

Endothermy in African Platyleurine Cicadas: The Influence of Body Size and Habitat (Hemiptera: Cicadidae)

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ABSTRACT

The platyleurine cicadas have a wide distribution across Africa and southern Asia. We investigate endothermy as a thermoregulatory strategy in 11 South African species from five genera, with comparisons to the lone ectothermic platyleurine we found, in an attempt to ascertain any influence that habitat and/or body size have on the expression of endothermy in the platyleurine cicadas. Field measurements of body temperature (T_b) show that these animals regulate T_b through endogenous heat production. Heat production in the laboratory elevated T_b to the same range as in animals active in the field. Maximum T_b measured during calling activity when there was no access to solar radiation ranged from 13.2° to 22.3°C above ambient temperature in the five species measured. The mean T_b during activity without access to solar radiation did not differ from the mean T_b during diurnal activity. All platyleurines exhibit a unique behavior for cicadas while warming endogenously, a temperature-dependent telescoping pulsation of the abdomen that probably functions in ventilation. Platyleurines generally call from trunks and branches within the canopy and appear to rely on endothermy even when the sun is available to elevate T_b , in contrast to the facultative endothermy exhibited by New World endothermic species. The two exceptions to this generalization we found within the platyleurines are *Platyleura wahlbergi* and *Albanycada albigera*, which were the smallest species studied. The small size of *P. wahlbergi* appears to have altered their thermoregulatory strategy to one of facultative endothermy, whereby they use the sun when it is available to

facilitate increases in T_b . *Albanycada albigera* is the only ectothermic platyleurine we found. The habitat and host plant association of *A. albigera* appear to have influenced the choice of ectothermy as a thermoregulatory strategy, as the species possesses the metabolic machinery to elevate to the T_b range observed in the endothermic species. Therefore, size and habitat appear to influence the expression of thermoregulatory strategies in African platyleurine cicadas.

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. 1995a, 1995b; Sanborn 1997, 2000) and the African platyleurines (Sanborn et al. 2003b; Villet et al. 2003). We describe and quantify endothermic behavior in several species of African cicadas of the platyleurine tribe in this study. The platyleurines contrast with the New World endothermic cicadas in that endothermy appears to be the main mechanism of thermoregulation, rather than a means to supplement radiant solar energy in the thermoregulatory process. It appears that endothermy allows crepuscular singing in these cicadas, which can have adaptive value for their acoustic ecology and predator avoidance (Sanborn et al. 2003b; Villet et al. 2003). Data for a related ectothermic platyleurine cicada, *Albanycada albigera* (Walker), that does not exhibit crepuscular acoustic activity are 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. 1995a, 1995b, 2003b; Sanborn 1997, 2000; Villet et al. 2003). The widespread use of endothermy in the platyleurines as a group provides a unique opportunity to investigate the potential influence of body size and habitat choice on the evolution of various thermoregulatory strategies within the platyleurine cicadas.

Material and Methods

Twelve species in six genera (Table 1) were collected in the Eastern and Western Cape provinces of South Africa during

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Table 1: Live mass, cooling rate, and oxygen consumption of platypleurine cicadas

