

BODY TEMPERATURE AND SINGING IN THE BLADDER CICADA, *CYSTOSOMA SAUNDERSII*

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(Received 19 July 1978)

SUMMARY

1. Body temperatures during singing were measured in the cicada, *Cystosoma saundersii* Westwood, both in the field and in tethered animals indoors.

2. The temperature of the sound-producing tymbal muscle rises rapidly during singing to reach a plateau approximately 12 °C above ambient. This produces a temperature gradient in the abdominal air sac which surrounds the muscle. When singing stops, the tymbal muscle cools exponentially.

3. Heat production during singing, estimated from the cooling curve, is 4.82 cal min⁻¹ g muscle⁻¹. Generation of the same temperature excess in the air sac by an artificial heat source yields an estimated heat production of 54.4 cal min⁻¹ g muscle⁻¹. This discrepancy may be caused by air mixing in the air sac during singing.

4. As temperature rises, tymbal muscle twitch contractions become faster and stronger. This and heat transfer to the thorax cause changes in the song pattern: a marked decrease in the interval between the two sound pulses produced by a single tymbal buckling and a lesser decrease in the interval between bucklings. The fundamental sound period remains unaltered. These effects are consistent with earlier data on sound production.

INTRODUCTION

Cicadas are virtuosos among sound-producing insects. In males, a large proportion of the body is devoted to acoustic functions. In particular, there is a pair of very large muscles, the tymbal muscles, the function of which is to buckle a pair of sound-producing tymbals. The buckling of the tymbals generates pulses of sound. High rates of buckling are maintained by repetitive twitch contractions of the tymbal muscles (Pringle, 1954; Hagiwara, 1955). The trains of sound pulses thus produced constitute the insect's song, which often continues for many minutes without interruption.

It is known from other insects that activities such as this, which involve large muscles with high contraction frequencies, result in elevated body temperatures during activity. In many cases such elevated temperatures are actively generated, by a warm-up procedure which involves the simultaneous contraction of antagonistic muscles. For example, this occurs in moth flight (Kammer, 1968; Hanegan & Heath,

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1970; Heinrich, 1971), bumblebee flight (Heinrich & Kammer, 1973) and katydid singing (Heath & Josephson, 1970; Josephson, 1973).

Therefore one might anticipate that cicadas would have elevated body temperatures during singing as a result of continuous tymbal muscle activity. In general, cicadas do not perform well in the laboratory and, hitherto, this has made it difficult to study this phenomenon experimentally. However, the Australian bladder cicada, *Cystosoma saundersii*, is an exception in that it will produce its calling song while tethered indoors (Simmons & Young, 1978). We have taken advantage of this in order to study body temperatures in tethered singing cicadas, by means of implanted thermistors, as well as making field measurements.

Some other species of cicadas generate elevated body temperatures by basking in the sun (Heath, 1967; Heath & Wilkin, 1970). Males of *C. saundersii* sing only at dusk (Scott, 1852; Young, 1972*a*) and so this option is not open to them. Therefore, any increase in body temperature that is observed must be due to muscular activity. In this paper we have paid particular attention to tymbal muscle temperature, have estimated heat production by two different methods and have studied the effects of muscle warming upon the song pattern.

MATERIALS AND METHODS

Specimens of the Australian bladder cicada, *Cystosoma saundersii* Westwood, were obtained at Port Macquarie on the coast of New South Wales. The animals were captured while singing in the early evening. All experiments were carried out in a rented flat at Port Macquarie as in Simmons & Young (1978). Five different experimental procedures were used to study temperature relations.

(1) Field recordings of tymbal muscle temperature were made using a temperature probe, similar to that described by Heath & Adams (1969), consisting of a bead thermistor mounted in the tip of a 22-gauge hypodermic needle. A singing insect was caught by hand, its expanded abdomen cut off quickly with a pair of scissors, and the probe inserted into one of the exposed tymbal muscles.

(2) Temperatures of tymbal muscles and other body structures were also measured chronically with thermistors implanted into animals allowed to sing in the laboratory. These animals were mounted by waxing the pronotum to a holder, which was held in a manipulator (Fig. 1). The thermistors were beads, 0.1 mm in diameter, which were soldered to long flexible wires. These were connected to a bridge circuit (Yellow Springs Telethermometer). Thermistors were calibrated against a laboratory thermometer and readings could be made to 0.1 °C. The thermistors were inserted into the desired area through holes made in the cuticle and held in place by wax applied around the entry point. Then the animals were fixed so that they walked on a polystyrene ball, 5 cm in diameter, which was floated on the surface of a beaker of water (Fig. 1). This operation was completed at least 4 h before the normal chorus time (dusk). The placement of the thermistors was always checked by dissection following the experiment.

