Body Temperature and the Acoustic Behavior of the Cicada *Tibicen winnemanna* (Homoptera: Cicadidae)

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Tibicen winnemanna *(Davis) produces a broad-band frequency- and amplitude-modulated advertisement call. Observations of the animals in the field show that the cicadas produce varied acoustic output. This work investigates the connection between the acoustic behavior of the cicada and the body temperature of the calling animal. The results show there is strong evidence to support the hypothesis that both acoustic output and song intensity are highly dependent on body temperature.*

INTRODUCTION

Most male cicadas produce a loud calling song to attract conspecific females. These calling songs are produced when rib-strengthened chitinous membranes on the dorsolateral surface of the first abdominal segment, the timbals, are buckled by the action of timbal muscles to produce sound pulses. These sound pulses are then modified by several body components (Pringle, 1954; Bennet-Clark and Young, 1992) before being radiated through the tympana (Young, 1990).

Production of the calling song is essential in bringing the sexes together for reproductive activities. Cicadas are capable of producing their species specific song over a restricted body temperature (T_b) range (Heath, J. E., 1967; Heath and Wilkin, 1970; Heath *et al.*, 1971; Heath, M. S., 1972; Sanborn, 1990; Sanborn *et al.*, 1992; Sanborn *et al.*, 1995). Song production, and ultimately reproduction, is therefore dependent on T_b.

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Tibicen winnemanna (Davis) is an endothermic cicada (Sanborn, 1990) which produces several distinct calls (see below). Davis (1912) described the call of *T. winnemanna* as a "low-pitched uniform note" and a "rising and falling note." I have described the changes to calling song structure of several endothermic cicadas during their activity period (Sanborn, 1990). A monotonous buzzing, similar to a "warm-up" period, precedes song production. The length of time spent "warming up" appears to increase at lower ambient temperatures (T_a) or when ambient conditions force the cicadas to raise their T_b endothermically. These changes in acoustic behavior may be related to the T_b of the calling individuals. Acoustic behavior has been shown to be temperature dependent in planthoppers (Vrijer, 1984), grasshoppers (Skovmand and Pedersen, 1983), crickets (e.g., Doherty and Callos, 1991; Ciceran *et al.*, 1994), and katydids (e.g., Gwynne and Bailey, 1988; Stiedl *et al.*, 1994), but the relationship has not been investigated in cicadas. There is, however, indirect evidence of song coordination being temperature dependent in cicadas. Several authors (Davis, 1894a, b; Myers, 1926; Beamer, 1928; Jacobs, 1953; Alexander, 1956) have noted that songs are produced at a rate slower than normal at low ambient temperatures or without access to solar radiation. Josephson and Young (1979) have shown that small changes in T_b due to activity in an ectothermic cicada alter song cycle period slightly. The objective of this paper is to determine if the observed changes in the acoustic behavior and intensity of *T. winnemanna* calls is related to changes in T_b.

MATERIALS AND METHODS

Tibicen winnemanna were captured in Greenbelt Park in the city of Maryville, Blount County, Tennessee. The animals were recorded and captured during their normal evening activity period during August and September from 1987 to 1991 and in 1993. Individuals were recorded with an Uher 4000 Report Monitor tape deck and an Electro-Voice RE55 dynamic microphone. All songs were recorded on $\frac{3}{4}$-in. audiotape at a tape speed of 19 cm/s. The microphone was placed between 0.15 and 2 m from the singing animal in an effort to reduce the background noise on the recording. A Kay Elemetrics Corporation Digital Sona-graph 7800 was used to analyze the recordings. Permanent copies were made with a Sona-graph printer. An intermediate-bandwidth analysis filter was used on the Sona-graph to produce sufficient resolution in both the frequency and the time domains.