Species	Body Mass ^a (g)	Cooling Rate ^a (°C min ⁻¹ °C gradient ⁻¹)	\dot{V}_{O_2} ^a (mL O ₂ min ⁻¹)	Maximal Gradient Capable of Producing En- dothermically (°C)
<i>Albanycada albiger</i> a (Walker)	.359 ± .067 (8)	.410 ± .046 (8)	.176 ± .060 (8)	19.79
<i>Kongota punctigera</i> (Walker)	.675 ± .007 (2)			
<i>Azanicada zuluensis</i> (Villet)	.724 ± .061 (8)	.281 ± .094 (8)	.524 ± .232 (8)	42.58
<i>Capcicada decora</i> (Germar)	.749 ± .175 (5)	.273 ± .064 (5)	.423 ± .202 (5)	34.14
<i>Platypleura capensis</i> (L.) ^b	.581 ± .064 (8)	.153 ± .011 (8)	.173 ± .058 (8)	32.21
<i>Platypleura divisa</i> (Germar) ^b	.683 ± .126 (5)	.199 ± .040 (5)	.187 ± .060 (4)	22.66
<i>Platypleura hirtipennis</i> (Germar) ^b	.802 ± .101 (6)	.186 ± .042 (6)	.354 ± .218 (6)	39.17
<i>Platypleura plumosa</i> (Germar)	.768 ± .137 (5)	.288 ± .021(5)	.483 ± .226 (5)	36.08
<i>Platypleura wahlbergi</i> (Stål)	.385 ± .056 (8)	.306 ± .063 (8)	.233 ± .112 (8)	32.68
<i>Platypleura cf. brunnea</i> (Villet) ^b	.893 ± .205 (4)	.177 ± .049 (4)	.327 ± .104 (4)	34.26
<i>Platypleura sp. 4</i> (Villet)	.676 ± .059 (5)	.399 ± .066 (5)	.328 ± .104 (5)	20.11
<i>Pycna semiclara</i> (Germar) ^c	.978 ± .153 (5)	.154 ± .027 (5)	.362 (1)	39.71

^a Number of individuals in parentheses.

^b Sanborn et al. 2003a.

^c Villet et al. 2003.

December 2001 and 2002 and January 2003. 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 until experiments could be performed. All 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.

Measurements of T_b were recorded with a type MT-29/1 29-gauge copper-constantan hypodermic microprobe and a digital thermometer sensitive to ± 0.1°C and a time constant of 0.15 s⁻¹ connected to a Physitemp BAT-12 digital thermocouple thermometer. The thermocouple probe 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 hand 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 to prevent solar heating when diurnal T_b measurements were obtained. Ambient temperature (T_a) was measured with the same equipment at a height of about 1 m above ground 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 warm-up. A flexible, 36-gauge copper-constantan thermocouple probe was implanted into the dorsal mesothorax of a cicada through a small piece of cork attached with glue (3M Super Weatherstrip Adhesive) and connected to the BAT-12 digital thermometer to measure changes to T_b during activity. Each cicada was prodded or stimulated to fly in order to measure endogenous heat production, and T_b was measured every 15 s as the individuals heated. The individual specimens were placed in a container after their T_b had reached a plateau or after 5 min, and T_b was recorded as they cooled for a period of 15 min.

The techniques described in Heath and Adams (1969) and Sanborn et al. (1995b) were used to construct heating and cooling curves from these data to estimate the energetic expenditure involved in heating. Oxygen consumption (\dot{V}_{O_2} [mL O₂ min⁻¹]) was determined using the formula

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

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), O₂ cal. eq. = the caloric equivalent of oxygen (4.8 cal mL O₂⁻¹), Q_l = heat loss to the environment (cal min⁻¹ °C⁻¹), and ($T_{th} - T_a$) = thoracic temperature minus ambient temperature (°C). \dot{V}_{O_2} was calculated so that we could make direct comparisons to other cicada data in the literature.

Bartholomew and Barnhart (1984) found the flight mus-

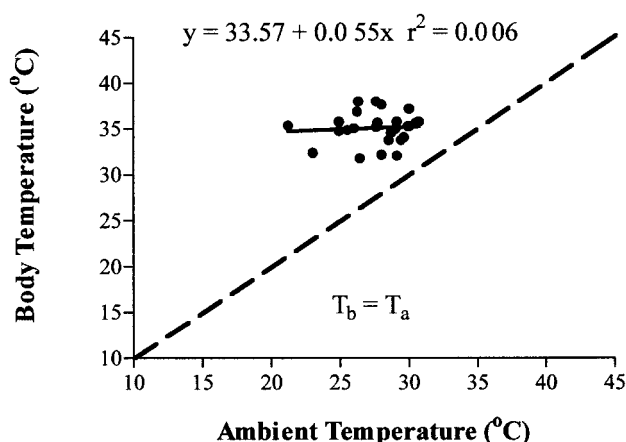


Figure 1. Body temperature as a function of ambient temperature in the ectothermic *Albanycada albigerana*. The slope is not significantly different from 0, suggesting thermoregulation.

culture of *Fidicina mannifera* (Fabricius) to be 35% of the total body mass. Sanborn et al. (1995a) confirmed this figure for two species of *Proarna*, so we used 35% of total mass in all calculations.

