

THEMOREGULATION BY ENDOGENOUS HEAT  
 PRODUCTION IN TWO SOUTH AMERICAN GRASS DWELLING  
 CICADAS (HOMOPTERA: CICADIDAE: *PROARNA*)

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ABSTRACT

*Proarna bergi* (Distant) and *Proarna insignis* Distant use metabolic heat to raise body temperature ( $T_b$ ) for activity when ambient conditions would prevent activity in ectothermic animals. Both species were observed singing during overcast or rainy conditions and at dusk.  $T_b$ s in the field exceeded ambient by as much as 7.4°C when solar radiation was unavailable to the insects. In the laboratory voluntary metabolic heat production raised  $T_b$  as much as 12.3°C and 10.7°C above ambient in *P. bergi* and *P. insignis* respectively. Estimates of metabolic rate from heating and cooling curves were 0.118 ml O<sub>2</sub> per min for *P. bergi* and 0.126 ml O<sub>2</sub> per min for *P. insignis*. Fine shiver-like movements of the thoracic musculature produced the heat. The  $T_b$  at which endogenous warm-up voluntarily stopped in the laboratory was similar to the  $T_b$ s measured in active animals in the field. Thermal responses measured in the laboratory also illustrate these animals are thermoregulating with endogenous heat. Endogenous heat production uncoupled reproductive behavior from environmental constraints.

Key Words: Endothermy, thermoregulation, temperature, shivering, cicadas, Cicadidae, *Proarna*

RESUMEN

*Proarna bergi* (Distant) y *Proarna insignis* Distant utilizan calor metabólico para elevar la temperatura del cuerpo ( $T_b$ ) y ser activos cuando las condiciones ambientales impiden la actividad en otros animales ectotérmicos. Ambas especies fueron observadas cantando bajo condiciones de cielo completamente nublado, bajo la lluvia y en la obscuridad. Las  $T_b$  en el campo excedieron las del ambiente en 7.4°C cuando la radiación solar no era disponible a los insectos. En el laboratorio la producción voluntaria de calor aumentó la  $T_b$  en 12.3°C y 10.7°C por encima del ambiente en *P. bergi* y *P. insignis* respectivamente. Los estimados de la tasa metabólica de las curvas de calentamiento y enfriamiento fueron de 0.118 ml de O<sub>2</sub> por minuto para *P. bergi* y 0.126 ml de O<sub>2</sub> por minuto para *P. insignis*. Finos movimientos en forma de temblor de la musculatura torácica producen el calor. La  $T_b$  a la cual el calentamiento endógeno voluntariamente cesó en el laboratorio fué similar a la  $T_b$  medida en animales activos en el campo. Las respuestas térmicas medidas en el laboratorio además ilustran que estos animales son termorreguladores con calor endógeno. La producción de calor endógeno

posibilitó el desarrollo de la conducta reproductiva independientemente de las condiciones ambientales.

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Cicadas must maintain their body temperature within a small range to coordinate reproductive activity (Heath 1967; Heath 1972). Thermoregulation is generally accomplished by altering the uptake of solar radiation (Heath 1967; Heath & Wilkin 1970; Heath et al. 1972; Sanborn et al. 1992). Endothermy was first described in cicadas by Bartholomew & Barnhart (1984) and has recently been described as a mechanism of thermoregulation in cicadas (Sanborn et al., in press).

This paper describes and quantifies an additional mechanism of endogenous heat production and its utilization by two grass dwelling cicadas in northern Argentina.