As an animal was approached in the field the sound an animal was producing was classified into one of five categories. These categories were designed so there was little subjectivity in assigning an animal to the correct category. Silent animals were those animals that produced no sound. Buzzing animals produced a characteristic "warm-up" buzz at the beginning of the activity period

without adding any frequency or amplitude modulations to the call. An animal classified as producing the buzzing/slow song initially produced the warm-up buzz but ended the acoustic bout by adding one or more frequency and amplitude modulations at the end of the call. Slow song animals produced the characteristic frequency and amplitude modulated call at a slow modulation rate. The slow song animals began their acoustic bout without producing a warm-up buzz but produced the modulated pattern from the beginning of the call. Finally animals classified into the fast song category were producing the call characteristic of the species when fully active again without producing a warm-up buzz at the beginning of the calling bout. No females were close to the calling males used in this study so sound output by an individual male was not altered due to production of a courtship call.

T_b was recorded during the different stages of acoustic behavior to determine if there is any relationship between T_b and the type of sound being produced. After classifying the sound the animal was producing into one of the five categories described above, the specimen was captured with an insect net and T_b was measured with a Physitemp Model BAT-12 digital thermocouple thermometer with a Type MT-29/1 copper/constantan hypodermic microprobe accurate to $\pm 0.1°C$. The microprobes were calibrated with a National Bureau of Standards mercury thermometer prior to use. T_b was determined by inserting the thermocouple through the net midway into the dorsal mesothorax. Each cicada was constricted within the net and oriented for insertion of the thermocouple probe to prevent heat transfer between the insect and the experimenter. Each T_b was measured within 5 s of the cicada being captured. All statistics are presented as mean $\pm$ SE.

Peak sound pressure levels were measured with a Brüel & Kjaer 2235 SPL meter, a Type 4155 $\frac{1}{2}$-in. prepolarized condenser microphone, and an UA 0237 wind screen which had been calibrated with a Brüel & Kjaer 4230 portable sound pressure calibrator. Measurements were taken using the procedures outlined by Sanborn and Phillips (1995). All intensity measurements are relative to 1×10^{-16} W/cm^2. There was no vegetation between a calling cicada and the microphone during measurements in the field.

Since intensity is measured on a logarithmic scale, all intensity measurements (dB readings) were converted to power levels (W) prior to calculating statistical measures using the equation $Q = 4\pi r^2 (I)$, where Q is the sound power (W), r the distance from the source (= 50 cm), and I the intensity reading for the individual (dB). Mean power output was then used to calculate mean sound intensity at 50 cm for each species. Power levels were logarithmically transformed before performing an ANOVA on the intensity measurements because there was a positive correlation between variances and means. This logarithmic transformation of the data made the variances independent of the mean so the ANOVA could be performed (Sokol and Rohlf, 1995).

RESULTS

The species-specific calling song of *T. winnemanna* is a broad-band frequency- and amplitude-modulated call (Fig. 1). Recordings of the alarm call produced by *T. winnemanna* while manipulating the abdomen show that the emphasized frequency is lower when the abdomen is raised. Major sound energy is between 2000 and 8000 Hz. The peak frequency is 4.70 $\pm$ 0.106kHz ($n = 11$) during the constant-frequency portion of the call and 3.56 $\pm$ 0.080kHz ($n = 11$) after the frequency modulation. Song intensity is greatest during the frequency sweep.

T_b of singing *T. winnemanna* was recorded to determine if the T_b affected the acoustic output. Silent animals have the lowest T_b (Table I). T_b increases as the animals begin to produce sound (buzzing) and continues to increase as the sound progresses toward the fast song. There is strong evidence that the mean T_b differs during the various categories of acoustic output (ANOVA, $F = 72.123$, df $= 4,103$. $P < 0.00001$). This suggests that the type of sound produced by an animal is highly dependent on the T_b.

Sound intensity also increases as *T. winnemanna* acoustic output moves toward the fast song (Table I). There is strong evidence to support the inference that intensity is dependent on T_b (ANOVA, $F = 356.784$, df $= 3,59$, $P = 0$).

Fig. 1. Calling song of *Tibicen winnemanna*. The call is frequency and amplitude modulated, with the peak sound energy approximately 4.7 kHz during the constant-frequency portion of the call and 3.6 kHz after the frequency sweep. Song intensity is greatest during the frequency sweep. Upper trace is the time wave; lower trace is the sonogram.

