Cicada Thermoregulation (Hemiptera, Cicadoidea)

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Abstract

A review the mechanisms and thermoregulatory strategies used by cicadas is presented. The behavioral and physiological processes used to regulate body temperature are discussed. Behavioral strategies include changes in body orientation to the sun, basking, shade-seeking, microclimate selection, vertical migration, using the wings as a parasol, and suspension of activity. The effect of temperature on the biology of cicadas and the strategies used to deal with temperature are discussed. Physiological responses include thermal adaptation, endothermy, and evaporative cooling.

Key words: temperature regulation, endothermy, evaporative cooling, thermal responses.

Temperature is a physical parameter of the environmental that affects all organisms at the cellular level through the temperature dependent nature of chemical reactions. The daily fluctuations in ambient temperature (T_a) can have a significant influence on the activity of any terrestrial animal. Animals have two options with respect to body temperature (T_b) and the changing thermal environment: they

Figs. 1:
Basking *Tympanoterpes elegans* BERG. Cicadas will bask at low body and/or ambient temperature to elevate body temperature to a range necessary to coordinate activity. Cicadas maximize radiant energy uptake by orienting the greatest body surface area to the sun. The dorsal surface is perpendicular to the sun in this photograph.

can be thermoconformers or thermoregulators. A thermoconformer is an animal whose T_b changes with and is approximately equal to T_a. Any animal that is a thermoconformer is unable to function efficiently physiologically over a wide temperature range because enzymes function most efficiently over a restricted temperature range. The alternative strategy that reduces the negative aspect of fluctuating T_b is thermoregulation. An animal that thermoregulates maintains T_b within a "preferred" temperature range so its enzymes are functioning near optimal levels while the animal is active.

Temperature has been shown to affect cicadas at all levels, from controlling the rate of neural firing (WAKABAYASHI & HAGIWARA 1953, WAKABAYASHI & IKEDA 1961) or the contraction kinetics of muscles (AIDLEY & WHITE 1969, JOSEPHSON 1981, JOSEPHSON & YOUNG 1979, JOSEPHSON & YOUNG 1985, SANBORN in press) to determining the rate of development (AZUMA 1976, HARTZELL 1954, NAGAMINE and TERUYA 1976), when a population emerges (HEATH 1968) or even the distribution of the species (OHGUSHI 1954, SCHEDL 1986, TOOLSON 1998). Therefore, temperature and the regulation of body temperature (T_b) are essential in the lives of cicadas as in any other terrestrial animal.

Previous studies (HEATH 1967, HEATH 1972, SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 1997, SANBORN 2000, SANBORN & MATÉ 2000) have shown that cicadas must maintain their T_b within a small range to coordinate reproductive activity, the main purpose of the adult life stage. The daily variations of T_a are large enough to prevent the passive development of a constant T_b, but it is not always practical for an organism to delay activity until ambient conditions are favorable while spending the remainder of the day in a thermal shelter. Cicadas, therefore, spend time and energy thermoregulating to permit activity for a significant portion of the day.

The strategies used by animals to regulate T_b can be divided into two major types of responses: behavioral and physiological. A common method of thermoregulation in cicadas is to use behavioral mechanisms to alter the uptake of solar radiation (Heath 1967, HEATH & WILKIN 1970, HEATH et al. 1972, HEATH 1972, HASTINGS 1989, HASTINGS & TOOLSON 1991, TOOLSON 1998, SANBORN 2000, SANBORN & MATÉ 2000) (Fig. 1). This type of organism is termed ectothermic because it uses exogenous heat to regulate T_b. However, there have been studies (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 1997, SANBORN 2000) showing cicadas using the physiological mechanisms of endothermy (the generation of endogenous heat for thermoregulation) and evaporative cooling (KASER & HASTINGS 1981, TOOLSON 1984, TOOLSON 1985, TOOLSON 1987, TOOLSON & HADLEY 1987, HADLEY et al. 1989, HASTINGS 1989,

STANLEY-SAMUELSON et al. 1990, HADLEY et al. 1991, HASTINGS & TOOLSON 1991, SANBORN et al. 1992, TOOLSON 1993, TOOLSON et al. 1994) in the field to regulate T_b.

Behavioral Responses

All animals use behavioral thermoregulation as a first option to regulate T_b. Behavioral thermoregulation is the quickest and most accessible mode of regulation since the effect is immediate and behavioral temperature regulation does not require changes in cellular composition or activity to be effective. Therefore, it is not surprising that the majority of cicadas regulate T_b through behavioral mechanisms (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1972, HEATH 1972, HASTINGS 1989, HASTING & TOOLSON 1991, SANBORN et al. 1992, SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 1997, TOOLSON 1998, SANBORN 2000, SANBORN & MATÉ 2000).

As stated previously, the majority of cicadas use solar radiation as a mechanism to elevate T_b. Cicadas move from their nocturnal feeding locations to perches where their exposure to the sun will be maximal early in the morning. Cicadas bask in order to keep T_b elevated to a range necessary for activity. Cicadas have been shown to congregate in areas where exposure to the sun is greatest (HUDSON 1890, RAMSAY 1959, HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1972, HEATH 1972, FLEMING 1975, YOUNG 1975, YOUNG 1980, YOUNG 1981, JOERMANN & SCHNEIDER 1987, HASTINGS 1989, HASTINGS & TOOLSON 1991, SANBORN et al. 1992, TOOLSON 1998, SANBORN 2000, SANBORN & MATÉ 2000). The concentration of animals moves within the habitat to stay exposed to the sun as the sun moves through the day (HEATH 1967, SANBORN et al. 1995a, DURIN 1981). These generalization are true of both ectothermic (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1972, HEATH 1972, HASTINGS 1989, HASTINGS & TOOLSON 1991, SANBORN et al. 1992, TOOLSON 1998, SANBORN 2000, SANBORN & MATÉ 2000) and endothermic species (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000).