#### MATERIALS AND METHODS

##### Insects

*Proarna bergi* (Distant) and *Proarna insignis* Distant are medium-sized cicadas. Live weight averages  $342 \pm 12$  (n=41) and  $434 \pm 14$  (n=21) milligrams respectively. Although the data was collected mainly from males, both sexes were used in field and laboratory measurements. Animals captured for laboratory experimentation were placed in a cardboard container along with plant samples and a wet paper towel. The containers were kept on ice until the experiments could be performed during the afternoon or evening of the day of capture. Live weights were measured on a Cent-O-Gram triple beam balance (Model CG 311, Ohaus Scale Corporation) accurate to  $\pm 5$  mg. All statistics are presented as mean  $\pm$  standard error. Voucher specimens are deposited in the collection of the Museo Nacional de La Plata, La Plata, Argentina.

##### Temperature Measurements

*Equipment.* Body temperature ( $T_b$ ) of the cicadas was measured with a Sensortek Model BAT-12 digital thermocouple thermometer with a type MT-29/1 copper/constantan hypodermic microprobe (accurate to  $\pm 0.1^\circ\text{C}$ ) which had been calibrated with a National Bureau of Standards mercury thermometer. The probes were inserted dorsally midway into the mesothorax of each cicada to measure  $T_b$ . All  $T_b$ s were measured within five seconds of the insect being captured or the insect performing the behavior under study.

*Laboratory Measurements.* Laboratory experiments were performed to determine the range of temperature in which the cicadas can be fully active. The procedures used to determine the thermal responses were described in previous cicada studies (Heath 1967; Heath & Wilkin 1970).

Cooling curves of *P. bergi* and *P. insignis* were measured from tethered cicadas. A copper/constantan thermocouple wire (30 gauge) was implanted into and secured to the dorsal mesothorax of the cicadas to measure changes in  $T_b$ . The tethered animal was permitted to fly to increase  $T_b$  above ambient. The animal was placed into a styrofoam box immediately after the flight terminated. The box served as a controlled radiant environment and prevented forced convective heat loss.  $T_b$  was recorded with the BAT-12 every 15 sec as the animal cooled until  $T_b$  remained relatively constant (10 min).

Heat production was determined by inducing warm-up behavior in room temperature animals ( $T_a$  21-27°C) and measuring the duration of warm-up behavior and the difference between  $T_b$  and  $T_a$  when the animal stopped warm-up behavior. This provided a rate of warm-up for the calculation of heat production. Warm-up behavior was induced by gently tapping the dorsal thorax of a cicada with a finger. The mechanical disturbance was usually sufficient to induce endogenous heat production.  $T_b$ s at the end of warm-up were measured with the BAT-12 system. Specimens were secured by the wings before probe insertion to prevent conductive heat transfer between our fingers and the insect.

Oxygen consumption ( $V_{O_2}$ ) was estimated using the following formula (Heath & Adams 1969):

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

where  $\Delta T$  = rate of change of temperature during heating (°C/min), sp. ht. = specific heat of the object [83 cal/g°C (Bartholomew 1981)], mass = thoracic mass in grams,  $O_2$  cal. eq. = the caloric equivalent of oxygen (4.8 cal/ml  $O_2$ ),  $Q_1$  = heat loss to the environment (cal/min°C), and  $(T_{th} - T_a)$  = thoracic temperature minus ambient temperature (°C). The thoracic mass of the individual *P. bergi* and *P. insignis* used to produce our cooling curves was 32.4% and 36.8% of total body mass, respectively. We used these percentages for determining thoracic mass in all calculations. We calculated  $V_{O_2}$  from the rate of heat change so direct comparisons could be made with published data.

*Field Temperatures.* The  $T_b$ s of singing cicadas were measured in the field in an attempt to ascertain the  $T_b$  range in which the cicadas are normally active. Insects in the field were caught either with an insect net or by hand. After an insect was captured in a net, the net was constricted around the animal to prevent movement. The thermocouple was inserted through the net into the insect to obtain the  $T_b$  measurement within five seconds of capture. This procedure prevented heat transfer between the insect and experimenter while the specimen was being oriented for insertion of the temperature probe. The insect was shaded by the experimenter during the measurement to prevent solar heating.

