm 0.85 days). We found no interaction between age and temperature, indicating that the data meet the parallelism assumption of MANCOVA (Wilks' λ = 0.059, $F_{[30,8]} = 0.8301$, $P = 0.6704$). MANCOVA revealed significant effects of temperature (Wilks' λ = 0.0005, $F_{[30,12]} = 18.1$, $P < 0.0001$), but no effect of age (Wilks' λ = 0.9254, $F_{[15,6]} = 0.9254$, $P = 0.5832$).

Univariate analysis of calling-song characteristics using a mixed-model ANOVA showed that most varied with temperature and all exhibited significant variation among males within temperature (Table 1). Almost all aspects of the long chirp (duration, number of chirps, pulse duration, and interpulse interval) decreased with increasing temperature (Table 2). However, the long-chirp pulse rate increased with temperature. Many characteristics of the short chirp also varied with temperature but the duration of the short chirp did not (Tables 1, 2). The number of chirps in the short chirp increased between 23 and 25 °C but not between 25 and 30 °C. The chirp rate increased in a linear fashion with temperature. Pulse duration, interpulse interval, and interchirp interval for the short chirp all decreased with temperature. Total song duration and the proportion of long chirp decreased at higher temperatures (Table 2). The song was significantly shorter at 30 °C than at 23 or 25 °C and the proportion of long chirp was significantly lower at 25 and 30 °C than at 23 °C. Carrier frequency increased with temperature in both the long and short chirp and was highest at 30 °C.

Teleogryllus oceanicus song exhibited significant variation in carrier frequency within sound pulses and between the long and short chirps (Table 3, Fig. 2). Carrier frequency was significantly lower in the short chirp than in the long chirp (Tables 2, 3). Frequency modulation occurred in both the long and the short chirp. However, there was greater frequency modulation in the long chirp than in the short chirp. This was due to the long chirp starting at a higher carrier frequency than the short chirp (Fig. 2). Interestingly, temperature had no effect on the difference in carrier frequency between the short and the long chirp or on the degree of frequency modulation as evidenced by the nonsignificant interaction terms between temperature and the other factors (Table 3).

Discussion

Male *T. oceanicus* have a complex song and elements of the song vary with temperature but not with age. Songs recorded at higher temperatures were shorter at higher frequency, and contained a smaller proportion of long chirp. There were also changes in pulse rate, number of pulses, pulse duration, interpulse interval in the long chirp, and

Table 1. Results of mixed-model ANOVAs examining variation in characteristics of the calling song of *Teleogryllus oceanicus* across temperatures.

Trait	Temperature		Male(temperature)	
	$F_{[2,21]}$	P	$F_{[21,120]}$	P
Duration of long chirp	31.99	<0.0001	6.55	<0.0001
No. of pulses in long chirp	9.93	0.0009	7.54	<0.0001
Pulse rate in long chirp	123.1	<0.0001	11.95	<0.0001
Pulse duration in long chirp	17.42	<0.0001	4.80	<0.0001
Interpulse interval in long chirp	29.68	<0.0001	5.03	<0.0001
Duration of short chirp	3.36	0.0542	20.37	<0.0001
No. of chirps in short chirp	8.54	0.0019	14.88	<0.0001
Chirp rate in short chirp	53.03	<0.0001	5.50	<0.0001
Pulse duration in short chirp	75.56	<0.0001	2.65	0.0005
Interpulse interval in short chirp	23.64	<0.0001	5.45	<0.0001
Interchirp interval in short chirp	47.92	<0.0001	6.59	<0.0001
Total song duration	8.27	0.0022	13.08	<0.0001
Carrier frequency in short chirp	18.59	<0.0001	9.78	<0.0001
Carrier frequency in long chirp	15.56	<0.0001	9.74	<0.0001
Proportion of song that is long chirp	9.43	0.0012	14.53	<0.0001

Table 2. Characteristics of *T. oceanicus* calling song at different temperatures.