Similar patterns of movement and exposure to solar radiation occur in endothermic species. Endothermic species use radiant heat when it is available to assist in the elevation of T_b. This behavioral strategy saves the animals metabolic energy that can then be used for activity at a time when solar radiation is not available (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000). This behavior may also potentially increase the life span of the individual adult since the adults do not receive significant amounts of energy from the xylem fluid on which they feed (CHEUNG & MARSHALL 1973a).

We had the opportunity to see importance of basking as a means to elevate T_b to a level necessary for activity during a partial (about 70%) solar eclipse in 1991 (SANBORN & PHILLIPS 1992). T_a decreased by approximately 1°C during the eclipse but remained at a level where activity had been recorded previously in the species active in the habitat (SANBORN et al. 1992). The cicadas were forced to suspend activity due to a loss of radiant input, which is required to maintain an elevated T_b. A similar effect has also been reported several times with decreased radiation due to cloud cover (see references in SANBORN & PHILLIPS 199).

A common mechanism used by ectothermic animals to decrease T_b is to decrease the radiant heat load. A simple behavior animals can employ to decrease radiant heat gain is to move into a shaded location. This strategy is widely used by cicadas exposed to elevated T_a and radiant energy from the sun to regulate T_b (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1972, HASTINGS, 1989, HASTINGS & TOOLSON 1991, SANBORN et al. 1992, SANBORN et al. 1995a, TOOLSON 1998, SANBORN 2000, SANBORN & MATÉ 2000). Cicadas also change the location of activity from the external regions of plants to inner shaded locations as T_a or T_b increase. This is an especially important strategy in active animals whose metabolism would further increase T_b.

Shade-seeking behavior has been measured directly in the field. HEATH (1967) measured the T_b when animals voluntarily moved to the shade. He demonstrated cicadas moved from sun to shade over a very narrow range of

T_b (1.5-2.0°C). In addition, the T_b range of the laboratory shade-seeking response corresponded to the maximum T_bs measured in the field suggesting a finely tuned response is controlling behavioral changes that regulate T_b (HEATH 1967).

Animals can also regulate the amount of radiant heating by changing the orientation of their body to the sun. This will change the

Figs. 2:
A specimen of *Cacama valvata* (UHLER) that has partially rotated around its perch. The radiant heat load decreases when the animal exposes the lateral body surface to the sun permitting the cicada to maintain body temperature in the range necessary for activity. Further increases in body temperature will stimulate movement into the shade.

surface area of the body being exposed to the sun which will alter the heat transfer. As T_b increases animals can decrease the total surface area exposed to the sun through three main mechanisms: an animal can orient the side of the body to the sun, rotate the body around a branch (Fig. 2, 3), or face the head into the sun (HEATH & WILKIN 1970, HEATH et al. 1972, HEATH 1972, SANBORN et al. 1992, SANBORN & MATÉ 2000). Changes in orientation in the field have been correlated with

changes of T_b in *Cacama valvata* (UHLER) (HEATH et al. 1972).

Changing the orientation of the body can also alter radiant heat uptake if the animal has differences in the reflective pattern of different parts of the body. Animals such as *Cacama valvata* (HEATH et al. 1972) and *Okanagodes gracilis* DAVIS (SANBORN et al. 1992) have a morphological adaptation that assists in decreasing radiant input at elevated T_b. The ventral surface of these, and many other desert inhabiting species, is white in color (Fig. 3). The difference in coloration between the dorsal and ventral surfaces facilitates reducing the radiant heat gain when the animals become negatively oriented to the sun as the white ventral surface reflects a greater portion of the radiant heat. Animals from less thermal rigorous habitats do not have this type of reflective ventral surface (HEATH 1967, HEATH 1972).

The periodical cicada *Magicicada cassinii* (FISHER) has been shown to adopt an unusual posture at low T_a and when the sun is low on the horizon (HEATH 1967). The wings are spread away from the midline exposing a greater area of the black thorax and abdomen to solar radiation. By the late morning, the wings have returned to their usual position, peaked over the midline of the abdomen. This strategy acts to increase the area of the body exposed to radiant heating at low T_a, thus increasing the heating rate. Similarly when T_b, T_a or the sun angle is elevated the wings act as a parasol decreasing the radiant heat load and the temperature excess of the animal.

There is also some evidence that cicadas use the wings as a shade in a different manner. Active *Magicicada cassinii* orient their bodies with the head facing directly away from the sun in the afternoon. This behavior permits the wings to "shade" the body and decrease heat uptake (HEATH 1967).

Selection of a specific microhabitat can be used in addition to the gross body movements associated with shade-seeking behavior. This was best illustrated by the description of movements in *Diceroprocta apache* (DAVIS) associated with T_a (HEATH & WILKIN 1970). *Diceroprocta apache* is able to keep T_b below T_a, in part, by selecting an appropriate microclimate.

