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DIURNAL ACTIVITY, TEMPERATURE RESPONSES AND ENDOTHERMY IN THREE SOUTH AMERICAN CICADAS (HOMOPTERA: CICADIDAE: *DORISIANA BONAERENSIS*, *QUESADA GIGAS* AND *FIDICINA MANNIFERA*)

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Abstract—1. Measurements of body temperature (T_b) in the field demonstrated that endothermic cicadas regulate T_b by behavioral mechanisms as well as by endogenous heat production.

2. The T_b of endothermically active cicadas without access to exogenous heat is approximately the same as the T_b of basking cicadas.

3. *Dorisiana bonaerensis* (Berg) and *Quesada gigas* (Olivier) raise T_b in the field with the heat produced in flight.

4. The thermal responses of a particular species are related to its activity patterns and habitat.

5. Endothermy in cicadas may serve to uncouple reproductive behavior from environmental constraints; to circumvent possible thermoregulatory problems; to permit the utilization of habitats unavailable to strictly ectothermic cicadas; to reduce predation; and to optimize broadcast coverage and sound transmission.

Key Word Index: Endothermy; thermoregulation; temperature; adaptation; cicadas; *Dorisiana*; *Quesada*; *Fidicina*

INTRODUCTION

Cicadas must maintain body temperature (T_b) within a specific range to coordinate reproductive activity (Heath, 1967, 1972). Thermoregulation in cicadas is generally accomplished through a combination of behavioral and physiological means. Most cicadas alter the uptake of solar radiation through behavioral adjustments to regulate body temperature (Heath and Wilkin, 1970; Sanborn *et al.*, 1992). Physiological mechanisms used by cicadas to thermoregulate include thermal tolerances (Sanborn *et al.*, 1992), evaporative cooling (Hadley *et al.*, 1991; Sanborn *et al.*, 1992), and endothermy (Bartholomew and Barnhart, 1984).

Bartholomew and Barnhart (1984) stated that "the functional significance of endogenous warm-up in *Fidicina mannifera* remains problematic". To answer that question this study compares daily T_b cycles, thermoregulatory strategies, thermal responses, endothermic heat production, and the influence of temperature on behavior in three endothermic species.

MATERIALS AND METHODS

Insects

Dorisiana bonaerensis (Berg), *Quesada gigas* (Olivier), and *Fidicina mannifera* (Fabricius) are medium-sized to large cicadas. Mean live weights are 1890 ± 62 ($n = 35$), 2340 ± 75 ($n = 12$) and 2505 ± 113 ($n = 19$) mg, respectively (unless specified otherwise, all statistics are presented as mean $\pm$ standard error). *D. bonaerensis* is distributed throughout the tropical thornscrub of South America [Cabrera's (1971) Chaco floristic province]. *Q. gigas* can be found in the adult phase any month of the year in some part of its distribution from southern Texas to central Argentina (Davis, 1944). *F. mannifera* inhabits tropical and subtropical rainforests of Central and South America (Young, 1983). Voucher

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specimens are deposited in the collection of the Museo Nacional de La Plata, La Plata, Argentina.

Animals captured for laboratory experimentation were placed in a cardboard container along with plant samples and a damp paper towel. The containers were kept on ice until experiments could be performed, during the afternoon or evening of the day of capture. Live weights were measured with a triple beam balance (Cent-O-Gram Model CG 311, Ohaus Scale Corporation) sensitive to ± 5 mg.

Temperature measurements

Body temperature (T_b) of the cicadas was measured with a Telethermometer and a 26 gauge hypodermic thermistor probe or a Physitemp Model BAT-12 digital thermocouple thermometer with a type MT-29/1 copper–constantan 29 gauge hypodermic microprobe accurate to ± 0.1°C. The telethermometer was calibrated with the Physitemp BAT-12 system which had been calibrated with a National Bureau of Standards mercury thermometer. Probes were inserted to a depth of about 5 mm, midway into the mesothorax, to record deep T_b. T_b and thermal responses of the cicadas were determined as described by Heath (1967) and Heath and Wilkin (1970). Each T_b was recorded within 5 s of the cicada performing a desired behavior. Ambient temperature (T_a) was measured at a height of about 1 m in the shade.

