Hot-blooded singers: endothermy facilitates crepuscular signaling in African platypleurine cicadas (Hemiptera: Cicadidae: *Platypleura* spp.)

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Abstract The cicada genus *Platypleura* has a wide distribution across Africa and southern Asia. We describe endothermic thermoregulation in four South African species that show crepuscular signaling behavior. This is the first evidence of thermoregulation in platypleurine cicadas. Field measurements of body temperature (T_b) show that these animals regulate T_b through endogenous heat production. Maximum T_b measured was 22.1°C above ambient temperature during calling activity at dusk. The mean T_b during dusk activity did not differ from the mean T_b during diurnal activity. A unique behavior for cicadas, a temperature-dependent telescoping pulsation of the abdomen, was observed in the laboratory during endogenous warm-up. This behavior is part of a unique method of heat generation in endothermic cicadas. Males generally call from trunks and branches within the canopy and appear to use endothermy even when the sun is available to elevate T_b. Endothermy may provide the cicadas with the advantage of decreasing predation and acoustic competition by permitting calling from perches that most complement their cryptic coloration patterns and that ectotherms cannot use due to thermal constraints. In addition, endothermy may permit calling activity during crepuscular hours when atmospheric conditions are optimal for acoustic communication and predation risks are minimal.

Introduction

Animals must maintain body temperature (T_b) within a limited range in order for physiological systems to function effectively. Most cicadas are ectotherms that use solar radiation to regulate T_b (see summary in Sanborn *2002*). However, endothermy is a physiological thermoregulatory strategy used by some New World cicada tribes (Bartholomew and Barnhart *1984*; Sanborn et al. *1995*a, *1995*b; Sanborn *1997*; *2000*). We describe and quantify endothermic behavior in several species of African cicadas of the genus *Platypleura* Amyot & Serville. These species represent endothermic cicadas from an Old World tribe that has not been shown previously to contain endothermic species. It appears that endothermy allows crepuscular singing in these cicadas, which can have adaptive value for their acoustic ecology. Data for a related ectothermic platypleurine cicada, *Albanycada albigera* (Walker), which does not exhibit crepuscular acoustic activity, is provided for comparison. Although endothermy in other acoustic insects has been investigated in detail (see summary in Heinrich *1993*), the study of endothermy in cicadas has received much less attention (Bartholomew and Barnhart *1984*; Sanborn et al. *1995*a, *1995*b; Sanborn *1997*; *2000*).

Materials and methods

Albanycada albigera, *Platypleura capensis* (L.), *P. divisa* (Germar), *P. hirtipennis* (Germar), and *P.* cf. *brunea* Villet were collected in the Eastern Cape province of South Africa during December 2001. Animals captured for laboratory experimentation were placed on ice in a cardboard container with a moist paper towel to minimize metabolism during transport to the laboratory, where the specimens were placed in a refrigerator. Experiments were performed during the afternoon or evening of the day of capture. Live mass was recorded with a triple beam balance (O'Haus Scale Corporation, Cent-O-Gram Model CG 311) sensitive to ±5 mg.

T_b measurements were recorded with a Physitemp BAT-12 digital thermocouple thermometer with a type MT-29/1 29 gauge copper-constantan hypodermic microprobe sensitive to ±0.1°C and a time constant of 0.15 s^{-1} which had been calibrated to a National Institute of Standards and Technology mercury thermometer. All T_b measurements were made by inserting the thermocouple midway into the mesothorax to obtain thoracic temperature.

Field temperatures were recorded from insects captured with a net. The net was collapsed around the insect to restrict movement and the thermocouple probe was inserted through the net into the insect within 5 s of capture to obtain the T_b measurement. This procedure minimizes any heat transfer between the insect and the experimenter while orienting the animal for thermocouple insertion. The experimenter shaded the insect when diurnal T_b measurements were obtained, in order to prevent solar heating. Ambient temperature (T_a) was measured with the same equipment at a height of about 1 m in the shade immediately after the T_b measurement was recorded.