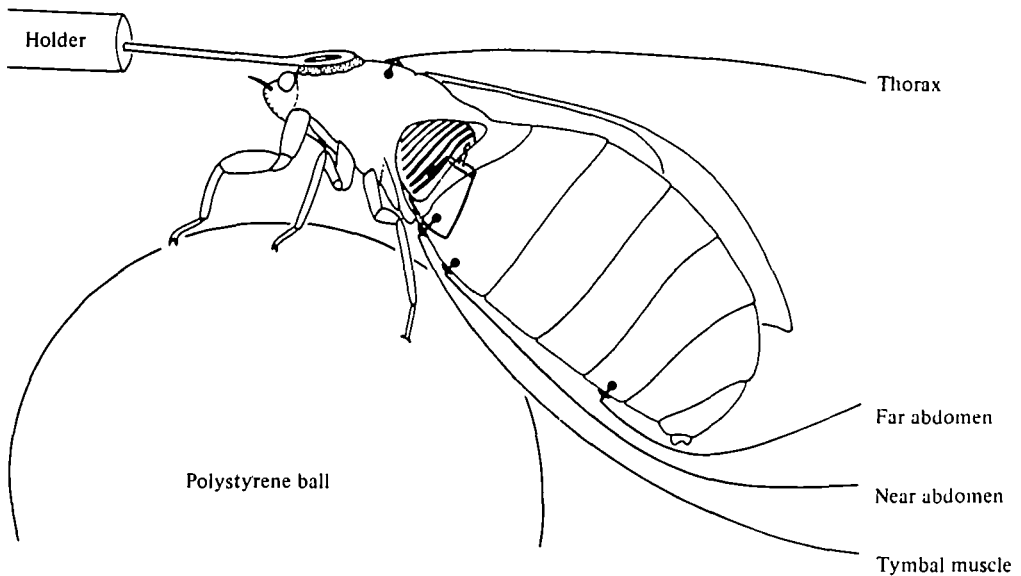


Fig. 1. A tethered specimen of *Cystosoma saundersii*, showing the location of thermistors (●) implanted for recording body temperatures during singing. The ribbed tymbal is drawn in and its associated tymbal muscle is indicated by a bold outline.

(3) In several of these animals, after completion of the above experiment, the rate of heat production was estimated by placing a small resistor ($\frac{1}{8}$ W, 100Ω) between the paired tymbal muscles and passing sufficient a.c. current through it to warm the animal to the same extent as occurred during singing. Heat dissipation from the resistor was calculated as V^2/R , where V = RMS voltage measured across the resistor and R = value of the resistor in ohms. In this experiment the posterior nerves leaving the thoraco-abdominal ganglion were cut to denervate the tymbal muscles and thus inactivate them.

(4) Mechanical responses from the tymbal muscles were recorded with a transducer constructed from a pair of semiconductor strain gauges (Pixie 8101, Endevco Co., San Juan Capistrano, California). The strain gauges formed two arms of a bridge circuit. The tymbal muscles were exposed by removing the posterior abdomen and the dorsal region of the anterior abdomen and posterior thorax. The muscles were fixed to a dissecting dish by pins which penetrated one of the muscles near the ventral mid-line. On the side with the undamaged muscle, the tymbal was cut away except for a small disc surrounding the tymbal apodeme. An insect pin bent into a small hook at one end was fixed to the transducer. The hook was slipped around the tymbal apodeme to link the muscle and transducer. The transducer was mounted in a manipulator so that the length of the muscle could be varied. Mechanical measurements were made with the muscle stretched 0.5 mm greater than its slack length (= approximately 6% greater than slack length). The muscle was stimulated through a pair of fine wires, insulated except at the tip, which were inserted into the ventral region of the muscle. The temperature of the tymbal muscles was controlled by varying the intensity of a microscope lamp directed equally at the muscle from which the

mechanical recordings were made and its contralateral partner. A thermistor probe in the contralateral muscle monitored muscle temperature.

(5) The relation between temperature and song pattern was studied by recording the songs of males which had been rendered unilateral by destruction of one tymbal. This operation was performed at least 3 h before sunset and the operated individuals were sleeved on to shrubs out-of-doors. Their songs were recorded with a Sennheiser MKH 815 directional microphone and a Nagra IVS tape recorder at a tape speed of $7\frac{1}{2}$ in/s. The tape recordings were displayed on an oscilloscope and filmed for analysis.