Table I. Mean (±SE) Body Temperature and Sound Intensity Levels During the Different
Categories of Acoustic Output in *Tibicen winnemanna*[a]

Sound produced	Body temperature (°C)*	Intensity (dB)**
Fast song	35.36 ± 0.218	105.74 + 0.232, −0.251
	(n = 53)	(n = 40)
Slow song	31.99 ± 0.294	101.76 + 0.499, −0.560
	(n = 20)	(n = 12)
Buzzing/slow song	30.56 ± 0.706	97.51 + 0.710, −0.844
	(n = 10)	(n = 6)
Buzzing	30.38 ± 0.521	79.64 + 0.722, −0.866
	(n = 11)	(n = 5)
Silent (no activity)	27.91 ± 0.525	
	(n = 14)	

[a]Note that body temperature and intensity levels increase as the sound produced by the cicada
progresses to the fast song. Intensity measurements are relative to 1×10^{-16} W/cm^2 (=2 $\times$ 10^{-4}
dynes/cm^2) at a distance of 50 cm. The logarithmic intensity scale produces the unequal deviation
about the mean intensity values.
*ANOVA, F = 72.123, df = 4,103, $P < 0.00001$.
**ANOVA, F = 356.784, df = 3,59, $P = 0$.

Table I shows how the acoustic output of *T. winnemanna* varies with and
is dependent on T_b. These T_b changes occur while the animals warm endo-
thermically at dusk (Sanborn, 1990). Numerous measurements from a single
individual also illustrate the relationship between T_b and SPL. As the individual
T. winnemanna proceeds from the "warm-up" buzz to full song production,
there is an increase in the call SPL as the acoustic output of the individual
changes with increasing T_b. Although the intensity changes with the type of call
produced, there is also considerable variation in SPL within a single call cate-
gory. These data illustrate how physiological state can affect the acoustic output.

DISCUSSION

The "low-pitched uniform note" and a "rising and falling note" described
by Davis (1912) probably refer to the warm-up buzz and the full calling song,
respectively. The fundamental frequency of a cicada call is determined by the
natural vibration period of the timbal (Pringle, 1954) and is related to the body
size (Daniel *et al.*, 1993; Bennet-Clark and Young, 1994). The mean measured
peak frequency of *T. winnemanna* calls before and after the frequency sweep is
within the 95% confidence interval for the predicted frequency based on the
scaling relationship determined by Bennet-Clark and Young (1994). Modifica-
tions to the fundamental frequency during the calls are accomplished through
abdominal movements in the dorsal–ventral plane.

Changes in calling song intensity are produced by increasing the strength

of timbal muscle contraction (Josephson and Young, 1979), changing the activity in the timbal tensor muscle (Pringle, 1954; Simmons and Young, 1978; Weber et al., 1987; Fonseca, 1991; Hennig et al., 1994), or altering the position of the abdomen. Extension of the abdomen brings the abdominal air sacs into resonance with the timbals, increasing the sound intensity (Pringle, 1954). Intensity changes of 5–6 dB have been reported by Young (1972, 1990) due to abdominal movements. Periods of increased intensity correspond to the time the abdomen is elevated in T. winnemanna. The song intensity of multiple cicada species has been reported to be greatest when the abdomen is raised (Beamer and Beamer, 1930; Hagiwara and Ogura, 1960; Alexander and Moore, 1962; Young, 1973; Weber et al., 1987; Villet, 1988). The sound intensity is increased by changing the tension on the timbal, folded membrane, and tympanum when the abdomen is raised (Pringle, 1954; Weber et al., 1987; Villet, 1988; Young, 1990; Hennig et al., 1994).

Changes in acoustic behavior in T. winnemanna may also be related to timbal muscle temperature. Measurements of timbal muscle temperature during activity show that muscle temperature is elevated well above ambient (Josephson and Young, 1979; 1985; Sanborn, in preparation). The buzzing observed in T. winnemanna may serve to elevate the timbal muscle temperature. Thermal constraints of the timbal muscles may necessitate a "warm-up" period prior to the production of the calling song. Timbal muscle temperature and contraction kinetics in T. winnemanna will be discussed in a forthcoming paper.