Similarly, microhabitat choice is reported to be responsible for the difference in T_b recorded in two syntopic species (HASTINGS & TOOLSON 1991). *Tibicen chiricahua* DAVIS is reported to exhibit a higher T_b because it is active closer to the ground and in less shade. In contrast, *T. duryi* DAVIS uses more elevated perches in deeper shade and has an average T_b 3.1°C lower than *T. chiricahua*. The differences are not due to biophysical factors as *T. duryi* is the larger of the two species and should, therefore, equilibrate at a higher T_b. These differences may be realted to distribution of *T. chiricahua* which would require adaptation to warmer T_a and the selection of elevated T_bs for activity since it lives in warmer habitats (HASTINGS & TOOLSON 1991).

Selection of a proper microhabitat is also important for one of the physiological responses to temperature to be effective. The decrease in T_b due to evaporative cooling disappears when the animals are placed in high humidity environments (TOOLSON 1985, TOOLSON 1987, HASTINGS 1989). Selection of an improper microhabitat could lead to an ineffective evaporative cooling response.

Related to the selection of a particular microclimate is a vertical change in position with changes in T_a. This is especially well exemplified by the vertical migrations of *Okanagodes gracilis* (SANBORN et al. 1992). When T_a is less than <40-42°C, *O. gracilis* is active on low, scrubby plants (*Atriplex* spp.) on which they are difficult to find due to cryptic coloration. However, when T_a elevates to as much as 50°C during the heat of the day, *O. gracilis* will abandon the low plants for a higher perch on plants like *Larrea tridentata* (Fig. 4). These elevated perches place the animals in lower temperature microclimates by elevating the animals above the boundary layer. These vertical migrations also facilitate the efficiency of the evaporative cooling response in *O. gracilis* (SANBORN et al. 1992). By decreasing the temperature gradient with a vertical migration, *O. gracilis* decreases the amount of water that must be evaporated to maintain T_b at a safe level and permits the evaporative response to occur for a greater time period.

Another strategy for dealing with extreme temperature is to suspend activity altogether. Cicadas are torpid at low T_b and low T_a (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1971, HEATH et al. 1972, HEATH 1972, SANBORN et al. 1992, SANBORN 2000, SANBORN & MATÉ 2000). This torpidity can be a benefit to ectothermic animals in that metabolic rate decreases as T_b decreases. The

Figs. 3:
A cicada that has moved to a negative orientation. This specimen of *Diceroprocta eugraphica* (DAVIS) has rotated around its perch to decrease the radiant heat load and maintain body temperature in the range necessary for calling behavior. By moving to the underside of the perch, the cicada exposes a white ventral surface to the sun and the perch cn be used for shade by the insect which decreases the radiant heat gain from the sun.

only behaviors exhibited at low T_b or T_a are basking, in an effort to elevate T_b, and feeding.

High T_as, combined with the metabolic heat produced as a byproduct of normal activity, could lead to lethal increases in T_b. When T_as are elevated, calling activity has been reported to be inhibited or depressed in several species (SWINTON 1908, TALHOUK 1959, WARD 1967, HEATH & WILKIN 1970, HEATH et al. 1972, YOUNG 1974, HADLEY et al. 1991). The potential dangers of activity at elevated T_a were described by HEATH & WILKIN (1970). They calculated that a *Diceroprocta apache* that initiated flight at a T_b of 43°C would lose motor control after 20 seconds due to the metabolic heat produced in flight. A loss of motor control at elevated T_as would most likely result in death for these animals as surface temperatures in their habitat can reach 70°C (HEATH & WILKIN 1970).

Physiological Responses

Although behavioral thermoregulation has several benefits, there are still limitations placed on reproductive activity due to the limits to changes in T_b through behavior. Physiological mechanisms assist behavioral strategies in regulating T_b to a more precise level, thus permitting activity over a wider range of T_a. There are three main physiological responses used by cicadas to survive the thermal environment: endothermy, evaporative cooling and thermal responses.

Endogenous heat production used specifically for thermoregulation constitutes the definition of endothermy (ANONYMOUS 1987). Endogenous heat production with the potential for thermoregulation was first shown in the tropical cicada *Fidicina mannifera* (FABRICIUS) (BARTHOLOMEW & BARNHARDT 1984). When BARTHOLOMEW & BARNHARDT (1984) described endothermy in *F. mannifera*, they stated that the functional significance of the endogenous heat was problematic. My colleagues and I have begun to investigate endothermy in cicadas in order to determine its biological significance (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 1997, SANBORN 2000, SANBORN in press).

Diel T_b distribution of endothermic cicadas is similar to that in ectothermic species in that T_b is elevated above T_a during daylight hours. Endothermic cicadas differ, however, in that the T_b of cicadas "active" at dusk or when solar energy is unavailable is approximately the same as the diurnal distribution of T_bs. A distinction between "active" and "inactive" individuals must be made because the T_b of "inactive" animals approximates T_a (SANBORN et al. 1995a, SANBORN 2000) as is found in ectothermic species under these conditions (HEATH 1967, SANBORN 2000). T_bs of *Guyalna bonaerensis* (BERG), *Quesada gigas* (OLIVIER), *Proarna insignis* DISTANT, and *Tibicen winnemanna* (DAVIS) measured in the field show that these cicadas are endothermic. Recorded T_bs were respectively as much as 13.0°C, 12.0°C, 7.4°C, and 12.6°C greater than T_a when solar heating was unavailable to the species (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000).

All cicadas bask at low T_bs. The endothermic species augment solar heating with metabolic heat production. At dusk or when environmental conditions prevent the use of solar radiation, the endothermic cicadas use metabolic heat to become or to remain active. Thus, the endothermic species do not rely on metabolic heat alone to regulate T_b. They will use radiant solar energy to elevate T_b for activity when it is available (SANBORN et al. 1995a, SANBORN 2000). 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's mass from one location to another or the cost of maintaining a particular posture which represents a small fraction of the energy cost to maintain T_b using metabolic heat (HEATH 1970).

