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Thermoregulation in the cicada *Platypedia putnami* variety *lutea* (Homoptera: Tibicinidae) with a test of a crepitation hypothesis

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Abstract

- 1. Measurements of body temperature (T_b) in the field demonstrate that *Platypedia putnami* var. *lutea* Davis regulates T_b through behavioral mechanisms.
- 2. Thermal responses (minimum flight temperature 17.3°C, maximum voluntary tolerance-temperature 32.5°C, and heat torpor temperature 44.4°C) of *P. putnami* var. *lutea* are related to the altitude of their habitat.
- 3. Water loss rates increase with ambient temperature (T_a). Water loss rates are not significantly different at the extremes of the active T_b range but increase significantly when exposed to elevated T_a .
- 4. Acoustic activity was restricted at 6.7° C $T_{\rm b}$ range. This is similar to the lower end of the $T_{\rm b}$ range for singing measured in cicada species that produce sound with a timbal mechanism.
- 5. The use of the wing musculature to produce acoustic signals in *P. putnami* var. *lutea* does not increase the T_b range over which the species can call compared to timbal calls produced by other cicada species. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The body temperature (T_b) of cicadas must remain within a specific range in order to coordinate reproductive activity (Heath, 1967, 1972). Thermoregulation in cicadas is often accomplished through behavioral mechanisms (Heath, 1967; Heath and Wilkin, 1970; Heath et al., 1972; Heath, 1972; Hastings, 1989; Hastings and Toolson, 1991; Sanborn et al., 1992, 1995a, b; Sanborn, 2000; Sanborn and Maté, 2000). Physiological mechanisms to regulate T_b in cicadas include endothermy (Sanborn et al., 1995a, b; Sanborn, 2000), evaporative cooling (Kaser and Hastings, 1981; Hadley et al., 1991; Hastings and Toolson, 1991; Sanborn et al., 1992), and thermal adaptation (Heath, 1967; Heath et al., 1971, 1972; Heath and Wilkin, 1970; Heath, 1972; Sanborn et al., 1992, 1995a, b; Sanborn and Phillips, 1996; Sanborn, 2000; Sanborn and Maté, 2000).

Most cicadas produce mating calls with a timbal mechanism. An alternative form of sound production is crepitation (Moore, 1966, 1973, 1993; Sanborn and Phillips, 1999). Crepitating cicadas will snap their wings together, either against their body or against a substrate, to produce sound. It has been hypothesized that crepitation may permit calling activity over a greater

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 $T_{\rm b}$ range than cicadas that use a timbal mechanism to produce their mating call (Sanborn and Phillips, 1999). We investigate thermoregulation in *Platypedia putnami* var. *lutea* Davis and test that hypothesis with this work.

2. Materials and methods

A population of *P. putnami* var. *lutea* was sampled during June 1995 and May and June 2001 at Geology View (32°22.25'N, 110°42.67'W), Mt. Lemmon, Pima County, Arizona, at an altitude of 1,981 m. Animals captured for laboratory experimentation were placed on ice in a cardboard container with a plant sample and moist paper towel until the experiments could be performed during the afternoon or evening of the day of capture. The specimens used for the water-loss studies were collected in the early morning just as the population became active and brought immediately to the laboratory to minimize any effect passive dehydration of the specimens would have on the results.