The correlation between T_b and intensity in T. winnemanna (Table I) can be explained by the same physiological factors affecting the acoustic behavior. If the nerve and muscle systems which alter call intensity are temperature dependent, this makes intensity temperature dependent. The variability within the species is thus probably related to temperature and other factors such as age, physiological state, or the presence of rivals in the habitat. This type of SPL variation has been shown in other cicada species (Sanborn and Phillips, 1995).

The increased song intensity produced by cicadas with an elevated T_b may increase the reproductive success of individual cicadas. Warmer cicadas produce louder calls which will travel farther in the environment. A warmer cicada thus has the potential to interact with a greater number of prospective mates within a habitat. This may be one of the factors that stimulated the development of endothermy in cicadas.

ACKNOWLEDGMENTS

REFERENCES

Alexander, R. D. (1956). *A Comparative Study of Sound Production in Insects with Special Reference to the Singing Orthoptera and Cicadidae of the Eastern United States*, Ph.D. dissertation, Ohio State University, Columbus.

Alexander, R. D., and Moore, T. E.(1962). The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). *Misc. Publ. Mus. Zool. Univ. Mich.* **121:** 1–59.

Beamer, L. D., and Beamer, R. H. (1930). Biological notes on some western cicadas. *J. N.Y. Entomol. Soc.* **38:** 291–305.

Beamer, R. H. (1928). Studies on the biology of Kansas Cicadidae. *Univ. Kans. Sci. Bull.* **18**(2): 155–263.

Bennet-Clark, H. C., and Young, D. (1992). A model of the mechanism of sound production in cicadas. *J. Exp. Biol.* **173:** 123–153.

Bennet-Clark, H. C., and Young, D. (1994). Scaling of song frequency in cicadas. *J. Exp. Biol.* **191:** 291–294.

Ciceran, M., Murray, A.-M., and Rowell, G. (1994). Natural variation in the temporal patterning of calling song structure in the field cricket *Gryllus pennsylvanicus*: Effects of temperature, age, mass, time of day, and nearest neighbor. *Can. J. Zool.* **73:** 38–42.

Daniel, H. J., Knight, C., and Charles, T. M. (1993). Predicting species by call in three species of North Carolina cicadas. *J. Elisha Mitchell Sci. Soc.* **109:** 67–76.

Davis, W. T. (1894a). Staten Island harvest flies. *Am. Nat.* **28:** 363–364.

Davis, W. T. (1894b). Staten Island harvest flies. *Proc. Natl. Sci. Assoc. Staten Is.* **4:** 9–10.

Davis, W. T. (1912). A new cicada (Homop.) from Plummer's Island, Maryland. *Bull. Brooklyn Entomol. Soc.* **8:** 2–4.

de Vrijer, P. F. W. (1984). Variability in calling signals of the planthopper *Javesella pellucida* (F.) (Homoptera: Delphacidae) in relation to temperature, and consequences for species recognition during distant communication. *Nether. J. Zool.* **34:** 188–406.

Doherty, J. A., and Callos, J. D. (1991). Acoustic communication in the trilling field cricket, *Gryllus rubens* (Orthoptera: Gryllidae). *J. Insect Behav.* **4:** 67–82.

Fonseca, P. J. (1991). Characteristics of the acoustic signals in nine species of cicadas (Homoptera, Cicadidae). *Bioacoustics* **3:** 173–182.

Gwynne, D. T., and Bailey, W. J. (1988). Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). *Behaviour* **105:** 202–223.

Hagiwara, S., and Ogura, K. (1960). Analysis of songs of Japanese cicadas. *J. Insect Physiol.* **5:** 259–263.

Heath, J. E. (1967). Temperature responses of the periodical "17-year" cicada, *Magicicada cassini* (Homoptera, Cicadidae). *Am. Midl. Nat.* **77:** 64–67.

Heath, J. E., and Wilkin, P. J. (1970). Temperature responses of the desert cicada, *Diceroprocta apache* (Homoptera, Cicadidae). *Physiol. Zool.* **43:** 145–154.