It was preferable to catch the insects in a net but the habitat sometimes made capturing a cicada with a net impossible. If a cicada had to be captured by hand, it was oriented immediately after capture so that it could be held by the wingtips between the thumb and forefinger. This method of restraint reduces conductive heat transfer during the capture before the  $T_b$  is recorded and minimizes change in  $T_b$  due to heat exchange with the experimenter. Ambient temperature ( $T_a$ ) was recorded in the shade at a height of approximately one m above ground.

## RESULTS

Thermal responses of the two *Proarna* species are summarized in Table 1. Mean values for all thermal parameters are lower in *P. insignis* than in *P. bergi*. Minimum flight temperature (MFT) ( $t=1.84$ , d.f.=50,  $p<.04$ ) and heat torpor temperatures (HT) ( $t=4.90$ , d.f.=55,  $p<<.001$ ) are significantly lower in *P. insignis*, but there is no significant difference in maximum voluntary tolerance temperature (MVT) ( $t=1.63$ , d.f.=55,  $p=.0545$ ). The MVT represents an upper thermoregulatory temperature (Heath 1970).

Endogenous heat to raise  $T_b$  in cicadas is produced by the thoracic musculature. *P. bergi* and *P. insignis* raise  $T_b$  by producing fine shiver-like movements of the wings. The wings of a cicada at rest are held in an "umbrella" position over the body. When

TABLE 1. TEMPERATURE RESPONSES ( $^{\circ}\text{C}$ ,  $\bar{X} \pm \text{S.E.}$ ) OF ARGENTINE ENDOTHERMIC CICADAS.

Species	Minimum Flight Temperature	Maximum Voluntary Tolerance	Heat Torpor
<i>Proarna bergi</i>	20.7 $\pm$ 0.51 (n=34)	37.6 $\pm$ 0.38 (n=40)	46.3 $\pm$ 0.26 (n=39)
<i>Proarna insignis</i>	19.3 $\pm$ 0.40 (n=18)	36.4 $\pm$ 0.60 (n=17)	44.0 $\pm$ 0.37 (n=18)

endogenous warm-up is initiated in the two *Proarna* species, the costal margin of the wings is raised laterally, flattening the wings in the dorso-ventral plane. The wings are then vibrated in a shiver-like motion of the thoracic musculature to produce heat.

Rates of cooling and estimated  $V_{\text{O}_2}$  determined from the heating and cooling curves for the species in this study are shown in Table 2. The rate at which cicadas cool is consistent with Newton's Law of cooling ( $r^2 > .99$  when an exponential model was fit to the data) so the animals were not regulating heat loss.

Maximum  $T_b$  differences upon cessation of warm-up behavior measured in the laboratory in *P. bergi* and *P. insignis* are 12.3 $^{\circ}\text{C}$  and 10.7 $^{\circ}\text{C}$  greater than  $T_a$ , respectively. The histogram of the body temperature of cessation of warm-up behavior shows a bimodal distribution (Figs. 1 and 2). This distribution may represent the  $T_b$  range of reproductive activity for the particular species and suggests that the cicadas are regulating heat production to achieve a certain body temperature. Mean  $T_b$  when warm-up behavior stopped was 33.60  $\pm$  3.70 $^{\circ}\text{C}$  (n=14) for *P. insignis* and 33.81  $\pm$  3.04 $^{\circ}\text{C}$  (n=23) for *P. bergi*. There is no significant difference in the  $T_b$  of cessation of warm-up behavior between the two species (t=0.187, d.f.=35, p=.43).

Figure 2 also shows the relationship between  $T_b$  of *P. insignis* active in the field (singing temperatures) and the  $T_b$  distribution of the species when it ceases voluntary warm-up behavior (field temperatures were measured under an overcast sky with  $T_a = 31.9^{\circ}\text{C}$ ). The upper peak of the warm-up temperature distribution is greater than or equal to the modal singing temperature in *P. insignis*. The figure demonstrates that the cicadas possess the mechanisms necessary to raise  $T_b$  endothermically to the level necessary for activity and that heat production is regulated to maintain  $T_b$  in a biologically significant temperature range. The upper peak of the bimodal distribution for both species encompasses the MVT temperatures determined for each species.