 $T_{\rm b}$ was measured with a Physitemp BAT-12 digital thermocouple thermometer with a type MT-29/1 copper-constantan 29 gauge hypodermic microprobe accurate to $\pm 0.1^{\circ}$ C, which had been calibrated with a National Institutes of Standards and Technology mercury thermometer. The probe was inserted midway into the dorsal mesothorax to record deep T_b . Field temperatures were measured after the cicadas were collected by hand after the behavior and position of the cicadas was determined. The animals were immediately oriented and held by the wing tips in an effort to decrease heat transfer between the experimenter and the specimen. $T_{\rm b}$ was stable during measurement for >15 s while a cicada was being held so that any heat transfer during capture should have been minimal. Thermal responses were determined in the laboratory following the procedures of Heath (1967) and Heath and Wilkin (1970). All measurements were recorded within 5 s of the animal being captured in the field or performing the desired activity in the laboratory. Perch temperature $(T_{\rm p})$ was measured immediately after $T_{\rm b}$ was recorded by placing the tip of the thermocouple above the perch where the animal was captured at the approximate height of the middle of the thorax (5mm). Ambient temperature (T_a) was measured at a height of about 1 m in the shade after T_p was recorded.

Evaporative water loss was determined using a modification of techniques described by Edney (1971) and Sanborn et al. (1992). Individual specimens were placed in plastic film canisters above 5 g of calcium sulfate (Drierite) to produce an approximate 0% humidity environment. The specimens were separated from the calcium sulfate by a screen. The canisters were placed in water baths that maintained water temperature within $\pm 0.1^{\circ}$ C. Animals were tested at 20.5°C, 29.6°C,

 $35^{\circ}C,$ and $40^{\circ}C.$ Six males were tested at each waterbath temperature.

Water loss rates were determined by measuring the mass loss of the individuals within the canisters over time. Specimens were removed from their respective canisters every 30 min and weighed on a Sartorius electronic scale sensitive to ± 0.00001 g. All mass loss was assumed to be water loss.

Cooling curves were determined by placing a thermocouple wire into the dorsal thorax of a freshly killed cicada. The cicada was warmed with a heat lamp, then suspended in a Styrofoam box which acted as a controlled radiant environment. T_b was measured with the Physitemp BAT-12 thermometer every 15s for 15 min. Cooling curves were analyzed using the procedure of Heath and Adams (1969).

All statistics are reported as mean \pm standard deviation.

3. Results

P. putnami var. lutea is a small cicada $(303 \pm 47 \text{ mg})$ [n = 35] [Sanborn and Phillips, 1999]) that forms aggregations in pointleaf manzanita (Arctostaphylos pungens) and silverleaf oak (Quercus hypoleucoides). They are a classic example of a behavioral thermoregulator. In the morning or when T_a or T_b was low, the cicadas migrated to the outer edges of the eastern side of the host plants. Cicadas would even leave the small branches (their usual perch) and sit on leaves where it was possible to maximize the uptake of solar radiation. As T_a and T_b increased, the cicadas would move deeper into the shaded portion of the host plants. In the evening as $T_{\rm a}$ and $T_{\rm b}$ became more difficult to maintain within the shaded portions of the plants, the cicadas migrated to the exposed western edges of the plants. In the evening, active cicadas were found only on the exposed, sunny perches of the western side of the host plants.

 $T_{\rm b}$'s were recorded over a $T_{\rm a}$ range of 18.2–30.2°C (n = 167) and a $T_{\rm p}$ range of 19.6–32.0°C (n = 167). Mean $T_{\rm b}$ of cicadas was 33.1 ± 1.49 °C (n = 167) with a range of 26.7–35.9°C. $T_{\rm b}$ shows a significant relationship as a function of either $T_{\rm a}$ (ANOVA F = 11.736, df = 1, 165, P < 0.001) (Fig. 1) or $T_{\rm p}$ (ANOVA F = 24.700, df = 1, 165, P < 0.001) (Fig. 2). The slope of the regression line of $T_{\rm b}$ as a function of $T_{\rm a}$ or $T_{\rm p}$ is significantly different than the one (for $T_{\rm b}$ vs. $T_{\rm a}$, t = -24.39, df = 165, P < 0.001; for $T_{\rm b}$ vs. $T_{\rm p}$, t = -22.11, df = 165, P < 0.001) suggesting thermoregulation (May, 1985).

