J. exp. Biol. 159, 269–283 (1991)
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EVAPORATIVE COOLING IN THE DESERT CICADA: THERMAL EFFICIENCY AND WATER/METABOLIC COSTS

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Accepted 26 April 1991

Summary

Using plant xylem water for evaporative cooling, the desert cicada *Diceroprocta apache* can maintain a body temperature as much as 5°C below ambient (T_a=42°C). Simultaneous measurements of water loss and gas exchange for cicadas feeding on perfused twigs show substantial increases in transpiration at temperatures at which evaporative cooling begins (between 37 and 38°C), but only modest increases in $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$. The extent and duration of evaporative cooling depend on the cicada's hydration state and the rate of water flux from cuticular pores located on the surface of the thorax and abdomen.

Introduction

Because of their small size and limited water stores, few terrestrial arthropods use evaporative cooling to unload excess heat (Edney, 1977). An important exception to this is the desert cicada *Diceroprocta apache* Davis. By feeding on the xylem of desert plants, this species has access to a constant and abundant water supply which it uses for evaporative cooling over prolonged periods (Toolson, 1987). Individuals actively extrude water through pores in the dorsal thorax and abdomen in a manner analogous to thermoregulatory sweating in mammals. Moreover, this discontinuous release of water begins at the point where cicadas seek milder microclimates to prevent body temperatures from reaching lethal levels (Toolson and Hadley, 1987; Hadley *et al.* 1989).

These findings in the cicada raise several interesting questions. For example, what rate of water input from feeding is needed to balance transpirational losses during evaporative cooling? What is the maximum differential between ambient temperature and body temperature during peak evaporative cooling? Does the acquisition and subsequent transfer of water to the cuticle surface constitute a significant metabolic cost to the cicada?

These questions were explored using a flow-through system to monitor water loss and gas exchange concurrently in cicadas feeding on twigs perfused with water. We report here the dramatic increase in evaporative water loss that occurs

Key words: cicada, evaporative cooling, metabolism, water loss, *Diceroprocta apache*.

when ambient temperatures exceed 38–40 °C as well as changes in metabolism that accompany feeding and the transcuticular pumping of water.

Materials and methods

Animal capture, housing and preparation

Cicadas were collected in Tempe, Arizona, between 1 July and 15 September 1989 and maintained in individual containers at 30 °C (L:D 14 h:10 h) prior to testing. Animals were generally used within 24 h of capture, and all animal preparation was made as soon after capture as possible. Fresh branches of the desert fern *Lysiloma microphylla* were provided daily as a food source.

All test animals carried a thermocouple (0.076 mm diameter copper–constantan) whose junction contacted the central pore tract of the dorsal thorax (see Hadley *et al.* 1989 for location of pore tracts). To minimize conduction along the thermocouple leads, the final segment of the thermocouple (approx. 3–4 mm) was placed in close contact with the pore tract and the leads were attached to the thorax laterally with beeswax. A second group of cicadas had an additional thermocouple implanted in the thoracic flight muscles (insertion depth=2 mm) approximately 4 mm caudolateral to the surface thermocouple and secured with wax. Thermocouple leads were long enough to allow soldering to permanent lead wires in the respirometer. Test animals were subdued prior to thermocouple mounting by brief cooling in a refrigerator. Animals with surface thermocouples were given at least 3 h to recover; cicadas with both thermocouples were given a minimum of 11 h to recover. Both thermocouples gave essentially identical readings and were presumed to reflect body temperature (T_b).

Respirometry system

The air-flow system used to measure $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, evaporative water loss (EWL) and body temperatures of cicadas is shown in Fig. 1. All gas connections were made with metal tubing. Air entering the system was split at the mass flow controller (Brooks 5840) into a reference and a sample circuit. The sample circuit consisted of a glass respirometer, water sensor (Al_2O_3 chip, see Hadley *et al.* 1982, for details), carbon dioxide analyzer, CO_2/H_2O scrubbing column (Drierite/Ascarite/Drierite) and oxygen analyzer. The respirometer vessel (30 ml volume) was constructed of a 19/22 female taper fitting fused to a larger glass body. All gas tubes, thermocouple ports and perfusion lines entered the respirometer *via* a rubber stopper seated in the taper. The CO_2 analyzer (Anarad 411) has a range of 0–500 p.p.m., and was calibrated using a certified span gas (Matheson). The O_2 analyzer, an Ametek S-3A/II, was used in the differential mode where it is sensitive to $\pm 0.001\ \% O_2$.