Graphs are plotted in Argentine standard time (approx. 1.5 h ahead of sun time). T_bs are discussed in terms of diurnal, evening, and dusk time periods. The term diurnal represents the time that the sun is above the horizon. Evening and dusk are used interchangeably and represent the light period after sunset.

Heat production in *D. bonaerensis*, and *Q. gigas* was calculated from heating and cooling curves produced by tethered cicadas. A thermocouple probe was implanted into the dorsal mesothorax to measure changes in T_b with the Physitemp BAT-12 thermometer as they warmed during flight and cooled after flight. Flight was initiated by lifting the cicada off the substrate. T_b was then recorded every 15 s until the animal stopped flying. When the flight terminated, the animal was immediately placed into a styrofoam box which served as a controlled radiant environment and prevented forced convective heat loss, and T_b continued to be recorded every 15 s as the animal cooled until it approximated T_a (10–15 min).

Oxygen consumption (V_{O_2}) was determined from the formula

$$V_{O_2} = \frac{(\Delta T \times \text{sp. ht.} \times \text{mass})}{O_2 \text{ cal. eq.}} + \frac{(Q_1)(T_{th} - T_a)}{O_2 \text{ cal. eq.}}$$

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 in grams, O_2 cal. eq. = the caloric equivalent of oxygen (4.8 cal ml O_2^{-1}), Q_1 = heat loss to the environment (cal. min^{-1} °C^{-1}), and ($T_{th} - T_a$) = thoracic temperature minus ambient temperature (°C). We calculated V_{O_2} so we could make direct comparisons to other cicada data in the literature.

Bartholomew and Barnhart (1984) found the flight musculature of *F. mannifera* to be 35% of the total body mass. We confirmed this figure for another species and used 35% of total mass in all calculations.

Field sites

T_b of *D. bonaerensis* and *Q. gigas* was recorded on the 13th December 1986 in Mina Clavero, Córdoba, Argentina. This is an ecotone of the Chaco and Espinal floristic provinces. The study site contained a pair of large *Prosopis alba* (algarrobo blanco) surrounded by many smaller *Prosopis* and *Acacia* trees in which the animals congregated. Comparative T_bs were measured on the 21st December 1986, when an active population of *D. bonaerensis* was discovered in a light rain in the Province of Salta, Argentina, and on 3rd January 1988 in the Province of Entre Rios, Argentina.

RESULTS

Diurnal distribution of body temperature

Figure 1 shows the distribution of T_bs recorded in the field on the 13th December. There was a rain shower from 07.00 to 08.00 h followed by a misting rain until the sky began to clear about 09.45 h which delayed the start of normal activity. However the general activity patterns were normal when compared to other collection sites.

T_bs were near or below T_a in the early morning hours. As T_a rose, T_b increased through the use of solar radiation and the metabolic heat produced during flight. T_b during activity was then regulated above T_a. T_b measured between 10.00–12.30 h (morning activity period) ranged between 34.6 and 40.6°C.

The range of T_bs measured in the cicadas decreased to 30.7–36.9°C between 17.00 and 19.00 h. T_bs were elevated with respect to T_a again at dusk. Cicadas that were singing or flying in the evening had T_bs as much as 13.0°C higher than T_a. Cicadas not participating in the evening chorus had T_bs slightly higher than T_a (<2°C) during the same activity period.

Male cicadas were found singing from *Prosopis* trees and two females were seen ovipositing in a

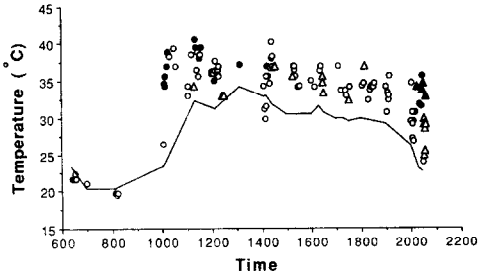

Fig. 1. Diurnal distribution of T_b of *Dorisiana bonaerensis* and *Quesada gigas* on the 13th December 1986. A rainstorm from 07.00 to 08.00 h followed by a misting rain until 09.45 h delayed the start of activity approx. 2 h. Body temperatures are below ambient temperature before activity begins. Body temperatures are elevated at the start of activity (10.00 h) and regulated throughout the day. Body temperatures of quiescent animals decrease with ambient temperature after sunset (20.10 h). Animals participating in the evening chorus have body temperatures in or near the body temperature range measured during the day. Closed circles, T_b of singing *D. bonaerensis*; open circles, T_b of *D. bonaerensis* engaged in other activities (including no activity); closed triangles, T_b of singing *Q. gigas*; open triangles, T_b of *Q. gigas* performing other activities; solid line, ambient air temperature.

rainstorm on the 21st December 1986. T_b distribution of cicadas from this population is shown in Fig. 2. T_bs of the singing males were 6.8–11°C greater than T_a and were within the temperature range of dusk singing *D. bonaerensis* recorded on the 13th December 1986.