The thermal responses determined in the laboratory were as follows: minimum flight temperature—17.3±1.60°C (n = 31), maximum voluntary tolerance temperature—32.5±2.24°C (n = 26), and heat torpor—44.4±1.64°C (n = 31). Two animals were observed moving from sun to shade in the field. Their $T_{\rm b}$'s were 35.0°C and 35.1°C similar to upper maximum



Fig. 1. T_b as a function of T_a in *P. putnami* var. *lutea*. The slope of the regression is significantly different from the one suggesting thermoregulation.



Fig. 2. T_b as a function of T_p in *P. putnami* var. *lutea*. The slope of the regression is significantly different from the one suggesting thermoregulation.

voluntary tolerance temperatures determined in the laboratory.

Water loss rates increased with increasing T_a . Average mass loss was 1.27% h⁻¹ at 20.6°C (95% CIE 1.046–1.489% h⁻¹), 3.28% h⁻¹ at 29.6°C (95% CIE 2.817–3.746% h⁻¹), 3.77% h⁻¹ at 35.0°C (95% CIE 3.185–4.365% h⁻¹), and 6.05% h⁻¹ at 39.9°C (95% CIE 5.646–6.454% h⁻¹). The water loss rates at the extremes of the T_b range for activity (29.6°C and 35.0°C) do not differ significantly (P > 0.05) since the CIE. values overlap the slope of the other regression. The rate of water loss at 20.6°C is significantly less than



Fig. 3. Distribution of crepitating *P. putnami* var. *lutea* T_b 's. The mean T_b for the population of *P. putnami* var. *lutea* is 33.1°C. The mean maximum voluntary tolerance temperature is 32.5°C.

at 29.6°C (P < 0.05) and the rate of water loss at 39.9°C is significantly greater than at 35.0°C (P < 0.05) since the CIE. ranges do not overlap the slope of the comparative regression (Sokal and Rohlf, 1995).

Freshly killed *P. putnami* var. *lutea* passively cool at a rate of $0.407 \pm 0.0324^{\circ}$ C min⁻¹°C gradient⁻¹ (*n* = 4).

Crepitating cicadas had a T_b of $33.0\pm1.34^{\circ}$ C (n = 50). This value is not significantly different from the mean T_b value determined for the population (t = 0.4257, df = 215, P = 0.6646) or from the maximum voluntary tolerance temperature determined in the laboratory (t = 1.213, df = 74, P = 0.8855). The range of T_b 's in crepitating cicadas was $29.2-35.9^{\circ}$ C. The distribution of crepitation T_b 's is shown in Fig. 3.

4. Discussion

P. putnami var. *lutea* follows the basic thermoregulatory pattern in cicadas—behavioral heliothermy. They will alter their exposure to the sun through gross body movements in one location or through movements from the edge of their host plants to deep shade within the host plant and back again. They have been shown to use microclimates effectively in maintaining T_b at a range suitable to maintain activity. This mechanism of thermoregulation has been shown to be common in cicadas (see summary in Sanborn, 1998, 2000; Sanborn and Maté, 2000).

The thermal responses of *P. putnami* var. *lutea* are related to the habitat in which the species lives. The

minimum flight temperature is similar to species that inhabit cooler environments such as Okanagana hesperia (Uhler) (Heath, 1972) and Magicicada cassinii (Fisher) (Heath, 1967) although minimum flight temperature is difficult to relate strictly to habitat (Sanborn, 1998). The maximum voluntary tolerance temperature and heat torpor temperature are similar to species that inhabit cooler environments such as O. hesperia (Heath, 1972) and M. cassinii (Heath, 1967). The maximum voluntary tolerance and heat torpor temperature are less than the values reported for other desert species (Heath et al., 1972; Sanborn and Phillips, 1996). The values for all the thermal tolerances in P. putnami var. lutea are less than the values reported for Cacama valvata (Uhler) (Heath et al., 1972) and Okanagodes gracilis Davis (Sanborn et al., 1992) both of which are found at lower altitudes around Mt. Lemmon. The thermal responses of P. putnami var. lutea illustrate adaptation to an altitudinally based cooler habitat.

