Thermal responses in some Eastern Cape African Cicadas (Hemiptera: Cicadidae)

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Abstract

Thermal responses were measured in cicadas collected in the Eastern Cape Province of South Africa.
The thermal responses of 22 species from 5 biomes were determined.
Shade-seeking temperature was the most variable and related to the various biomes.
Mean shade-seeking temperature was greatest for species inhabiting the thicket biome and lowest for species inhabiting the forest biome.
The animals that live in the thicket biome may adapt to the greater thermal stress to take advantage of a habitat that permits lower predation pressure.
There is a correlation between body size and shade-seeking temperatures with smaller species exhibiting lower thermal responses within a particular habitat. This may be related to the greater heat exchange in smaller species.
Heat torpor temperatures did not differ between the various biomes.

1. Introduction

Animals must maintain body temperature (T_b) within a limited range in order to function effectively physiologically. Most cicadas are behavioral thermoregulators that use solar radiation to regulate T_b (see summary in Sanborn, 2002; Sanborn et al (2002a) and Sanborn et al (2002b)). Physiological mechanisms used by cicadas to thermoregulate include endothermy (Bartholomew and Barnhart, 1984; Sanborn et al (1995a); Sanborn et al (1995b); Sanborn et al (2002b) and Sanborn et al (2003); Sanborn (1997) and Sanborn (2000); Villet et al., submitted) and evaporative cooling (Kaser and Hastings, 1981; Hadley et al., 1991; Hastings and Toolson, 1991; Sanborn et al., 1992). An additional physiological process to deal with temperature is thermal adaptation (see

summary in Sanborn, 2002; Sanborn et al (2002a) and Sanborn et al (2002b)). We describe the thermal responses of several African cicada species with this work.

2. Materials and methods

All cicadas were collected in the Eastern Cape Province of South Africa during December 2001. Animals were captured in the field and placed on ice in a cardboard container with a moist paper towel to minimize metabolism during transport to the laboratory. Specimens were stored in a refrigerator until experiments could be 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 deep thoracic temperature.

The thermal responses of the species were determined using the procedures of Heath (1967) and Heath and Wilkin (1970). To summarize, minimum flight temperature was determined by tossing a cooled animal 1–2 m in the air until the animal made a controlled flight or landing. Maximum voluntary tolerance or shade-seeking temperature was determined by heating a cooled animal on a vertical surface with a heat lamp at a distance of 40–50 cm until the animal walked or flew from the heat source. Heat torpor was determined by heating an animal in a cardboard container with a heat lamp until movement ceased. The minimum flight and heat torpor temperatures represent the T_b range of full activity. The shade-seeking temperature represents an upper thermoregulatory temperature (Heath, 1970). Animals were oriented for insertion of the thermocouple by pinching the wing tips together with the thumb and forefinger. This procedure prevented heat transfer between the insect and the experimenter that could alter the T_b reading. T_b was recorded within 5 s of the animals performing the desired behavior. All statistics are reported as mean±standard deviation.

We use the terminology of Low and Rebelo (1996) in describing habitat associations for the individual species.

3. Results

The thermal limits and masses of the twenty-two cicada species studied are listed in Table 1. The data are separated by biomes, based on where the various specimens were collected. In some cases, a species may be listed in more than one biome. This may be due to a species being less particular about its host plants (e.g. *Platypleura plumosa*) or

because the host plant may be distributed in several biomes (e.g. *Platypleura divisa*).
When possible, the primary biome habitat is indicated for each species.