TABLE 2. COOLING RATES AND ESTIMATED OXYGEN CONSUMPTION ( $V_{\text{O}_2}$ ) OF THE CICADAS DETERMINED IN THE PRESENT STUDY. REPORTED VALUES ARE MEAN  $\pm$  STANDARD ERROR.

Species	Cooling Rate ( $^{\circ}\text{C}/\text{min.}^{\circ}\text{C}$ )	$V_{\text{O}_2}$ Max (ml $\text{O}_2/\text{min}$ )
<i>Proarna bergi</i>	0.282 (n=1)	0.110 $\pm$ 0.0176 (n=6)
<i>Proarna insignis</i>	0.257 (n=1)	0.132 (n=1)

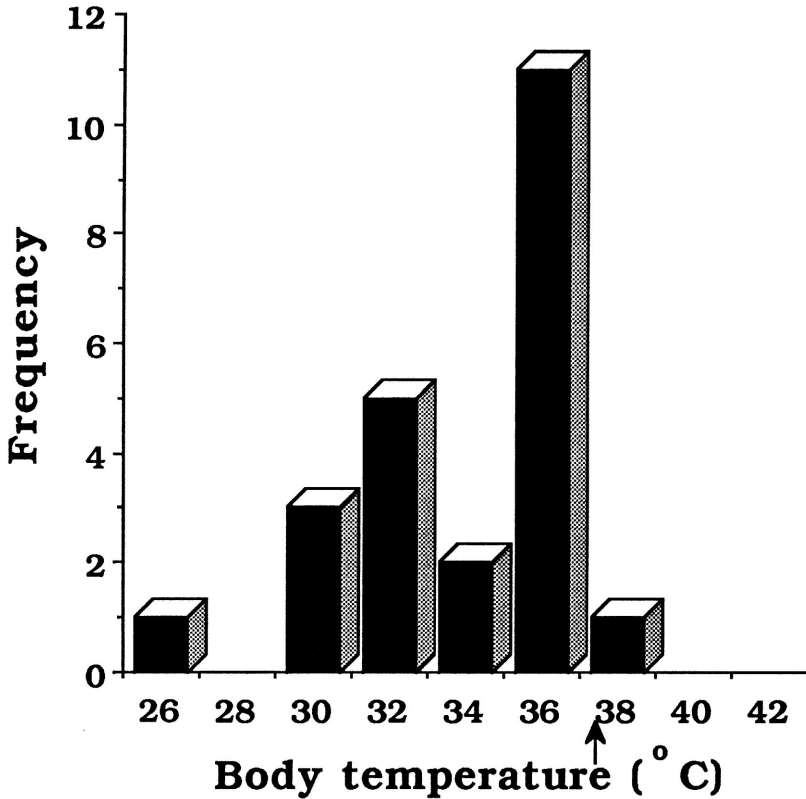


Fig. 1. Distribution of body temperatures of *Proarna bergi* recorded when endogenous warm-up behavior ceased. The bimodal distribution of warm-up temperatures may represent the body temperature range of reproductive activity. The thermoregulatory maximum voluntary tolerance temperature measured in the laboratory is indicated by the arrow.

*Proarna bergi* and *P. insignis* were found to use endogenous heat production to remain active under adverse environmental conditions. We observed populations of both species singing under heavy overcast, during rainy conditions, and at dusk. The lack of solar radiation coupled with environmental conditions means that the elevated  $T_b$ s observed in these species were a result of endogenous heat production. Recorded  $T_b$ s in *P. insignis* were as much as  $7.4^\circ\text{C}$  greater than  $T_a$  when solar heating was unavailable to the species.

