

Energetics of Singing in Crickets: Effect of Temperature in Three Trilling Species (Orthoptera: Gryllidae)

Kenneth N. Prestwich¹ and Thomas J. Walker²

Department of Zoology¹ and Department of Entomology and Nematology², University of Florida, Gainesville, Florida 32611, USA

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Summary. 1. Oxygen consumptions of resting and trilling crickets were measured at various temperatures. Oscillograms taken at comparable temperatures were used to identify the major factors determining the cost of stridulation.

2. Species used were *Anurogryllus arboreus* (mass ≈ 0.4 g), wing stroke rate at 23 °C of 71 strokes per s; and *Oecanthus celerinictus* and *O. quadripunctatus*, two sibling species, (masses ≈ 0.06 g), wing stroke rates at 23 °C of 57 and 38 strokes per s respectively.

3. At 23 °C the three species have similar total mass-specific metabolism during singing ($\dot{V}_{O_2} \approx 3,710 \mu\text{l} \cdot (\text{g} \cdot \text{h})^{-1}$; Table 3) even though their wing stroke rates are different.

4. *A. arboreus* has no change in net singing metabolism with increasing T_a ; however, cost per wing stroke decreases slightly. The *Oecanthus* both increase their net singing costs with increased T_a and the cost per wing stroke remains roughly constant. *O. quadripunctatus* has a cost per wing stroke about 1.6 times *O. celerinictus* (Tables 1, 3; Fig. 10). *A. arboreus* does not elevate its thoracic temperature significantly while stridulating and it is doubtful that tree crickets thermoregulate due to their small size.

5. The cost of singing in *A. arboreus* varies from 10 to 16 times resting; in *Oecanthus*, from 6 to 12 times resting (Table 3).

6. Although the two tree cricket species have different wing stroke rates at any common temperature, the number of file teeth struck per s is almost the same; *A. arboreus* strikes nearly twice as many teeth per s as do either of the tree crickets (Fig. 9).

7. The two factors that explain most of the variation in net cost of trilling are the wing stroke rate (Fig. 10) and the number of teeth struck $(\text{wing stroke})^{-1}$. Related factors that merit study are inter-

specific differences in file tooth depth and angle, wing mass, and wing velocity.

8. For three species of crickets and two species of katydids the average net cost of trilling is about $1.5 \times 10^{-5} \text{ ml O}_2 \cdot (\text{g} \cdot \text{wing stroke})^{-1}$ (Fig. 10).

9. Chirping should be energetically less expensive than trilling, with costs equivalent to the average cost per wing stroke times the total number of wing strokes per time. The latter factor is 10–95% lower in chirping species than in trillers.

10. An estimated daily respiratory energy budget shows calling taking about 56% of the daily respiratory budget of *O. celerinictus* and 26% for *A. arboreus* (Table 4).

Introduction

Crickets and katydids produce song by rubbing specialized areas on the forewings together. This tegminal movement, termed stridulation, results in both the familiar auditory signals of these animals and also in substrate vibrations, both of which can be important in attracting a mate (Bell 1980). The only previous measurements of the energetics of this vital activity have been on katydids by Heath and Josephson (1970) and Stevens and Josephson (1977). These katydids maintain a high thoracic temperature that probably helps them stridulate at extremely high wing stroke rates. Most crickets are probably too small to permit elevated thoracic temperatures during stridulation. In addition, and perhaps related to this fact, they tend to have lower wing stroke rates than the katydids previously studied. We selected three species of crickets to use in a study of the metabolic costs of stridulation at different ambient and body temperatures. To allow us to partition the various determi-

Abbreviations: CF carrier frequency; TBM total body mass; WS wing stroke; WSR wing stroke rate

nants of these costs at different temperatures, we analyzed their songs.

Crickets stridulate in the following manner: First the tegmina are raised at an angle to the body, the particular angle greatly influencing both the directionality and form of the song (Huber 1964). Next, the tegmina are rapidly opened and closed against each other; during the closing stroke the scraper (plectum) of the left tegmen is rubbed against the file (pars stridens) of the right tegmen. (In katydids the closing stroke involves the contact of the right scraper and the left file (Dumortier 1964)). Because of the arrangement of the teeth, the steeper edges of both the scraper and file strike each other (Fig. 1a). Each tooth catches the scraper and considerable force must be applied before the scraper skips onto the next tooth. In this manner, some of the kinetic energy of the tegmina is transferred to the cells via the file and scraper, causing the cells of both tegmina to vibrate. The frequency with which the cells vibrate determines the pitch or carrier frequency (CF) of the song. At the end of the wing closure these oscillations quickly die out and a silent period ensues while the tegmina are being opened. Normally, the file and scraper do not contact each other during wing opening, but if they do, teeth and plectum cannot gather each other as strongly because the teeth are set at shallow angles in this direction (Bennet-Clark 1970). Thus, the overall intensity of sound produced per wing closure is a function of the friction between the file and scraper and the efficiency of the transfer of this energy to the wing cells and to the air.

A complete cycle of tegminal movement, a wing stroke (WS), consists of a silent opening phase followed by a sound-producing closing phase. Wing stroke rates (WSR) are characteristic in each species for a given temperature and vary from a few to several hundred per s. If many wing strokes occur without a stop, the song produced is termed a trill; if a few wing strokes are followed by a pause and then more wing strokes, etc., the calling pattern is referred to as chirping (Walker 1962).

For this study, we selected three species that reliably produce trilling calls for at least one-half hour each night. The first, *Anurogryllus arboreus*, the short-tailed cricket, has been extensively studied as to its life history and song (West and Alexander 1963; Walker 1973, 1980; Paul and Walker 1979). In north Florida, males call nightly for about 45 min at sundown, producing a trill with a CF of 5 to 5.5 kHz and a WSR of about 71 oscillations-s⁻¹ at a T_a of 23 °C. Their mass varies from 0.3 to 0.5 g.

The other two are sibling species of tree crickets: *Oecanthus celerinictus* and *O. quadripunctatus*. Morphologically and ecologically the two are extremely

similar and are nearly impossible for the untrained worker to distinguish. The males of both species are quite small compared to *A. arboreus*, having an average mass of between 0.05 and 0.06 g with essentially no differences in wing and body dimensions. Their CF's are nearly identical (about 3.5 kHz), but they are readily distinguishable on the basis of different WSR's: 57 in *O. celerinictus* at 23 °C as compared to 38 in *O. quadripunctatus*. This difference was the clue that led to their recognition as different species (Walker 1963). Males call for as long as 7 h, most frequently at night.

Materials and Methods

Animals

Crickets were collected in Alachua County, Florida, and housed in small jars provided with either dirt for burrowing (*A. arboreus*) or screens and vegetation for perching (*Oecanthus*). They were maintained on a diet of sweet potato and apple and kept on a dark:light cycle appropriate to the season but shifted by 1 to 2 h to facilitate data collection.

Temperature Measurements

Thoracic temperatures of *A. arboreus* were measured in the field on two evenings using a hypodermic probe with a Veco #32A130 thermistor (Heath and Adams, 1969) in conjunction with a calibrated Yellow Spring Instrument Co. Telethermometer Model 43TD. Crickets were located as they sang from tree trunks. Temperature measurement was made by quick insertion of the hypodermic probe into the thorax; it was not necessary to touch the animals except with the probe. Ambient temperatures were recorded at each perch site using the same probe after cleaning it.

Measurements of Oxygen Consumption

Measurements of oxygen consumption (\dot{V}_{O_2}) were made manometrically using Gilson Differential Respirometers. Soda lime was used as a CO₂ absorbant. Animals were placed in 50 ml flasks on the afternoon of the day during which measurements were planned. A small amount of sterile soil was provided for *A. arboreus* and some crumpled paper for *Oecanthus*. The flasks were attached to the respirometer with the waterbath set several degrees above the planned temperature for the experiments. Near the accustomed sundown time the temperature was dropped to the planned value and the lights were turned off. This combination of changes encouraged individuals to begin stridulation. Crickets would then sing over a period of several hours, although not usually the same individuals. Cost of singing was obtained by measuring \dot{V}_{O_2} as a function of time of singing. Individual crickets had very repeatable \dot{V}_{O_2} values per song length. Tree crickets occasionally showed signs of burst release of CO₂, resulting in more variation in these species.

