

## Effects of temperature on chirp rates of tree crickets (Orthoptera: Oecanthidae)

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The relationship between temperature and chirp rate is described for three African tree crickets, *Oecanthus capensis*, *O. karschi* and *O. sycmorus*. Knowledge of the variation in the chirp rates of *O. karschi* and *O. capensis* makes it possible to discriminate between the songs of these species with a stopwatch. Their songs can also be used to estimate air temperature. When signals like cricket songs change with temperature, the response may also be affected. Some problems associated with temperature dependent communication systems are discussed.

Die verhouding tussen temperatuur en tjirptempo word beskryf vir drie Afrika boomkriekke, *Oecanthus capensis*, *O. karschi* en *O. sycmorus*. Kennis van die verskille in die tjirptempo's van *O. karschi* en *O. capensis* maak dit moontlik om tussen die sang van die twee spesies te onderskei met 'n stophorlosie. Hulle sang kan ook gebruik word om lugtemperatuur te meet. Wanneer seine soos kriekklanke verander met temperatuur, kan die reaksies ook beïnvloed word. Sommige probleme geassosieer met temperatuur afhanklike kommunikasie-stelsels, word bespreek.

Surprisingly little is known about the effects of temperature on rates within poikilotherm nervous systems (Walker 1975). Since poikilotherm metabolic rates generally increase with temperature, pulse rates and chirp rates of the calling songs of crickets generally increase with temperature. Since songs that are utilized during the process of mate location can change with temperature, it may also be necessary for the response to change with temperature (e.g. Walker 1957). Since cricket songs play a crucial role in the location of conspecifics of the opposite sex, it is also probable that we will have to understand evolutionary changes in the neurophysiology of sound production much better, before we can hope to understand speciation.

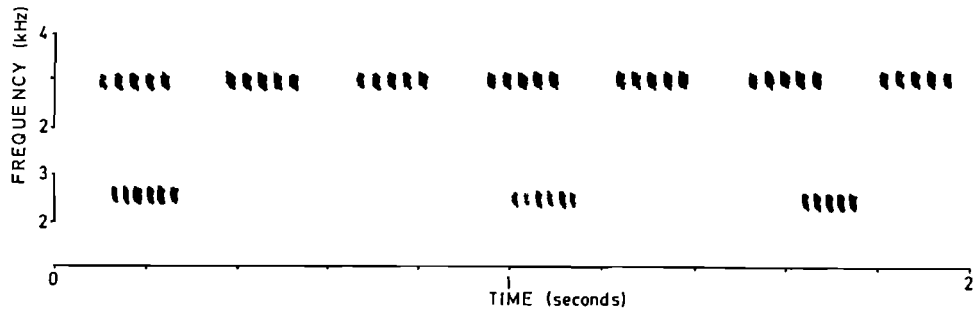
Of all the changes in songs which are correlated with changes in temperature, by far the most conspicuous, and the easiest to monitor, are changes in chirp rate. In some species this phenomenon is so distinct that it can be used to calculate air temperature reasonably accurately. Although it has been incorrectly suggested that almost any cricket can be used to calculate temperature with one formula (e.g. Skaife 1953), most crickets have unique songs and are totally unsuitable as 'thermometer' crickets for a variety of reasons. Since most crickets sing with a pulse rate (= wing closure rate) that is too fast to count without instruments, a good thermometer cricket would need to have its song broken into chirps. The chirp rate should be regular, slow enough to count, and loud enough to hear clearly. Ideally, the cricket should have a large surface area to volume ratio, so that its body temperature quickly adjusts to changes in air temperature. The more pronounced the change in chirp rate with temperature, the more accurate the estimates will be. Finally, the animal should sing from an elevated position, such as a tree, shrub or grass, and not from a concealed place, such as a burrow or crack, so that it is quickly exposed to changes in air temperature. Few crickets possess all of these characteristics, apart from the chirping members of the genus *Oecanthus*, generally known as tree crickets.

Several studies have been made on the relationship between temperature and chirp rate of the American snowy tree cricket *Oecanthus fultoni* (e.g. Brooks 1882; Dolbear 1897; Block 1966; Walker 1969). Although the calls of most southern African species have now been described (Toms & Otte 1988), and *O. karschi*, incorrectly referred to as *O. burmeisteri*, is known for its baffle-making behaviour (Prozesky-Schulze, Prozesky, Anderson, and van der Merwe 1975; Bennet-Clark 1989) few data on chirp rates have been published for any African species of the genus *Oecanthus*.