The relationship between field temperatures and the T_b when voluntary endogenous heat production ceased in *Proarna bergi* (DISTANT) and *P. insignis* presents further evidence that the cicadas are warming to a level necessary for activity. Captive animals generally cease warm-up behavior in the same T_b range of those animals active in the field. The data also illustrate that the animals possess the metabolic machinery necessary to raise their T_b to a biologically significant range (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000). Similarly, the mean T_b of endothermically active *Tibicen winnemanna* does not differ significantly from the mean T_b during the day (SANBORN 2000) and the mean peak T_b measured by BARTHOLOMEW & BARNHARDT (1984) during warm-up behavior in *Fidicina mannifera* is similar to the upper thermoregulatory temperature we determined for the species *F. torresi* BOULARD & MARTINELLI (which was split out from *F. mannifera*) (SANBORN et al. 1995a).

Female endothermic cicadas raise T_b during the chorusing activity of the males. Female *Guyalna bonaerensis* with elevated T_bs have been observed ovipositing in the rain (SANBORN et al. 1995a). Female *Tibicen winnemanna* captured during the species' evening activity period also had elevated T_bs (SANBORN 2000). The females may be required to elevate T_b for species recognition. Female planthoppers (VRIJER 1984) and

crickets (WALKER 1957, WALKER 1963, DOHERTY 1985) have been shown to respond only to the calls produced by males at the same T_b as the female. Some evidence to support a similar temperature dependent recognition system in *Tibicen winnemanna* is that T_bs of the mating females observed were within 0.5°C of the males with which they were copulating (SANBORN 2000).

The heat for thermoregulation is produced by the thoracic musculature. The relatively large percentage of body mass (35% in cicadas [BARTHOLOMEW & BARNHARDT 1984, SANBORN et al. 1995b]), the high metabolic scope, and the inefficiency of flight all make the flight musculature an ideal tissue to generate heat for thermoregulation. The extremely high metabolic rate of insect flight muscles makes them well suited for heat production (BARTHOLOMEW & EPTING 1975). *Guyalna bonaerensis*, *Quesada gigas*, *Fidicina torresi* (SANBORN et al. 1995a) and *Tibicen winnemanna* (SANBORN 2000) have been observed to use the heat produced in flight to raise T_b endothermically.

Insect flight is a mechanically inefficient process. Flight is normally assumed to have an efficiency of 20% (WEIS-FOGH 1972, WEIS-FOGH 1976, CASEY 1981a), but studies of several insect species demonstrate that flight efficiency ranges from 3.3-27.5% (WEIS-FOGH 1972, WEIS-FOGH 1976, CASEY 1981b, ELLINGTON 1984, ELLINGTON 1985, CASEY et al. 1985). The efficiency of insect flight is thus much lower than the assumed value of 20% and as a class insects have a mean flight efficiency between 10-15%. This means that a significant amount of the energy used in flight (85-90%) is released as heat.

Behavior similar to that observed in the endothermic cicadas has been described in many dusk singing cicadas and endothermy may be a wide spread phenomenon in the superfamily Cicadoidea. It has been reported that *Tibicen auletes* (GERMAR) and *Tibicen resonans* (WALKER) are active for a greater period of time than environmental conditions should permit (ALEXANDER 1960). "Sing and fly" behavior has been described in these and many other species active at dusk (DAVIS 1894a, DAVIS 1894b, MATSUMURA 1898, ANNANDALE 1900, KERSHAW 1903, DAVIS 1922, DISTANT 1906, ALEXANDER 1956,

MOORE 1962, HAYASHI 1982, POPOV et al. 1985, DUFFELS 1988). These species may well be endothermic since the ectothermic dusk singer *Cystosoma saundersii* (JOSEPHSON & YOUNG 1979) does not exhibit "sing and fly" behavior (DOOLAN & MACNALLY 1981).

Fidicina mannifera (BARTHOLOMEW & BARNHARDT 1984) and *Tibicen winnemanna* (SANBORN 2000) are capable of endothermically warming without flight. Non-flapping warm-up in *F. mannifera* was accompanied by barely perceptible low frequency (1-2 s^{-1}) wing movements and telescoping of the abdomen at 15-36 cycles min^{-1}. Non-flapping warm-up was not observed in *T. winnemanna* in the laboratory, but individuals were observed to progress from a buzzing call to producing a full mating call without changing singing perches in the field. Since the mean T_b of a cicada producing the fast song is significantly greater than one producing a buzz (SANBORN 1997), the cicadas were capable of raising T_b without flight. Species of Coleoptera, Hymenoptera, Diptera, and Lepidoptera also have been shown to raise T_b without wing movements (MAY 1976, BARTHOLOMEW & HEINRICH 1978, HEINRICH 1981, CHAPPELL & MORGAN 1987).

Proarna bergi and *P. insignis* generate metabolic heat with shiver-like movements of the wings (SANBORN et al. 1995b) (Fig. 5). The amplitude of the wing vibrations is found to change with increasing T_b in some moth species (DORSETT 1962, Kammer 1981) but this did not occur in these cicadas. The mechanism producing the wing vibrations in the cicadas is probably similar to the near synchronous activation of wing elevator and depressor muscles described by KAMMER (1970) in the butterfly *Danaus plexippus* (L.) but this has yet to be shown with electrical recordings in the cicadas.