All data are reported as mean \pm standard deviation. Instat (GraphPad Software) was used in the statistical analyses. Two-tailed *t*-tests were used to compare means. Statistical significance is considered to be $\alpha = 0.05$ for all tests.

Results

Thermoregulation is indicated if the slope of the regression of T_b as a function of T_a is significantly different from 1 or not significantly different from 0 (May 1985). *Albanycada albigerana* did not follow the characteristic behaviors exhibited by the other platypleurines. Specimens of *A. albigerana* were observed to thermoregulate behaviorally; that is, they used the sun as a radiant heat source, along with changes to body orientation and perch location, to regulate T_b as the thermal environment changed throughout the day. *Albanycada albigerana* was observed to call only when the sun was available as a heat source, and it 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 0 ($F_{1,25} = 0.1383$, $P = 0.7133$), suggesting that *A. albigerana* thermoregulates through behavior (Fig. 1).

The distribution of T_b as a function of T_a in the endothermic platypleurines is similar to that seen in the ectothermic *A. albigerana*. Thermoregulation continues 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 0 ($F_{1,24} = 0.6797$, $P = 0.4181$ for *Platypleura hirtipennis*; $F_{1,7} = 0.2857$, $P = 0.6095$ for *P. plumosa*) or significantly different from 1

($t = -11.363$, $df = 16$, $P \ll 0.0001$ for *P. capensis*; $t = -3.827$, $df = 10$, $P = 0.0017$ for *P. wahlbergi*), confirming active thermoregulation (Figs. 2–5).

The range of T_b of calling males was 37.3°–41.1°C in *P. capensis*, 32.7°–40.8°C in *P. hirtipennis*, 36.9°–39.1°C in *P. plumosa*, and 34.2°–40.6°C in *P. wahlbergi*. There was no statistical difference between T_b measured in diurnally calling males and those calling in the evening without access to solar radiation ($39.2^\circ \pm 1.19^\circ\text{C}$ [$n = 10$] and $40.2^\circ \pm 1.03^\circ\text{C}$ [$n = 9$], respectively; $t = 1.904$, $P = 0.963$) for *P. capensis*, ($38.9^\circ \pm 2.27^\circ\text{C}$ [$n = 13$] and $38.8^\circ \pm 1.40^\circ\text{C}$ [$n = 12$], respectively; $t = 0.1717$, $P = 0.567$) *P. hirtipennis*, and ($38.16^\circ \pm 1.11^\circ\text{C}$ [$n = 5$] and $37.75^\circ \pm 0.31^\circ\text{C}$ [$n = 4$], respectively; $t = 0.7090$, $P = 0.501$) *P. plumosa*. Although there is a significant difference in the means for *P. wahlbergi* ($38.57^\circ \pm 1.55^\circ\text{C}$ [$n = 10$] and $35.9^\circ \pm 1.75^\circ\text{C}$ [$n = 3$], respectively; $t = 2.555$, $P = 0.027$), this is probably due to the very low sample size of the evening measurements, as two of the three values are within the range of T_b measured during the day. T_b measured in animals without access to solar radiation was $19.8^\circ \pm 1.17^\circ\text{C}$ ($n = 9$), $16.9^\circ \pm 1.81^\circ\text{C}$ ($n = 12$), $19.63^\circ \pm 0.39^\circ\text{C}$ ($n = 4$), and $13.27^\circ \pm 1.70^\circ\text{C}$ ($n = 3$) above T_a in *P. capensis*, *P. hirtipennis*, *P. plumosa*, and *P. wahlbergi*, respectively. Maximum recorded T_b elevations for *P. capensis* and *P. hirtipennis* during the evening chorus were 22.1° and 20.7°C above T_a , respectively.