Field temperatures were recorded for comparative purposes on the morning of the 3rd January 1988. These data contrast the data of the 13th December 1986 because the entire morning was clear and sunny on the 3rd January 1988. Of the ten recorded T_bs, nine fell within the T_b range previously measured for each of the various activities observed. The lone exception was a copulating female whose T_b was 0.2°C lower than any mating animal previously recorded.

The daily distribution of *Q. gigas* T_b is similar to that seen in *D. bonaerensis* (Fig. 1).

Thermoregulation

D. bonaerensis spends the night feeding on small to medium-sized *Prosopis* branches. By 2–2.5 h after sunrise the cicadas were observed to have moved to the eastern side of their host plant to bask in the morning sunlight. In addition, metabolic heat produced in flight is used to increase T_b. After the cicadas have elevated T_b to the level necessary for reproductive activities, thermoregulation maintains T_b within a preferred temperature range. As T_a increases, the cicadas retreat to interior, shaded portions of the trees. T_b is then regulated through behavioral and metabolic mechanisms throughout the afternoon as can be seen by the distribution of T_b in Fig. 1. There is a general movement toward the outer edges on the western side of the tree as the afternoon progresses and T_a begins to decrease. This movement permits the utilization of radiant energy to maintain an elevated T_b until the sun has set.

Individuals that participate in the evening chorus increase their T_b with metabolic heat using a patterned "sing and fly" behavior. After sunset cicadas turn to metabolic heat to raise T_b to the level necessary for activity. The T_b of "inactive" cicadas, those not seen to be participating actively (singing) in the evening chorus remains near ambient (Fig. 1). When "active" cicadas have finished their activity, their T_b falls to near T_a, fluctuating with T_a until the next activity period.

The slope of the regression line of T_b as a function of T_a can indicate if T_b is being regulated. If the slope is significantly different from one, regulation is occurring. Similarly, if the slope is not significantly different from one, there is no temperature regulation (May and Casey, 1983; May, 1985). Figures 3 and 4 show the distribution of T_b as a function of T_a in *D. bonaerensis*. In both figures the data are separated as to whether the animals were "active" or "inactive".

Figure 3 shows the T_b distribution for all *D. banaerensis* measured in the field. The slope of the regression analysis for all "active" animals is significantly different from one ($t = 6.34$, $df = 44$, $P \ll 0.0001$) suggesting the cicadas are thermoregulating. In contrast, the slope of the regression for all "inactive" animals is not significantly different from one ($t = 1.99$, $df = 21$, $P > 0.05$) suggesting the cicadas are not thermoregulating when they are not active.

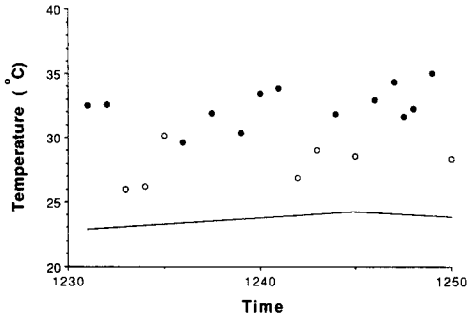

Fig. 2. T_b of *Dorisiana bonaerensis* during a light rain under a heavy overcast on the 21st December 1986. These animals were not exposed to direct solar radiation before the T_b was recorded. Closed circles, represent body temperatures of singing *D. bonaerensis*; open circles, represent body temperatures of *D. bonaerensis* engaged in other activities (including no activity). Details as in Fig. 1.