There have been diverse functions described for endogenous heat production of insects (HEINRICH 1993). It has been estimated that an endothermic cicada would use more than five times as much energy during activity as an ectothermic animal (SANBORN et al. 1995a). The use 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 (CHEUNG & MARSHALL 1973a, WHITE &

461

STREHL 1978), the nutrients available for energy conversion are limited. This raises the question as to why an animal would expend energy stores to become active when it could use solar radiation during the day and save metabolic energy.

Endothermic behavior in cicadas may serve to increase reproductive fitness in several ways including: uncoupling of reproductive

Figs. 4:
Okanagodes gracilis DAVIS thermoregulating during the warmest portion of the day. Ambient temeprature was 48°C when the image was taken. The picture illustrates the combined use of behavioral and physiological strategies to thermoregulate. The animal is exhibiting a negative orientation which shades the body with the branch and exposes a white ventral surface to the sun to reflect more solar radiation and decrease heat load. The animal has also abandoned the normal host plant for a higher perch which places the animal in a cooler microclimate. The animal is feeding to get the water necessary for evaporative cooling which depresses the body temperature below ambient. These activities combine with elevated thermal tolerances permit reproductive activity at a time when other animals are seeking shelter from the heat.

behavior from possible physiological constraints of the environment, avoidance of possible thermoregulatory problems of midday by restricting activity to the cooler portions of the day, permitting the use of habitats unavailable to strictly ectothermic animals, helping species to avoid predators, optimizing broadcast coverage and sound transmission, or to permit avoidance of acoustic interference through temporal separation of singing (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 1997, SANBORN 2000).

A second physiological mechanism to regulate T_b is evaporative cooling. Evaporation of water represents a potentially significant mechanism for the dissipation of excess heat from any organism. The amount of energy lost is dependent upon the coefficient of evaporation, the surface area of the evaporating surface, and the partial pressure gradient of water between the evaporating surface and the surrounding air. The use of evaporative cooling by insects is a relatively rare occurrence due to their relatively small body size. Their high surface to volume ratio, and the limitations of sufficient water reserves can quickly lead to osmoregulatory problems for insects that attempt to use evaporative cooling. PRANGE (1996) has provided a fairly recent review of evaporative cooling in insects as a group.

The use of evaporative cooling in cicadas was first described by KASER and HASTINGS (1981) in *Tibicen duryi*. It has since been described in *Cacama valvata* (TOOLSON 1993), *Diceroprocta apache* (TOOLSON 1985, TOOLSON 1987, TOOLSON & HADLEY 1987, HADLEY et al. 1989, HADLEY et al. 1991), *Okanagodes gracilis* (SANBORN et al. 1992), *T. chiricahua* (HASTINGS & TOOLSON 1991), *T. dealbatus* (DAVIS) (TOOLSON 1984, STANLEY-SAMUELSON et al. 1990, TOOLSON et al. 1994), and further descriptions for *T. duryi* (TOOLSON 1984, HASTINGS 1989, HASTINGS & TOOLSON 1991). All species inhabit environments in which T_b could elevate to lethal levels. Significant evaporative cooling has only been described for species that inhabit hot, dry environments even though they have different phylogenetic histories (HEATH 1978). An evaporative cooling mechanism was described in a species from a warm, humid environment but it was found the species had limited evaporative capabilities (TOOLSON & TOOLSON 1991). The ability to decrease T_b below T_a disappears when animals are placed in a saturated environment (TOOLSON 1985, TOOLSON 1987, HASTINGS 1989). It appears a significant selection pressure in the evolution of evaporative cooling is the environment inhabited by the species.

Cicadas will attempt to use behavioral mechanisms to decrease T_b before evaporation of water begins (HADLEY et al. 1991, SANBORN et al. 1992). However, *Diceroprocta apache* can maintain T_b 5°C below T_a

(TOOLSON 1987) and *Okanagodes gracilis* can maintain a 6.7°C gradient (SANBORN et al. 1992) once evaporation begins. Water loss rates increase as much as 600% during the evaporative response (TOOLSON & HADLEY 1987) with the amount of water loss increasing with increasing T_a (HADLEY et al. 1991).

The onset of evaporative cooling occurs at a thermoreglatory point that is similar to the maximum voluntary tolerance temperature. Evaporation begins at a T_b of 39.2°C in *Diceroprocta apache* (HADLEY et al. 1989) which is the same as the maximum voluntary tolerance temperature determined by HEATH & WILKIN (1970). Evaporative cooling in *Okanagodes gracilis* occurs at a T_b slightly above the maximum voluntary tolerance temperature but this may have been an artifact of the experimental procedure (SANBORN et al. 1992). Evaporative cooling begins at lower T_bs when animals are well hydrated and have access to food (TOOLSON & HADLEY 1987, HADLEY et al. 1991) and T_bs elevate as water reserves decrease (HASTINGS 1989).

Water is evaporated through pores in the cuticle (Fig. 6) (TOOLSON & HADLEY 1987, HADLEY et al. 1991, SANBORN et al. 1992). These pores are located on the thorax and abdomen in both *Diceroprocta apache* and *Okanagodes gracilis*. The pore structure and distribution is also similar in the two species. *Magicicada tredecim* (WALSH & RILEY), a species from a higher humidity, lower T_a environment, has a limited number of pores and a limited ability to cool evaporatively (TOOLSON & TOOLSON 1991). The main site of evaporative water loss is the abdomen in *D. apache* (HADLEY et al. 1989) which would explain the lower abdominal temperatures also observed in *Tibicen duryi* (HASTINGS 1989).