The rate at which platypleurine species cool follows Newton's law of cooling, suggesting that the animals do not regulate heat loss. Heat production in all species occurred without visible wing movement or tangible vibration from the flight muscles. Specimens of all genera that were increasing their T_b endothermically exhibited a characteristic abdominal movement that

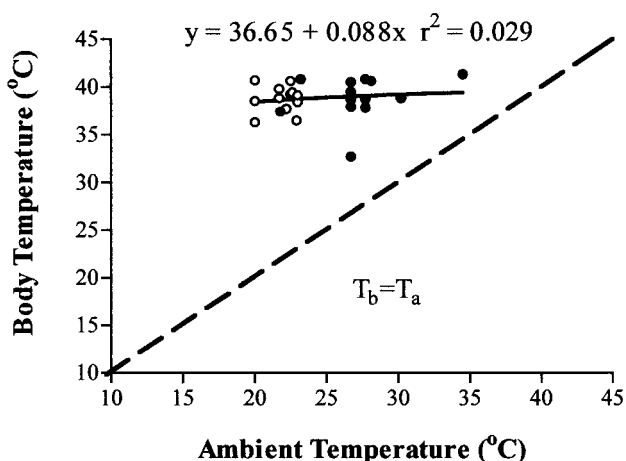


Figure 2. Body temperature as a function of ambient temperature in the endothermic *Platypleura hirtipennis*. The slope is significantly different from 1, suggesting thermoregulation. Filled circles represent diurnally calling animals, and open circles represent animals calling without access to solar radiation.

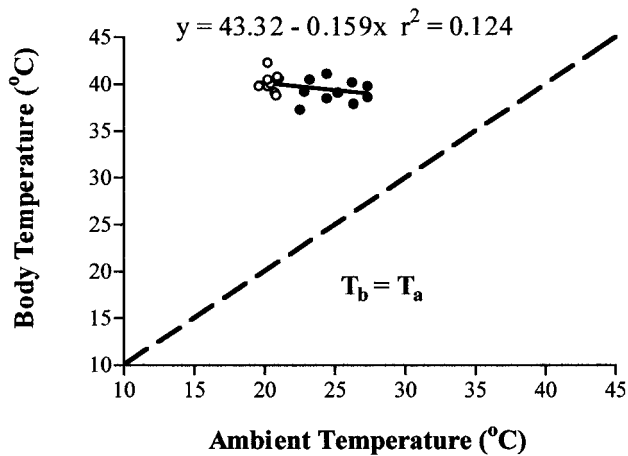


Figure 3. Body temperature as a function of ambient temperature in the endothermic *Platypleura capensis*. The slope is significantly different from 1, suggesting thermoregulation. Filled circles represent diurnally calling animals; open circles represent animals calling without access to solar radiation.

is unique in the cicadas to the platypleurines. 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. Maximal calculated oxygen consumption ($\dot{V}O_{2max}$) and cooling rates are summarized in Table 1 for all the platypleurine species studied except *Kongota punctigera*, of which only the second of the two specimens collected exhibited the abdominal pumping in the laboratory and we were unable to collect additional specimens for experimentation.

The habitats, host(s), and microhabitat choices for the platypleurines studied are listed in Table 2. The host plant(s) listed represent consistent associations of the adults with the plants and include observations of adults feeding on the plants. We were not able to substantiate nymphal feeding with the plant species.

Discussion

The platypleurine cicadas contrast with most cicada groups in that the platypleurines regulate T_b almost exclusively through endothermy. Endothermy appears to be the ancestral system in the group, as it is found in most of the species studied from multiple genera. The selection pressures for the group must have been strong, since we were able to find only one species that regulated T_b through behavioral methods. There appears to be an influence of habitat choice on the use of ectothermy rather than endothermy in *Albanycada albigera*. It is not a result of size, because *Platypleura wahlbergi* does not differ significantly in size ($t = 0.8542$, $df = 14$, $P = 0.4074$), yet *P. wahlbergi* is endothermic and will call at dusk.