Air temperature was controlled to ± 0.1 °C with a circulating water bath (Haake A82) connected to a cylindrical acrylic jacket surrounding the respirometer. Air entering the respirometer was pre-heated by passing it through 2 m of coiled tubing in the jacket (not shown in Fig. 1). Temperatures [air (T_a) and body] were

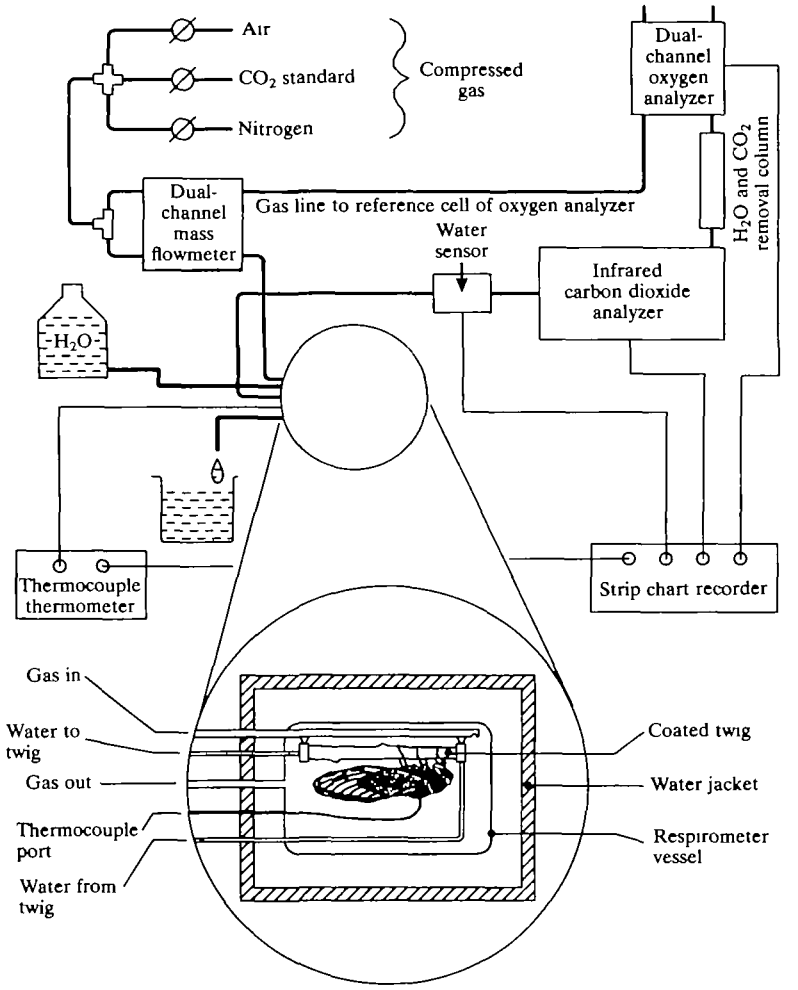

Fig. 1. Air-flow system used to measure $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, evaporative water loss and body temperatures of cicadas. See text for description.

measured with a BAT-12 thermocouple thermometer and CHL-1 multiplexer (Physitemp).

Perfused feeding twigs were prepared from small (0.4 cm×3.2 cm) segments of *Lysiloma* branches coated with spray-on plastic (Plastidip) to reduce transpiration. Trimming of the twigs was carried out under water to maintain the fluid column in the xylem. Twig ends were glued (silicone) to 20 gauge stub adapters and the twig assemblies secured to the gas inlet tube with tape. Twig inflow (degassed distilled water) came from an aspirator bottle suspended 0.5 m above the twig; outflow was collected in a graduated cylinder. Our choice of distilled water rather than artificial xylem fluid as the perfusate was based on Cheung and Marshall's (1973) report that xylem fluid of host plant species used in their study was very dilute (approx.

28 mosmol kg^{-1}), with only trace amounts of organic materials present. Also, since cicadas were maintained overnight on large cut branches of *Lysiloma*, they should have received at least some of the normal nutrients. All twig connections were made with polyethylene tubing (Intramedic PE 90). Fresh twigs were generally mounted daily as water flow through the xylem decreased rapidly with time. Twig perfusion averaged 3.7 ml h^{-1} for all runs.

Run protocols

Preliminary experiments revealed the O_2 analyzer to be less sensitive and more unstable than either the CO_2 or water analyzer. Flow rates low enough to provide $\dot{V}_{O_2}$ values often saturated the other two instruments, and the O_2 analyzer tended to drift during extended runs. To accommodate these instrument characteristics, it was necessary to employ two run protocols. In the first procedure, T_a was increased ('ramped') in a step-wise fashion from 30 to 42 °C with steps at 33, 36, 38 and 40 °C; $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and EWL were measured at 30 °C (air flow 50 ml min^{-1}), but only $\dot{V}_{CO_2}$ and EWL at the other temperatures (air flow 150 ml min^{-1}). Step duration ranged from 30 to 60 min. CO_2/O_2 ratios (respiratory quotients, RQs) determined at 30 °C were then used to calculate $\dot{V}_{O_2}$ values at higher temperatures. To determine whether RQ was affected by temperature, a second group of animals was ramped from 30 °C directly to 40 °C and both $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured (air flow 50 ml min^{-1}).