Heath, J. E., Hanagan, J. L., Wilkin, P. J., and Heath, M. S. (1971). Adaptation of the thermal responses of insects. *Am. Zool.* **11:** 147–158.

Heath, M. S. (1972). Temperature requirements of the cicada *Okanagana striatipes beameri*: A study from Flagstaff, Arizona. *Plateau* **45:** 31–40.

Hennig, R. M., Weber, T., Moore, T. E., Huber, F., Kleindienst, H.-U., and Popov, A. V. (1994). Function of the tensor muscle in the cicada *Tibicen linnei*. *J. Exp. Biol.* **187:** 33–44.

Jacobs, M. E. (1953). Observations on the two forms of the periodical cicada *Magicicada septendecim* (L.). *Proc. Ind. Acad. Sci.* **63**: 177–179.

Josephson, R. K., and Young, D. (1979). Body temperature and singing in the bladder cicada, *Cystosoma saundersii*. *J. Exp. Biol.* **80**: 69–81.

Josephson, R. K., and Young, D. (1985). A synchronous insect muscle with an operating frequency greater than 500 Hz. *J. Exp. Biol.* **118**: 185–208.

Myers, J. G. (1926). New or little-known Australasian cicadas of the genus *Melampsalta*, with notes on songs by Iris Myers. *Psyche* **33**: 61–76.

Pringle, J. W. S. (1954). A physiological analysis of cicada song. *J. Exp. Biol.* **31**: 525–560.

Sanborn, A. F. (1990). *Endothermy in Cicadas (Homoptera: Cicadidae)*, Ph.D. dissertation, University of Illinois, Urbana.

Sanborn, A. F., and Phillips, P. K. (1995). Scaling of sound pressure level and body size in cicadas (Homoptera: Cicadidae; Tibicinidae). *Ann. Entomol. Soc. Am.* **88**: 479–484.

Sanborn, A. F., Heath, J. E., and Heath, M. S. (1992). Thermoregulation and evaporative cooling in the cicada *Okanagodes gracilis* (Homoptera: Cicadidae). *Comp. Biochem. Physiol.* **102A**: 751–757.

Sanborn, A. F., Heath, M. S., Heath, J. E., and Noriega, F. G. (1995). Diurnal activity, temperature responses and endothermy in three South American cicadas (Homoptera: Cicadidae: *Dorisiana bonaerensis*, *Quesada gigas* and *Fidicina mannifera*). *J. Therm. Biol.* **20**: 451–460.

Simmons, P., and Young, D. (1978). The tymbal mechanism and song patterns of the bladder cicada *Cystosoma saundersii*. *J. Exp. Biol.* **76**: 27–46.

Skovmand, O., and Pedersen, S. B. (1983). Song recognition and song pattern in a shorthorned grasshopper. *J. Comp. Physiol.* **153A**: 393–401.

Sokol, R. R., and Rohlf, F. J. (1995). *Biometry, the Principles and Practice of Statistics in Biological Research*, 3rd ed., W. H. Freeman, New York.

Stiedl, O., Hoffmann, E., and Kalmring, K. (1994). Chirp rate variability in male song of *Ephippigerida taeniata* (Orthoptera: Ensifera). *J. Insect Behav.* **7**: 171–181.

Villet, M. (1988). Calling songs of some South African cicadas (Homoptera: Cicadidae). *S. Afr. J. Zool.* **23**: 71–77.

Weber, T., Moore, T. E., Huber, F., and Klein, U. (1987). Sound production in periodical cicadas (Homoptera: Cicadidae: *Magicicada septendecim*, *M. cassini*). *Proc. 6th Auchen. Meet.*, Turin, Italy, 7–11 Sept. 1987, pp. 329–336.

Young, D. (1972). Neuromuscular mechanisms of sound production in Australian cicadas. *Z. Vergl. Physiol.* **79**: 343–362.

Young, D. (1973). Sound production in cicadas. *Austral. Nat. Hist.* **Sept.**: 375–380.

Young, D. (1990). Do cicadas radiate sound through their ear-drums? *J. Exp. Biol.* **151**: 41–56.