The evaporative cooling mechanism appears to be mediated by an active transport system (TOOLSON & HADLEY 1987, HADLEY et al. 1989, HADLEY et al. 1991). Death or the injection of NaCN causes a rapid decrease in transcuticular water flux in *Diceroprocta apache*. The system probably operates by the coupling of an actively transported ion across the cell membrane of the dermal glands or dermal gland ducts which then causes water to move by osmosis. The water can then evaporate
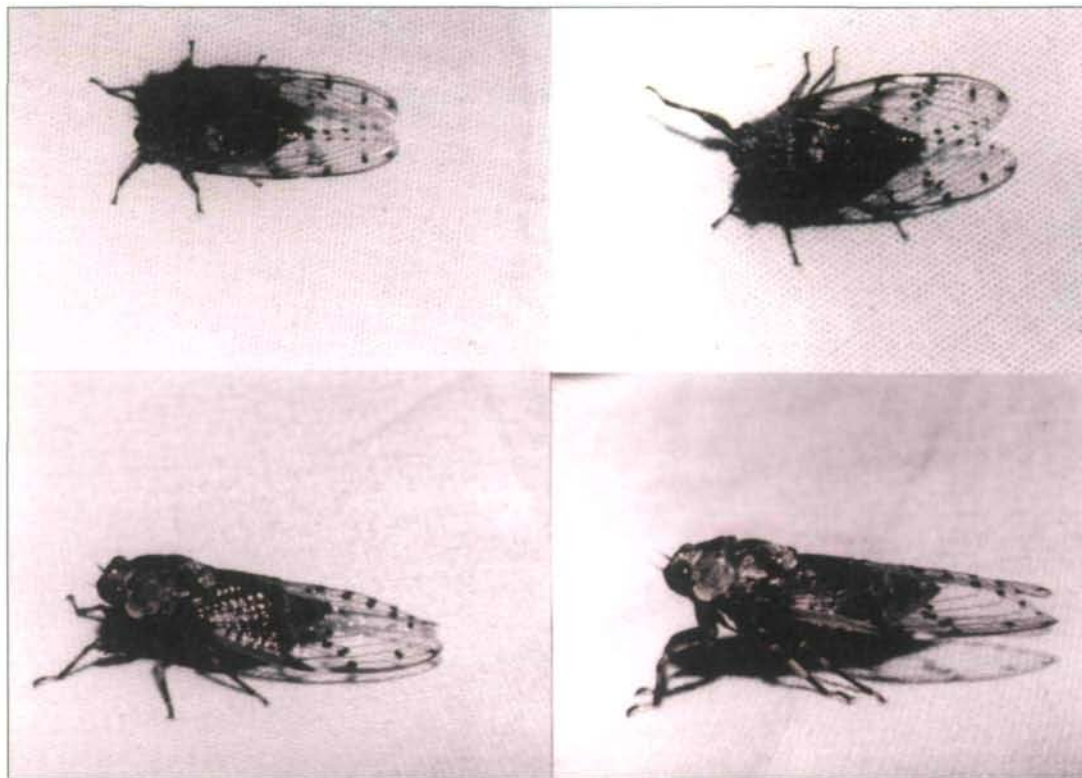
Figs. 5: Endogenous heat production in *Proarna insignis* DISTANT. The images on the left depict an animal at rest with the wings held over the body. The images on the right were taken while the animal was generating heat to elevate body temperature. The wings flatten in the dorso-ventral plane and are vibrated in a shiver-like manner during heat production. The shivering stops when the animals have elevated their body temperature to the range necessary for activity.
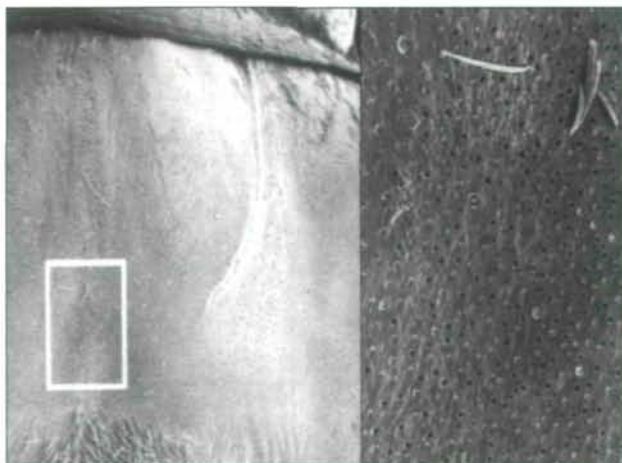
Figs. 6: The dorsal mesothorax of *Okanagodes gracilis* DAVIS. The pores are used to evaporate water to cool the animal in extreme heat. The individual pores are about 7 mm in diameter.

once it is outside the cuticle. There is a cyclical rate of water loss at higher T_a, which is similar to evaporative cooling mechanisms described for mammals (HADLEY et al. 1989).

Prostaglandins have been suggested to regulate the control of transcuticular water flux in cicadas (STANLEY-SAMUELSON et al. 1990, TOOLSON et al. 1994). Blocking the synthesis of prostaglandins prevents the initiation of the sweating response in *Tibicen dealbatus*. The results of these experiments suggest a complex interaction of chemicals in the 20 carbon, polyunsaturated fatty acids and arachidonic acid synthesis pathway that regulate the sweating response by regulating the set point for initiation (TOOLSON et al. 1994).