RESULTS

(1) *Field recordings of tymbal muscle temperature*

During the dusk chorus individual males of *C. saundersii* were captured and their tymbal muscle temperature measured with the thermistor probe. The ambient temperature was recorded with the probe within 30 cm of the animal before its capture. The tymbal muscle temperatures recorded in this way in six individuals are summarized in Table 1. There is a delay between the cessation of singing at capture and the first temperature reading. This delay was measured from tape recordings and is included in Table 1. The tymbal muscle temperature drops rapidly at the cessation of singing (see below) and so the recording delay allows the muscle to cool somewhat. Therefore the measured difference in temperature of 10.5°C between the tymbal muscle and the animal's environment is an underestimate of the true difference in an undisturbed cicada.

Table 1. *Tymbal muscle temperature recorded in the field*

	Mean	Range
Tymbal muscle temperature ($^{\circ}\text{C}$)	30.8	28.0-33.9
Ambient temperature ($^{\circ}\text{C}$)	20.3	18.5-22.2
Muscle temperature excess ($^{\circ}\text{C}$)	10.5	9.0-12.1
Recording delay (s)	13.7	11-22

(2) *Chronic temperature measurements from tethered cicadas*

In the tethered animals, thermistors were implanted in the tymbal muscle and in other regions of the body which might be warmed by tymbal muscle activity. These regions were the thorax and the large air sac, which surrounds the tymbal muscles and fills most of the abdomen (see Simmons & Young, 1978, figs. 2, 4). Near abdomen measurements were made in the air sac 1-6 mm posterior to the tymbal muscles and far abdomen measurements from 16 to 32 mm posterior to the tymbal muscles. As many as four thermistors could be implanted in one animal, as in Fig. 1, without impairing its singing performance. Most of the tethered cicadas sang in chorus with the non-captive males at dusk on the day of their operation. They walked on the polystyrene ball, adopted the singing posture and sang continuously for 15-30 min.

In a non-singing animal the tymbal muscle temperature is within 1°C of ambient, typically slightly less than ambient. Full singing is often preceded by a number of short bursts of sound. The tymbal muscle temperature rises slightly during these

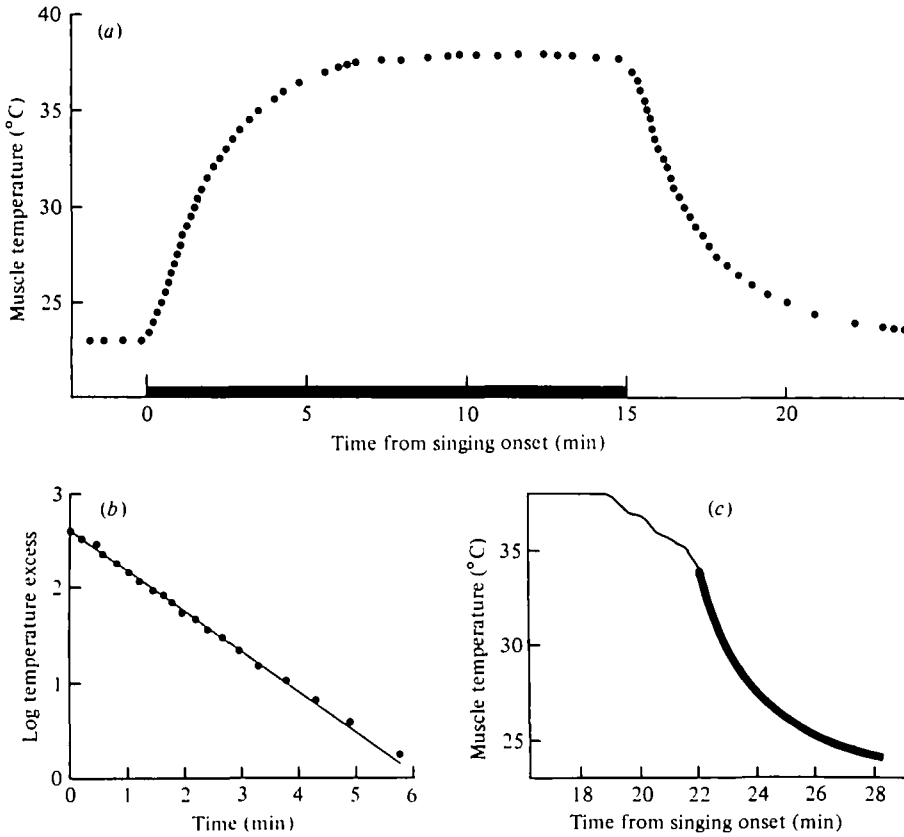


Fig. 2. Tymbal muscle temperature recorded with implanted thermistors. (a) Muscle temperature during singing and subsequent cooling in one individual. The duration of the calling song is indicated by a heavy line above the abscissa. (b) The temperature excess during the cooling portion of (a). Note that the curve approximates to a simple exponential process. (c) Muscle temperature at the end of singing in another animal. Full singing, during which muscle temperature reached a constant plateau, was followed by intermittent singing and irregular cooling. When singing stopped altogether, cooling became exponential, as indicated by the thicker line.