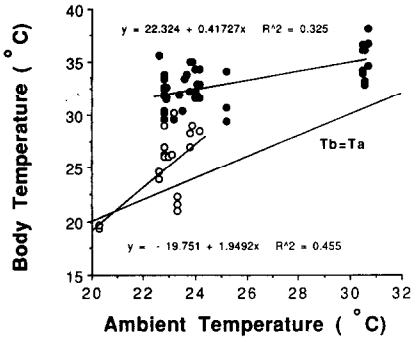

Fig. 3. Distribution of *Dorisiana bonaerensis* T_b as a function of T_a. The slope of the linear regression for "active" animals (closed circles) is significantly different from one, suggesting thermoregulation. The slope of the linear regression for "inactive" animals (open circles) is not significantly different from one, suggesting no thermoregulation is occurring.

Figure 4 shows the T_b distribution for *D. bonaerensis* measured in the field without access to solar radiation, either after the sun had set or during a rainstorm. The regression analysis for animals classified as "active" is significantly different from one ($t = 2.63$, $df = 21$, $P < 0.01$) while the slope of the regression for animals classified as "inactive" does not differ significantly from one ($t = 0.524$, $df = 14$, $P > 0.30$). These analyses show that *D. bonaerensis* is thermoregulating with endogenous heat.

Temperature ranges for various activities

T_bs were measured during a variety of activities. A wide temperature range for an activity indicates temperature independence. A narrow range implies

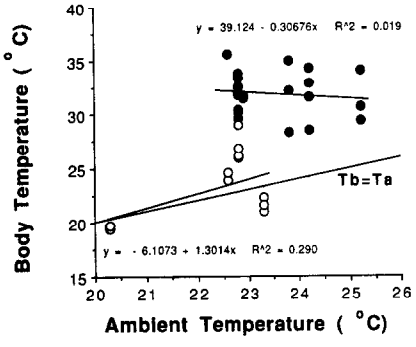

Fig. 4. Distribution of T_b of as a function of T_a when *Dorisiana bonaerensis* were not exposed to solar radiation. The slope of the linear regression for "active" animals (closed circles) is significantly different from one, suggesting thermoregulation is occurring with endogenous heat. The slope of the linear regression for "inactive" animals (open circles) is not significantly different from one, suggesting no thermoregulation is occurring when the animals do not generate heat for activity.

Table 1. Body temperature ranges for various activities in the cicada *Dorisiana bonaerensis*

Activity	Range (°C)	*n*
Feeding	19.4–38.9	48
Oviposition	28.3–40.2	15
Mating	32.8–37.6	12
Singing		
Total	29.4–40.6	34
Diurnal	34.3–40.6	16
Evening	29.4–35.6	5
Rain	29.6–35.0	13
Evening + rain	29.4–35.6	18

that the activity is dependent on temperature (Heath, 1967). A summary of the temperature ranges for various activities in *D. bonaerensis* is shown in Table 1.

Feeding behavior occurred over the greatest T_b range. Feeding animals had T_bs ranging from 19.4 to 38.9°C ($T_a < 19.4$°C was not encountered).

Oviposition had a greater temperature dependence than feeding. The data from 13 December 1986 show a T_b range of 34.3–40.2°C for ovipositing females. The temperature range in which oviposition was observed was increased when two females were captured while ovipositing in the rain on 21 December 1986. The T_bs of these two females were 28.3 and 28.5°C. The small number (2) of females seen ovipositing in the rain suggests that the lowest T_b necessary for oviposition is approx. 28°C.

The T_b range recorded for singing males was 29.4–40.6°C. Animals singing during the day had a T_b range of 34.3–40.6°C. The range of T_bs found in animals singing at dusk was 29.4–35.6°C. T_bs of animals singing in the rain (29.6–35.0°C) were within the temperature range of animals singing at dusk.

Mating occurs over the smallest temperature range (32.8–37.6°C) of the recorded activities suggesting a higher degree of temperature dependency. No mating was observed in the evening or during the rainstorm. Mating usually occurs on the interior branches of the host tree protected from possible overheating due to solar radiation.

Temperature responses

Temperature tolerance and thermal preference data are summarized in Table 2. Minimum flight temperature (MFT) and heat torpor temperatures delineate the T_b range within which cicadas are fully active. Cicadas are torpid outside of this temperature range. The maximum voluntary tolerance temperature (MVT) or shade-seeking temperature is an upper thermoregulatory point (Heath, 1970).