Measurements of resting metabolism were made in a similar manner on animals treated like those used for calling experiments. Resting metabolism (not standard metabolism) was measured in that the animals were well-fed prior to their use in both this and calling experiments. Resting metabolism was defined as that metabolism consistently observed on quiescent animals. Many observations were taken on each animal at each temperature; runs at each temperature lasted at least 3 h.

A blank was used during all measurements, both active and

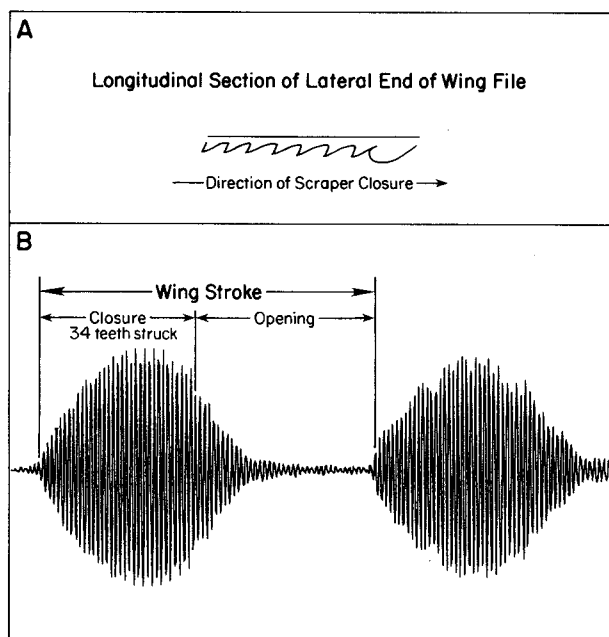


Fig. 1. **A** A side view of the stridulatory file showing the difference in the pitch of the teeth in the direction of tegminal closure as compared to opening. **B** Oscillogram of *O. celerinictus*. The wing stroke is defined as the time between two sound pulses. Wing closure is defined acoustically, starting at the beginning of sound production and ending when the sound pulse begins to decay. Wing opening comprises the remainder of the wing stroke. The number of teeth struck is equal to the number of fundamental oscillations during the closing phase

resting. Corrections were seldom necessary. All \dot{V}_{O_2} measurements were converted to STPD.

Measurements of Carbon Dioxide Production

Carbon dioxide production (\dot{V}_{CO_2}) was estimated simultaneously with \dot{V}_{O_2} on *A. arboreus* using 10 ml Scholander gas analyzers. The crickets were sealed together, 5 to a 100 ml container. Two air bags were attached to each flask, giving a total air capacity of about 250 ml. Initial samples were drawn and analyzed; then after the animals called 0.5 to 1.0 h, the air was mixed using the air bags, and 3 replicate samples were withdrawn and analyzed. From this data, a respiratory quotient (RQ) was calculated and used to obtain the energy equivalence of the \dot{V}_{O_2} measurements made on the respirometer.

Analysis of Song

Songs were recorded on professional-quality, reel-to-reel tape recorders at 38.1 cm/s. Recordings were made both in the field and the lab; those free of reverberations and high background noise levels were oscillographically analysed with a Honeywell Visicorder or a Nicolet Scientific Model 444A Computing Spectrum Analyzer in conjunction with a Tectronix 4662 Interactive Plotter.

The following procedures were used in interpreting the oscillograms (see Fig. 1B):

Wing Stroke Rate (WSR). The reciprocal of the time necessary for a complete cycle of opening and closing the tegmina, i.e., of the time from the onset of one pulse to the onset of the next.

Carrier Frequency (CF). The number of fundamental oscillations produced during a wing closure divided by the period of time over which they were produced.

Time Spent Closing Wings. According to Sismondo (1979) both the termination of a wing closure and missing of teeth by the scraper result in either a change in carrier frequency or a decrease in amplitude, or both. We used both criteria, especially the latter, to establish the end of a wing closure. The beginning of the production of sound was taken as the start of wing closure and the beginning of the major decay in amplitude was taken as the end of wing closure (Fig. 1b). The wing may have actually continued in the closing movement or may have begun closure before the first sound (Sismondo 1979), but if it did, the file and scraper were not making contact. Thus we define wing closure only in terms of the time when energy is being used to generate tegminal oscillations.

Time Spent Opening Wings. The difference between the time for a total wing stroke and wing closing time.

Number of Teeth Struck per Closure. Koch (1980), Sismondo (1979), Nocke (1971), and Huber (1964) have all indicated that for the species they studied (*Gryllus bimaculatus*, *Oecanthus nigricornis*, *G. campestris*), tooth impact rate = carrier frequency. Thus, the number of cycles during the wing closure equaled the number of teeth struck.

Number of Teeth Struck per Second. The product of the WSR and the number of teeth struck per wing closure.

All of the above measurements were made on 5 or more complete wing strokes per recording of an individual at a given T_a ; the averages obtained from these measurements for each recording were then used in calculating least squares regressions. An effort was made to analyze the most repetitious portion of each tape.

Statistics

Regression lines were calculated using the method of least squares. Coefficients of determination (r^2) were calculated for each regression line; these indicate the degree that variation in the dependent variable is explained by changes in the independent variable. Differences between the slopes of regression lines were sometimes tested for homogeneity of regression. Regression lines having indistinguishable slopes based on homogeneity of regression tests were tested for difference in elevation using analysis of covariance. For all statistical tests, the 0.05 level was considered as the critical value for rejecting a null hypothesis. Error terms are given as standard errors. N signifies the number of individuals used, n the total number of observations.

Results

Temperature

Field measurements of thoracic temperature in *A. arboreus* revealed no evidence of significant heating during calling. Thoracic temperatures (T_{th}) of crickets singing at 20.5 °C ($N=5$) and 23.2 °C ($N=6$) were no more than 2 °C above ambient; most were less than 1 °C above ambient (mean $T_{th}=21.3 \pm 0.3$ °C at $T_a=20.5$ °C; 23.9 ± 0.4 °C at $T_a=23.2$ °C). Calling time should not have been a factor in the measurements since all had been singing for several minutes

Table 1. Metabolic cost of trilling song in 3 species of crickets. V_{O_2} = oxygen consumption in $\mu\text{l O}_2 \cdot \text{g}^{-1}$ STPD. t = singing time in s

Species	T_a (°C)	Regression equation	Number of observations	r^2	Average mass (g)	Number of individuals
<i>A. arboreus</i>	20	$V_{O_2} = 1.034 t - 1.8$	17	0.97	0.317	3
	22	$V_{O_2} = 1.115 t - 2.2$	94	0.87	0.405	14
	24	$V_{O_2} = 1.082 t - 3.8$	75	0.95	0.392	12
	26	$V_{O_2} = 1.010 t + 12.4$	76	0.92	0.408	9
<i>O. celerinictus</i>	16	$V_{O_2} = 0.6382 t - 8.3$	50	0.91	0.058	4
	23	$V_{O_2} = 0.9365 t - 3.9$	51	0.88	0.063	5
	28	$V_{O_2} = 1.3244 t - 4.6$	36	0.91	0.055	5
<i>O. quadripunctatus</i>	23	$V_{O_2} = 1.0611 t - 2.4$	93	0.86	0.056	9
	28	$V_{O_2} = 1.4166 t - 10.7$	43	0.97	0.051	7

prior to measurement. These results are expected: *A. arboreus* neither warms up before calling nor does the quality or intensity of the call change appreciably. Also, unlike some species that at least passively heat during stridulation (such as the southern mole cricket, *Scapteriscus acletus*, Prestwich unpublished), *A. arboreus* does not possess an insulated thorax. Thus, while there is a small amount of heating occurring during stridulation in *A. arboreus*, it is less than 1 °C and we choose to ignore it.

We did not measure thoracic temperatures of the *Oecanthines*: they are extremely small with body masses of ca. 0.055 g and with the thorax less than half of this. Given this small size it is extremely unlikely that they maintain an elevated T_{th} , even at high work loads. Thus, it appears that all three species are true poikilotherms.