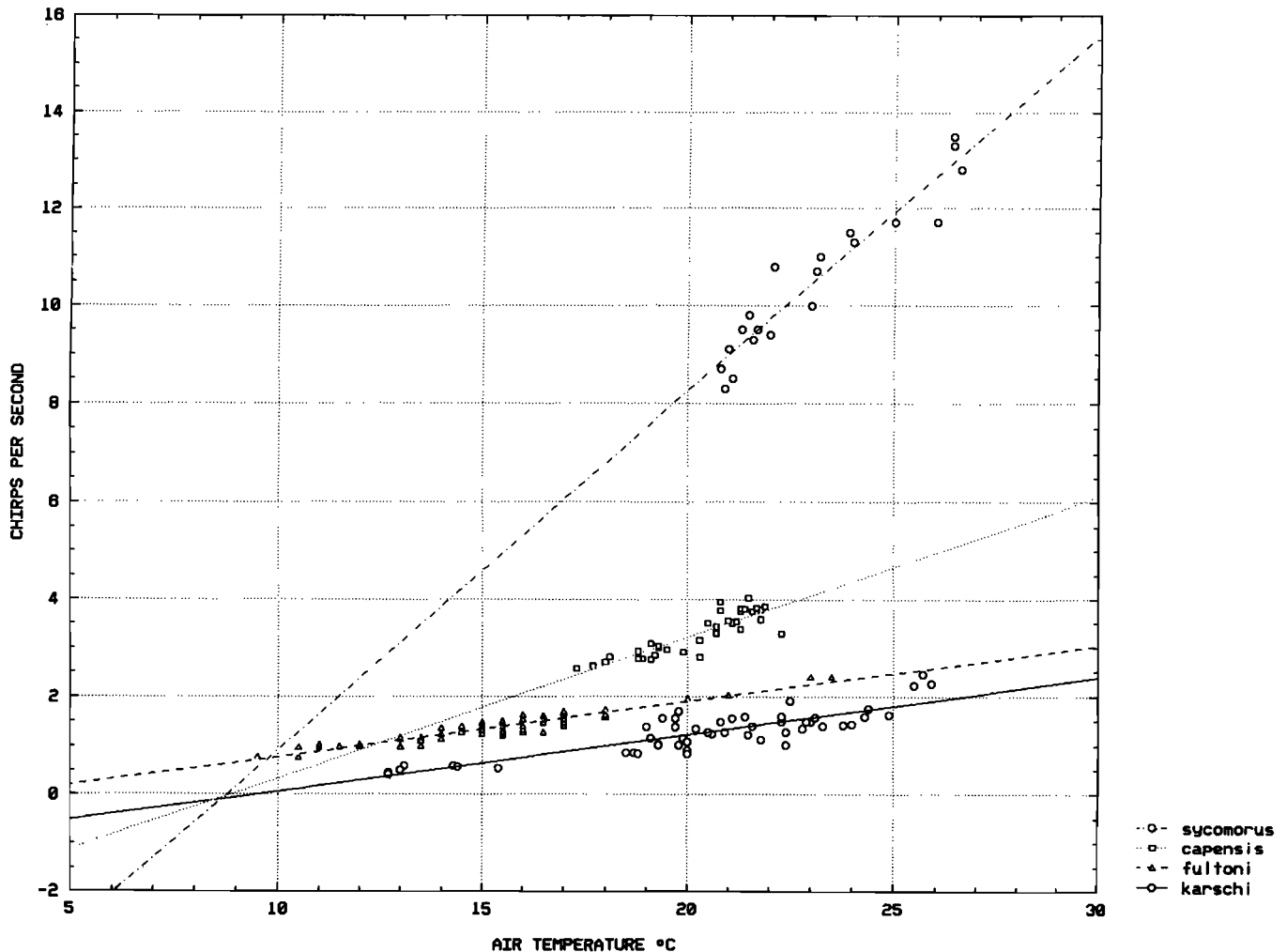
Most male crickets are capable of producing sounds by rubbing their modified forewings (tegmina) together. During stridulation a scraper on one wing comes into contact with a file on the other. Two factors affect the frequency of the song, the rate at which the scraper makes contact with the file teeth, and the physical attributes of the resonating membrane (Sismondo 1979). File tooth impact rate depends on the distance between successive teeth and tegminal closure rate. In tree crickets, tooth impact rate is more important than the characteristics of the vibrating membrane in frequency determination, so frequency also changes with temperature. Each tooth impact causes one vibration of the tegminal membranes, so the frequency of the sound in Hz is directly related to the tooth impact rate. One sound pulse is produced during each tegminal closure, while one chirp consists of a group of pulses produced at more or less regular intervals (Figure 1; Toms 1984; Bennet-Clark 1989).