Trait	23 °C	25 °C	30 °C
Duration of long chirp (ms)	528±23 a	363±20 b	285±21 c
No. of pulses per long chirp	7.2±0.4 a	5.6±0.3 b	5.2±0.3 b
Pulse rate in long chirp (no./s)	13.6±0.2 a	15.5±0.2 b	18.3±0.2 c
Pulse duration in long chirp (ms)	49.8±1.4 a	42.6±1.2 b	38.8±1.3 c
Interpulse interval in long chirp (ms)	45.9±1.8 a	41.2±1.6 a	27.8±1.7 b
Duration of short chirp (ms)	870±77	1045±69	809±72
No. of chirps per short chirp	4.9±0.5 a	7.4±0.4 b	6.9±0.4 b
Chirp rate in short chirp (no./s)	6.0±0.2 a	7.1±0.2 b	8.6±0.2 c
Pulse duration in short chirp (ms)	42.5±0.9 a	33.1±0.8 b	28.4±0.8 c
Interpulse interval in short chirp (ms)	27.6±1.3 a	19.9±1.2 b	15.4±1.2 c
Interchirp interval in short chirp (ms)	104.3±3.7 a	71.5±3.2 b	56.3±3.4 c
Total song duration (ms)	1432±67 a	1470±59 a	1141±63 b
Carrier frequency in short chirp	4.66±0.03 a	4.75±0.03 a	4.90±0.03 a
Carrier frequency in long chirp	4.70±0.03 a	4.81±0.03 a	4.96±0.03 b
Proportion of song that is long chirp	0.38±0.02 a	0.25±0.02 b	0.26±0.02 b

Note: Data are shown as the mean ± 1 SE. Different letters within a row indicate significant differences between temperatures ($P < 0.05$).

chirp rate, number of chirps, and interpulse and interchirp intervals in the short chirp. In addition, in all song characteristics we examined we found significant variation among males.

In several species, male age is correlated with calling-song characteristics (Stiedl et al. 1991; Simmons and Zuk 1992; Ritchie et al. 1995). The relationships between calling song characteristics and age are important, since females prefer to mate with older males in some species, and females may base this choice on male song characteristics (e.g., Simmons 1995). However, even when females prefer older males, the traits that indicate male age may not be clear. For instance, female *Gryllus pennsylvanicus* prefer older males (Zuk 1987), but calling-song characteristics are not related to age in this species (Ciceran et al. 1994). We found no relationship between age and calling-song characteristics in male *T. oceanicus*. This is consistent with the results of

many other studies of signaling in field crickets and suggests that male age may not be reflected in calling songs (Hedrick 1986; Souroukis et al. 1992; Ciceran et al. 1994; Gray 1997; Gray and Cade 1999).

As in other studies, we found that pulse and chirp rates increase with temperature (Walker 1962a, 1962b; Doherty 1985; Doherty and Callos 1991; Souroukis et al. 1992; Ciceran et al. 1994; Martin et al. 2000). Changes in the pulse rate of the long chirp are due to decreases in both pulse duration and interpulse interval. Similarly, changes in the chirp rate of the short chirp are due to decreases in pulse duration, interpulse interval, and interchirp interval. From 23 to 30 °C, changes in the interpulse interval are greater than changes in pulse duration in the short and long chirps. Changes in interpulse interval result from changes in the rate at which the wing opens, while variation in pulse duration is a function of how fast the wing closes (Bennet-Clark 1989).

Table 3. Results of a mixed-model ANOVA examining the effects of temperature, chirp (long or short), and time (first, middle, or last third) on the carrier frequency of individual pulses of sound in *T. oceanicus*.