Table 2. Steady-state temperature excess during singing in tethered animals (°C)

	Mean	
Tymbal muscle	13.6	(S.E. = 0.7, n = 8)
Near abdomen	4.2	(S.E. = 1.7, n = 8)
Far abdomen	0.7	(S.E. = 0.2, n = 7)
Thorax (flight muscle)	2.0	(S.E. = 0.3, n = 5)

short bursts but drops in the intervening quiet periods so that typically full singing begins with the muscle at ambient temperature. Following the onset of full singing the tymbal muscle temperature rises, at first rapidly and then more slowly, before finally reaching a plateau, 12–17 °C above ambient, in 10–20 min (Fig. 2a, Table 2). The maximum rate of rise for a 5 °C temperature interval averaged 4.4 ° min⁻¹ in the 8 animals from which chronic temperature measurements were taken.

Table 2 summarizes the steady-state temperature excess recorded from different

parts of the body during singing. The ambient temperature averaged 23.5 °C during these measurements and these parts of the body were at ambient temperature shortly before the onset of singing. The abdominal thermistors always protruded into the air sac for at least 1 mm so that they recorded internal air temperature and not that of the body wall. There is a significant temperature gradient in the abdominal air sac during singing, indicating that the air within the sac is not well mixed by the movements of the tymbal muscles. The temperature of the flight muscle in the thorax does increase during singing but the rise is small and the flight muscles almost certainly represent a route of heat loss from the tymbal muscle and not a source of heat. The wings are raised from the body during singing but they do not move. The tonic activity of the small group of muscles required to raise the wings is unlikely to be a significant source of heat. There is no reason to believe that flight muscle activity contributes to the elevated temperature of the tymbal muscle and the abdominal air sac.

Singing may stop abruptly or continuous singing may be followed by a period of irregular sound production, with bursts of song separated by intervals of increasing length, before complete cessation of singing. Following an abrupt stop, tymbal muscle temperature falls rapidly (Fig. 2*a*), the decline being approximately exponential (Fig. 2*b*). The tymbal muscle temperature falls irregularly during interrupted singing but when singing finally stops the decline in temperature is approximately exponential (Fig. 2*c*).

(3) *Heat production during singing estimated from cooling curves*

Heat loss from the tymbal muscles during cooling is a complex phenomenon, involving heat transfer from the muscles to the abdominal air sac and from the air sac, whose temperature is not spatially uniform, to the environment. Nevertheless, the overall result of heat transfer during cooling is effectively an exponential decline in muscle temperature (Fig. 2*b*). Hence, even without knowledge about the details of the cooling process, the exponential cooling curves can be used empirically to estimate heat production during singing. One assumption that must be made is that the rate of heat loss from the tymbal muscles is the same function of muscle temperature during cooling as during singing.

The rationale for the procedure used is as follows. The straight line in a cooling curve plotted as in Fig. 2(*b*) is described by the equation:

$$\log_e T_E = Kt + C, \quad (1)$$

where T_E is the muscle temperature excess (°C) defined as the difference between the muscle temperature, T_M , and the equilibrium muscle temperature in a non-singing animal, T_A , t is the time from the onset of cooling (min), K is the slope of the cooling curve (min⁻¹) and C is the ordinal intercept of the line.

From this it follows that

$$T_E = T_E^\circ \exp. (Kt), \quad (2)$$

where T_E° is the muscle temperature excess (°C) at the onset of cooling, i.e. when $t = 0$, and

$$dT_E/dt = T_E^\circ K \exp. (Kt). \quad (3)$$

From the definition of muscle temperature excess, given that T_A is constant,

$$dT_E/dt = dT_M/dt. \quad (4)$$

Now the rate of change in muscle temperature is directly proportional to the rate at which the muscle gains or loses calories and this is inversely proportional to the mass of the muscle and the specific heat of the muscle tissue. The relation may be expressed:

$$dT_M/dt = (1/MS)(dH_p/dt - dH_L/dt), \quad (5)$$

where M is the mass of the muscle (g), S is the specific heat of muscle tissue (cal deg⁻¹ g⁻¹), dH_p/dt is the rate of heat production by the muscle (cal s⁻¹) and dH_L/dt is the rate of heat loss from the muscle (cal s⁻¹).