### Methods

Data collected at several localities and various ambient temperatures (Toms 1988; Toms & Otte 1988) were used to compare changes in chirp rates of African Oecanthidae with published data for *Oecanthus fultoni*. In the species which call slowly enough for chirp rate to be counted without special techniques (*capensis* and *karschi*), tape recordings of each individual were analysed by timing the duration of 10 or more chirps and interchirps with a stopwatch and then



**Figure 1** Audiospectrograms showing the constant chirp rate of the song of *Oecanthus capensis* at 21,8°C and the variable chirp rate of *O. karschi* at 22,4°C. The song of *O. sycomorus* has been published elsewhere (Toms & Otte 1988).



**Figure 2** Change in chirp rate with temperature in *Oecanthus capensis*, *O. fultoni*, *O. karschi* and *O. sycomorus*, with extrapolations to show how the regression lines of the African species converge where  $Y = 0$  on the  $X$ -intercept. Data obtained from audiospectrographs were used for *O. capensis* and *O. sycomorus*, while the data for the other species were obtained with a stopwatch (see Table 1).

calculating the chirp rate. These results were compared with chirp rates obtained by measurement, using dial callipers, of the duration of a single chirp and inter-chirp period (10 chirps were measured and averaged in *O. sycomorus*), from an audiospectrogram produced with a Kay 7029A spectrum analyser. Special care was exercised in the collection of ambient-temperature data after each recording, at or as near to the calling site as possible, but always < 2 m from the calling site. A  $50^{\circ}\text{C} \pm 0,1^{\circ}\text{C}$  thermometer was exposed to

the air at least 1 min before any temperatures were recorded. Least-squares linear regression equations were calculated with a microcomputer.

## Results

As is the case with *O. fultoni*, the relationship between chirp rate and temperature of all three African species appears to be linear (Figure 2, Table 1).

The regression lines for *O. karschi* and *O. fultoni* are almost parallel but the slope of the regression line for *O. capensis* is greater. In *O. sycomorus*, the rate of change of chirp rate is even more pronounced than in *O. capensis* (Figure 2, Table 1).

## Discussion

The songs of three chirping African Oecanthidae change significantly with temperature in a predictable way. The chirp rates of *O. karschi* and *O. capensis* are slow enough to count in the field, so they can be used to identify the species concerned. If the chirp rate is greater than three chirps per second, it is probably *capensis*. Below 20°C a chirp rate exceeding two chirps per second is probably produced by *capensis*. It is also possible to estimate temperature from the chirp rates of these species, in a similar way to *O. fultoni* (Table 2). Although the chirp rate of *O. sycomorus* changes rapidly with temperature, it sings at a rate which is too fast to count without the use of instruments.

Walker (1975) showed that a linear relationship generally provided more accurate predictions than an exponential one, and that the extrapolated regression lines of most species tended to converge where  $Y = 0$  on the X-intercept. The chirp rates of the species in this study converge at about 9°C, providing further evidence for this phenomenon. In contrast, the X-intercept for *fultoni* and *rileyi*, another American chirping species, is about 4°C (Walker 1962b). The fact that the regression lines for African and American species converge at different temperatures, suggests that there may be a basic physiological difference between African and American chirping *Oecanthus*. The African species studied here would not be capable of singing at temperatures

**Table 1** Regression equations of chirp rate plotted against temperature for *Oecanthus fultoni*, *O. capensis*, *O. karschi* and *O. sycomorus*

Species	Method	Regression equation	$r^2$	$n$
<i>fultoni</i>	stopwatch	$y \text{ chirps} / \text{min} = -21,9 + 6,81x$	0,91	77
<i>fultoni</i>	stopwatch	$y \text{ chirps} / s = -0,36 + 0,11x$		
<i>capensis</i>	stopwatch	$y \text{ chirps} / s = -1,95 + 0,26x$	0,72	32
<i>capensis</i>	spectrograph	$y \text{ chirps} / s = -2,57 + 0,29x$	0,78	35
<i>karschi</i>	stopwatch	$y \text{ chirps} / s = -1,10 + 0,12x$	0,73	51
<i>karschi</i>	spectrograph	$y \text{ chirps} / s = -1,13 + 0,12x$	0,54	48
<i>sycomorus</i>	spectrograph	$y \text{ chirps} / s = -6,44 + 0,74x$	0,90	21

**Table 2** Simplified regression equations for the calculation of temperature from chirp rate. The first equation for *O. fultoni* was published by Walker (1962a)

Species	Regression equation
<i>fultoni</i>	$x^\circ\text{F} = \text{No. chirps in } 13 \text{ s} + 40$
<i>fultoni</i>	$x^\circ\text{C} = \text{No. chirps in } 8 \text{ s} + 4$
<i>capensis</i>	$x^\circ\text{C} = \text{No. chirps in } 3 \text{ s} + 11$
<i>karschi</i>	$x^\circ\text{C} = \text{No. chirps in } 6 \text{ s} + 12$