Measurements of Oxygen Consumption

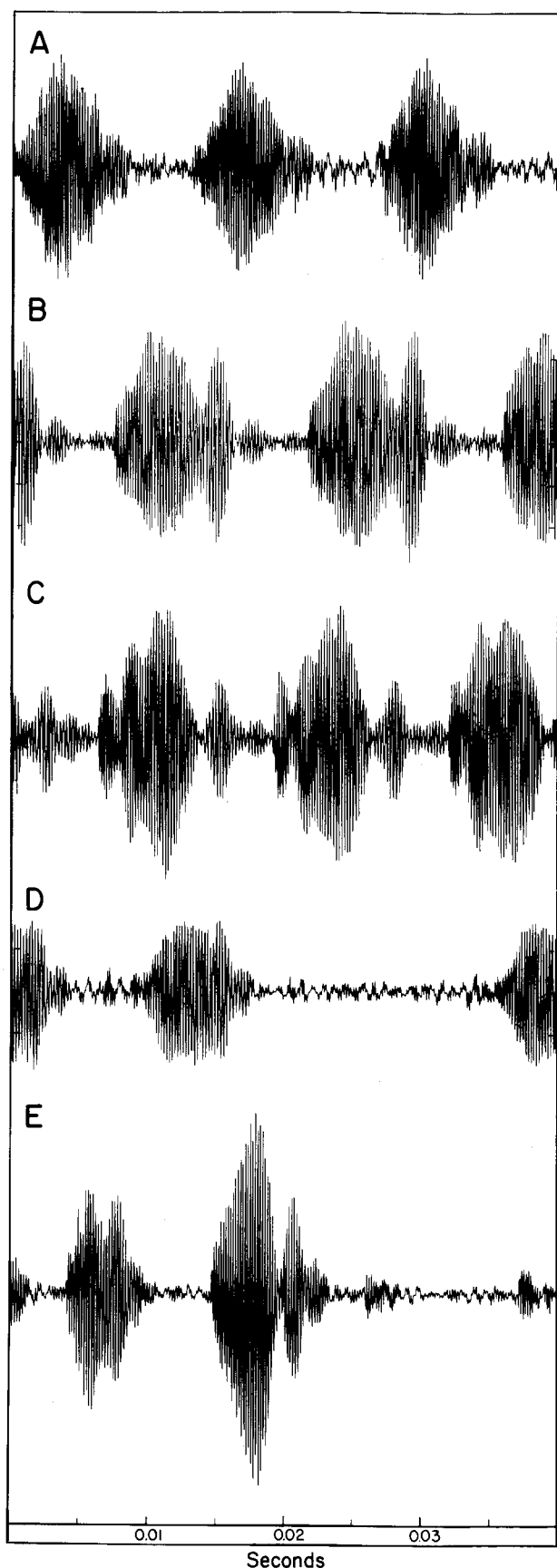
The results of measuring \dot{V}_{O_2} during trilling are in Table 1. Within the resolution of our respirometer, there was no evidence of any type of oxygen debt after singing: metabolic rates went from resting level to a much higher value with the initiation of stridulation and quickly fell to resting levels at the end of singing. Finally, there was no evidence of variation in the cost of singing as length of the song changed: measurements based on the first 30 s of calling were, within error, the same as those taken for an equal period later in the calling bout. Measurements of costs in tree crickets were complicated by their apparent tendency to release CO_2 in bursts. This was noted when a large increase in pressure occurred in the sealed flask during the course of a measurement. This increase usually disappeared in less than a minute and this disappearance is consistent with the idea that the gas was being absorbed by the soda lime in the respirometer. Measurement intervals in which this occurred tended to give lower V_{O_2} readings and

were followed by intervals with higher V_{O_2} readings than normal: this contributed to the variability of the *Oecanthus* data.

There are no statistically significant differences between either the slopes or elevations of the 4 regression lines for *A. arboreus*. Among the tree crickets, within each species the regression coefficients are significantly different from each other at each temperature. However, the regression coefficients for *O. celerinictus* and *O. quadripunctatus* at common temperatures of 23 and 28 °C do not differ significantly: the total oxygen consumption of these two species at common temperatures are unexpectedly similar. The total cost of singing for the three species on a mass-specific basis (assuming an interpolated coefficient of regression for *A. arboreus* at 23 °C of 1.096) are extremely close.

The Y-intercept term for each equation should be close to zero since an animal that is measured for zero seconds should have zero metabolism. The deviations from this are small, especially in light of the size the first term of the equation takes compared to the Y-intercept during typical singing times of 10^2 to 10^4 s.

The regressions in Table 1 have high r^2 values; this is in spite of considerable variation between individuals. For instance, at 24 °C for *A. arboreus* the coefficients of regression for individuals varied from 0.786 to 1.229 ($N=8$; mass range 0.272–0.476 g; r^2 range 0.87 to 1.0); most, of course, clustered near the overall regression coefficient of 1.082 (Table 1). This variation probably comes from two sources: (1) variation in body mass due to feeding and defecation: an animal's weight often fluctuated by $\pm 10\%$; (2) variation in the total force with which the file and scraper were rubbed together. Examination of oscillograms of *A. arboreus* shows some individuals commonly miss rubbing their tegmina together (silent wing closures), make tegminal contact during opening phases, and may even vary the force of contact between file and scraper (Fig. 2). These departures from 'ideal' sound production appear to be behavioral and



not related to morphological factors such as wear of the file. The same type of records is shown for *O. celerinictus* in Fig. 3; in general, calls in this species are much freer of the 'defects' seen in *A. arboreus* where approximately 70% of the oscillograms we examined are as imperfect as those depicted in Fig. 2.

Table 1 estimates the *total* metabolism of singing crickets. To estimate the net oxygen consumption in singing, the resting metabolism must be subtracted from the total metabolism. We assumed that resting metabolism reflects maintenance costs and that these costs remain constant during activity except for systems directly involved in the activity. We have no proof that this is the case but it seems reasonable. Table 2 presents the measured resting rates of oxygen consumption as a function of temperature in these crickets. We measured resting – not standard – metabolism since the latter implies animals acclimated to constant temperature regimes and in a post-absorptive (starved) state (Hemmingsen 1960). Had we measured standard rates, the values would undoubtedly be lower, but we were interested in the rates of resting crickets physiologically as identical to those used in the calling experiments as possible. Since feeding may affect the likelihood of calling, we fed the crickets. The rates for *A. arboreus* are lower than those for the two *Oecanthus*, as expected, given that metabolism scales allometrically to body size at a slope less than zero for mass-specific interspecific comparisons (Hemmingsen 1960). The sibling *Oecanthus* have essentially identical metabolic functions with temperature; this is as expected due to their relationship, size, and ecological similarities. All three functions are typical for poikilotherms and have Q_{10} values of between 2 and 3.2 in the normal temperature range to which the species is exposed.

Calculations of net cost of singing are shown in Table 3. The values for metabolic rates were calculated as follows: column 1, total V_{O_2} during singing for a 1 h period ($t=3,600$ s) was calculated from each regression equation in Table 1. Resting values in column 2 were obtained by using Q_{10} values calculated

Fig. 2 A–E. Oscillograms for *A. arboreus* at a series of temperatures. B–E are from one individual and illustrate the typical imprecision of tegmental contact in this species. A Teeth are struck only during the wing closure, waveform variations in the silent period are due to noise in the background ($T_a=24.5$ °C). B, C The presence of tooth strikes during wing opening is indicated by small pulses. Changes in pulse shape probably indicate variation in the force with which the file and scraper are rubbed against each other ($T_a=22$ °C and 24 °C). D Missed contact between file and scraper. Regular repetition of this pattern produces a sputtery call ($T_a=22.7$ °C). E Variation in pressure during both opening and closing portions of the wing stroke producing different sized sound pulses and a complete miss ($T_a=33.6$ °C)