#### DISCUSSION

*Proarna insignis* was originally described from Nicaragua and Panama (Distant 1881). Its range extends from Mexico in the north (Jacobi 1907) to northwestern Argentina where it inhabits grasses in clearings in the cloud forest.

Torres (1961) synonymized *P. bergi* (Distant) with the closely related *P. bufo* Distant. Our collections in Argentina show two distinct varieties or subspecies. The

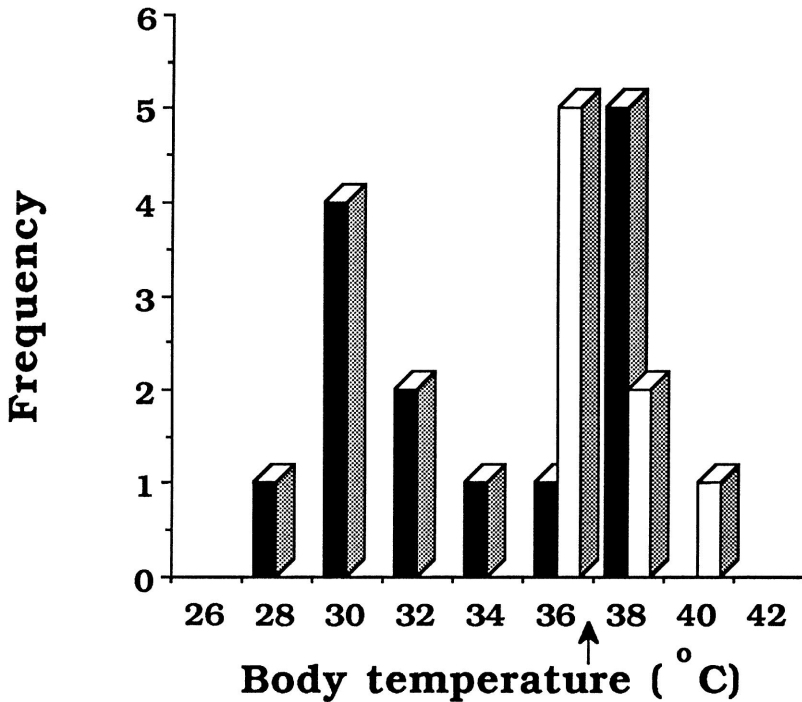


Fig. 2. Body temperature distribution of singing *Proarna insignis* (open columns) and the body temperature distribution when voluntary endogenous warm-up ceased in the laboratory (closed columns). A bimodal distribution of warm-up temperatures is clearly evident and probably corresponds to the temperature range of reproductive activity. There is a clear correspondence between the upper peak of the warm-up temperatures with body temperatures recorded in the field. The upper thermoregulatory temperature measured in the laboratory is indicated by the arrow.

southern variety corresponds to the type of *P. bufo* in the British Museum. We did not observe endothermic behavior in this group. The northern variety is found in open grasslands from the province of Cordoba and the northern edge of Buenos Aires province in the south northward throughout Argentina. Its range also extends marginally into the cloud forests of northwestern Argentina. The limits of its distribution in South America have not been established. We considered this northern variety to be the original *P. bergi* and have restricted the data presented here to that variety.

In most cicadas  $T_b$  increases are accomplished by behaviorally altering the heat gain from solar radiation (Heath 1967; Heath & Wilkin 1970; Sanborn et al. 1992). *P. bergi* and *P. insignis* are similar to ectothermic cicadas in that they use radiant solar energy to raise  $T_b$  for activity. The *Proarna* species will bask at low  $T_b$ s and augment this solar heating with metabolic heat production as has been described in other endothermic cicadas (Sanborn et al. in press). The endogenous heat production of the *Proarna* species is generated and used for thermoregulation. The endothermy described here is not simply the result of activity in an isolated, active body region, e.g. the timbal muscles, as has been described by Josephson & Young (1979; 1985).