All runs were started during daylight hours and conducted under full light conditions. Animals were weighed immediately before and after the runs; dry mass was also determined. Behavioral activities were monitored continuously and summarized for each 30-s interval.

Data analysis

Outputs from the instruments were recorded on strip chart recorders and areas of interest integrated on a digitizing tablet (Kurta) connected to a personal computer. Only periods when the animals were observably resting or feeding were considered for analysis, except where noted. Evaporative water loss was determined as previously described (Hadley *et al.* 1982), and surface area corrections were calculated using the standard equation relating body mass to area ($A=12M^{0.67}$, where A is area in cm^2 and M is body mass in g). Urination was a frequent event, especially in animals that were able to feed effectively. Evaporative water loss measurements, however, were never made until all urine had visibly evaporated from the respirometer. For some animals, it was not possible to obtain valid EWL data, resulting in sample sizes of EWL values being slightly less than those of other variables listed in Table 1. $\dot{V}_{O_2}$ was calculated using equation 2 of Hill (1972); calculation of $\dot{V}_{CO_2}$ required different equations depending on whether or not $\dot{V}_{O_2}$ was measured. If $\dot{V}_{O_2}$ was measured (30 °C), then the following expression was used:

$$\dot{V}_{CO_2} = \frac{(\dot{V}_I - \dot{V}_{O_2} + \dot{V}_{H_2O})FE_{CO_2}}{1 - FE_{CO_2}},$$

where $\dot{V}_I$ is the air flow into the respirometer (CO_2- and H_2O-free, in $ml\,h^{-1}$), $F_{E_{CO_2}}$ is the fractional concentration of CO_2 leaving the respirometer and $\dot{V}_{O_2}$ and $\dot{V}_{H_2O}$ are the rates of O_2 and H_2O consumed or released, respectively. At temperatures where $\dot{V}_{O_2}$ was not measured, the individual RQ values from the 30°C step were used as follows:

$$\dot{V}_{CO_2} = \frac{(\dot{V}_I + \dot{V}_{H_2O})F_{E_{CO_2}}}{(1 + F_{E_{CO_2}}[(1/RQ) - 1])}.$$

The derivations of these equations are presented in the Appendix. All volumes were corrected to STP.

Data are reported as means±standard deviations. Statistical tests are those of Zar (1974).

Results

Behavior and patterns of gas exchange

Behavioral activities of the cicadas were closely associated with thermal and gas exchange patterns. Fig. 2 shows the physiological and behavioral responses of a representative cicada at 40°C. For the first 15 min, the cicada displayed low-level escape and walking activity. During this period, $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and evaporative water loss (EWL) patterns were characterized by numerous small, irregularly spaced peaks that were not correlated with any observable ventilatory activity. The two large peaks at 5 and 10 min, however, represent short bouts of abdominal pumping. At 20 min the cicada successfully penetrated the twig and characteristically became completely motionless. Unsuccessful twig penetrations were common and were accompanied by gentle rocking motions of the body and rapid withdrawal of the proboscis. A latent period between penetration and onset of evaporative cooling was common, and in this case totalled 15 min. The two co-occurring dips in the gas exchange tracings during the evaporative cooling period indicate brief closures of the spiracles. EWL increased approximately 2.5-fold during the evaporative cooling bout, depressing the cicada's body temperature (T_b) nearly 4°C below ambient. Both $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ declined in parallel with the decrease in T_b. These physiological responses are discussed in greater detail in the sections that follow and are summarized for all cicadas tested in Table 1.

Water and temperature relations

Water status of the test cicadas during the runs was quite variable. The mean initial water content, in $g\,H_2O\,g^{-1}$ dry mass, was 2.296±0.154 (N=12, range: 2.030–2.530). In contrast, their final water content averaged only 1.973±0.349 $g\,H_2O\,g^{-1}$ dry mass (range: 1.544–2.572 $g\,H_2O\,g^{-1}$ dry mass), a decrease of 14.1 %. Three animals were able to increase their water contents, while three others suffered losses between 25 and 30 % (all survived). The animals'