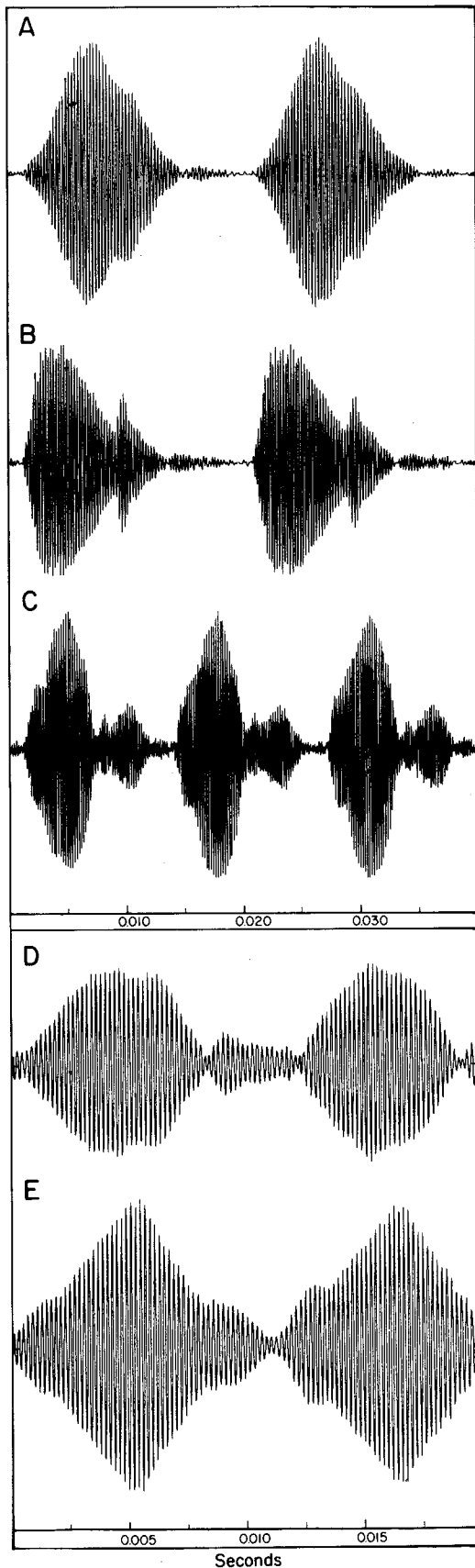


Table 2. Resting rates of oxygen consumption in 3 species of crickets. \dot{V}_{O_2} = rate of oxygen consumption, $\mu\text{l O}_2 \cdot (\text{g} \cdot \text{h})^{-1}$ STPD. Values in parentheses are the \pm standard error (SE) and number of animals used (N), respectively

T_a (°C)	\dot{V}_{O_2}		
	<i>A. arboreus</i>	<i>O. celerinictus</i>	<i>O. quadripunctatus</i>
	$0.377 \pm 0.20, 8^a$	$0.053 \pm 0.01, 12$	$0.049 \pm 0.01, 12$
10	64 ($\pm 9.2, 8$)	89 ($\pm 6.4, 12$)	103 ($\pm 3.3, 12$)
15	197 ($\pm 12.0, 8$)	176 ($\pm 5.9, 12$)	222 ($\pm 8.3, 12$)
20	236 ($\pm 11.9, 8$)	311 ($\pm 10.5, 12$)	358 ($\pm 12.4, 12$)
25	378 ($\pm 15.3, 8$)	558 ($\pm 21.9, 12$)	586 ($\pm 11.5, 12$)
30	486 ($\pm 16.4, 8$)	932 ($\pm 35.4, 12$)	947 ($\pm 25.4, 12$)
35	—	1,669 ($\pm 42.8, 12$)	1,461 ($\pm 37.3, 12$)

^a Mean mass (g) \pm SE, N

for the appropriate 5 °C temperature interval (Table 2). (Calculation of resting cost for *A. arboreus* at 22 °C: $Q_{10} 20-25^\circ\text{C} = 2.57$, thus, \dot{V}_{O_2} at 22 °C = $289.4 \mu\text{l O}_2 \cdot (\text{g} \cdot \text{h})^{-1}$.)

The difference between columns 1 and 2 is the net cost or arithmetic metabolic scope for singing. The factorial metabolic scope is also calculated. The decrease in factorial scope values with increase in temperature is mainly due to a proportionately higher resting \dot{V}_{O_2} with an increase in T_a . The net cost, on the other hand, is either roughly constant as in the case of *A. arboreus* or increases with T_a as with the *Oecanthus*. Thus, even when resting metabolism is taken into account, the same trends that appear on Table 1 are still present. The factorial scopes for singing are intermediate to those observed for insects in other activities: for flight these values range from 50 to 400 times standard (not resting) rates (Weis-Fogh 1964); for activity in mole crickets (walking, digging) it is 4 to 6 times resting at 25 °C (Prestwich,

Fig. 3A-E. Variation in the oscillograms of *O. celerinictus* (18–34 °C). The oscillograms (except for A and D) are for songs of different individuals. Note the much greater precision of these sound pulses compared to *A. arboreus* (Fig. 2). **A** An example of a clean sound pulse. $T_a = 18^\circ\text{C}$. **B** Wing closure with a period of reduced pressure followed by increased pressure (second peak in each pulse), a slight amount of file and scraper contact occurs during the opening phase (small sound pulses after decay of second peak in main sound pulse). $T_a = 18^\circ\text{C}$. **C** An example of a sound pulse which is difficult to interpret due to the large secondary pulse. Closing probably occurs until the rapid decay of sound at the end of the major pulse, the smaller pulse is probably due to contact during the opening phase. Closure could not be continuing throughout the minor pulse since there are not enough teeth in the file for this to happen. $T_a = 23^\circ\text{C}$. **D** A long period of contact during the opening phase probably produced the small pulse. $T_a = 31^\circ\text{C}$. **E** An oscillogram for which it is difficult to discern when the wing closure ends. (This category of oscillogram was excluded in constructing Figs. 4–9). $T_a = 33.9^\circ\text{C}$

Table 3. Net metabolic rates ($\mu\text{O}_2 \cdot (\text{g} \cdot \text{h})^{-1}$) and metabolic scope during trilling. Metabolic rates can be converted from \dot{V}_{O_2} to Joules assuming $\text{RQ}=1.0$ (see text) with $1 \mu\text{l O}_2 \cong 2.197 \times 10^{-2} \text{ J}$

Species	T_a (°C)	Metabolic rates			Factorial aerobic scope (total ÷ rest)
		Total	Resting	Net	
<i>A. arboreus</i>	20	3,721	236	3,485	15.8 ×
	22	4,012	273	3,739	14.7 ×
	24	3,891	315	3,576	12.4 ×
	26	3,648	364	3,284	10.0 ×
<i>O. celerinictus</i>	16	2,289	191	2,098	12.0 ×
	23	3,368	437	2,931	7.7 ×
	28	4,763	761	4,002	6.25 ×
<i>O. quadripunctatus</i>	23	3,818	476	3,342	8.0 ×
	28	5,089	782	4,307	6.5 ×

unpubl.); about 2 times resting for walking and feeding in two species of katydids, and about 15 to 30 times resting during warm-up and stridulation in these same species (Stevens and Josephson 1977); and from 4.8 to 113 times resting in two species of beetle that are endothermic when they walk (Bartholomew and Casey 1977).

Energy equivalents of \dot{V}_{O_2} data were obtained by assuming an RQ of 1. This assumption was based on the result of the 5 determinations of ΔCO_2 and ΔO_2 using *A. arboreus*. Mean changes were $\Delta\text{CO}_2 = 0.0097 (\pm 0.0005)$ and $\Delta\text{O}_2 = 0.0095 (\pm 0.0012)$ for an

RQ of 1.02. These data are from 25 animals, only some of which sang. Thus, this is a rough estimate for singing and resting *A. arboreus* and could be refined. Given the much greater metabolic rate during calling, this RQ should be thought of as a calling RQ. It is supported by one isolated measurement on katydids (Stevens and Josephson 1977), but then crickets are not katydids. Nevertheless we assumed $\text{RQ}=1.0$ at both rest and activity in all species. Thus $1 \mu\text{l O}_2 = 2.1297 \times 10^{-2} \text{ J}$.