When the muscle temperature reaches a plateau during singing, $dT_M/dt = 0$ and the rates of heat production and loss are necessarily equal (i.e. $dH_p/dt = dH_L/dt$). Heat production must be negligible when singing stops for the muscle temperature rapidly falls to an equilibrium temperature very close to that of the animal's environment. When heat production is zero, equations (3), (4) and (5) can be combined to give:

$$dH_L/dt = -MST_E^0 K \exp. (Kt). \quad (6)$$

Finally, if it is assumed that the rate of heat loss from the animal is the same just before and just after singing, the rate of heat loss during singing is given by letting $t = 0$ in equation (6). This rate of heat loss is also the rate of heat production during the temperature plateau preceding cessation of song. Hence:

$$dH_p/dt = -MST_E^0 K. \quad (7)$$

Equation (7) was used to determine heat production during singing in eight animals in which the tymbal muscle temperature reached a plateau during tethered singing. The muscle temperatures during cooling were plotted as in Fig. 2(b) and the cooling rate constant, K , was determined as the slope of the straight line fitted by eye to the data points. When singing did not stop abruptly, as in Fig. 2(c), only the exponential portion of the cooling curve, following total cessation of singing, was used to determine K . The average value of K was 0.445 min⁻¹ (s.e. = 0.020 min⁻¹). The average weight of the paired tymbal muscles in these eight animals was 85.8 mg (s.e. = 5.3 mg). The value for specific heat, s , used was 0.8 cal g⁻¹ deg⁻¹, which was determined for insect muscle by Krogh & Zeuthen (1941). The estimated rate of heat production for the eight animals averaged 0.41 cal min⁻¹ (s.e. = 0.037 cal min⁻¹) or 4.82 cal min⁻¹ g muscle⁻¹.

(4) *Heat production during singing estimated from artificially heating the animal*

Five of the cicadas of the preceding series were used to estimate heat production in the following way. After measurement of tymbal muscle temperature rise and cooling had been completed, an electrically heated resistor was introduced between the tymbal muscles as an artificial heat source. These animals had a thermistor in both near and far abdominal air sac, as in Fig. 1.

Ideally the heat dissipation from the artificial source should be adjusted to replicate exactly the distribution of temperature excess in the abdomen which is produced by

the muscles during singing. In practice, this was possible in only one of the five preparations. In the other preparations, when the current through the resistor was adjusted so that the temperature excess was the same as during singing at the near thermistor, the temperature excess at the far thermistor was either too high or too low. Probably the problem is one of geometry. The near thermistor is close to the heat source (muscle or resistor), where the temperature gradient is presumably steep, and so small differences in the distance between the thermistor and the two heat sources could alter significantly the heat dissipation from the resistor required to match the temperature excess during singing. The far thermistor, being rather far removed from both real and artificial heat sources, is much less affected by small inaccuracies in the placement of the resistor. But we could measure temperatures only to within $0.1\text{ }^{\circ}\text{C}$ which is a significant fraction of the total temperature excess at the far thermistor ($0.7\text{ }^{\circ}\text{C}$). In short, matching the temperature excess resulting from the two heat sources is subject to inaccuracies at the near thermistor because of small differences in the distance between the thermistor and the two heat sources, and resolution is poor when using the far thermistor as the reference because of the small temperature change there.

Realizing this, we chose the near thermistor when, upon dissection after the experiment, the distances between thermistor and muscle and between thermistor and resistor were within 1 mm and we chose the far thermistor when these distances were obviously different. Using this approach, the heat production by the resistor required to match the temperature excess during singing averaged 0.32 W (S.E. = 0.03 W). When only the near thermistor was used as a reference, the best match between muscle and resistor averaged 0.44 W (S.E. = 0.07 W) and when only the far thermistor was used, the best match averaged 0.35 W (S.E. = 0.04 W).

The estimated rate of heat production of 0.32 W is equivalent to 4.56 cal min^{-1} or, using the muscle weights from section (3) above, $54.4\text{ cal min}^{-1}\text{ g muscle}^{-1}$. This is an order of magnitude greater than the heat production estimated from the cooling curves. A possible reason for this discrepancy is considered in the Discussion.