It appears cicadas that use evaporative cooling are adapted to survive the loss of a large percentage of their total body water during the evaporative cooling response. Mean water loss rates of 14.1% h^{-1} in *Diceroprocta apache* (HADLEY et al. 1991), 10.67% h^{-1} in *Tibicen duryi*, 11.01% h^{-1} in *T. chiricahua* (HASTINGS & TOOLSON 1991), and 9.73% h^{-1} in *Okanagodes gracilis* (SANBORN et al. 1992) with a maximum rate of 30-35% h^{-1} in *Diceroprocta apache* (TOOLSON 1987) have been reported.

Insects in general simply do not have sufficient body water reserves to employ evaporation as a main mechanism of thermoregulation. However, cicadas are an exception in that they have access to a water source that other organisms in their environment do not. Cicadas feed on xylem fluid (CHEUNG & MARSHALL 1973a) which is mostly water. In fact, the digestive system of cicadas is modified to eliminate the excess water load they get with their food (CHEUNG & MARSHALL 1973b, MARSHALL & CHEUNG 1973, MARSHALL & CHEUNG 1974, MARSHALL & CHEUNG 1975, MARSHALL 1983). Thus, the use of a specific food source in a dry environment has permitted certain cicadas to use evaporative cooling as a means to regulate T_b. This has allowed the cicadas to remain active in a thermally stressed environment at times when other animals, especially their predators, have retreated to thermal shelters due to the excessive heat of the environment.

Water uptake in evaporatively cooling cicadas has become an integral daily activity. Access to water is required for the cicadas to maintain T_b less than T_a (KASER & HASTINGS 1981, HASTINGS 1989) and appears to alter the T_b at which the evaporative response is initiated (HADLEY et al. 1991, SANBORN et al. 1992, TOOLSON et al. 1994). *Okanagodes gracilis* continually feeds during the day even while performing reproductive activities such as singing and ovipositing (SANBORN et al. 1992) to maintain water balance (Fig. 4). *Tibicen duryi* also feeds during the day (KASER & HASTINGS 1981, HASTINGS 1989) but this species suspends other activities while it is feeding (HASTINGS 1989).

A final physiological mechanism cicadas employ is adaptation to particular thermal environments. An analysis of the thermal responses for a particular insect can give insights into how the animal is adapted thermally to its environment. Early work (HEATH et al. 1971, HEATH et al. 1972) suggested the thermal responses of a particular species were related to the habitat type and the elevation of the habitat. This relationship has proven to be an over simplification as the number of species investigated has increased and endothermy was discovered. Our further analyses have suggested that the thermal responses of cicadas are related to the activity patterns, thermoregulatory strategies, and habitat of a particular species.

Three measurements are required to determine the thermal responses of a species (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1971, HEATH et al. 1972, HEATH 1972, SANBORN et al. 1992, SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN & PHILLIPS 1996, SANBORN 1997, SANBORN 2000, SANBORN & MATÉ 2000, SANBORN & PHILLIPS 2001). The minimum flight temperature (MFT) represents the lowest T_b at which an animal is considered fully coordinated. The maximum voluntary tolerance (MVT) or shade-seeking temperature is a measure of an upper thermoregulatory set point (HEATH 1970). The heat torpor temperature (HTT) is the upper T_b limit of coordinated activity and can represent an ecologically lethal T_b since the animal is unable to prevent further increases in T_b. The T_b range of full activity is the difference between the MFT and HTT. Table 1 is a summary of the reported cicada temperature responses.

The MFTs are the most difficult thermal response to analyze. There is no clear correlation between habitat type and MFT. For example, the desert inhabiting *Diceroprocta cinctifera* (UHLER) has the second lowest reported MFT (SANBORN & PHILLIPS 1996). Similarly, *Okanagana hesperia* (UHLER) lives at altitude (HEATH 1972) but has a higher MFT than desert dwelling species (HEATH & WIL-

MVT when it is endothermically active. On the other extreme are *Diceroprocta apache* (HEATH & WILKIN 1970) and *Okanagodes gracilis* (SANBORN et al. 1992). These species inhabit the Sonoran Desert where T_a can approach or exceed 50°C. The animals must have elevated thermal tolerances to be active for a significant portion of the day in their environment. In addition, the elevated MVT

Species	Minimum Flight Temperature	Maximum Voluntary Tolerance	Heat Torpor	Range of Full Activity
Magicicada cassinii[1]	20.9	31.8	43.0	22.1
Okanagana hesperia[2]	22.9	36.3	43.5	20.6
Diceroprocta apache[3]	21.9	39.2	45.6	23.7
Okanagodes gracilis[4]	22.7	41.2	48.7	26.0
Cacama valvata[5]				
Camp Verde	23.7	37.3	44.6	20.9
Agua Fria	24.0	34.9	44.3	20.3
Diceroprocta cinctifera[6]	17.6	34.0	45.8	28.2
Diceroprocta cinctifera var. *limpia*[6]	16.8	34.7	46.0	29.2
Diceroprocta cinctifera var. *viridicosta*[6]	16.7	35.3	46.0	29.3
Diceroprocta aurantiaca[7]	17.7	36.3	46.0	28.3
Diceroprocta delicata[7]				
Northern population	19.8	33.9	46.8	27.0
Southern population	21.4	35.3	46.5	25.1
Diceroprocta olympusa[8]	20.4	37.0	46.7	26.3
Tibicen chloromerus[9]	19.2	34.4	45.3	26.1
Tibicen winnemanna*[9]	16.4	32.7	45.6	29.2
Guyalna bonaerensis*[10]	16.7	34.6	44.6	27.9
Fidicina torresi*[10]	19.8	32.0	42.0	22.2
Quesada gigas*[10]	19.1	33.8	44.9	25.8
Proarna bergi*[11]	20.7	37.6	46.3	25.6
Proarna insignis*[11]	19.3	36.4	44.0	24.7

Table 1:
Mean temperature responses (°C) reported in the literature for cicadas. Endothermic species are marked with an asterisk(*).