Heating and cooling curves of tethered animals were used to calculate metabolic rate during endothermic behavior. A flexible copper/constantan thermocouple probe was implanted into the dorsal mesothorax of a cicada to measure changes in T_b during activity. Each cicada was disturbed mechanically (prodded) or stimulated to fly in order to measure endogenous heat production. Individual specimens were then placed in a container after their T_b had reached a plateau and T_b was recorded as they cooled. T_b was measured every 15 s as they heated (up to 5 min) and cooled (for a period of 15 min) with the BAT-12 digital thermometer.

Heating and cooling curves constructed from these data were used to estimate the energetic expenditure involved in heating, using the techniques described in Heath and Adams (*1969*) and Sanborn et al. (*1995*b). Oxygen consumption $\left(V_{O_2}\left[\text{ml } O_2 \text{ min}^{-1}\right]\right)$ was determined using the formula:

$$V_{O_2} = \frac{(\Delta T \times \text{sp. ht.} \times \text{mass})}{O_2 \text{ cal. eq.}} + \frac{(Q_l)(T_{th} - T_a)}{O_2 \text{ cal. eq.}}$$

Where ΔT = rate of change of temperature during heating (°C min^{-1}), sp. ht. = specific heat of the object [0.83 cal g^{-1} °C^{-1} (Bartholomew *1981*)], mass = thoracic mass (g), O_2 cal. eq. = the caloric equivalent of oxygen (4.8 cal ml $O_2{}^{-1}$), Q_l = heat loss to the environment (cal min^{-1} °C^{-1}), and (T_{th} – T_a) = thoracic temperature minus ambient temperature (°C). We calculated V_{O2} so we could make direct comparisons to other cicada data in the literature.

Bartholomew and Barnhart (*1984*) found the flight musculature of *Fidicina mannifera* (Fabricius) to be 35% of the total body mass. Sanborn et al. (*1995*a) confirmed this figure for another species, so we used 35% of total mass in all calculations.

The platypleurine cicadas were found to exhibit a characteristic telescoping of the abdomen while endogenously warming. We measured the rate of abdominal pumping while the animals were tethered to a thermocouple to determine whether the rate was temperature-dependent. The number of complete pumping cycles was counted for 10 s. The 10 s period was started and stopped by a second individual who also recorded the T_b of the tethered animal.

All data are reported as mean ± standard deviation. Two-tailed *t*-tests were used to compare means. Statistical significance is considered to be $\alpha=0.05$ for all tests.

Results

The range of T_b of calling males was 37.3–41.1°C in *P. capensis* and 32.7–40.8°C in *P. hirtipennis*. There was no statistical difference between T_b measured in diurnally calling males and those calling in the evening without access to solar radiation [39.2±1.19 (*n*=10) and 40.2±1.03 (*n*=9), respectively; *t*=1.904, *P*=0.963 for *P. capensis* and 38.9±2.27 (*n*=13) and 38.8±1.40 (*n*=12), respectively; *t*=0.1717, *P*=0.567 for *P. hirtipennis*]. T_b measured in animals without access to solar radiation was 19.8±1.17°C (*n*=9) and 16.9±1.81°C (*n*=12) above T_a in *P. capensis* and *P. hirtipennis*, respectively. Maximum recorded T_b elevation for *P. capensis* and *P. hirtipennis* during the evening chorus were 22.1°C and 20.7°C above T_a, respectively.

The slope of the regression of T_b as a function of T_a is an indication of T_b regulation (see Table 1). Thermoregulation is occurring if the slope of the regression is significantly different from one or not significantly different from zero (May *1985*). Specimens of *A. albigera* were seen to thermoregulate behaviorally, i.e., to change body orientation to the sun and perch location, as the thermal environment changed throughout the day. *Albanycada albigera* calls only when the sun is available as a radiant heat source, and does not call when the sun is obscured by clouds, or at dawn or dusk. The slope of the regression of T_b as a function of T_a is not significantly different from zero ($F_{1,20}=3.964$, *P*=0.0603), suggesting that *A. albigera* thermoregulates behaviorally.