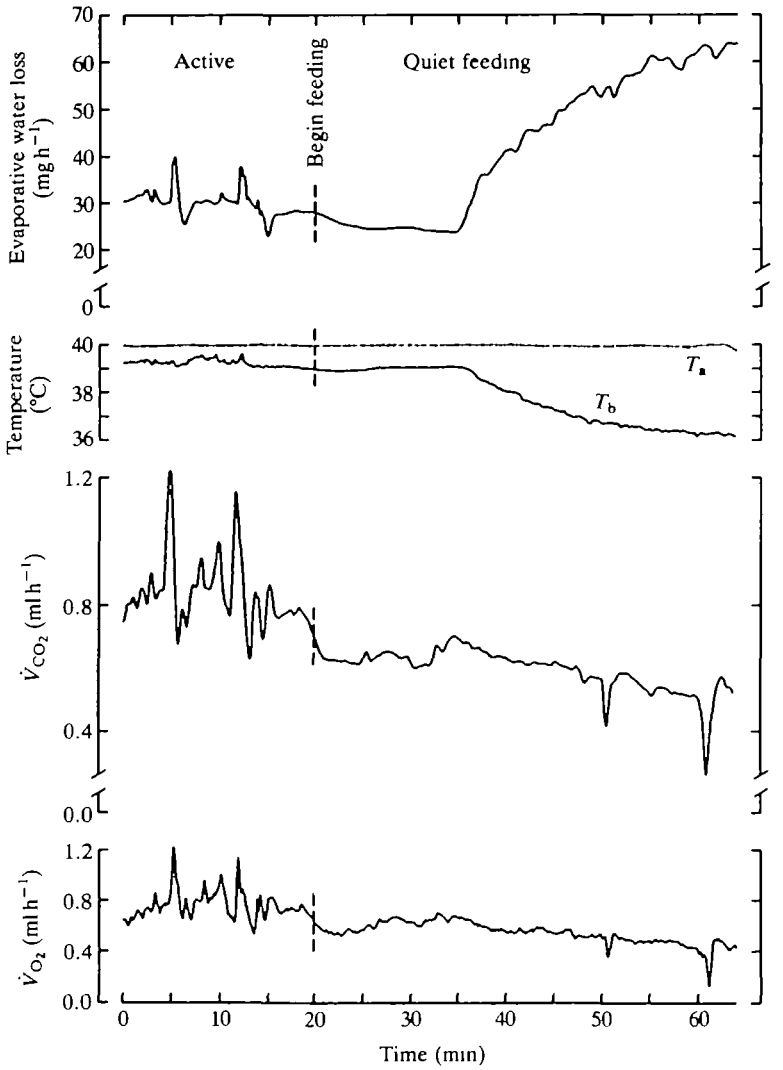

Fig. 2. A composite figure showing $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, evaporative water loss, T_a and T_b from a representative male cicada. The animal's initial mass was 0.493 g; its final mass was 0.554 g.

water content was undoubtedly very labile, as feeding, and in some cases urination, occurred intermittently throughout the runs.

Mean EWL increased exponentially with T_a, with rates at 42 °C being more than six times rates at 30 °C (Table 1). The relationship between EWL and T_a changed dramatically above 38 °C owing to the extrusion of water from the pores; in the ranges 30–36 °C and 38–42 °C, EWL Q_{10} averaged 1.742 and 12.142, respectively. Relative humidities inside the respirometer remained low (approx. 5 %) despite the high EWL.

EWL and body temperature depression (T_{a-b}) were strongly correlated with

ble 1. *Summary of the physiological responses to temperature of the desert cicada* Diceroprocta apache

Variable	Ambient temperature (°C)					
	30.0	33.0	36.0	38.0	40.0	42.1
T_b	29.8±0.22 (12)	32.7±0.23 (12)	35.6±0.24 (12)	37.2±0.50 (12)	38.5±0.79 (9)	39.2±1.44 (11)
EWL ($mg\,cm^{-2}\,h^{-1}$)	0.81±0.23 (9)	0.93±0.24 (9)	1.13±0.36 (9)	1.76±0.89 (9)	2.60±0.98 (8)	4.89±2.85 (8)
$\dot{V}_{CO_2}$ ($ml\,g^{-1}\,h^{-1}$)	0.57±0.07 (9)	0.76±0.15 (12)	0.91±0.12 (12)	1.07±0.13 (12)	1.18±0.09 (9)	1.27±0.24 (11)
$\dot{V}_{O_2}$ ($ml\,g^{-1}\,h^{-1}$)	0.63±0.18 (9)	0.80	0.97	1.13	1.25	1.35

T_b, body temperature; EWL, evaporative water loss; $\dot{V}_{O_2}$, rate of oxygen consumption; $\dot{V}_{CO_2}$, rate of CO_2 production; RMR, resting metabolic rate; FMR, feeding metabolic rate; RQ, respiratory quotient.

Values are means±S.D., with sample size in parentheses.

Metabolic rates include resting and feeding animals, with a correction applied to rates for feeding cicadas (i.e. RMR=0.944FMR).

$\dot{V}_{O_2}$ was measured only at 30°C; values at other temperatures are derived from $\dot{V}_{CO_2}$ using the RQ at 30°C for each animal (mean RQ=0.946±0.185, N=9).

Mean initial mass of the animals was 0.622±0.061 g (N=12).

the cicadas' water contents (Fig. 3). This relationship was assessed by regressing T_{a-b} and EWL during the last 5 min of each run against final water content. The highest values were from two cicadas that increased their water contents during the runs (1.6 and 2.6% for the resting and feeding individuals, respectively). Nevertheless, even dehydrated animals were able to cool evaporatively to some extent. There was no obvious correlation between type of activity and ability to exploit this cooling mechanism. Fig. 3 also suggests that T_{a-b} is highly dependent on EWL; regressing the former on the latter yields a value of r^2 of 0.882. This situation prevailed at all T_a values, implying that the cicadas' principal mode of heat loss in the respirometer was evaporative cooling.