Characteristics of Stridulation

The three most important features of a trilling cricket's call are amplitude, WSR, and CF. The former must be above a female's threshold for hearing (Paul and Walker 1979; Forrest 1980) while the latter two should fall within a species-specific range of values (Huber 1964; Bentley and Hoy 1974). Fig. 4 shows the relationship between WSR and T_a . The *A. arboreus* WSR regression line is calculated only for the data points between 20 and 28 °C; field animals rarely if ever sing at temperatures outside this range. *A. arboreus* has the highest WSR: the *Oecanthus* differ from each other in both their WSR at any given temperature and in their response to changes in temperature. Considering the great importance of the WSR to males in obtaining females of the proper species (Walker 1957a, b) it is not surprising that

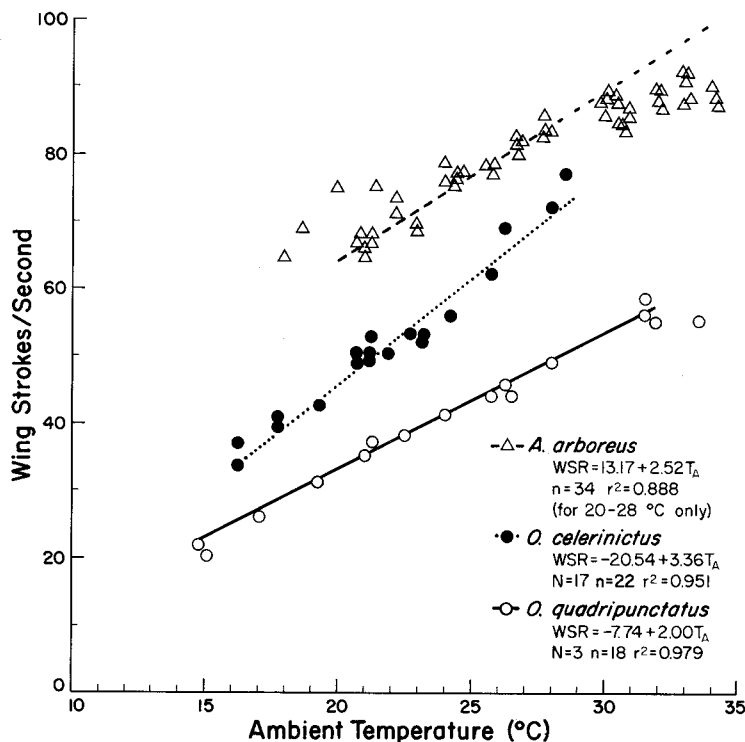


Fig. 4. Relationship between wing stroke rate and ambient temperature (T_a). For *A. arboreus*, the regression line is drawn only for the points from 20–28 °C; animals in the field do not sing outside of this range. (The regression line for all *A. arboreus* points is: $\text{WSR} = 34.90 + 1.67 T_a$, $n = 55$, $r^2 = 0.86$).

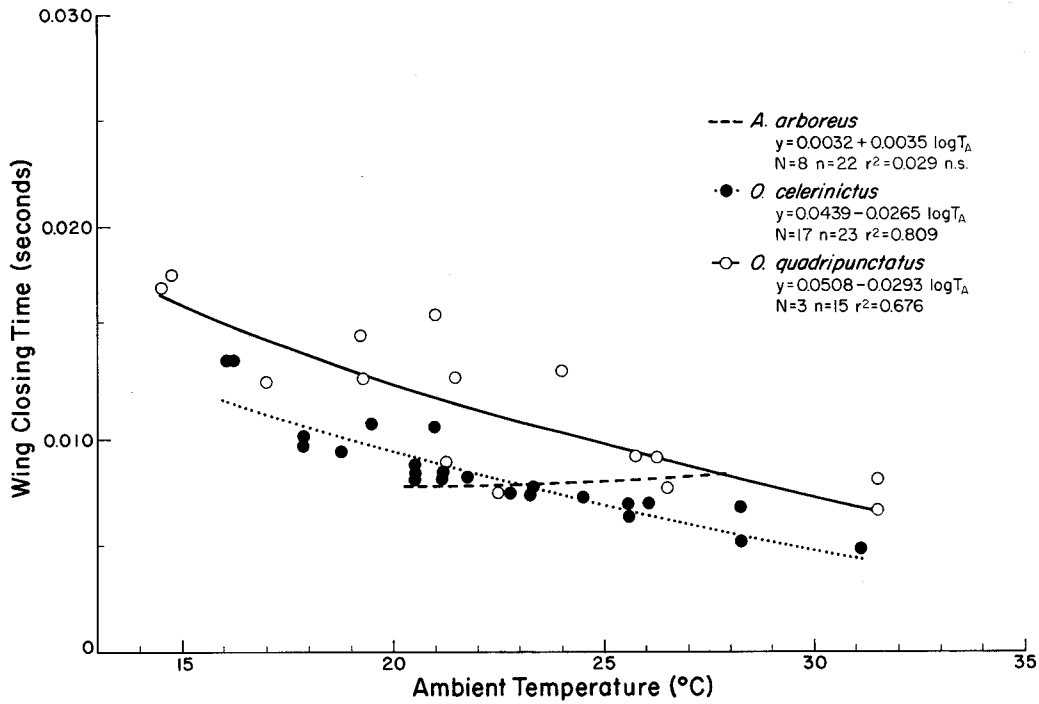


Fig. 5. Wing closing time during stridulation as a function of T_a . Data points for *A. arboreus* are not shown since their regression on T_a is not significant and they would obscure those for *Oecanthus*. *A. arboreus* line is based on closing times over the T_a range of 20 to 28 °C

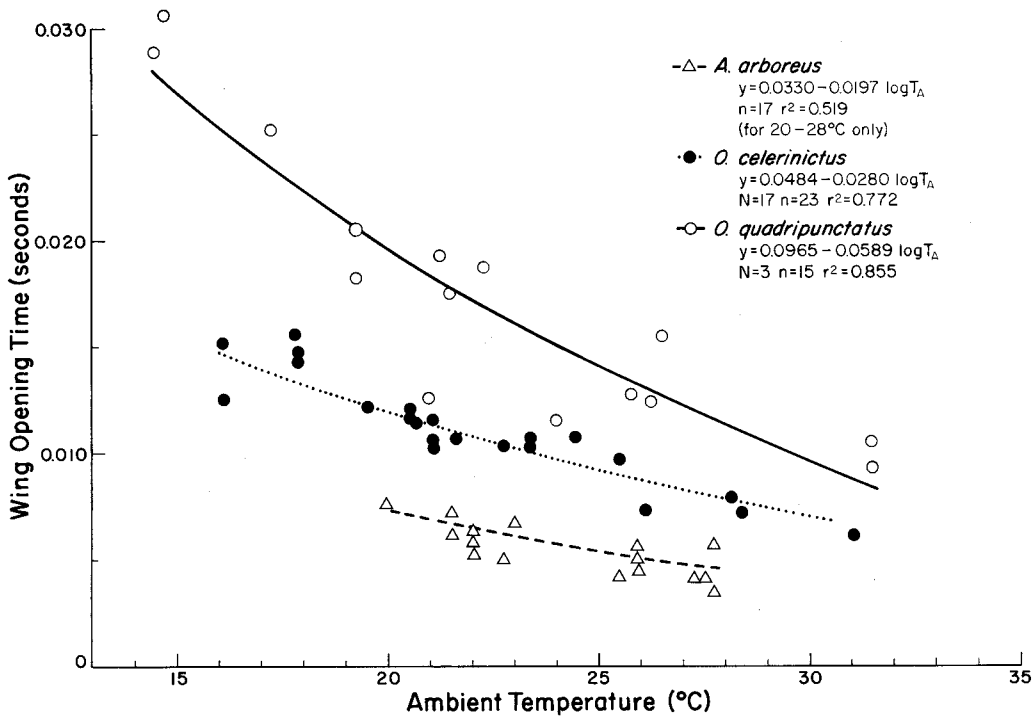


Fig. 6. Wing opening time during stridulation as a function of T_a . *A. arboreus* data points are from 20–28 °C