Albanycada albigera thermoregulates (Fig. 1) 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). However, *A. albigera* is also able to generate sufficient heat to maintain elevated thermal gradients similar to those of the endothermic species (Table 1). It appears to be capable of using endothermy, but other selection factors have determined that ectothermy is a better thermoregulatory strategy in *A. albigera*. The colonization of the valley bushveld habitat may have been an important stimulus in the loss of endothermy in *A. albigera*. The bushveld and the host species provided the opportunity to use radiant solar energy and to use exposed perches as calling sites in place of the shaded perches in the understory used by the majority of platypleurines (Table 2).

A similar pattern of thermoregulation is seen in the endothermic species of *Platypleura* that sing during crepuscular hours. The distribution of T_b (Figs. 2–5) in these endothermic species is similar to that seen in the ectotherm (Fig. 1). Furthermore, there is no difference in the mean T_b of active animals with the potential to use solar radiation and those calling at dusk. These data are very similar to the 35.3°–40.3°C T_b range of calling *Pycna semiclara*, whose diurnal and dusk T_b 's also do not differ significantly (Villet et al. 2003). The T_b regulation through endogenous heat occurs in a manner similar to that observed in New World endothermic cicada species (Sanborn et al. 1995a, 1995b; Sanborn 2000). The endothermic platypleurines call from shaded perches within the canopy, where T_b would approximate T_a if not for the endogenous heat pro-

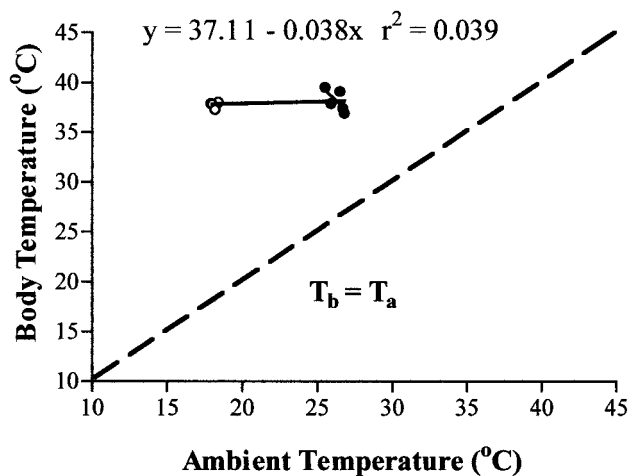


Figure 4. Body temperature as a function of ambient temperature in the endothermic *Platypleura plumosa*. The slope is significantly different from 1, suggesting thermoregulation. Filled circles represent diurnally calling animals, and open circles represent animals calling without access to solar radiation.

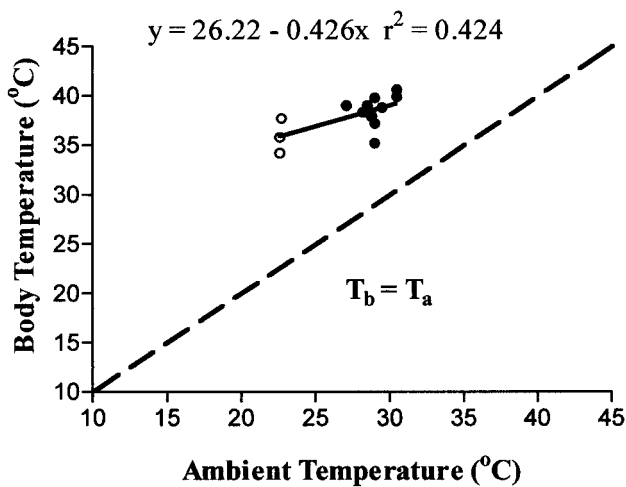


Figure 5. Body temperature as a function of ambient temperature in the endothermic *Platycleura wahlbergi*. The slope is significantly different from 1, suggesting thermoregulation. Filled circles represent diurnally calling animals, and open circles represent animals calling without access to solar radiation.

duction in this heavily 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 when it is available to the animals (Sanborn et al. 1995a, 1995b; Sanborn 2000, 2004). Most platycleurines appear to regulate T_b exclusively with endogenous heat.