The relationship between T_b and T_a is not linear throughout the temperature range (Fig. 4). A break occurs between 36 and 38°C that corresponds to the onset of evaporative cooling (T_b at break=T_{ec}). T_{ec} was determined from individual plots of T_b on T_a using the method of Nickerson *et al.* (1989) for continuous two-phase regressions. Only resting or feeding intervals were used in any given animal. The mean T_{ec} was 37.5± 1.01°C (N=6, range: 36.2–38.8°C); no differences were noted between resting and feeding animals.

Metabolic rate

The dependence of resting metabolic rate ($\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$) on body mass was determined at 30°C using the standard allometric model ($V_x=aM^b$). Values for constants a and b were determined from regressions of $\log V_x$ ($ml\,h^{-1}$) on log mass

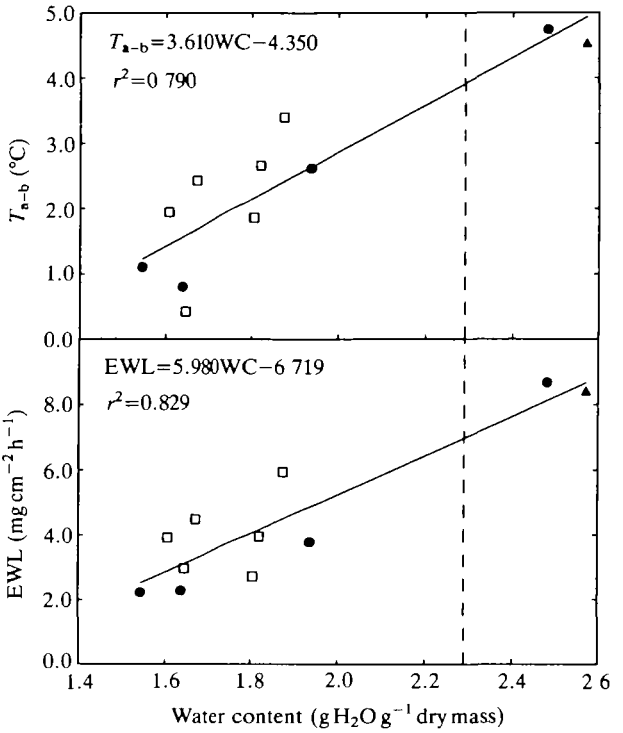

Fig. 3. Evaporative water loss and T_{a-b} as a function of water content in 11 cicadas. Air temperature was 42°C. See text for method of determining these variables. ▲, animal resting; ●, feeding; □, active. Vertical dashed line indicates the mean initial water content of the cicadas. WC, water content.

(g). With initial mass as the independent variable, $\dot{V}_{O_2}=0.591M^{1.005}$ ($r^2=0.282$, $N=18$) and $\dot{V}_{CO_2}=0.659M^{1.259}$ ($r^2=0.709$, $N=19$). Using dry mass as the independent variable improved the values of r^2 only slightly. Oxygen consumption was not as strongly correlated with mass as was CO_2 production; we attribute this to the superior sensitivity and stability of the CO_2 analyzer. Respiratory quotients at 30°C indicate a predominantly carbohydrate metabolism (RQ=1.030±0.248, $N=18$). In another group of experiments, RQ was found to be independent of temperature: RQ at 30°C=1.002±0.046, RQ at 40°C=0.963±0.169 ($N=3$). Note that our definition of 'resting' means quiescent and does not conform to the more rigorous standard definition (Cossins and Bowler, 1987).

To assess the effect of quiet feeding on metabolic rate, we compared the $\dot{V}_{CO_2}$ values of resting and feeding periods occurring during the same temperature step in individual cicadas. Such events were uncommon: only 13 occurrences were observed in all of the test animals. Four of these episodes occurred at 30°C, three at 42°C, two at 33 and 40°C, and one each at 36 and 38°C. To correct for temperature differences, $\dot{V}_{CO_2}$ values were scaled back to a common T_b of 30°C using the mean Q_{10} (see below). Animals that had paired resting/feeding periods

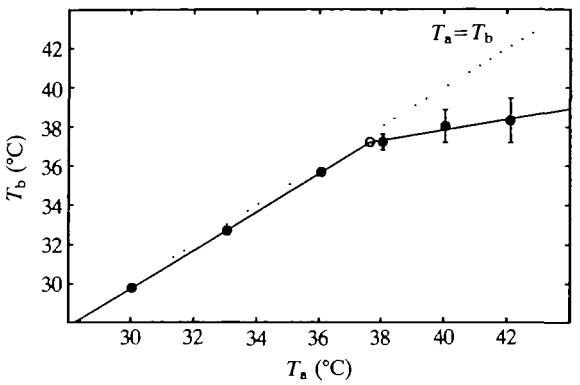

Fig. 4. Relationship between T_a and T_b in *Diceroprocta apache*. Filled symbols are mean values±S.D. of T_a and T_b; $N \geq 5$. The open symbol is the calculated intersection (T_{ec}) of the regressions shown with solid lines (see text).

at two or more T_a steps were represented by a single averaged value. The mean increase in resting $\dot{V}_{CO_2}$ associated with feeding was 5.6±6.29 % (N=8, range: −3.4 to +14.5 %). No correlation with temperature was evident.