(5) *The effect of muscle warming on the song pattern*

Because the tymbal muscle warms during singing, changes may be expected in those features of the song which are influenced by temperature-dependent processes. The mechanical response of the tymbal muscle was studied at different temperatures and found to be temperature-dependent. Table 3 summarizes data from eight animals for twitch duration (onset to 90% return) and twitch tension. As the muscle becomes warmer, its twitches become faster and it develops greater twitch tension (Fig. 3). Consequently, as singing progresses and the muscles warm up, the sound pulses are produced by muscles which contract more rapidly and more strongly.

Possible effects on the song pattern, due to this change, may be predicted from the detailed analysis of sound production in *C. saundersii* by Young (1972*b*), Simmons (1977) and Simmons & Young (1978). Each tymbal muscle is innervated by a single motor neurone. During singing, each motor neurone fires at about 40 Hz and so each tymbal buckles at this frequency. The tymbal bears seven stiffening ribs. Each contraction of a tymbal muscle produces two major sound pulses – the first associated

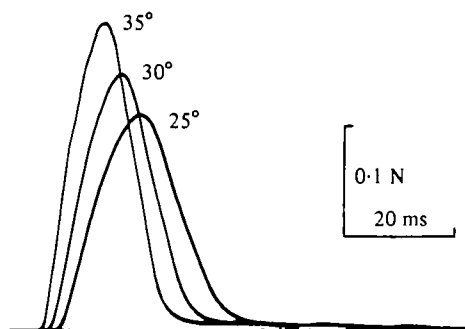


Fig. 3. Mechanical recordings of single twitches of the tymbal muscle at three different temperatures.

Table 3. *Twitch contraction of the tymbal muscle as a function of muscle temperature (mean \pm S.E.)*

	25°	30°	35°
Twitch duration (ms)	34.5 \pm 2.0	30.5 \pm 3.0	25.3 \pm 5.4
Twitch tension (mN)	200 \pm 20	227 \pm 18	241 \pm 18

with the buckling of rib 1 and the second associated with the buckling of ribs 2-4, which collapse synchronously. The sound is radiated into the environment by the large abdomen, the air sac being resonant at the fundamental frequency of the song.

This analysis may be considered in relation to the three main parameters of the song. Expressed as intervals, these are: the fundamental *sound period*, the *cycle period* of tymbal buckling and the *interpulse interval* between the two major sound pulses generated by a single tymbal buckling. These intervals are labelled respectively A, B and C in Fig. 4(a). The interpulse interval reflects the rate at which the ribs of the tymbal collapse and this is governed partly by the contraction kinetics of the muscle. Hence a progressive decrease in this interval is to be expected as the muscle warms and its twitches become faster. The cycle period of tymbal buckling is determined by the rate of firing of the motor neurone and this is controlled in the thoraco-abdominal ganglion (Simmons, 1977). If the ganglion warms to about the same degree as the flight muscle and if the neuronal song generator is temperature-dependent, then a slight decrease in the cycle period may be expected as warming occurs. The fundamental sound period primarily reflects the resonance of the abdominal air sac, which is determined by its mechanical properties and dimensions (Fletcher & Hill, 1978). One would not expect these to be affected by the small rise in temperature of the air in the abdominal air sac.

These predictions were examined in four animals. The tymbal on one side of each animal was destroyed so that the sound output reflected the activity of only a single tymbal. The tensor muscle on the side with the intact tymbal was disconnected by cutting out its insertion (see Simmons & Young, 1978). This was necessary since the tensor muscle alters the tension on the tymbal (Pringle, 1954) and the interpulse interval (Simmons & Young, 1978). All four of these animals sang at dusk in chorus with nearby wild animals. Results from three animals were clear and consistent with