Table 2. Temperature responses (°C, mean ± SE) of Argentine endothermic cicadas

Species	Minimum flight temperature	Maximum voluntary tolerance	Heat torpor
Dorisiana bonaerensis	16.7 ± 0.35 (n = 28)	34.6 ± 0.55 (n = 27)	44.6 ± 0.24 (n = 26)
Fidicina mannifera	19.8 ± 0.56 (n = 10)	32.0 ± 0.87 (n = 11)	42.0 ± 0.58 (n = 10)
Quesada gigas	19.1 ± 0.93 (n = 17)	33.8 ± 0.73 (n = 16)	44.9 ± 0.51 (n = 17)

Endothermy

Endogenous heat to raise T_b is produced by the thoracic musculature of cicadas. *D. bonaerensis* and *Q. gigas* raised their T_b in the field by taking short flights (1–3 m) during their activity period. The cicadas alternately sang and flew when solar radiation was unavailable to elevate T_b.

We observed *F. mannifera* making similar flights in the field. However, Bartholomew and Barnhart (1984) showed that *F. mannifera* could raise T_b endothermically without flight or large wing movements.

The heating and cooling curves obtained for each species were used to quantify heat production (Table 3). The T_b of a flying insect under uniform heat input increases as a decaying exponential curve (Heath and Wilkin, 1970) until it reaches a maximum temperature difference. The rate at which cicadas cool is consistent with Newton's Law of cooling.

DISCUSSION

Diurnal distribution of body temperature

The T_bs of *D. bonaerensis* and *Q. gigas* measured in the field show that these cicadas are endothermic in their natural environment. Recorded T_bs were respectively as much as 13.0 and 12.0°C greater than T_a when solar heating was unavailable to the species. The diel distribution of T_bs in endothermic cicadas is similar to that in ectothermic species in that T_b is elevated above T_a during daylight hours. Endothermic cicadas differ in that T_bs of "active" cicadas are approximately the same as diurnal T_bs at dusk or when solar energy is unavailable.

Female cicadas endothermically raise T_b in the manner described above during the chorus activity of the males. Female *D. bonaerensis* elevate T_bs while ovipositing in the rain. The females may also elevate T_b for specific song recognition. Female planthoppers (de Vrijer, 1984), crickets (Doherty, 1985), and frogs (Gerhardt, 1983) respond only to the calls produced by males at the same T_b as the female.

Thermoregulation

In most cicadas thermoregulation is accomplished by behaviorally altering the heat gain from solar radiation (Heath, 1967, 1972; Heath and Wilkin, 1970; Heath *et al.*, 1972; Hastings and Toolson, 1991; Sanborn *et al.*, 1992). In the endothermic species solar heating is augmented with metabolic heat production. When environmental conditions prevent the utilization of solar radiation, endothermic cicadas use metabolic heat to become active. These cicadas can be

Table 3. Cooling rates and oxygen consumption (V_{O_2}) of the cicadas determined in the present study

Species	Cooling rate (min^{-1})	V_{O_2max} (ml O_2 min^{-1})
Dorisiana bonaerensis	0.214 ± 0.0375 (n = 8)	0.650 ± 0.1638* (n = 7)
Quesada gigas	0.183 ± 0.0127 (n = 2)	0.907 ± 0.1315* (n = 2)
Fidicina mannifera†	0.257 (n = 1)	
Fixed flapping		1.837 ± 0.1125 (n = 11)
Non-flapping warm-up		0.470 ± 0.0278 (n = 6)

Reported values are mean ± standard error.
*Estimated.
†Bartholomew and Barnhart (1984; calculated from Fig. 4).

Table 4. Mean temperature responses (°C) reported in the literature for cicadas

Species	Minimum flight temperature	Maximum voluntary tolerance	Heat torpor	Range of full activity
*Dorisiana bonaerensis**	16.7	34.6	44.6	27.9
*Quesada gigas**	19.1	33.8	44.9	25.8
*Fidicina mannifera**	19.8	32.0	42.0	22.2
Magicicada cassini[a,b]	20.9	31.8	43.0	22.1
Diceroprocta apache[c]	21.9	39.2	45.6	23.7
Cacama valvata[d]				
Camp Verde	23.7	37.3	44.6	20.9
Agua Fria	24.0	34.9	44.3	20.3
Okanagana hesperia[e]	22.9	36.3	43.5	20.6
Okanagodes gracilis[f]	22.7	41.2	48.7	26.0