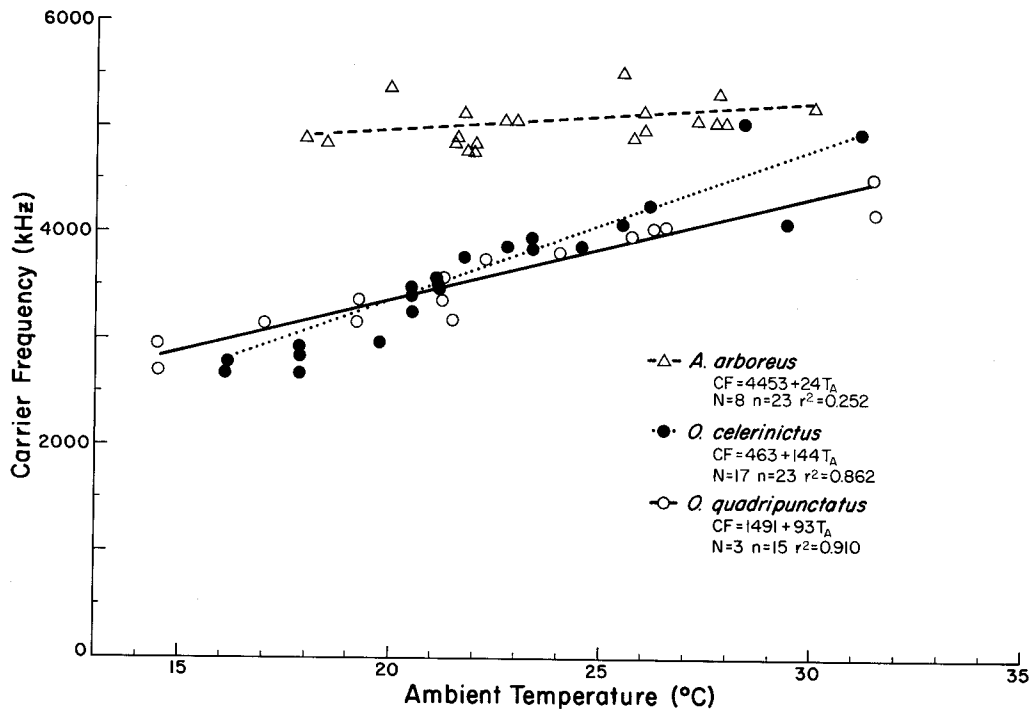


Fig. 7. The relationship between carrier frequency (pitch) of song and ambient temperature

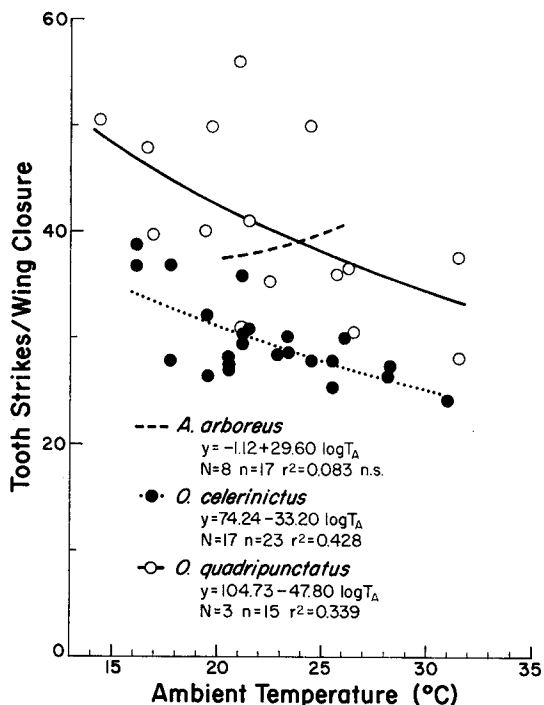


Fig. 8. The number of file teeth struck during wing closures at different ambient temperatures. The relationship for *A. arboreus* has a slope not significantly different from zero. In the tree crickets, both species strike less than their full file on each wing closure. The mean number of teeth per file and tooth densities are: *A. arboreus*, 72 teeth, 30/mm; *O. celerinictus* 41.1 teeth, 38.5/mm; and *O. quadripunctatus* 56.7 teeth, 38.7 mm (Walker 1963, 1973)

the coefficients of determination for these regression lines are extremely high. Any male stridulating at a different rate might either attract a female of the wrong species or none at all.

The patterns of tegminal opening and closing are different in all three species (Figs. 5, 6). Due to the variability in sound pulse shapes (Figs. 2 and 3) we had difficulty in determining accurately wing closure time (and therefore opening time) from oscillograms. Nevertheless, using Sismondo's (1979) interpretation of the oscillograms of the tree cricket *O. nigricornis* (a sibling species of the two tree crickets we used in this study) and using the most unambiguous pulse sequences we had, we obtained closing and opening times. One further caveat should be made: we had no data comparable to Sismondo's to help us analyze the song of *A. arboreus*, which is more variable than those of tree crickets (Figs. 2 and 3). Nonetheless, we used the same criteria for *A. arboreus* as for *Oecanthus*, since it seems logical that cessation of tooth impacts and thus power input to the wing cells results in a decaying signal as in *Oecanthus*.

To prevent their obscuring the data for *Oecanthus* we did not plot the points for *A. arboreus* in Fig. 5. Examination of the regressions shows that *A. arboreus* has a tegminal closing time that is very similar to *Oecanthus* and that it achieves its higher WSR through a much shorter opening time. *O. quadripunctatus*, as expected, has the slowest wing closures and

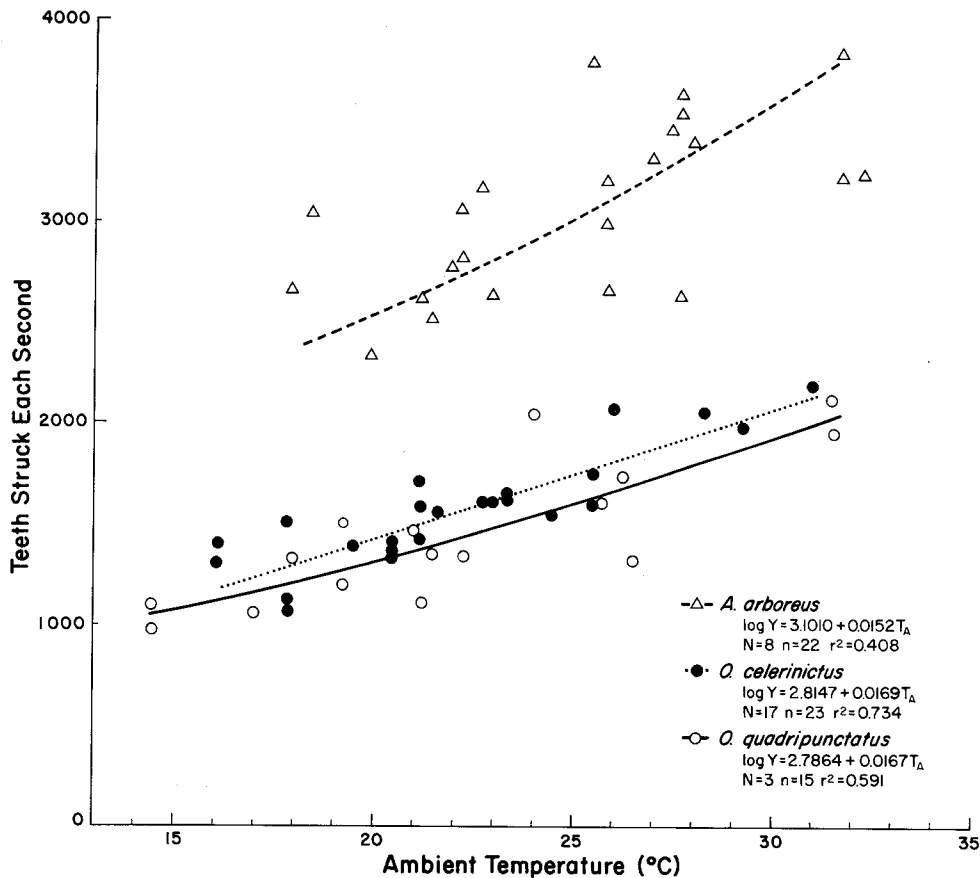


Fig. 9. The number of teeth struck each second as a function of T_a . Although the *Oecanthus* species have very different wing stroke rates (Fig. 4) the number of teeth struck each second are similar due to the greater number of teeth struck per wing closure in *O. quadripunctatus* (Fig. 8)

openings, but its wing closure time changes at the same rate as does *O. celerinictus* with the only difference between the two species being a constant 0.003 s per wing stroke. In opening time, *O. quadripunctatus* shows a greater response to temperature than either of the other species (Fig. 6).