Table 1. Thermal responses of Eastern Cape cicadas

Species	Mass (mg)	Minimum flight (°C)	Shade seeking (°C)	Heat torpor (°C)
Forest biome species				
[a,b] *Platypleura divisa* (Germar, 1834)	682±44 (n = 10)	18.00±1.53 (n = 10)	34.3±1.86 (n = 10)	46.8±1.70 (n = 10)
[b] *Platypleura* cf. *brunnea*	982±211 (n = 9)	18.1±0.95 (n = 8)	37.7±2.19 (n = 9)	46.5±1.26 (n = 9)
[b] *Pycna semiclara* (Germar, 1834)	1320±244 (n = 8)	19.5±1.67 (n = 8)	33.1±3.16 (n = 7)	44.9±1.67 (n = 8)
Bavea concolor (Walker, 1850)	175±35 (n = 2)	16.5±0.99 (n = 2)	30.3±0.42 (n = 2)	44.2±1.56 (n = 2)
n.gen. n.sp.	280 (n = 1)	20.4 (n = 1)	31.8 (n = 1)	43.8 (n = 1)
Thicket biome species				
Albanycada albigera (Walker, 1850)	454±76 (n = 18)	19.3±1.81 (n = 18)	36.2±3.11 (n = 18)	47.0±1.87 (n = 17)
Azanicada zuluensis (Villet, 1987)	760 (n = 1)	19.3 (n = 1)	36.8 (n = 1)	45.4 (n = 1)
[a,b] *Platypleura capensis* (Linné, 1764)	609±77 (n = 15)	19.2±3.34 (n = 11)	34.3±2.33 (n = 14)	46.1±2.15 (n = 15)
[a,b] *Platypleura divisa* (Germar, 1834)	682±44 (n = 10)	18.00±1.53 (n = 10)	34.3±1.86 (n = 10)	46.8±1.70 (n = 10)
[a,b] *Platypleura hirtipennis* (Germar, 1834)	951±175 (n = 13)	17.8±2.00 (n = 9)	37.9±2.33 (n = 13)	46.9±1.53 (n = 13)
Platypleura wahlbergi (Stål, 1855)	373±97 (n = 3)	21.5±1.72 (n = 3)	37.0±3.32 (n = 3)	46.5±3.04 (n = 3)
Quintilia wealei (Distant, 1892)	274±52 (n = 8)	20.8±1.35 (n = 8)	34.5±2.79 (n = 8)	47.3±2.66 (n = 7)
Stagira caffrariensis (Villet, 1997)	78±10 (n = 10)	20.1±2.03 (n = 10)	33.6±2.48 (n = 9)	44.0±1.77 (n = 9)
Xosopsaltria thunbergi (Metcalf, 1955)	112±31 (n = 17)	20.7±1.92 (n = 15)	32.3±1.95 (n = 17)	45.6±1.42 (n = 15)
Savanna biome species				
[b] *Platypleura divisa* (Germar, 1834)	682±44 (n = 10)	18.00±1.53 (n = 10)	34.3±1.86 (n = 10)	46.8±1.70 (n = 10)
[b] *Platypleura hirtipennis* (Germar, 1834)	951±175 (n = 13)	17.8±2.00 (n = 9)	37.9±2.33 (n = 13)	46.9±1.53 (n = 13)
[b] *Platypleura plumosa* (Germar, 1834)	729±76 (n = 5)	20.1±2.14 (n = 5)	35.8±4.30 (n = 5)	45.7±0.78 (n = 5)
[a] *Platypleura wahlbergi* (Stål, 1855)	373±97 (n = 3)	21.5±1.72 (n = 3)	37.0±3.32 (n = 3)	46.5±3.04 (n = 3)
Melampsalta sp. b	64±15 (n = 16)	23.8±1.48 (n = 12)	33.5±1.61 (n = 16)	45.3±1.36 (n = 16)
Stagira simplex (Germar, 1834)	49±13 (n = 12)	22.2±0.83 (n = 5)	35.4±1.49 (n = 11)	44.9±1.34 (n = 8)
Tettigomyia vespiformis (Amyot and Serville, 1843)	87±21 (n = 19)	21.2±1.53 (n = 12)	33.5±1.66 (n = 19)	45.3±1.54 (n = 17)
Xosopsaltria annulata (Germar, 1830)	97±14 (n = 14)	18.9±1.52 (n = 13)	32.4±3.32 (n = 14)	45.6±1.66 (n = 14)
Xosopsaltria n. sp	66±11 (n = 17)	22.6±1.47 (n = 9)	34.7±1.95 (n = 16)	45.3±1.67 (n = 15)
Grassland/fynbos biome species				
[b] *Platypleura divisa* (Germar, 1834)	682±44 (n = 10)	18.00±1.53 (n = 10)	34.3±1.86 (n = 10)	46.8±1.70 (n = 10)
Cicadettini sp. a	53±29 (n = 3)	21.3±2.76 (n = 3)	34.6±0.56 (n = 3)	45.6±1.46 (n = 3)
Cicadettini sp. b	72±11 (n = 13)	20.6±1.18 (n = 13)	33.2±2.12 (n = 13)	46.4±1.21 (n = 13)
Melampsalta sp. a	95±12 (n = 8)	21.2±2.06 (n = 7)	33.8±1.55 (n = 8)	45.9±1.34 (n = 8)
[b] *Platypleura capensis* (Linné, 1764)	609±77 (n = 15)	19.2±3.34 (n = 11)	34.3±2.33 (n = 14)	46.1±2.15 (n = 15)