Endothermic species are marked with an asterisk (*).
[a]Heath (1967).
[b]Heath *et al.* (1971).
[c]Heath and Wilkin (1970).
[d]Heath *et al.* (1972).
[e]Heath (1972).
[f]Sanborn *et al.* (1992).

termed facultative or partial endotherms. *Magicicada tredecim* (Walsh and Riley) has been described as another endothermic cicada (Toolson and Toolson, 1991). The small difference between T_b and T_a reported (range −0.1–2.6°C) is insufficient to free the species from thermal constraints imposed by the environment as was described by Heath (1968). The passive heat production in *Magicicada* does not represent heat produced for thermoregulatory purposes and therefore does not correspond to endothermy as defined by the Commission for Thermal Physiology of the International Union of Physiological Sciences (Anonymous, 1987).

Temperature ranges for various activities

The T_b range over which cicadas are optimally active represents a small portion of the temperature range an animal can tolerate. The temperature range required for specific activities is dependent on the complexity of the task (Heath *et al.*, 1971). Feeding, a simple solitary activity, occurs over a wide temperature range. More complex activities, such as singing and oviposition, occur over a more restricted temperature range. Behaviors involving the coordination of several muscle groups or involving more than one animal such as copulation occur over the most limited temperature range (Heath, 1967, 1972; Heath *et al.*, 1971).

The T_b ranges for various activities in the endothermic *D. bonaerensis* correspond well to values reported in ectothermic cicada species. Similar temperature ranges for singing are described in *Cacama valvata* (Uhler) (Heath *et al.*, 1972) and *Magicicada cassini* (Fisher) (Heath *et al.*, 1971). The temperature ranges for feeding, copulation, and ovipositing in *D. bonaerensis* are also similar to the temperature ranges reported for *Magicicada cassini* (Heath, 1967; Heath *et al.*, 1971).

Temperature responses

The thermal responses of cicadas can be related to their activity patterns and their habitat. Table 4 summarizes the reported cicada temperature responses. Endothermic cicadas generally have a lower MFT and a greater temperature range of full activity than the ectothermic species. Heath *et al.* (1972) suggested the MFT probably relates more to the physical design of the cicada flight motor system than to the habitat of the cicada. However, the low MFTs of the endothermic cicadas may be necessary for dusk activity. A low MFT permits the cicada to utilize heat produced in flight to raise T_b even at low T_a.

The MVTs for the endothermic species are variable but generally are lower than those described in ectothermic species. The MVT values obtained for *D. bonaerensis* and *Q. gigas* probably represent a balanced response to the elevated T_as encountered during the day coupled with the lower T_as encountered during the dusk activity period. The MVT value obtained for *F. mannifera* is probably an adaptation to the preferred microenvironment of the species, the trunks of primary forest trees (Young, 1983). It avoids radiant solar heating through activity under the canopy of the tropical forest it inhabits.

F. mannifera has the lowest reported heat torpor temperature (Table 4). This also can be related to activity in the understory of the tropical forest. The environment is more thermally stable and temperature extremes are avoided with activity in the understory.

The heat torpor temperatures of *D. bonaerensis* and *Q. gigas* are similar to the desert grassland adapted *Cacama valvata* (Heath *et al.*, 1972) and lower than the Sonoran desert adapted *Diceroprocta apache* (Davis) (Heath and Wilkin, 1970) and *Okanagodes gracilis* Davis (Sanborn *et al.*, 1992). The elevated heat torpor temperatures of *D. bonaerensis* and *Q. gigas* may be a response to the hot and humid Chaco environment and activity in the canopy. High thermal tolerances may have helped *Q. gigas* colonize and survive in a wide range of habitats.

Endothermic heat production

Cicadas use the heat produced by the flight muscles to raise T_b. *D. bonaerensis* and *Q. gigas* fly to elevate T_b in the field. Because insect flight is a mechanically inefficient process (3.3–27.5% efficiency; Weiss-Fogh, 1972, 1976; Casey, 1981; Casey *et al.*, 1985; Ellington, 1984, 1985), insect flight muscles are well suited for heat production. In addition to flapping flight Bartholomew and Barnhart (1984) showed *F. mannifera* is capable of endothermically warming by low frequency (1–2/s) wing movements and telescoping of the abdomen at 15–36 cycles/min.