Table 1. Statistics calculated from regression analysis of T_b as a function of T_a in platypleurine cicadas. Probability value is significance from a slope of zero. Although *A. albigera* is ectothermic and the two *Platypleura* species are endothermic, all species thermoregulate

Species	Slope	Intercept	*r*	*F* (*df*)	*P* value
A. albigera	0.055	33.57	0.0757	3.964 (1,20)	0.0603
P. capensis	–0.159	43.32	–0.3524	2.040 (1,19)	0.1694
P. hirtipennis	0.088	36.65	0.1694	0.6797 (1,23)	0.4181

The distribution of T_b as a function of T_a in *P. capensis* and *P. hirtipennis* is similar to the pattern seen in the ectothermic *A. albigera*, even when solar radiation is not available for heating, suggesting that these species are thermoregulating using endothermy. Again the slopes of the regressions are not significantly different from zero ($F_{1,19}$=2.040, P=0.1694 for *P. capensis*; $F_{1,23}$=0.6797, P=0. 4181 for *P. hirtipennis*), confirming active thermoregulation.

The rate at which *Platypleura* species cool follows Newton's law of cooling, suggesting that the animals do not regulate heat loss. Heat production occurred without visible wing movement or vibration from the flight muscles. All specimens that were increasing their T_b endothermically exhibited a characteristic abdominal movement not seen previously in other endothermic cicadas. The abdomen was alternately extended and withdrawn in a telescoping manner during endothermic warm-up, probably to facilitate ventilation to provide sufficient O_2 for endogenous heat production. The rate of these telescoping movements was correlated with T_b (Fig. 1) with a significant relationship between telescoping frequency and body temperature ($F_{1,8}$=7.568, P=0. 0250). Maximal calculated oxygen consumption (V_{O2max}) and cooling rates are summarized in Table 2 for four species of *Platypleura* that exhibited endothermic behavior in the laboratory.
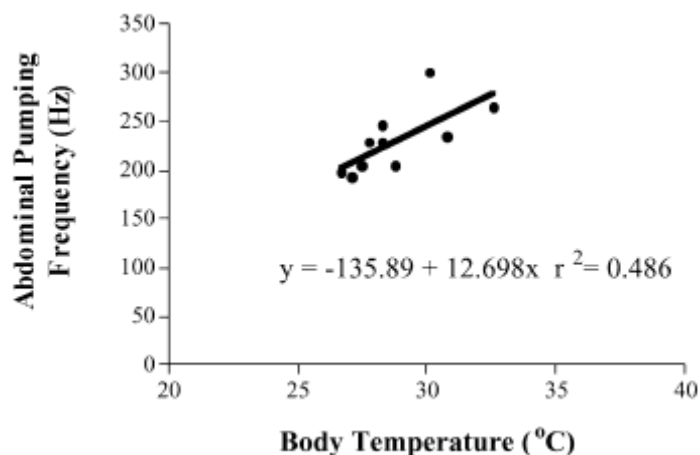

$$y = -135.89 + 12.698x \quad r^2 = 0.486$$

Fig. 1. Rate of abdominal pumping frequency (Hz) as a function of body temperature (T_b, °C) in *Platypleura capensis*

Table 2. Cooling rate and oxygen consumption of endothermic platypleurine cicadas

Species	Body mass (g)	Cooling rate (°C min^{-1} °C gradient^{-1})	V_{O2} (ml O$_2$ min^{-1})
P. capensis	0.581 ± 0.064	0.153 ± 0.011	0.332 ± 0.060
	($n = 8$)	($n = 8$)	($n = 8$)
P. hirtipennis	0.802 ± 0.101	0.186 ± 0.042	0.642 ± 0.260
	($n = 6$)	($n = 6$)	($n = 6$)
P. divisa	0.683 ± 0.126	0.199 ± 0.040	0.465 ± 0.137
	($n = 5$)	($n = 5$)	($n = 4$)
P. cf. *brunea*	0.893 ± 0.205	0.893 ± 0.177	0.631 ± 0.282
	($n = 4$)	($n = 4$)	($n = 4$)

Discussion

Albanycada albigera is a platypleurine cicada that thermoregulates ectothermically and does not call at dawn or dusk. Specimens were observed to use changes in body orientation and perch selection to regulate radiant solar uptake and maintain T_b in a range necessary to coordinate activity. This is the general pattern of thermoregulation found in many cicada species (see summary in Sanborn *2002*).