The exception to the generalization that platycleurines use endothermy exclusively for thermoregulation that we found is *P. wahlbergi*. This is the smallest of the African platycleurines used in this study (Table 1), and like the New World cicadas it employs facultative endothermy (Sanborn et al. 1995a, 1995b; Sanborn 2000, 2004). *Platycleura wahlbergi* were observed to use the sun as a heat source when it was available but used metabolic energy at dusk to elevate T_b . The more rapid heat transfer of the smaller animal may support the use of facultative endothermy by *P. wahlbergi*. Facultative endothermy permits the conservation of metabolic energy by using radiant solar energy when it is available. The smaller size of *P. wahlbergi* would require greater metabolic cost to maintain the same T_b difference through endothermy as a larger platycleurine due to a more rapid rate of heat loss. Switching to facultative endothermy will increase the survival time of the animals while maintaining the benefits of endothermy in the platycleurines.

All endothermic platycleurine 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 with-

out wing movements (Sanborn 2000). In contrast, *Fidicina mannifera* (Fabricius; tribe Fidicinini) was described as producing small wing movements while warming endothermically (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. 1995a). Heat generation in the platycleurines may be through a mechanism similar to the tetanic contractions described during warm-up in bees (Esch and Goller 1991), since no wing movements were observed or vibrations felt in the temperature probe. Circumstantial evidence to support this method of heat generation comes from the inability to stimulate flight activity in animals exhibiting abdominal movements characteristic of endogenously warming animals.

The platycleurines produce a characteristic telescoping abdominal movement while warming endothermically that is a unique behavior in endothermic cicadas. The rate of the telescoping abdominal movements of *P. capensis* was correlated to T_b and occurred at frequencies as high as 300 min^{-1} (Sanborn et al. 2003b). Bartholomew and Barnhart (1984) described minute movements of the abdomen in *F. mannifera*, occurring at a rate of $15\text{--}36 \text{ min}^{-1}$ during nonflapping warm-up. The abdominal movements probably function to increase ventilation and O_2 availability to the muscles during warm-up (Bartholomew and Barnhart 1984; Sanborn et al. 2003b).

The allometric relationship between $\dot{V}\text{O}_{2\text{max}}$ and body size for cicadas is illustrated in Figure 6. $\dot{V}\text{O}_{2\text{max}}$ scales with body size with a slope of 0.76 in cicadas as a group, a value first shown through scaling by Kleiber (1932). The lowest absolute values of $\dot{V}\text{O}_{2\text{max}}$ are not produced by the smallest species, *A. albigera* and *P. wahlbergi*. The lowest mean value we determined for a species was in *P. capensis*, a complete endotherm. The lower cooling rate in *P. capensis* may facilitate the reliance on endothermy when compared to the ectothermic *A. albigera*.

The rate at which the platycleurine species cool (Table 2) is related to their size but also appears to be related, in part, to their habitat and choice of thermoregulatory strategy. For example, *A. albigera* has the highest cooling rate of the species examined in this study. The higher cooling rate is advantageous in the selected microhabitat, which exposes the animals to the sun and a more elevated T_a and thus to a potentially higher T_b . Figure 7 illustrates the allometric relationship between cooling rate and body size in cicadas as a group. It is interesting to note that in general, the endotherms have lower cooling rates than the ectotherms, with many of the endothermic platycleurines having very low cooling rates. The exception in the endothermic platycleurines is *Platycleura* sp. n. Again, habitat may play a role in the deviation from the generalized relationship, in that *Platycleura* sp. n. inhabits the semiarid Karoo, which has the potential to become much warmer than the understory habitats of the other endothermic platycleurines. The lowest cooling rates are found in species that are restricted to understory habitats and avoid the sun.