At dusk or when environmental conditions prevent the utilization of solar radiation, *P. bergi* and *P. insignis* use metabolic heat to become active. These cicadas produce metabolic heat only when necessary and can be termed facultative or partial endotherms. Restriction in the use of metabolic heat saves energy stores in the cicadas. The energetic expense of behavioral thermoregulation is the cost of transporting the animal mass from one location to another or the cost of maintaining a particular posture. The energetic expense of behavioral thermoregulation represents a small fraction of the energy cost to maintain  $T_b$  using metabolic heat (Heath 1970). Conservation of energy is very important in cicadas since they have limited access to nutrients in the xylem fluid on which they feed (Cheung & Marshall 1973).

The cooling rate is greater than, and the estimated  $V_{O_2}$  less than (Table 2), the values determined for other endothermic cicada species (Bartholomew & Barnhart 1984; Sanborn et al. in press). The differences are expected due to the smaller size of the *Proarna* species. The values we obtained by indirect methods scale as expected when compared to the values reported for larger cicadas (Bartholomew & Barnhart 1984; Sanborn et al. in press).

The thermal responses of cicadas can be related to their activity patterns and their habitat. Table 3 summarizes the reported cicada temperature responses. The 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 origin of the cicada. However, the low MFTs of the endothermic cicadas may be necessary for dusk activity. A low MFT permits the cicada to use the heat produced in flight to raise  $T_b$ . If the MFT were elevated, activity could possibly be inhibited by low  $T_a$ . The lower MFT of *P. insignis* may also be related to the cloud forest habitat of the species.

The temperatures of thermoregulatory responses determined for the *Proarna* species are higher than the those determined for the other endothermic cicadas. Both species of *Proarna* are diurnally active so the potential of radiant solar heat gain may necessitate a higher MVT than found in other endothermic cicadas. The other endothermic cicadas either have a brief period of activity in the morning hours, specialize in dusk activity, or are found in deep tropical forests and are protected from temperature extremes (Sanborn et al. in press).

The temperature of heat torpor in *P. bergi* is greater than in *P. insignis*. *P. bergi* may require a higher heat torpor temperature in the grassland in which the species lives. The open grassland is susceptible to extremes of temperature that may not occur in the cloud forest habitat of *P. insignis*. Since *P. insignis* is probably not exposed to temperature extremes in the cloud forest, *P. insignis* can survive with a lower heat torpor temperature.

Metabolic heat for thermoregulation is generated by the flight musculature in cicadas. Bartholomew & Barnhart (1984) described non-flapping warm-up occurred with "barely visible wing movements of low frequency" in *Fidicina mannifera*. Sanborn et al. (in press) describe two cicada species using heat generated during flight for endothermic temperature regulation. Metabolic heat in *P. bergi* and *P. insignis* was produced by rapid shiver-like movements of the wings and is a new mechanism of heat production not previously described in cicadas. The amplitude of the wing vibrations did not change noticeably with increasing  $T_b$ , as is found in some moths (Dorsett 1962; Kammer 1981). The mechanism producing the wing vibrations was probably similar to the near synchronous activation of wing elevator and depressor muscles described in Lepidoptera (Kammer 1968; 1970; Kammer & Rheuben 1976) and bees (Esch & Goller 1991).

The relationship between field temperatures and the  $T_b$  when voluntary endogenous heat production ceased in *P. bergi* and *P. insignis* presents good evidence that the

TABLE 3. MEAN TEMPERATURE RESPONSES (°C) REPORTED IN THE LITERATURE FOR CICADAS. ENDOTHERMIC SPECIES ARE MARKED WITH AN ASTERISK (\*).