Temperature effects on metabolism were pronounced, as shown in Table 1. Q_{10} values were determined by assuming $\dot{V}_{CO_2}$ is related to temperature (T_b) by the exponential model described in Cossins and Bowler (1987, page 29). This technique derives a single Q_{10} from regressions of $\log\dot{V}_{CO_2}$ on T_b from individual animals. The mean Q_{10} was 2.338±0.301 (N=12); separate Q_{10} values calculated for resting and feeding intervals did not differ statistically. Using the mean values in Table 1, the relationship between metabolic rate and T_b is given by the equation: $\dot{V}_{CO_2}=0.049\ (1.086)^T$

Discussion

An integral part of this study was the development of a system that would measure simultaneously temperature, evaporative water loss and gas exchange in a feeding insect. Although this system shares some features with other multiparameter systems used to measure gas exchange and water loss (Hadley and Quinlan, 1982; Quinlan and Hadley, 1982; Nicolson and Louw, 1982; Louw and Hadley, 1985; Lighton, 1988; Paul *et al.* 1989), our system advances this technology by coupling a water sensor of superior sensitivity (see Hadley *et al.* 1982, and Quinlan and Hadley, 1982, for details) to commercially available O_2/CO_2 sensors, and by providing a means of rapidly and accurately changing T_a. Other refinements are now available that further improve CO_2 measurement and data analysis (Lighton, 1988, 1990), and we expect that systems combining these technologies will greatly improve our understanding of metabolic and water relations in small organisms.

The results of this investigation of cicadas clearly illustrate the importance of body water content in both driving and limiting the various physiological variables

measured. We expected cicada water contents to be quite variable based on our understanding of their biology, but this proved to be only partly true. Body water content was very consistent at the start of runs (69.7 % of live mass; coefficient of variation=6.7 %). This mean value is slightly higher than that reported for *Diceroprocta apache* (66.2 %) (Toolson and Hadley, 1987) or other cicadas (*Tibicen dealbatus*, 67.5 %; Toolson, 1984). Our values suggest that our housing system provided adequate water and that *D. apache* regulates its water content within narrow limits when water is available. In contrast, variation in water content at the end of the runs was large, with changes in the cicadas' body water ranging from −30.5 % (21.4 % of initial mass) to +8.9 % (6.0 % of initial mass).

Much of the variation in water content during a run was a direct consequence of an individual cicada's feeding success. Feeding effort did not appear to be a factor. *D. apache* will attempt to insert its proboscis into any cylindrical object to which it is clinging when dehydrated. Feeding attempts were always noted in the test animals, especially at higher temperatures. We also do not feel that fluid flow to the twig was a problem, despite the rapid increase in flow resistance with time. Fluid was always under positive pressure and twigs were changed frequently. A more likely explanation is that twig diameter was too small for reliable feeding; *D. apache* was rarely observed to feed on such small twigs in the field. Unfortunately, technical considerations restricted the use of larger twig segments.

Despite these shortcomings, perfused twigs allowed cicadas partially to offset dehydrating conditions in the respirometer. Cicadas used in preliminary runs (2.8 h duration) without a water source experienced much larger mean losses of body water (23.0 %) than did those in runs with a twig (14.1 %, mean run duration 4.8 h). Fortunately, *D. apache* appears to be able to sustain considerable losses of water without long-term effect. This was also noted by Toolson (1987), who reported losses of 30–35 % of body water in *D. apache* without lethal effects.

Water content is also an important factor in determining evaporative water loss. For example, a change in water content of 10 % produces a 19.6 % change in EWL (Fig. 3). This relationship explains the large variation (coefficients of variation: 25.8–58.3 %) in rates of EWL (Table 1). Further evidence of this relationship is seen in animals that had resting and feeding periods at the same T_a, in that EWL was usually greater during feeding.

Evaporative water loss is also highly dependent on temperature; however, the extent of this relationship is partially concealed by the fact that EWL depresses body temperature, which in turn reduces the gradient for water loss. Using the T_b values and relative humidities in the respirometers, we were able to calculate gradient-corrected EWLs. In the T_a range 30–36 °C, corrected EWL values ranged from 0.194 to 0.210 $cm^2 h^{-1} Pa^{-1}$. At 38 °C and above, corrected EWLs increased dramatically, reaching a maximum of 0.813 $cm^2 h^{-1} Pa^{-1}$ at T_a=42 °C (mean T_b=39.4 °C).