Table 2: Habitat, host associations, and microhabitat choice in the studied African platypleurine cicadas

Species	Habitat	Host Species	Microhabitat Selection
<i>Albanycada albigera</i>	Valley bushveld	<i>Portulacaria afra</i> , <i>Euclea</i> spp., <i>Euphorbia bothae</i>	Exposed branches of bushes
<i>Kongota punctigera</i>	Coastal dune thicket	Various forest trees	Trunks and main branches of various trees, in shade and above herb layer
<i>Azanicada zuluensis</i>	Coastal dune thicket	<i>Maytenus undata</i>	Trunks and main branches of <i>M. undata</i> trees, in shade and above herb layer
<i>Capcicada decora</i>	Fynbos	<i>Protea grandiflora</i> and other <i>Protea</i> species	Trunks and main branches of <i>Protea</i> trees, which tend to have a relatively open growth form; the insects sit in the shade.
<i>Platypleura capensis</i>	Fynbos and Renosterveld, coastal and inland	<i>Brachylaena discolor</i> , <i>Chrysanthemoides monilifera</i> , and various heaths	Interiors of bushes of suitable hosts
<i>Platypleura divisa</i>	Various forms of open bushveld, bushclump savanna, and closed riverine thicket	<i>Maytenus heterophylla</i>	Interiors of <i>M. heterophylla</i> bushes
<i>Platypleura hirtipennis</i>	<i>Acacia</i> thornveld, secondary regrowth in disturbed habitats	<i>Acacia karroo</i>	Interior trunks and branches of <i>A. karroo</i> trees
<i>Platypleura plumose</i>	In karoid areas with <i>Acacia</i> thornveld, riverine thicket, or secondary regrowth in disturbed habitats	<i>A. karroo</i>	Interior trunks and branches of <i>A. karroo</i> trees
<i>Platypleura wahlbergi</i>	Mixed thicket, and disturbed habitats invaded by <i>A. karroo</i>	<i>A. karroo</i> , an unidentified composite, and various woods herbs	Exposed stems of shrubs and small trees, and interior branches of small <i>A. karroo</i> trees
<i>Platypleura</i> cf. <i>brunnea</i>	Coastal and inland forests	Various forest trees	Trunks and lower branches of trees in shade, above herb layer
<i>Platypleura</i> sp. n.	Karoo thornveld	<i>A. karroo</i>	Interior trunks and branches of <i>A. karroo</i> trees
<i>Pycna semiclara</i>	Coastal and inland forest, rarely in thickets	Various forest and commercial plantation trees, stands of oak (<i>Quercus</i> spp.), pines (<i>Pinus</i> spp.), gums (<i>Eucalyptus</i> spp.), and cottonwood (<i>Populus</i> spp.) with closed canopies	Trunks and thickest branches of various trees, in shade and above herb layer

Endothermy in the platyleurines has been hypothesized to provide several potential benefits to the cicadas (Sanborn et al. 2003b; Villet et al. 2003). It may decrease predation risks. Endothermic platyleurines are able to use shaded perches that maximize the benefits of their cryptic coloration. Endothermy permits the species to call from the large branches under the canopy of the trees in their habitat, where they are protected not only by the lower light levels in the microhabitat but also by the large spines found on the host species. The endothermic cicadas are not required to have access to solar radiation in order to elevate T_b to the range necessary for song production (Sanborn et al. 1995b; Sanborn 2001; Villet et al. 2003; Figs. 2–5) and are not exposed to potential predators while basking in the sun. Calling at dusk may also decrease predation risk due to a decrease in avian foraging efficiency that occurs with decreasing light intensities (Kacelnik 1979). Endothermy may permit these species to choose a habitat that is unavailable to strictly ectothermic species. Although some species are able to adapt thermally to cooler microclimates (Sanborn et al. 2003a), endothermy permits the use of cooler microclimates that do not have radiant energy available for thermoregulation. The spatial separation of habitats permitted by endothermy may decrease competition with other species for calling sites or resources for the nymphs. This spatial separation may also decrease sound attenuation due to scattering and absorption by the vegetation, by permitting the endotherms to select perches above the undergrowth and the ground but within the canopy (Wiley and Richards 1978). Endothermy permits calling at dawn and dusk, when sound travels farther in the environment (Wiley and Richards 1978; Henwood and Fabrick 1979), which