Effect	Mean square	df	F	P
Temperature ^a	5.25	2,21	22.4	<0.0001
Chirp ^b	0.43	1,21	63.17	<0.0001
Temperature × chirp ^b	0.013	2,21	1.95	0.1678
Time ^c	4.87	2,42	139.3	<0.0001
Time × temperature ^c	0.047	4,42	1.35	0.2681
Time × chirp ^d	0.164	2,42	40.89	<0.0001
Time × chirp × temperature ^d	0.0038	4,42	0.9521	0.4437
Individual(temperature) ^e	0.234	21,45	6.20	<0.0001
Individual × chirp(temperature) ^d	0.0068	21,42	1.69	0.0713
Individual × time(temperature) ^d	0.035	24,42	8.73	<0.0001
Individual × time × chirp(temperature)	0.004	42,720	1.53	0.0190
Error	0.002619	720		

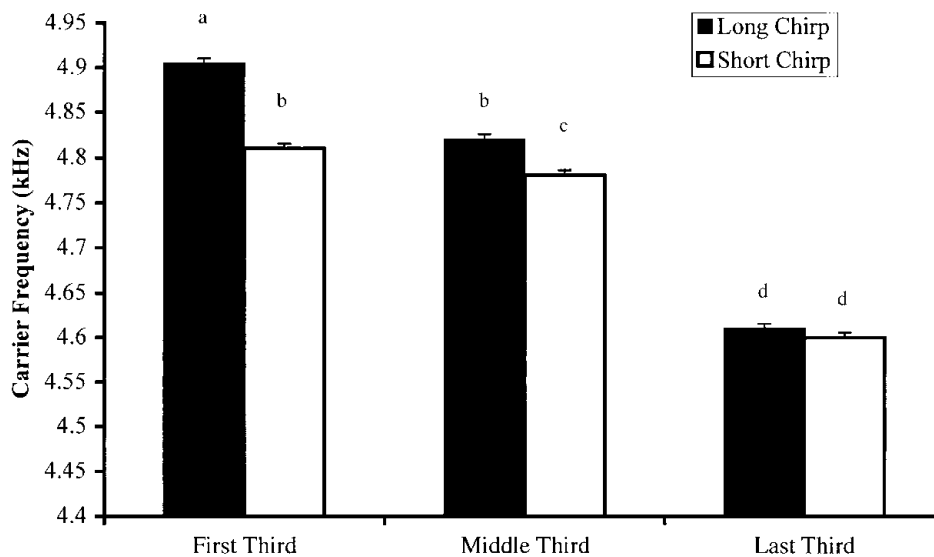
^aThe denominator mean square for this test is individual(temperature).

^bThe denominator mean square for this test is individual × chirp(temperature).

^cThe denominator mean square for this test is individual × time(temperature).

^dThe denominator mean square for this test is individual × time × chirp(temperature).

^eThe denominator mean square for this test is the sum of the means squares for individual × chirp(temperature) and individual × time(temperature) minus the mean square for individual × time × chirp(temperature).

Fig. 2. Carrier frequency (mean + 1 SE) of the first, middle, and last thirds of single pulses of sound from the short and long chirps. Groups with the same letter above them are not significantly different.

Martin et al. (2000) found a similar pattern in *G. texensis* (formerly *G. integer*) and suggested that there are two different mechanisms, either mechanical or neural, that control wing closure and opening. This is quite similar to our results and suggests that similar mechanisms are involved in the control of wing closure and opening in *T. oceanicus*.

Studies of tree crickets and some studies of field crickets demonstrate that carrier frequency increases with temperature (Walker 1962a, 1962b, 1963; Van Wyk and Ferguson 1995; Martin et al. 2000). However, not all studies have demonstrated shifts in carrier frequency with temperature (Doherty 1985; Doherty and Callos 1991) and it has been suggested that individual variation in carrier frequency could mask temperature effects (Walker 1962a). In field crickets, carrier frequency is determined by the rate at which the wing

closes, wing mass and reverberation, and where the plectrum strikes the file on the wing (Simmons and Ritchie 1996; Bennet-Clark 1999). Our data clearly show an increase in carrier frequency with temperature in *T. oceanicus*. In addition we found significant individual variation in peak frequency among males that was much smaller than the variation across temperatures. Our results also show significant differences in carrier frequency between chirp types and frequency modulation within sound pulses.