Whole-cicada EWL rates given in the present work are considerably lower than *in vivo* rates determined with ventilated capsules (Hadley *et al.* 1989). At a mean T_b of 40.5 °C, *in vivo* EWL rates ranged from 9.9 $mg\,cm^{-2} h^{-1}$ (lateral thorax) to

85.1 mg cm^{-2} h^{-1} (dorsal abdomen). In contrast, whole-animal rates at similar T_b values averaged only 2.6 mg cm^{-2} h^{-1} (Table 1). These discrepancies are probably due to a combination of errors in estimating surface areas in whole cicadas and local differences in cuticular permeabilities. Hadley *et al.* (1989) measured *in vivo* permeability from small areas (0.8 mm^2) at just three locations on the dorsal surface of *D. apache*, and it is clearly hazardous to extrapolate these values to the animals as a whole.

Our results indicate that the T_b at which evaporative cooling begins (T_{ec}) ranges between 37 and 38°C. This is in contrast to previous work. Toolson (1987) found that heating curves for live cicadas at 45.5°C diverged from those of dead controls at T_b values between 39 and 40°C, and Hadley *et al.* (1989) reported that water extrusion from pores commenced at a mean T_b of 39.2°C when the animals were step-ramped from room temperature to 41.5°C. These differences are probably due to a combination of physiological and methodological factors. Both Toolson (1987) and Hadley *et al.* (1989) used CO_2 anesthesia during preparation of the animals; recovery time was approximately 1 h. In the present study, animals were cooled and given at least 3 h to recover, with the mean recovery time being 17 h. The two earlier studies, in addition, abruptly ramped the cicadas from room temperature to the test temperature. Determining the exact value of T_{ec} in such cases is difficult as T_b changes so rapidly.

Perhaps a more important question revolves around what value of T_b, if any, the cicadas defend with evaporative cooling. Heath and Wilkin (1970), using field measurements, showed that, at ambient temperatures between 25 and 35°C, cicadas elevated their T_b behaviorally to approximately 38.2°C. At higher T_a values (43–45°C) later in the day, T_b rose to 41.5°C. Toolson (1987) reported T_b values ranging between 39 and 40°C in animals at a T_a of 45.5°C, though these values tended to increase with exposure time. Finally, our results showed that, at a T_a of 42°C, the stable T_b averaged 39.2°C.

Taken together, these studies suggest that T_b of *D. apache* varies depending on T_a and the behavior of the insect. The present work indicates that an additional factor, water content, influences EWL so profoundly that T_b is also affected (Fig. 3). This dependence of T_b on water content is supported by Kaser and Hastings' (1981) finding that the T_b of the cicada *Tibicen duryi*, which is subambient at T_a values above 36°C, increased significantly when the animals were denied access to water. Our results also indicate that *D. apache* can thermoregulate very effectively when well hydrated; the mean T_b of the three cicadas able to gain water during the runs was 37.0±0.38°C (T_a=42°C). Clearly, work is now needed to establish the relationship between water content and T_b of *D. apache* in the field.

The relationship between water loss, when expressed per unit body mass, and T_{a-b} provides a means of estimating the drinking rates demanded by *D. apache's* thermoregulatory activities. T_{a-b}, when regressed against mass-specific EWL (mg g^{-1} h^{-1}) for individual cicadas, yielded the mean expression: T_{a-b}=0.043EWL−0.186 (r^2=0.961). The reciprocal of the slope, 23.14 mg de-

gree^{-1} g^{-1} h^{-1}, represents the mass of water that must be lost (and ingested if animal mass is stable) to maintain a 1°C temperature depression per gram of cicada. For a 0.6 g cicada maintaining a T_{a-b} of 5°C, this represents a drinking rate of 69.4 mg h^{-1}. This drinking rate is similar to rates reported for other cicadas (51.5 mg h^{-1}; Cheung and Marshall, 1973).

Diceroprocta apache did not show the discontinuous mode of respiration commonly observed in insects (Miller, 1981; Kestler, 1985). With the exception of the perturbations noted below, $\dot{V}_{CO_2}$ (and $\dot{V}_{O_2}$ at 30°C) was more or less constant. Abdominal pumping did occur, especially when the animals became active; it was very rare in resting or feeding animals. Pronounced dips such as those shown at about 50 and 60 min in Fig. 2 were fairly common during periods of quiescence. We assume that they represent changes in spiracular closure. The most common pattern observed during resting and feeding periods was very small fluctuations averaging one or two per minute. These fluctuations were independent of temperature and apparently represent small changes in spiracular caliber as they occurred when the animals were completely motionless. The absence of discontinuous ventilation in this insect does not come as a surprise since the putative function of this respiratory mode is water conservation.