[1]Heath 1967, [2]Heath 1972, [3]Heath and Wilkin 1970, [4]Sanborn et al. 1992, [5]Heath et al. 1972, [6]Sanborn and Phillips 1996, [7]Sanborn and Phillips 2001, [8]Sanborn and Maté 2000, [9]Sanborn 2000, [10]Sanborn et al. 1995a, [11]Sanborn et al. 1995b.

KIN 1970, SANBORN et al. 1992). It has been suggested that the MFT probably relates more to the physical design of the cicada flight motor system than to the origin of the cicada (HEATH et al. 1972). My laboratory has now found evidence to support this hypothesis. We have been able to find several morphological variables that influence lift that correlate with MFT. However, it appears that the environment still plays a role in determining what the MFT will be for a particular species.

The MVT is easier to relate to the habitat than the MFT. There is an increase in MVT as habitats become warmer. *Fidicina torresi* is active on the trunks of primary forest trees in the tropics and has the lowest reported MVT (SANBORN et al. 1995a). The limited exposure to solar radiation due to the canopy means *F. torresi* will save energy with a depressed

also delays the start of the evaporative cooling response in these species which could be important in maintaining water balance.

HTT is strictly related to the habitat of a species. The HTT appears to have evolved to reflect the maximum thermal load a species might face in a particular environment. It does not appear to be related to the thermoregulatory strategy or behavior of a species (HEATH 1967, HEATH & WILKIN 1970, HEATH et al. 1971, HEATH et al. 1972, HEATH 1972, SANBORN et al. 1992, SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN & PHILLIPS 1996, SANBORN 2000, SANBORN & MATÉ 2000, SANBORN & PHILLIPS 2001).

There are some generalizations that can be made in the analysis of the thermal responses of endothermic species. The endothermic

cicadas generally have a lower MFT and a greater T_b range of full activity when compared to ectothermic species. The low MFT of the endothermic cicadas may be necessary because of their endothermic activity. A low MFT permits the cicada to utilize heat produced in flight to raise T_b. If the MFT were elevated, low T_a could possibly inhibit activity (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000).

The MVTs of the endothermic species are variable but generally are lower than those found in ectothermic species even if the habitats are similar (SANBORN et al. 1995a, SANBORN et al. 1995b, SANBORN 2000). The MVT values obtained probably represent a balanced response to the T_as encountered during their activity period and the maximum T_a encountered during the day. If the upper thermoregulatory point were elevated too high, the cicada might be unable to produce sufficient heat to become active at dusk. Similarly high T_as could prohibit activity if the MVT was depressed any further.

The HTTs of endothermic species show the same dependency to the environment as the HTT of ectothermic species. This is best illustrated in the HTT of the endothermic *Tibicen winnemanna* and the syntopic ectothermic *T. chloromerus* (WALKER). The HTT of both species are approximately equal even though the two species have vastly different behavioral strategies and thermoregulatory points (SANBORN 2000).

Elevated thermal tolerances may also be an adaptation to predator avoidance. *Diceroprocta apache* (HEATH & WILKIN 1970) and the syntopic species *Okanagodes gracilis* (SANBORN et al. 1992) have the highest reported thermal tolerances in cicadas. Their elevated thermal tolerances permit the species to be active in a habitat when their potential predators must retreat to a thermal shelter due to the extreme heat. This is an advantage to the cicadas since the males produce conspicuous acoustic signals to attract females. By calling when predators are not active, the cicadas should decrease their predation pressure since several types of predators have been shown to orient to the acoustic signals of insects (WALKER 1964,

CADE 1975, SOPER et al. 1976, MANGOLD 1978, BELL 1979, BUCHLER & CHILDS 1981, SAKALUK & BELWOOD 1984, FOWLER & KOCHALKA 1985, TUTTLE et al. 1985, BELWOOD & MORRIS 1987). An increase in cicada activity with a decrease in bird activity was also observed in tropical Brazil (Jones 1884).

The study of cicada thermal biology has led to some interesting insights into temperature effects and thermoregulation in insects. However, there is always more to learn about how temperature influences activity in animals. We have even applied thermal biology to systematics in helping to separate *Diceroprocta aurantiaca* DAVIS as a distinct species (SANBORN & PHILLIPS 2001). Continued research using integrated methods should attempt to answer more questions about the thermal biology of this interesting group of insects.

Zusammenfassung

Mechanismen und Strategien der Temperaturregelung bei Singzikaden werden im Überblick dargestellt, Verhaltensweisen und physiologische Vorgänge zur Regulation der Körpertemperatur diskutiert. Verhaltensweisen umfassen Lageveränderung des Körpers zur Sonne, sonnenbaden, Schatten aufsuchen, Auswahl günstiger mikroklimatischer Verhältnisse, Vertikalwanderung, Verwendung der Flügel als "Sonnenschirm" und die Einstellung der Aktivität. Die Auswirkungen der Temperatur auf die Biologie der Singzikaden und deren Reaktionen auf bestimmte Temperaturverhältnisse werden diskutiert. Physiologische Reaktionen umfassen Temperaturanpassung, Endothermie und Kühlung durch Evaporation.

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467

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