Frequency modulation has now been documented in several species of crickets (Simmons and Ritchie 1996; Bennet-Clark 1999; Prestwich et al. 2000; Bailey et al. 2001; Bennet-Clark and Bailey 2002). In species in which frequency modulation has been observed, carrier frequency decreases towards the end of the pulse. A similar phenomenon

occurs in *T. oceanicus*: carrier frequency is higher at the beginning of a pulse than at the end. Also, *T. oceanicus* exhibits a degree of frequency modulation that is within the range of that of other species of gryllids (5%–16%). Our data show that the degree of frequency modulation does not change with temperature; however, it differs between the two chirp types. Pulses in the long chirp start at a higher frequency than pulses from the short chirp and decay to approximately the same frequency. Bennet-Clark (1999) suggests that frequency modulation within a pulse is due to changes in the mass of the resonating system and that as the wings close, the mass of the system increases. If this is the case, pulse-to-pulse variation in carrier frequency may be due to differences in the point when the plectrum first contacts the file (Prestwich et al. 2000). This hypothesis suggests that differences in carrier frequency and frequency modulation between chirp types are due to differences in the point where the plectrum makes contact with the file. If this is true, we predict that the plectrum will contact the file earlier during wing closure in the long chirp than in the short chirp. This is supported by the observation that pulses are longer in the long chirp than in the short chirp.

We found no significant change in the duration of the short chirp, but an increase in the number of chirps. This was due to changes in pulse duration, interpulse interval, and interchirp interval, resulting in increase in chirp rate, while the duration of the short chirp stayed approximately the same. Thus, males perform the short-chirp portion of the song for a fixed amount of time rather than emitting a certain number of chirps. This results in little variation in the duration of the short chirp but changes in the number of chirps.

Temperature influenced the number of pulses in the long chirp, and the proportion of long chirp in the song decreased with temperature. The variation in the number of pulses in the long chirp is particularly interesting. In trilling species the number of pulses per trill does not vary with temperature (Martin et al. 2000) and in chirping species there is no variation in the number of pulses per chirp in relation to temperature (Doherty and Huber 1983; Ciceran et al. 1994; Van Wyk and Fergusun 1995). In addition, female *T. oceanicus* prefer male songs with a high proportion of long chirp (Simmons et al. 2001), and calls consisting of only long chirp are more attractive than those made up of only the short-chirp portion of the song (Pollack and Hoy 1981). Also, the temporal pattern of the long chirp is essential for song recognition (Hennig and Weber 1997). In species with simple songs, temperature-dependent changes in male song are reflected by temperature-dependent shifts in female preferences (Doherty 1985; Pires and Hoy 1992a, 1992b). It seems likely that similar shifts in female preference would occur in *T. oceanicus*. This suggests that changes in song structure due to temperature would not interfere with communication between the sexes.

Male *T. oceanicus* produce a complex calling song consisting of two different types of chirp. Song parameters in this species vary depending on geography (Zuk et al. 2001), whether or not they are parasitized by a tachinid fly, *Ormia ochracea* (Zuk et al. 1998), and differences in the prevalence of infestation with *O. ochracea* (Zuk et al. 1993; Rotenberry et al. 1996). Our data demonstrate that the calling song of

T. oceanicus also varies as a function of temperature but not age. Changes in the song of this species as a function of temperature are reflected by changes in pulse and chirp rates as well as by changes in the fine structure of the song. These changes occur in both the long- and short-chirp portions of the song, and temperature clearly affects the temporal aspects of the long and short chirps differently. This suggests that there are two mechanisms which respond differently to the temperature regulating the fine structure of the short- and long-chirp portions of the song. Given the complex changes in male calling song with temperature, females' preferences for male song characteristics may also vary with temperature.

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