The literature contains little data on the metabolic rate of cicadas. Bartholomew and Barnhart (1984) determined the mass-dependence of $\dot{V}_{O_2}$ in three species of tropical cicadas weighing between 0.2 and 3.0 g. $\dot{V}_{O_2}$ was measured during daylight hours, as it was in *D. apache*, but T_a ranged between 23 and 24°C. Assuming a live body mass of 0.6 g, the equation reported by Bartholomew and Barnhart (1984) yields a $\dot{V}_{O_2}$ of 0.354 ml h^{-1}. The same calculation using our $\dot{V}_{O_2}$/mass equation, after temperature correction (30 to 23.5°C) using the mean Q_{10}, gives a value of 0.207 ml h^{-1}. This value is only 58.5 % of that of tropical cicadas. A similar result was obtained by Bartholomew *et al.* (1985) in comparing four species of desert tenebrionids with a number of tropical beetles; the resting $\dot{V}_{O_2}$ of the desert forms was only 38 % that of the tropical beetles. Bartholomew *et al.* (1985) considered this difference to be an adaptation to an environment of low food productivity. Whether this explanation is applicable to xylem-feeding cicadas is presently unknown.

Evaporative cooling does not occur without cost to the cicada. Extracting water from the perfused twig resulted in a 5 % increase in metabolic rate over resting levels. This increase probably underestimates the cost of feeding in nature since the twig perfusate was under pressure, whereas xylem sap is generally under tension due to transpirational water loss, thus requiring the cicada to develop considerable suction to extract the fluid (Mittler, 1967). There are also probably costs associated with the physiological processing of the ingested fluid. Water must be rapidly removed from the xylem fluid and shunted to the ileum, while trace amounts of sugar, amino acids and various inorganic ions are absorbed into the hemolymph from the conical segment of the filter chamber and anterior tubular midgut (Cheung and Marshall, 1973). Finally, water responsible for the observed evaporative cooling must be pumped through and onto the thorax and abdominal

cuticle. Previous studies have clearly established that this is an energy-requiring process, as transcuticular water loss at these same temperatures greatly diminishes upon death (Toolson and Hadley, 1987; Hadley *et al.* 1989). Unfortunately, it is difficult to assess the metabolic costs associated with the cuticular pumping of water since some extrusion always occurs at the higher temperatures. The energy expended by the cicada, however, is fully compensated by the thermoregulatory benefits provided by evaporative cooling.

Appendix

Derivation of $\dot{V}_{CO_2}$ equations

The terminology is similar to that used by Hill (1972) (all volumes at STP): $\dot{V}_I$, volume of CO_2- and H_2O-free air entering respirometer; $\dot{V}_E$, volume of air leaving respirometer; $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$, volumetric rates of O_2 consumption and CO_2 production, respectively; $\dot{V}_{H_2O}$, volumetric rate of water loss from animal; $F_{I_{CO_2}}$, fractional concentration of CO_2 in inlet air; $F_{E_{CO_2}}$, fractional concentration of CO_2 in outlet air; RQ, respiratory quotient ($\dot{V}_{CO_2}/\dot{V}_{O_2}$).

$\dot{V}_{CO_2}$ *when* $\dot{V}_{O_2}$ *measured*

The general equation for $\dot{V}_{CO_2}$ is:

$$\dot{V}_{CO_2} = \dot{V}_E F_{E_{CO_2}} - \dot{V}_I F_{I_{CO_2}} \tag{A1}$$

Since inlet air is free of CO_2 and H_2O ($F_{I_{CO_2}} = 0$),

$$\dot{V}_{CO_2} = \dot{V}_E F_{E_{CO_2}} \tag{A2}$$

and outlet flow is given by:

$$\dot{V}_E = \dot{V}_I - \dot{V}_{O_2} + \dot{V}_{CO_2} + \dot{V}_{H_2O}\,. \tag{A3}$$

Substituting equation A3 for $\dot{V}_E$ in equation A2 and solving for $\dot{V}_{CO_2}$ gives:

$$\dot{V}_{CO_2} = \frac{(\dot{V}_I - \dot{V}_{O_2} + \dot{V}_{H_2O})F_{E_{CO_2}}}{1 - F_{E_{CO_2}}}. \tag{A4}$$

$\dot{V}_{CO_2}$ *when* $\dot{V}_{O_2}$ *is not measured but RQ is known*

$\dot{V}_{O_2}$ is given by:

$$\dot{V}_{O_2} = \dot{V}_{CO_2}/\mathrm{RQ}\,. \tag{A5}$$

Substituting equation A5 into equation A3 for $\dot{V}_{O_2}$ and solving for $\dot{V}_{CO_2}$ yields

$$\dot{V}_{CO_2} = \frac{(\dot{V}_I + \dot{V}_{H_2O})F_{E_{CO_2}}}{[1 + F_{E_{CO_2}}(1/\mathrm{RQ} - 1)]}. \tag{A6}$$

In practice, if the RQ is approximately 1, and FE_{CO_2} is kept low (<0.0005 in the present study), then equations A4 and A6 may be simplified to:

$$\dot{V}_{CO_2} = (\dot{V}_I + \dot{V}_{H_2O})FE_{CO_2}. \quad \text{(A7)}$$

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