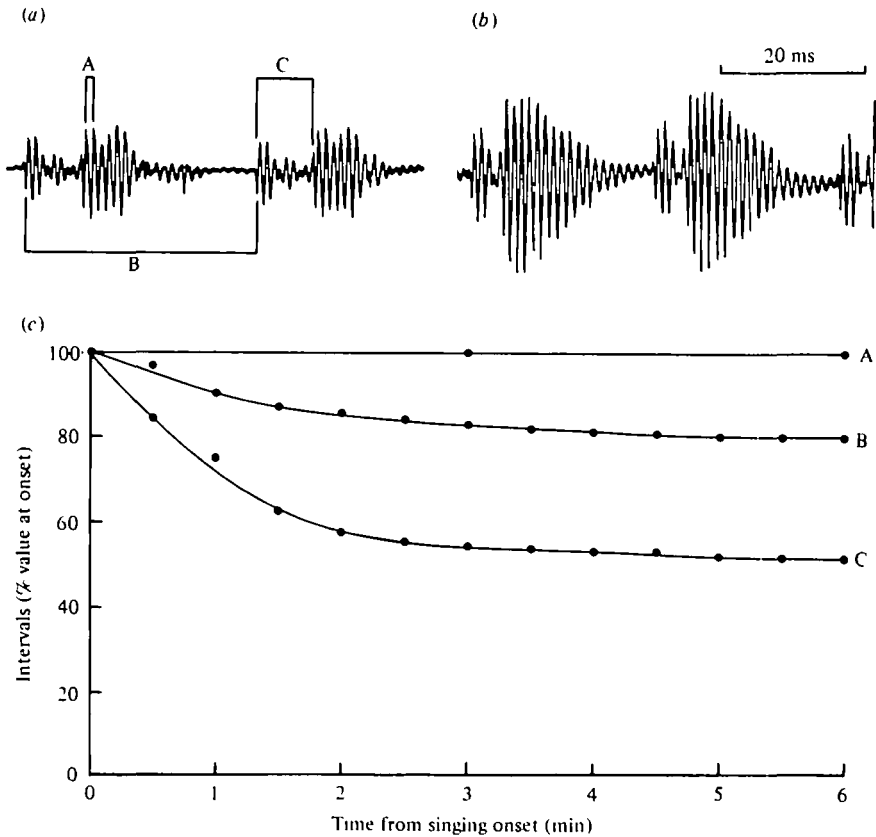


Fig. 4. Song parameters of an individual *Cystosoma saundersii* in which the ipsilateral tensor muscle and contralateral tymbal muscle have been severed. (a) Sample oscillogram of calling song a few seconds after onset, showing the intervals which are plotted in (c): sound period (A), cycle period (B) and pulse interval (C). (b) Sample of calling song 6 min after onset. Time scale also applies to (a). (c) Relative changes in intervals A, B, C, indicated in (a), during the first 6 min of song.

expectation (Fig. 4). The fundamental sound period remained constant at just under 1.2 ms. The cycle period shortened from about 31 ms at onset to just under 25 ms after 6 min. The interpulse interval shortened from 8.0 ms to about 4.1 ms after 6 min. The latter is proportionally a much larger change (Fig. 4c). For both the cycle period and interpulse interval the change followed a very similar time course to the rise in muscle temperature (cf. Figs. 2a, 4c). Although sound volume was not measured accurately, it was clear that there was a significant increase in volume, i.e. in pulse amplitude, as song progressed (cf. Fig. 4a, b). Most of this increase occurs in the first 3 min and so it is possible that it reflects the effect of temperature on the twitch tension of the tymbal muscle (see Discussion).

The fourth animal of this series was peculiar in that it sang in short bursts rather than continuously. The interpulse interval changed within each burst, becoming larger as the burst progressed. The impression given by this animal is that the tymbal muscle fatigued very readily, as evidenced by the increasing interpulse interval, the fatigue being relieved by the frequent breaks.

DISCUSSION

The tymbal muscle temperature excess recorded in the field (10.5°C) is an underestimate and the value recorded indoors (13.6°C) may be an overestimate due to the still air conditions of the room. The true value is probably about 12°C for ambient temperatures in the range $20\text{--}25^{\circ}\text{C}$. This accords well with the thoracic temperature excess range of $5\text{--}15^{\circ}\text{C}$, which is characteristic of medium to large insects (without special endothermic mechanisms) during flight (Krogh & Zeuthen, 1941; Church, 1960) or singing (Heath & Josephson, 1970; Josephson, 1973).

C. saundersii does not warm up before singing. This is understandable because the two principal methods, basking and shivering, are not available to it. Basking in the sun is not possible for an insect that sings at dusk and shivering is not possible because the tymbal is not moved by antagonistic muscles. Nevertheless, the warming and cooling curves (Fig. 2) closely resemble those from animals which do warm up prior to activity (e.g. Heath & Adams, 1967; Heath & Josephson, 1970; Heinrich & Bartholomew, 1971). The maximum warming rate of $4.4^{\circ}\text{C}/\text{min}$ falls in the centre of the range of warm up rates from other insects at ambient temperatures of $20\text{--}25^{\circ}\text{C}$ (table 1 in Heinrich & Bartholomew, 1971).