Metabolic rates calculated from heating and cooling curves have been shown to underestimate V_{O_2} measured by changes in O_2 concentration from about 15% (Heath and Adams, 1967; Casey *et al.*, 1981; May, 1979) to over 50% (Casey *et al.*, 1985). The discrepancy is possibly produced because measurements of T_b do not account for evaporation, heat transfer to the head or abdomen, or convection due to wing movements (May, 1985), and the insects do not produce normal lift during tethered flight (Casey, 1989). The values reported here for the cicadas correspond to the maximum calculated values of heat production during the initial stages of flight when heat transfer to the head or abdomen and/or abnormal flight should be minimal.

Bartholomew and Barnhart (1984) suggest that cicadas exhaust quickly during flight. The inability of these investigators to sustain cicada flight in the laboratory was thought to be the result of depleted energy reserves in the flight muscles. They rarely fly more than a few tens of meters. From the data collected in this research, it appears cessation of flight activity can be attributed to the cicadas reaching a thermoregulatory temperature rather than flying to exhaustion. The MVT temperature, an upper thermoregulatory temperature (Heath, 1970), we determined for *F. mannifera* in this study (Table 2) is not statistically different from either the mean thoracic temperature obtained by Bartholomew and Barnhart (1984) when endogenous warm-up stopped during fixed flapping ($t = 0.716$, $df = 20$, $P = 0.241$) or during non-flapping warm-up ($t = 1.02$, $df = 15$, $P = 0.837$). It appears the cicadas are regulating T_b with the heat produced during flight and they stop flying (producing heat) when they reach a fully active T_b.

Oxygen availability was not the limiting factor in *F. mannifera* flight (Bartholomew and Barnhart, 1984). *F. mannifera* was unwilling to make flights of normal duration after warm-up activity which was of greater duration and consumed more oxygen than a bout of fixed flapping (Bartholomew and Barnhart, 1984). *Diceroprocta apache* is reluctant to fly at T_bs above the reported MVT temperature for the species (Heath and Wilkin, 1970) and *Magicicada septendecim* (Linn.) has the endurance to fly nearly 1000 s (White *et al.*, 1983) further suggesting an inhibition of flight activity in *F. mannifera* was due to an elevated T_b. Other endothermic insects will pause at high T_as to permit T_b to decrease and prevent overheating (Kammer, 1981).

The cicada species in this study behaved in a similar fashion to *F. mannifera* when tethered. Flight times ranged from a little more than 100–300 s in the laboratory. However, the thoracic temperatures when tethered animals stopped flying were within the T_b range of endothermically active cicadas encountered in the field. As an example, heat output by *D. bonaerensis* at the initiation of flight could have achieved a T_b gradient of 19.77°C above T_a. The rate of heat production decreased throughout the flight. As the flight terminated, heat production could only maintain a 3.72°C gradient. T_b at this time was elevated 5.6°C above T_a and was within the temperature range of endothermic animals active in the field. This suggests that the cicadas stop flying when tethered because additional heat production is unnecessary.

The significance of endothermy

Endothermy is an energetically expensive process. Comparison of the data reported for *Cystosoma saundersii* Westwood, an ectothermic dusk singing cicada (Josephson and Young, 1979), with the endothermic *D. bonaerensis* illustrates the metabolic cost of endothermy. V_{O_2} during calling in *C. saundersii* (MacNally and Young, 1981) is less than 23% of the V_{O_2} necessary to maintain the 9°C average T_b gradient measured in endothermically active animals. If the metabolic cost of singing in *D. bonaerensis* is similar to that measured in *C. saundersii*, then dusk activity in the endothermic animal is more than five times as energetically expensive as activity in an ectothermic animal.

The utilization of metabolic heat to raise T_b for activity will decrease the life span of animals that

do not obtain large amounts of energy from their food. Since cicadas feed on xylem fluid, the nutrients available for energy conversion are limited. The question arises as to why an animal would expend energy stores to become active when it could utilize solar radiation during the day and save metabolic energy. Endothermy and the high T_bs of insects may have evolved for several reasons (recently summarized by Heinrich, 1993). Endothermic behavior in cicadas may serve to increase reproductive fitness in the following five ways:

1. Facultative endothermy is an uncoupling of reproductive behavior from possible physiological constraints of the environment. The ability to produce metabolic heat circumvents a reliance on environmental conditions to determine when an animal may or may not be reproductively active. This becomes important to cicadas because the adult phase of the life cycle is relatively brief.