Forest biome species were collected in the Coastal and Afromontane Forest. Thicket biome species were collected in the Valley Thicket and Dune Thicket. Savanna biome species were collected in the Eastern Thorn Bushveld. Grassland and Fynbos biome species were collected in Moist Cold Highveld Grassland, grassland patches within Valley Thicket, Grassy Fynbos, and S&SW Coast Renosterveld.

The Eastern Cape region of South Africa has examples of all seven major biomes found in South Africa (Low and Rebelo, 1996). We largely concentrated collecting in three of those major biomes: forest, thicket, and savanna. However, a fourth category of grassland/fynbos is included in Table 1. Technically, fynbos and grassland are two different major biome divisions thus this is obviously not a true biome division. We combined the species into this category for several reasons. The fynbos regions inhabited

by the species we collected, Grassy Fynbos (*Melampsalta* sp. a) and S&SW Coast Renosterveld (*Platypleura capensis*), are largely characterized by several grass species growing amongst heaths. Further, *P. capensis* is also found in Dune Thicket and it was difficult to determine into which biome it fit best. The two new Cicadettini species were collected in a region characterized as Valley Thicket but were associated with grassland patches within the thicket region. Since the thicket biome is described as lacking understory and grasses, it was clear that these grassy patches were an artifact, likely resulting from the small depression in the area which led to the soil being too wet to support thicket. This grassland area was much too small to show up on any distribution map. Only *Platypleura divisa* ventures into a true grassland habitat (Highveld Grassland in the Eastern Cape) and that does not appear to be its major habitat because it is associated with a bushy plant, *Maytenus heterophila*.

The mean shade-seeking data are highest for the thicket biome, 35.21±1.84°C (*n*=9 species) and lowest in the forest biome, 33.44±2.81°C (*n*=5 species). The savanna and grass/fynbos fall in between at 34.94±1.77°C (*n*=9 species) and 34.04±0.55°C (*n*=5 species), respectively. However, there are no statistical differences between the mean shade-seeking temperatures for all habitats (ANOVA, *F*=1.198, df=3, 24, *p*=0.3316). Mean heat torpor temperature was 45.64±0.95°C (*n*=22) with less than 0.6°C variation in the means between biome groupings and no significant differences between biome means (ANOVA, *F*=1.244, df=3, 24, *p*=0.3159).

Masses of the species varied from 49±13 to 1320±244 mg. Ten species averaged less than 115 mg. Seven species averaged more than 600 mg, six of which are endothermic platypleurines (Sanborn et al., 2003; Villet et al., submitted).

4. Discussion

The thermal data separates the species studied into groups with what appear to be biome-specific results. Minimum flight temperatures appear to be related to a group of several morphological characteristics (Sanborn et al., 2003) rather than the habitat as was previously thought (see summary in Sanborn, 2002). Heat torpor is relatively constant, regardless of species or habitat and may be more related to the maximum thermal extreme in each habitat being similar. We collected all species within ±100 km of Grahamstown. The limited geographic range without large changes in altitude over which the species were collected may explain why the heat torpor data show little variation.

The shade-seeking data best represent the biome preference of the insects. Several factors appear to affect the shade-seeking values of species within each biome. Size appears to be inversely related to the shade-seeking value of species within a biome. The higher rate of heat transfer in the smaller species may necessitate a lower thermoregulatory temperature. Microhabitat selection also appears to affect shade-seeking temperature. For example, *Bavea concolor* inhabits the vegetation of the understory within the forest biome and has the lowest of the shade-seeking values reported here. A similar relationship was found in another understory cicada in Argentina, *Fidicina torresi* Boulard and Martinelli (Sanborn et al., 1995a). Thermoregulatory behavior also appears

to affect shade-seeking temperature. An endothermic species has the highest shade-seeking temperature in all habitats except the Grassland and Fynbos biomes (although there is no statistical difference between the endotherm (*P. divisa*) and the ectotherm with the highest shade-seeking value (Cicadettini sp. a), $t=0.2682$, df=11, $p=0.7935$). This may be related to overall physiological efficiency being better at the elevated temperature. The elevated shade-seeking temperature of the African endotherms contrasts the shade-seeking temperature relationship seen in endotherms and ectotherms in New World species (Sanborn, 2000).