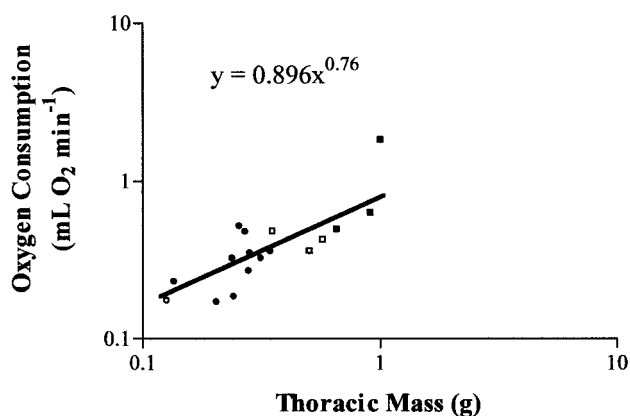


Figure 6. Allometric relationship between maximum calculated $\dot{V}O_2$ and body size in cicadas. Values represent the mean value determined for each species ($n = 1-8$). Filled circles represent endothermic platyleurines, the open circle represents the ectothermic *Albanycada albiger*, filled squares represent New World endotherms, and open squares represent New World ectotherms. Additional data are from Heath and Wilkin (1970), Heath et al. (1972), Bartholomew and Barnhart (1984), Sanborn (2000), Sanborn et al. (1995a, 1995b, 2003a), and Villet et al. (2003).

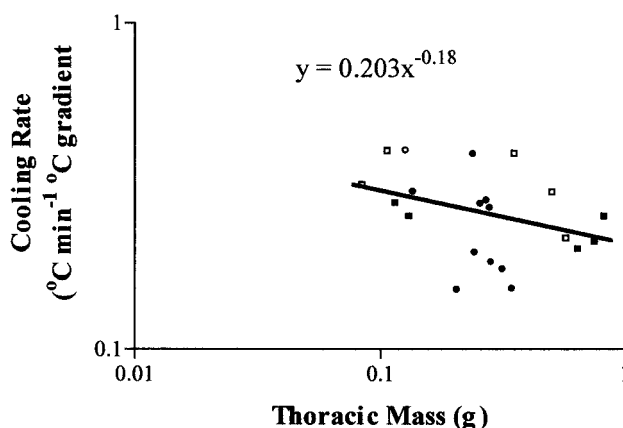


Figure 7. Allometric relationship between cooling rate and body size in cicadas. Values represent the mean value reported for each species ($n = 1-8$). Filled circles represent endothermic platyleurines, the open circle represents the ectothermic *Albanycada albiger*, filled squares represent New World endotherms, and open squares represent New World ectotherms. Additional data are from Heath and Wilkin (1970), Heath et al. (1972), Bartholomew and Barnhart (1984), Sanborn et al. (1992, 1995a, 1995b, 2002, 2003a), Sanborn (2000), and Villet et al. (2003).

will increase the potential number of mates with which an animal can interact. Endothermy permits the animals to produce a call that is consistently attractive to females, in that conditions in the thermal environment will not alter the temporal properties of the calls (Sanborn 2001; Villet et al. 2003). Finally, endotherms are not restricted in their activity by environmental conditions. Whatever the reasons, endothermy appears to have had strong selection pressures that favored it as the primary thermoregulatory strategy in platyleurine cicadas.

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