The CF in all three species increases with T_a (Fig. 7) but at a lower rate than the WSR. It is of interest that the CF's of the *Oecanthines* are essentially identical. Recent evidence suggests that the CF is equal to the tooth impact rate between file and scraper in crickets (Sismondo 1980; Koch 1980). Since the tooth spacing in these *Oecanthines* is the same ($38.5 \text{ teeth} \cdot \text{mm}^{-1}$; Walker 1963) then the velocity of wing closure must be the same. However, wing closure times are significantly longer in *O. quadripunctatus*. From these data, a greater number of teeth strikes per wing closure should occur in *O. quadripunctatus*. If tooth strikes per wing stroke are plotted against T_a the predicted relationship is obtained (Fig. 8): *O. quadripunctatus* strikes a greater number of teeth per wing closure than does its sibling. Since they close their tegmina at the same rate, if *O. quadri-*

punctatus strikes a greater number of teeth per closure then it does more work per closure. This longer closing stroke correlates well with the longer file in *O. quadripunctatus*: ca. 57 teeth vs 41 in the sibling (Walker 1963). Finally, while the work done during a single closure is greater in *O. quadripunctatus* it must be kept in mind that this species makes fewer wingstrokes per unit time than does its sibling (Fig. 4). In order to remove time as a variable, the number of tooth strikes per s can be plotted against T_a (Fig. 9): viewed this way *O. quadripunctatus* consistently strikes about 90% as many teeth as does *O. celerinictus* per unit time.

Discussion

One aim of this study is to identify the features of the call that allow the prediction of calling costs. It was for this reason that we analyzed acoustical and mechanical features of the call in addition to \dot{V}_{O_2} .

The work done by the tegminal musculature during a wing stroke is that of accelerating the tegminal mass (and supporting tissues) through a certain sized

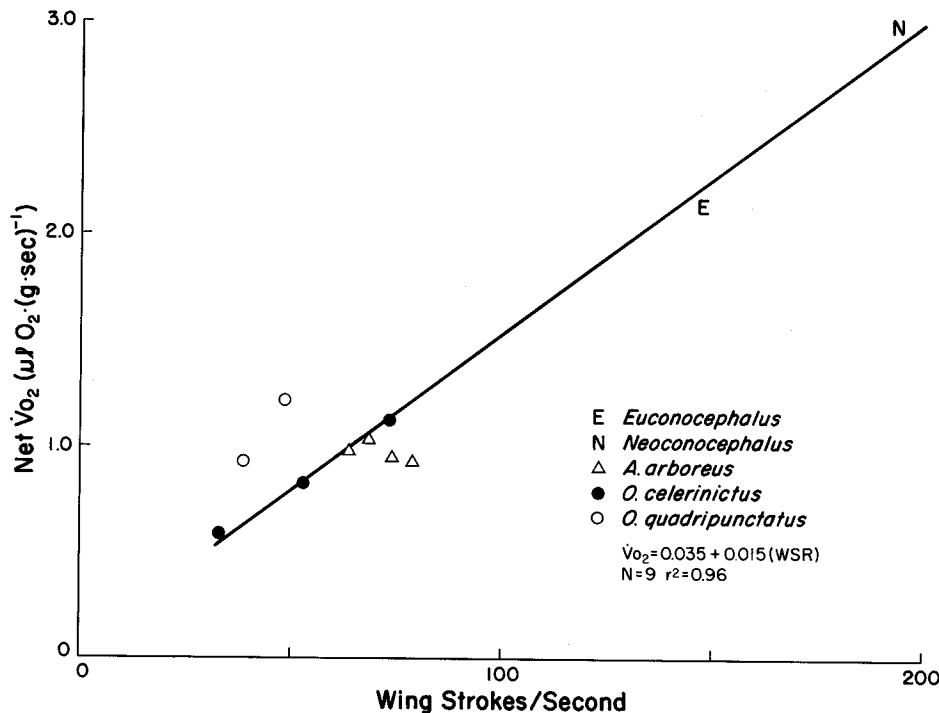


Fig. 10. The relationship between net cost of singing for 1 s ($\mu\text{l O}_2 \cdot (\text{g} \cdot \text{s})^{-1}$) and wing stroke rate. Data for two species of katydids (Stevens and Josephson 1977) and for the three species of cricket used in this study at each temperature investigated (Table 3). The regression line is drawn for all points except *O. quadripunctatus*; however, inclusion of these points does not greatly alter the regression, in part due to the extreme values for the katydids (*Euconocephalus* and *Neoconocephalus*). The general trend is that net cost is strongly determined by the wing stroke rate; however, an alternative model is possible where cost is independent of wing stroke rate (*A. arboreus*). In this case the number of teeth struck per wing closure may have a major effect. This possibility is also supported by the fact that *O. quadripunctatus* values do not fall on the overall regression but are above it. This species strikes more teeth per wing stroke than does its sibling *O. celerinictus*. The latter has costs that fall on the overall regression line

arc. Mass for any cricket is constant; however, acceleration varies with the calling pattern. Acceleration is related to three inter-dependent factors: (1) Wing velocity. Since the CF and tooth strike rate increase with T_a (Fig. 7) and, thus, with WSR (Fig. 4), then tegminal velocity also increases. The greater the tegminal velocity, the greater the acceleration since the wing must stop at least instantaneously twice each WS. (2) External frictional resistance. This is a result of three factors: (a) the number of file teeth struck per WS (Fig. 8), (b) the force with which they are struck (Figs. 2, 3) and (c) air resistance (probably a minor factor). (3) Internal friction. This is internal resistance by muscle, connective, and supportive tissues (Weis-Fogh 1964).

The interrelations between these factors are complex. Wing velocity and temperature influence internal resistance in flying locusts (Weis-Fogh 1964). Shorter WS's, which would decrease work, are accompanied by higher WSR's and wing velocities, both of which tend to increase work and power consumption. Thus, the question is to what degree do these factors influence the cost of stridulation. One factor that would seem to be very important is the WSR

since it varies greatly and has a major influence on the relative distances the tegmina move per unit time at different T_a 's.

We plotted net \dot{V}_{O_2} vs. WSR for 3 species of crickets and 2 katydids (Fig. 10). The average total metabolic rate during singing for katydids was obtained from Stevens and Josephson's Table 3 (1977). We corrected these values to make them mass-specific for the entire animal (instead of the tegminal musculature) and then subtracted the resting rate of metabolism to estimate a net cost. We assumed a resting \dot{V}_{O_2} at 25 °C of $400 \mu\text{l O}_2 \cdot (\text{g} \cdot \text{h})^{-1}$, a value consistent with ours and also that of Stevens and Josephson (1977). This value was corrected for temperature (40 °C) using a Q_{10} value of 2 (*A. arboreus*). The entire katydid was assumed to be at 40 °C (the errors induced if this assumption is false are slight).

The data in Fig. 10 are fitted to a linear model; they fit a logarithmic model as well ($\log \dot{V}_{\text{O}_2} = 0.0042 (\text{WSR}) - 0.3194$; $N=9$, $r^2=0.97$). The two data points for *O. quadripunctatus* have not been included in calculating either of these regressions for reasons discussed below; however, inclusion of these points on either regression model would change the overall

equation only slightly due to the extreme values of the katydids.

The relationship shown in Fig. 10 demonstrates the major importance of WSR in determining the cost of singing. The overall trend shows an increase in cost with WSR – not a surprising result since as long as resistance per WS remains constant, the more wing strokes per unit time the greater the work done. The slope of the regression line in Fig. 10 gives the average net cost of a wing stroke – $0.015 \mu\text{l O}_2 \cdot (\text{g} \cdot \text{WS})^{-1}$. For the comparison, we calculated the cost of flight per WS per total mass in two insects which, like crickets and katydids, use synchronous muscle. For the locust *Schistocerca* (cited in Stephens and Josephson 1977) the cost is ca. $0.36 \mu\text{l O}_2 \cdot (\text{g} \cdot \text{WS})^{-1}$, for a hawk moth *Hyles* (Casey 1976a, b) it is 0.54. These figures are from 13 to 36 times that of stridulation. The result is not surprising; the useful work of flight is lift and propulsion and is achieved by relatively long wing strokes, stridulation produces sound and while WSR's may be high, the strokes are short.