Based on the shade-seeking data, the species that inhabit the thicket biome appear to demonstrate the highest thermal tolerances. This habitat is clearly different from either forest or savanna and the editors of *Vegetation of South Africa, Lesotho, and Swaziland* (Low and Rebelo, 1996) recognize and categorize it as such. There are many microhabitats within the thicket and several species utilize this region, even if it is not their primary habitat. It is essentially impenetrable for the human collectors and most of the specimens were collected on the fringes. Virtually all of the plant species in the thicket have sharp spines or thorns, which may reduce predation and make it a relatively secure habitat for cicadas despite the apparent higher thermal stresses. There are a greater variety of sizes amongst the thicket biome species, supporting the suggestion that the potentially safer location compensates for the need for greater thermal tolerance. Furthermore, the Albany area of the Eastern Cape is recognized as a speciation "hotspot" (Lubke and de Moor, 1998) resulting from its complex topography and palaeoenvironmental history (Partridge et al., 1999).

Species collected in the savanna also had high thermal tolerances, but lower than the mean for the thicket group. This biome is found between thicket and grassland, made up of grassy ground layer with a distinct upper woody layer and outcroppings. Many of the plants still have spines, but it is a bit easier for both collector and insect to maneuver through this habitat. There are also a large number of microhabitats available here, as evidenced by the variety of species that were collected in savanna. Based on the lower shade-seeking values, it appears the requirement for high thermal tolerance is not as great which may attract more species, even while risk of predation is higher. This trade-off is clearly one many species are able to survive. The species collected in the savanna were either very small (<100 mg) or endothermic (Sanborn et al., 2003). The possible exception is *P. wahlbergi*, which did not exhibit endothermic behavior in the lab.

Size differences are not as obvious in the grass/fynbos grouping. This could be because it is not a true biome category, but additionally because the two larger species collected there were both endotherms (Sanborn et al., 2002b) that are found in several biomes. The three small species are all previously undescribed species with very high frequency calls. All three were found inhabiting grass and did not seem to migrate to the nearby woody plant areas. Little is known of these species, but their thermal responses were all similar, which may be due to size, biome and/or phylogenetic proximity.

Although each biome has different stresses resulting in the observed biome differences, there are obvious size-related differences within the biome. In each group, the larger

species (>300 mg) demonstrated higher thermal tolerances. The smaller animals in each biome except grass/fynbos had mean shade-seeking values at least 2°C lower than the larger species. The most dramatic example is found in the forest biome where the lowest shade-seeking values were found. The three larger species (>600 mg) were found at mid-level or higher in the canopy. The two smaller species (<300 mg) were collected in the understory, in low light areas where there is very little vegetation. Comparison of their thermal tolerances shows significantly lower values for the smaller animals (31.05±0.75°C vs. 35.0±1.95°C). This could be a result of the size differences, for the smaller insects would heat and cool more rapidly. It could be a habitat difference, since the ambient temperature is less in the understory and the potential for a heat source much lower.

Further, the larger species collected in the forest are all endothermic (Sanborn et al., 2003; Villet et al., submitted) and thus their responses can be uncoupled from their environment. In fact, with only one exception (*Albanycada albigera*), all of the collected species with masses greater than 600 mg were found to be endothermic. These species are smaller in comparison to most other endothermic cicadas that have been described (Sanborn et al., 1995a; Sanborn, 2000) but are not the smallest described endotherms in the family (Sanborn et al., 1995b). Nevertheless, the ability to regulate internal temperature without relying on external heat sources provides these insects with an advantage that they are not tied to the thermal constraints of a particular biome. This is further emphasized by the fact that many of the endotherms were collected in and inhabit more than one biome type.

Acknowledgements

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