**Table 3** Differences between predicted and actual temperatures using the formulae in Table 2

Species	Range °C	Standard deviation	Standard error	$n$
<i>fultoni</i>	-1,2 to 2,4	0,79	0,09	77
<i>capensis</i>	-2,0 to 1,4	0,68	0,11	35
<i>karschi</i>	-2,4 to 4,4	1,75	0,24	51

below about 10°C, while this may be possible for some American species and *O. fultoni* has been tape recorded below 10°C (Figure 2). The fact that *O. capensis* has not been tape recorded below 17°C, or above 23°C, is probably due to limited sampling. How and why different species should have different rates of change and why their rates should converge at the X-intercept is not known. It is interesting to note that the regression lines for *O. fultoni* and *O. karschi* are almost parallel, which suggests that something about the mechanism of changes in metabolic rates with temperature is similar in these two species.

In *O. capensis*, the  $r^2$  value is higher when chirp rates were calculated from audiospectrograms than with a stopwatch, while the opposite is true for *O. karschi* (Table 1). The measurement of a single chirp in *O. karschi* is not accurate because the chirp rate is not always constant (Figure 1). In contrast, the chirp rate of *O. capensis* is constant, but rates calculated with a stopwatch depend on the response time of the operator. Higher chirp rates of *O. capensis* (four or more chirps per second above 20°C), are also more difficult to count. It is interesting to note that the  $r^2$  value for *O. fultoni* is higher than those of *O. capensis* and *O. karschi* (Table 1). Differences in correlation coefficients can arise from differences in sample size, sample range, sampling bias and other factors. Some of the difference in correlation coefficients may also have arisen as an effect of the method of measurement. Data for *O. fultoni* were collected specifically for analysis of effects of temperature, while the data used here were collected primarily for taxonomic purposes. When Block collected his data the chirp rate was counted for 1 min in the field. Any breaks in the song would have made it necessary to start again. Tape recordings collected for taxonomic purposes may have several breaks, since only 2 s of singing are generally needed for a spectrograph. The fact that the chirp rate of *O. capensis* changes faster with temperature than that of *O. fultoni* or *O. karschi* means that it is a better thermometer cricket in certain respects. Calculation of temperature from chirp rate is accurate within the limits of  $\pm 2^\circ\text{C}$  for *O. capensis*, while in *O. karschi* this drops to  $\pm 4^\circ\text{C}$  (Table 3). This also means that two *O. karschi* males at the same locality, and the same temperature, could produce songs with different chirp rates. Convergence of regression lines at the X-intercept makes it possible to make relatively reliable predictions about variation in songs even if only one tape recording is available. However, the X-intercepts for crickets of different faunas may be different, so predictions of this nature will be more reliable for new members of a fairly well-known fauna than for completely unknown groups.

### Problems with mate recognition

Signals which change with temperature pose special problems for the receiver. A wide band receiver, capable of receiving the entire range of variation in signals, would also be capable of receiving excessive noise, including sounds produced by other species. For example, *O. capensis* and *O. karschi* both call at about 2,2 chirps per second, but at different temperatures (Figure 2). When additional data for *O. capensis* are available, I suspect that it will be found that they can continue to sing at temperatures down to at least 13°C, at rates at least as low as one chirp per second. This would mean that chirp rates between 1 and 2,2 could be produced by either species. With regard to pulse rates, a similar problem exists. *O. capensis* and *O. karschi* call at similar pulse rates and have similar ranges of pulse rates with some overlap in the available sample (Toms & Otte 1988: Figure 20). In trilling species *O. neosimilis*, *O. rufopictus* and *O. galpini* are all capable of singing at 30 pulses per second at different temperatures (Toms & Otte 1988: Figure 26a).

Although the extent to which cricket songs change with temperature can be considerable, Walker (1957) showed that the female response may also be affected by temperature. In other words, the female auditory system may only be capable of perceiving a limited range of the possible variation in male songs as appropriate signals at any given temperature. The fact that the regression lines of different species of crickets converge at the X-intercept means that the possibility for confusion may increase at low temperatures in certain species. In *Drosophila* almost no hybridization occurs between *Drosophila pseudoobscura* and *D. persimilis* at 24,5°C but at 16,5°C heterogametic and homogametic matings occur at almost the same frequency, when *D. persimilis* males are used (Mayr & Dobzhansky 1945). Temperature dependent changes in receptivity could occur as a result of different rates of change in metabolic rates of different species, and the convergence of regression lines at low temperatures. In order to understand these changes, it would be necessary to understand how changes in temperature affect emitters and receivers. Although little is known of the mechanisms of thermal variation in metabolic rates affecting transmitters, even less is known about thermal variation in receivers.

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