A similar pattern of thermoregulation is seen in two endothermic species of *Platypleura* that sing during crepuscular hours. The distribution of T_bs in these endothermic species is similar to that seen in the ectotherm. The T_b regulation through endogenous heat occurs in a manner similar to that observed in other endothermic cicada species (Sanborn et al. *1995*a, *1995*b; Sanborn *2000*). These platypleurines call from shaded perches within the canopy, where T_b would approximate T_a if not for the endogenous heat production in this shaded environment. They tend to avoid basking in spots of sunlight on the large branches or trunks that serve as perches. This behavior contrasts with the facultative endothermy described in New World cicadas, where solar radiation is used to regulate T_b (Sanborn et al. *1995*a, *1995*b; Sanborn *2000*). These platypleurines appear to regulate T_b exclusively with endogenous heat.

The four *Platypleura* species were able to elevate T_b without flight or visible wing movements, and no vibrations were felt in the temperature probe during endogenous heat generation. The endothermic cicada *Tibicen winnemanna* (Davis) (tribe Tibicenini) has also been observed to elevate T_b without wing movements (Sanborn *2000*). In contrast, *Fidicina mannifera* (Fabricius) (tribe Fidicinini) was described as producing small wing movements while endothermically warming (Bartholomew and Barnhart *1984*). *Proarna bergi* (Distant) and *P. insignis* Distant (tribe Fidicinini) produced shiver-like movements of the wings during heat generation (Sanborn et al. *1995*a). Heat generation in the platypleurines may be through a mechanism similar to that described in bees (Surholt et al. *1990*), since no wing movements were observed.

The high-frequency, temperature-dependent telescoping movements of the abdomen observed in the platypleurine species that were endothermically warming is a unique behavior in endothermic cicadas. Bartholomew and Barnhart (*1984*) described minute movements of the abdomen occurring at a rate of 15–36 min^{-1} during non-flapping warm-up in *F. mannifera*. The telescoping abdominal movements of *P. capensis* were correlated to T_b and occurred at frequencies as high as 300 min^{-1} (Fig. 1). The abdominal movements probably function to increase ventilation and O_2 availability to the muscles during warm-up (Bartholomew and Barnhart *1984*).

The rate at which the four *Platypleura* species cool (Table 2) is partially related to their size. However, when compared to other cicadas, they cool more slowly than larger endothermic species (Sanborn et al. *1995*b). This relationship may be related to phylogenetic differences in the general body shape of species in different tribes. Platypleurines are generally short-bodied and stocky. This shape has a lower surface to volume ratio than a longer, thinner cicada. Decreasing the surface to volume ratio decreases the animal's cooling rate. It is advantageous for endothermic platypleurines to have a lower cooling rate since they do not appear to use solar radiation for thermoregulation and are completely dependent on endogenous heat.

The rate of heat production in these platypleurine cicadas is greater than would be predicted based on their body size. The data for all four *Platypleura* species is similar to much larger endothermic

cicadas (Sanborn et al. *1995*b; Sanborn *2000*). This is probably related to the fact that endothermic platypleurines regulate T_b with endogenous heat at all times of the day, since they avoid sunlit perches, instead of the facultative endothermy observed in endothermic cicadas of other tribes.

Endothermy in these platypleurines may provide many of the same benefits that have been described in other cicada species (Sanborn et al. *1995*a, *1995*b; Sanborn *2000*). We hypothesize that they receive three potential benefits from endothermy. First, endothermy may decrease predation risks. Endothermic *Platypleura* species are able to use shaded perches that maximize their cryptic coloration. Thermoregulation through endogenous heat permits the species to call from the large branches under the canopy of the trees in their habitat. The cicadas are not required to have access to solar radiation in order to elevate T_b to the range necessary for song production (Sanborn *2001*) and are not exposed to potential predators while basking in the sun. In addition, calling at dusk may also decrease predation risk due to the decrease in avian foraging efficiency with decreasing light intensities (Kacelnik *1979*). Secondly, endothermy may permit these species to choose a habitat that is unavailable to strictly ectothermic species. The spatial separation of the habitat may decrease competition with other species for calling sites or resources for the nymphs, and sound attenuation due to scattering and absorption by the vegetation will be reduced by selecting perches above the undergrowth and the ground, but within the canopy (Wiley and Richards *1978*). Finally, endothermy permits calling at dawn and dusk when sound travels farther in the environment (Henwood and Fabrick *1979*; Wiley and Richards *1978*). This will increase the potential number of mates with which an animal can interact.

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