An interesting consequence of tymbal muscle warming is that some parameters of the song change as the song progresses (Fig. 4). From the point of view of intra-specific communication, the most reliable parameter is the fundamental sound frequency, which does not change, and the least reliable is the interpulse interval, which changes most. The nature of these effects agrees well with the mechanism of song generation put forward by Simmons & Young (1978). The lack of change in the fundamental sound frequency is consistent with its being determined primarily by physical factors. One would expect it to be temperature-sensitive if neuromuscular elements played a large part in determining it. The decrease in cycle period (= increase in motor neurone firing frequency) as song progresses, which is observed under natural conditions (Simmons & Young, 1978), is an expected consequence of the slight thoracic warming. In other cases, where thoracic muscles warm up prior to flight, the motor neurone firing frequency rises linearly with thoracic temperature (Heinrich & Bartholomew, 1971; Heinrich & Kammer, 1973). Similarly in orthopteran singing, a linear increase in wingstroke frequency (corresponding to motor neurone firing frequency) is observed with rising ambient temperature in those species where the thoracic muscles do not warm appreciably during singing (Walker, 1962, 1975*a*). However, in *Neoconocephalus robustus*, which warms up prior to singing, no increase in firing frequency is observed (Heath & Josephson, 1970).

The marked decrease in interpulse interval is exactly what was expected from the faster muscle contractions acting upon the tymbal rib buckling sequence. In orthopteran singing, the tooth-strike rate is the parameter which should be modified similarly by muscle contraction kinetics and this rises with ambient temperature, though not always linearly (Walker, 1962, 1975*b*). Similar relations between temperature and contraction kinetics have been reported for katydids (Josephson, 1973). However, in locust flight muscle, although twitch duration shortens with rising temperature, the tension developed remains unchanged (Neville & Weis-Fogh, 1963). Since the tymbal muscle contractions in *C. saundersii* become stronger as

well as faster with rising temperature (Fig. 3), this factor may well contribute significantly to the increasing pulse amplitude (= loudness of song) which is observed (Fig. 4*a, b*). Normally, contraction of the tensor muscle and extension of the abdomen also have this effect (Simmons & Young, 1978) but for these experiments the tensor muscle was disconnected and abdominal extension is usually complete before singing onset or within a few seconds of onset.

It is not at all obvious why the estimates of heat production by the two methods should be so different. Recently there has been controversy about the models used in estimating heat production from cooling curves (e.g. Strunk, 1971, 1974; Bakken & Gates, 1974; Bakken, 1976). However, our use of the cooling curve follows from the purely empirical use of an exponential function to describe cooling and assumes no particular model of the cooling process. The artificial heating method seemed to be a useful, and again entirely empirical, way of estimating heat production. An artificial heat source (a thermocouple) was used by Church (1960) to estimate heat transfer within the bodies of insects. This gave satisfactory results and he found no difference between living and dead insects.

In the present case there is one difference between the singing and non-singing insect, which may go some way towards explaining the discrepancy, and this is that there is actual movement of the tymbal muscles during twitch contractions when singing. This vibration at about 40 Hz will cause some mixing of the air in the air sac, though not a great deal judging by the temperature gradient, whereas the artificial heat source causes none. Consequently the artificial heat source will need to produce more heat than the paired tymbal muscles to generate a given temperature excess in the air sac. Similarly cooling will occur somewhat less rapidly after singing stops than during singing, whereas our use of the cooling curve assumes that there is no difference. Thus the cooling curve method will tend to underestimate heat production and the artificial heating method will tend to overestimate it. It is difficult to say whether this factor is sufficient to account for the discrepancy but it does illustrate the caution which needs to be exercised in estimating heat production in animals.

If the estimate from the cooling curve is used to calculate the metabolic rate, assuming an oxycalorific equivalent of 4.8 cal ml^{-1} , then the oxygen uptake is $1.0 \text{ ml min}^{-1} \text{ g muscle}^{-1}$. This value is on the low side compared to values obtained from other insects during warm up, flight and singing (Table 3 of Stevens & Josephson, 1977). Two reasons may be suggested for this. One is that the cooling curve may tend to underestimate heat production as explained above. The other is that a significant fraction of muscle energy will be expended in buckling the tymbal to produce sound; not all the energy will appear as heat. In tettigoniids (Counter, 1977) and mole crickets (Bennet-Clark, 1970), an appreciable part of the energy output of a singing animal appears as sound rather than heat and the same is likely to be the case in *Cystosoma*.

This work was supported by a grant from the Committee for Research and Graduate Studies of Melbourne University, by grant BNS 75-09530-AO1 from the National Science Foundation to R.K.J. and by a grant from the Guggenheim Foundation to R.K.J.

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