A 3 or 4°C increase in T_b could represent the difference between an active period and lost time. Forced endogenous heat production was shown to extend the activity period for a normally ectothermic cicada (Heath, 1968). While rain causes non-endothermic cicadas to decrease or suspend activity (Alexander and Moore, 1958), endothermic cicadas can remain active during a heavy overcast and/or light rainstorms by using endogenous heat production. Restriction in the use of metabolic heat saves energy stores in the cicadas.

2. By restricting activity to the cooler portions of the day, possible thermoregulatory problems of midday are avoided. High T_as combined with metabolic heat produced by normal activities could lead to a lethal increase in T_b. When T_as are elevated, calling activity is stopped or depressed in *Cacama valvata* (Heath *et al.*, 1972) and *Diceroprocta apache* (Heath and Wilkin, 1970).

Activity during the heat of the day could also affect the internal state of a cicada. *Diceroprocta apache* lose 30–35% of their body water within the first hour of evaporative cooling required to regulate T_b when exposed to high T_a (Toolson, 1987). The endothermic cicadas eliminate problems associated with high T_as by restricting their activity to the cooler portions of the day, i.e. early morning and dusk.

3. Utilization of habitats unavailable to strictly ectothermic animals. The endothermic *F. mannifera* is a deep forest dwelling cicada (Young, 1980a, 1983; personal observation). It is active on the lower trunks of primary forest trees at a height of 2–3 m (Young, 1983) and at times when other cicadas are less active (Young, 1980b). Most of the cicadas active in the same geographic area have a tendency to aggregate in exposed areas (Young, 1975, 1980a, 1981a). Optimal calling sites are presumably related to the acoustic and thermoregulatory requirements of each species (Young, 1981b).

Endothermy has permitted *F. mannifera* the use of a habitat in which other cicadas are unable to reproduce efficiently. *F. mannifera* has the ability to reproduce under conditions of less sunlight and increased wetness compared with other synchronously emerged cicadas (Young, 1972). Spatial partitioning of the environment is adaptive in reducing interspecific competitive conflicts (Young, 1972, 1980b, c). Decreasing competition between species is achieved in adults by eliminating competition for singing perches, and oviposition sites.

Flexibility in choice of habitat and microhabitat has allowed *Q. gigas* to become the most widely distributed cicada (Young, 1976). The ability to choose a wide variety of habitats and microhabitats is associated with the facultative endothermy utilized by *Q. gigas*.

4. Predator avoidance. Insects that have gathered together for activity represent prey of high energy content with low searching and handling costs (Burk, 1982). Dusk cicada choruses occur after the burst of activity characteristic of many insectivorous birds (Alexander, 1960; Young, 1981c). Avian foraging efficiency decreases as light intensity decreases (Kacelnik, 1979). Thus the poor profitability at dawn and dusk makes foraging behavior uneconomical for the birds. Doolan and MacNally (1981) report bird predation on the dusk singing *Cystosoma saundersii* only in the first few minutes of chorus activity. Flying female cicadas normally were taken as prey. However, when the chorus was started early, either by temporary cloud cover or from artificial stimulation in playback experiments, and light levels were higher than normal, avian predation occurred much more frequently than in normal choruses with the birds preying not only on the flying individuals but also on the sedentary singing males (Doolan and MacNally, 1981).

5. Optimization of broadcast coverage and sound transmission. Young (1981c) hypothesizes selection favoring cicada dawn/dusk chorusing as an adaptation for communicatory optimization. Acoustic data support this hypothesis (Henwood and Fabrick, 1979; Marten *et al.*, 1977; Waser and Waser, 1977; Wiley and Richards, 1978). Endothermy permits communication by cicadas at a time when they can communicate over the largest area and increases the potential number of interactions with members of their own species.

Thoracic temperature in cicadas must be within a restricted temperature range for coordinated

reproductive activities. Endogenous heat production functions to raise and maintain thoracic temperature at an optimal level for reproductive activity.

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