The rate of water loss increases in P. putnami var. lutea as T_a increases. The rate of water loss is approximately constant over the active range of $T_{\rm b}$. It appears that P. putnami var. lutea can evaporatively cool at higher T_{as} but the ability to cool evaporatively appears to be limited. In contrast to most desert cicadas (Kaser and Hastings, 1981; Hastings, 1989; Hastings and Toolson, 1991; Hadley et al., 1991; Sanborn et al., 1992), P. putnami var. lutea actually loses a lower percentage of body mass per hour than does Magicicada tredecim (Walsh and Riley), a species from a warm, humid environment (Toolson and Toolson, 1991). The pattern of water loss with increasing temperature contrasts with the results of a similar experiment on O. gracilis where water loss rates decreased with increasing $T_{\rm a}$ until after the thermoregulatory point was reached when the species began to cool evaporatively (Sanborn et al., 1992).

The rate at which *P. putnami* var. *lutea* passively cool is similar to other small cicadas (Sanborn et al., 1992). The cooling rate is related predictably to the size of the species (Heath and Wilkin, 1970; Heath et al., 1972; Sanborn et al., 1995a, b; Sanborn, 2000).

The rate at which *P. putnami* var. *lutea* cool would mean an individual would need to evaporate 0.175 mg of water/min or the equivalent of 3.5% of body mass/h in order to maintain a 1°C gradient below T_a . Animals were able to survive mass losses of as much as 22.2% of their initial mass during the experimental period. We did not encounter a $T_a > 35^{\circ}$ C even though there were record high temperatures at lower altitude so we do not know if the evaporative cooling response is necessary to thermoregulate or if *P. putnami* var. *lutea* can find sufficiently cool microclimates if T_a rises to a potentially dangerous level.

Crepitation occurred at the same mean T_b as the mean T_b of the population. Crepitation occurred at T_b 's below

the maximum voluntary tolerance temperature. The maximum voluntary tolerance temperature is an upper thermoregulatory set-point (Heath, 1970) and many cicadas sing at $T_{\rm b}$'s below the maximum voluntary tolerance temperature (Heath, 1967; Heath and Wilkin, 1970; Heath et al., 1972; Sanborn et al., 1992, 1995a, b; Sanborn and Maté, 2000; Sanborn, 2000, but see for exceptions).

P. putnami var. lutea exhibited acoustic behavior over a $T_{\rm b}$ 6.7°C range. The $T_{\rm b}$ range for crepitating is similar to the $T_{\rm b}$ range reported for singing in the ectothermic cicadas O. hesperia (2.8°C, Heath, 1972), C. valvata (9.5°C, Heath et al., 1972), M. cassinii (6.8°C, Heath, 1967), O. gracilis (4.9°C, Sanborn et al., 1992), Diceroprocta apache (Davis) (4.8°C, Heath and Wilkin, 1970), Diceroprocta olympusa (Walker) (5.8°C, Sanborn and Maté, 2000) and Tibicen chloromerus (Walker) (8.1°C, Sanborn, 2000). The range for acoustic activity in P. putnami var. lutea is less than the total range of acoustic activity in the endothermic cicadas Guyalna bonaerensis (Berg) (11.2°C, Sanborn et al., 1995b), Proarna bergi (Distant) (3.6°C, Sanborn et al., 1995a), P. insignis Distant (3.6°C, Sanborn et al., 1995a) and Tibicen winnemanna (Davis) (13.2°C, Sanborn, 1997, 2000). Therefore, these data do not support the hypothesis that crepitation can permit acoustic activity over a greater $T_{\rm b}$ range than a timbal system. It appears that the acoustic activity for reproduction is restricted by temperature in cicadas regardless of the type of sound generating system employed.

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