Species	Minimum Flight Temperature	Maximum Voluntary Tolerance	Heat Torpor	Range of Full Activity
<i>Proarna bergi</i> <sup>1*</sup>	20.7	37.6	46.3	25.6
<i>Proarna insignis</i> <sup>2*</sup>	19.3	36.4	44.0	24.7
<i>Dorisiana bonaerensis</i> <sup>2*</sup>	16.7	34.6	44.6	27.9
<i>Quesada giga</i> <sup>2*</sup>	19.1	33.8	44.9	25.8
<i>Fidicina mannifera</i> <sup>2*</sup>	19.8	32.0	42.0	22.2
<i>Magiccicada cassini</i> <sup>3,4</sup>	20.9	31.8	43.0	22.1
<i>Diceroprocta apache</i> <sup>5</sup>	21.9	39.2	45.6	23.7
<i>Cacama valvata</i> <sup>6</sup>				
Camp Verde	23.7	37.3	44.6	20.9
Agua Fria	24.0	34.9	44.3	20.3
<i>Okanagana hesperia</i> <sup>7</sup>	22.9	36.3	43.5	20.6
<i>Okanagodes gracilis</i> <sup>8</sup>	22.7	41.2	48.7	26.0

<sup>1</sup>Present study.<sup>2</sup>Sanborn et al., in press.<sup>3</sup>Heath, 1967.<sup>4</sup>Heath et al., 1971.<sup>5</sup>Heath and Wilkin, 1970.<sup>6</sup>Heath et al., 1972.<sup>7</sup>Heath, 1972.<sup>8</sup>Sanborn et al., 1992.

cicadas are warming to a level necessary for activity. The animals generally cease warm-up behavior in the same  $T_b$  range of animals active in the field (Fig. 2). The data also illustrate that the animals possess the metabolic machinery necessary to raise their  $T_b$  to a biologically significant range. The  $T_b$  that the *Proarna* species cease warm-up behavior in the laboratory is equal to the modal singing temperatures recorded in the field. This suggests the regulation of  $T_b$  through endogenous heat production.

Reproductive adult cicadas live for a limited time period, usually 6-8 weeks. Endothermy in the *Proarna* species may serve to increase reproductive fitness by uncoupling reproductive behavior from possible physiological constraints imposed by the environment. The ability to produce metabolic heat circumvents a reliance on environmental conditions to determine when an animal may or may not be active. Decreases in solar radiation by clouds or rain causes non-endothermic cicadas to decrease or suspend activity (Alexander & Moore 1958; Sanborn 1990; Sanborn & Phillips 1992). *P. bergi* and *P. insignis* can initiate activity and remain active during heavy overcast and/or rainstorms by using endogenous heat production thereby increasing the duration of activity on a given day and the number of days they are potentially active. Endothermy may permit *P. insignis* to inhabit the cloud forest. The seemingly ever present clouds and fog could inhibit reproductive activity in an ectothermic species for the majority of the adult life cycle. If environmental conditions were to prevent reproductive activity, the local population would become extinct.

Endothermy may also decrease predation on *P. bergi* and *P. insignis* populations. Acoustic insects represent a potential food source that advertise their location to po-



tential predators with the calling song. Many predators have been shown to use the reproductive signals of insects in locating their prey (summarized in Bailey 1991). The endothermic species can decrease predation pressure on the population by calling when environmental conditions decrease the hunting success of predators, e.g. at dusk.

A second manner in which endothermy may decrease predation in *P. bergi* and *P. insignis* populations deals with their choice of habitat. The thick grass and intertwining vegetation of their habitats at times made capturing a specimen difficult. In certain locations the use of an insect net was impossible. The easiest way to locate a singing cicada in these habitats was to compress the grass where the animal was singing. By orienting on the alarm call emanating from the compressed grass, the specimen could be localized and captured. By singing from deep within the grass, the *Proarna* species decrease their exposure to potential predators and decrease the risk of predation.

The *Proarna* species use endogenous heat production to become and/or to remain reproductively active. They regulate endogenous heat production through an on-off control system to elevate and maintain a  $T_b$  within the range required to coordinate the physiological processes of reproduction.

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