Figure 10 shows that stridulators do not all do the same amount of work per WS. If that were the case, all points would fall along the regression line. Some *A. arboreus* values and all those of *O. quadripunctatus* fall off the line. The per WS cost of *O. quadripunctatus* averages about $1.6 \times$ greater than the other species, including its sibling, to which we will compare it. What is the source of the different costs?

Morphologically, the two siblings are nearly identical and even when they stridulate at the same WSR the cost differences remain. Thus, it is unlikely that differences in internal resistance are responsible for the different costs. The CF's of the two species are nearly identical as are their file tooth densities. Thus, the average velocity during file and scraper contact is the same and so acceleration is not a factor. However, Fig. 8 shows that the number of teeth struck per WS was greater in *O. quadripunctatus*. Assuming a constant force between file and scraper, the greater the number of teeth struck per WS, the greater the resistance presented and work done per WS.

In order to evaluate this explanation, we calculated cost per tooth strike in both species of tree crickets using the net V_{O_2} (Table 3) and number of teeth struck per s (Fig. 9). At 23 and 28 °C the values for *O. celerinictus* are 5.1×10^{-4} and $5.7 \times 10^{-4} \mu\text{l O}_2 \cdot (\text{g} \cdot \text{tooth})^{-1}$; for *O. quadripunctatus* they are 6.3×10^{-4} and 6.7×10^{-4} . The costs still are not identical: at 23 °C the ratio of costs is 1.23; at 28 °C it is 1.16. Thus, on the average, the cost per tooth strike is about $1.2 \times$ greater in *O. quadripunctatus*. This is considerably less than the $1.6 \times$ difference which exists

when costs are compared on a per WS basis. Other factors being equal, the number of teeth struck per WS is also an important determinant of cost. The remaining difference in cost could come from several sources: (1) longer wing opening time per WS (Fig. 6); (2) change in the friction per tooth strike. Friction per tooth strike is determined by the morphology of the teeth and the scraper (see below) and by the behavior of the cricket. While the morphology of the files of the tree crickets is similar, it is possible that *O. quadripunctatus* rubs its file against its scraper harder than does its sibling. Variation in the loudness of calling probably as a result of variable file and scraper contact is suggested in Figs. 2 and 3. In addition, at least one cricket, *Gryllus integer*, is known to call at two distinct sound levels (Cade 1979, 1980), possibly by variation in tegminal contact.

Any equation which seeks to predict calling costs will also need to take into account two factors in addition to those discussed above. First, there is the mass of the tegmina, since they are what must be accelerated. Second, the morphology of the file teeth may indicate something about the force with which they are pressed together: it seems reasonable that files having deep teeth with steep angles would gather the scraper more strongly than shallow teeth set at slight angles. Thus, file morphology may be a good indicator as to the frictional forces to be overcome during stridulation.

The factors discussed in this section can be substituted into the work equation:

$$W \propto m_t \cdot (a_t \cdot n_t + a_o) \cdot \text{WSR}. \quad (1)$$

Where the work of calling is W , m_t is the tegminal mass, a_t the deceleration per tooth strike, n_t the number of teeth struck, and a_o is the acceleration of the tegmina during the opening phase. To test the relative importance of these factors and the usability of an equation derived from this proportionality, it will be necessary to evaluate these factors in a larger number of species. At the present, a very rough estimate of the net cost of trilling is suggested from Fig. 10:

$$V_{\text{O}_2} = \text{WSR} \left(1.5 \times 10^{-2} \frac{\mu\text{l O}_2}{\text{g} \cdot \text{WS}} \right). \quad (2)$$

It must be remembered that this equation yields costs that are ca. 50% too low for *O. quadripunctatus* and ca. 15% too high for *A. arboreus* at 26 °C. However, it may serve as a useful estimator for trilling costs.

This study has only dealt with trilling calls; however, many stridulators chirp and the cost of chirping calling songs relative to trilling calling songs is of

Table 4. Estimated daily respiratory energy budgets for *A. arboreus* and *O. celerinictus*

	Resting	Singing	Daily activity	Totals	% total body mass
<i>A. arboreus</i> (0.38 g)			2.5 × rest		
Assumptions-time ^b	19.4 h	0.6 h	4 h	—	—
T_a	20 °C	22 °C	17 °C	—	—
V_{O_2}	1.740 ml	0.915 ml	0.805 ml	3.460 ml	—
Fat energy stores used ^a	8.7×10^{-4} g	4.6×10^{-4} g	4.0×10^{-4} g	1.72×10^{-3} g	0.5
% of daily respiration	50%	26%	23%	—	—
<i>O. celerinictus</i> (0.055 g)			2.5 × rest		
Assumptions-time ^c	12 h	6 h	6 h	—	—
T_a	30 °C	26 °C	25 °C	—	—
V_{O_2}	0.615 ml	1.342 ml	0.460 ml	2.417 ml	—
Fat energy stores used ^a	3.1×10^{-4} g	5.5×10^{-4} g	2.3×10^{-4} g	1.20×10^{-3} g	2.2
% of daily respiration	25%	56%	19%	—	—

^a To convert these to carbohydrate, multiply by 2.56

^b Walker (1980)

^c Walker (1957b)

interest. Unlike trilling, chirping is characterized by long periods when the tegmina are not being oscillated. They are, however, maintained in the elevated position. To estimate the cost of calling in a chirper we make three assumptions: (1) during the times when the tegmina are oscillating the processes involved are identical with that of trilling species and therefore the cost per wing stroke is the same in chirping and trilling species; (2) the cost of maintaining the tegmina elevated is negligible; (3) the cost per wing stroke is constant, there being no warm-up, a phenomenon that (if it occurs) would be insignificant in a long trill but could be very important in a short chirp. [In some chirping crickets the power output apparently increases during the first few wing closures of the chirps (oscillograms in Popov and Shuvalov, 1977) while in other species, this does not occur (audiospectrograms in Walker, 1969).] Thus, the cost of chirping should be equivalent to the cost of trilling at a similar WSR times the percentage of time the cricket is actually stridulating. A cricket that chirps for an hour but only moves its wings during 5% of this hour will have a cost similar to a triller that sings 3 min.

More formally, the rate of oxygen consumption during chirping (\dot{V}_{O_2}) should equal the cost per wing stroke ($V_{O_2} \cdot WS^{-1}$) times the number of wing strokes or

$$\dot{V}_{O_2} = (V_{O_2} \cdot WS^{-1}) \cdot (WS \cdot \text{chirp}^{-1}) \cdot (\text{chirps} \cdot \text{time}^{-1}). \quad (3)$$

Preliminary measurements of the cost of chirping in two unrelated species (*Oecanthus fultoni* and *Orocharis luteolira*) with very different chirping and wing stroke patterns support the above relationship.

Finally, earlier investigators have concluded that stridulation in thermoregulating katydids is an expensive way to attract a mate (Heath and Josephson 1970; Stevens and Josephson 1977). Our data show this is also true for poikilothermic stridulators (Table 4). The proportion of the total daily respiratory budget used for song varies from about 26% in *A. arboreus* to 56% in *O. celerinictus* for only 2.5% and 25% of the day, respectively. By singing, a cricket presumably increases its cost benefit ratio by attracting more females per unit time than it could find by searching. It probably has less risk of encountering predators than would occur in a random search for females. There is some evidence of nocturnal phonotactic predation on *A. arboreus*, but none on *Oecanthus*. Male *A. arboreus* spend a considerable time each night searching, probably for both food and burrows of females. They apparently suffer heavy predation, probably from spiders, during this time (Walker 1980). Thus the calling period offers a time when males advertise themselves and attract mates, perhaps at a low risk of predation, while females have a greater change of locating a male than would occur if mating only occurred in female burrows.

Given the high cost of calling, we wondered how long a male could call if it did not feed. Under the conditions assumed in Table 4, *A. arboreus* loses about 0.5% of its body mass daily to respiration while *O. celerinictus* loses 2.2%. These figures do not seem to be especially high or limiting. This interpretation has been borne out in preliminary experiments: in *A. arboreus* eight days of starvation resulted in neither termination nor reduction of singing time when compared to controls. Thus, while calling is metabolically

expensive, it is not so expensive in the crickets we studied as to severely deplete a male's metabolic reserves over several days, even if it cannot feed.

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