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TEMPERATURE REGULATION BY RESPIRATORY EVAPORATION IN GRASSHOPPERS

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Summary

Grasshoppers of the species *Schistocerca nitens* (Thünberg), *Locusta migratoria* (L.) and *Tmethis pulchripennis* (Bolivar) are able to withstand air temperatures higher than lethal internal temperature (48°C) for more than an hour, during which time they maintain an internal temperature as much as 8°C below air temperature.

Rates of evaporation at high air temperatures are much greater than those observed for cuticular transpiration alone. The rate of evaporation and the ventilation frequency remain relatively constant at temperatures of up to about 45°C, above which they both increase markedly.

The depression of internal temperature thus appears to be caused by increased tracheal ventilation for evaporative cooling. This finding contradicts the common assumption that evaporative cooling is of little adaptive advantage for thermoregulation in insects.

In *L. migratoria*, the increase in ventilation appears to be achieved almost entirely by an increase in frequency of ventilation, although other species may alter tidal volume as well.

Introduction

Because of their small body size and consequently limited water reserves, temperature regulation by evaporative cooling has been presumed to be a generally unavailable or unimportant component of the thermoregulatory strategy for quiescent insects (Whitman, 1988; Tschinkel, 1985; May, 1979; Parker, 1982; Casey, 1981; Kammer, 1981). In the case of active insects, Church (1960) concluded that flying locusts could not cool sufficiently by evaporation to have any important effect on their internal temperature.

The alternative strategy, behavioral temperature regulation, has been observed by many authors (e.g. Whitman, 1988; Parker, 1982; Anderson *et al.* 1979; Waloff, 1963; Ellis and Ashall, 1957; Rainey *et al.* 1957) to be employed by grasshoppers in hot arid environments. Thus, selection of microhabitat and postural adjustment

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seem widely assumed to be the only available means by which grasshoppers can cope with environmental heat loads.

In the course of observations on behavioral temperature regulation, I found that a grasshopper (*Schistocerca nitens*) in my laboratory would voluntarily tolerate and survive more than an hour of exposure to an air temperature of 50°C, even though escape was readily available. Because insects of a similar range of body masses have been shown to reach temperature equilibrium in much shorter times (Bartholomew and Epting, 1975), this finding meant either that the grasshopper was extraordinarily able to withstand a high internal temperature or that it was, contrary to the general assumption, cooling itself by evaporation. In this paper I report the results of an investigation, stimulated by these observations, of physiological mechanisms of temperature regulation in *S. nitens* and, in greater detail, two other species of grasshoppers.

Materials and methods

In addition to *S. nitens*, two species of grasshoppers found in Israel were used in this study: *Locusta migratoria*, which typically lives in more humid environments, such as cultivated areas, and *Tmethis pulchripennis*, which is common to more arid environments in the Negev desert (Fishelson, 1985).

In Israel, grasshoppers were collected in the field (*T. pulchripennis*) or obtained from laboratory colonies (*L. migratoria*). They were maintained in individual containers with abundant fresh grass for forage and were used within a few days of capture. *S. nitens* were maintained in my laboratory colony. In the course of measurements, a grasshopper was confined within a cylindrical wire mesh (mesh: 6 mm×12 mm) cage approximately 1.5 cm in diameter and 5 cm long in which it could move its body and appendages freely. The length of the cage was adjusted to fit the individual grasshopper.

The body masses of the animals used in this study were (mean±S.E.): *S. nitens*, 2.29±0.14 g; *L. migratoria*, 1.54±0.17 g; *T. pulchripennis*, 1.52±0.18 g. Both genders were used and no distinction was made between them in the measurements.

Studies on *S. nitens* were carried out in my laboratory at Indiana University; *L. migratoria* and *T. pulchripennis* were studied at the Mitrani Center for Desert Ecology, Blaustein Institute for Desert Research, Sede Boqer, Israel.

A convective chamber, constructed of styrofoam for good insulation and low thermal capacity, was used to provide controlled but quickly changeable air temperatures for these experiments. Air drawn in by a low-speed fan and heated by electrical resistance elements was directed upwards through a wire mesh floor on which the animal cage was placed. The temperature of the air could be maintained within ±0.1°C through a range of 25–55°C by a proportional controller that controlled the output of the heater and responded to a thermistor located just beneath the chamber floor. Air flowed through the chamber at a speed of 0.2 m s^{-1}; its measured relative humidity was always less than 20%.

The internal temperature of the grasshopper was measured by insertion of a 36 gauge thermocouple through the pronotum to the approximate center of the prothorax. Dissection revealed that, in this position, the tip of the thermocouple bypassed the flight muscles and was positioned just above the gut. Where any seepage of hemolymph occurred, it dried quickly and animals prepared in this manner did not have measurably higher rates of water loss than those without thermocouples inserted.

Thermocouple voltages were converted to temperatures with either a digital thermometer or a datalogger. The output from these instruments was stored on diskette with a portable computer for subsequent analysis.

Ventilatory movements and contractions of the heart were recorded simultaneously from electrodes made of 30 gauge hypodermic needles inserted in the abdomen. Changes in the impedance between the electrodes were converted to voltage and recorded on an oscillographic chart recorder. Chart records were synchronized with temperature data and data transferred to the computer from visual inspection of the record. The accuracy of the method was confirmed by direct observation of abdominal pumping and heart contractions through a dissecting microscope.

For measurements of internal temperature at different air temperatures, the grasshopper, implanted and confined as described above, was allowed to come to steady state at room temperature, 25–30°C. The cage and animal were then moved to the chamber which was preheated to the experimental temperature. When a steady state was reached, the animal was either moved to room air to cool or remained in the chamber while the temperature was reset. Temperatures of the grasshopper and the air adjacent to the animal were recorded every 15 s throughout the experiment. Each animal was used in only one experimental preparation.

For measurements of evaporative water loss, the grasshopper and its cage were sealed in a cylindrical glass container 4 cm in diameter and 10 cm long through which dry air was passed. The container and grasshopper were allowed to come to a steady temperature in the temperature-controlled chamber. The water vapor in the air leaving the chamber was collected by absorption in anhydrous $CaSO_4$ (Drierite) and its change in mass determined to 0.1 mg. A blank was collected and its value subtracted from the amount collected during each experiment. The water vapor leaving the container was collected for a period of 30–60 min. The procedure was repeated at various temperatures within a range of 25–50°C.

Results

Internal temperature at different air temperatures

The internal temperatures of all three species had similar and overlapping distributions across the range of temperatures studied. The combined data for these measurements, expressed as the difference between air temperature (T_a) and internal temperature (T_b), are shown in Fig. 1. The maintenance of an

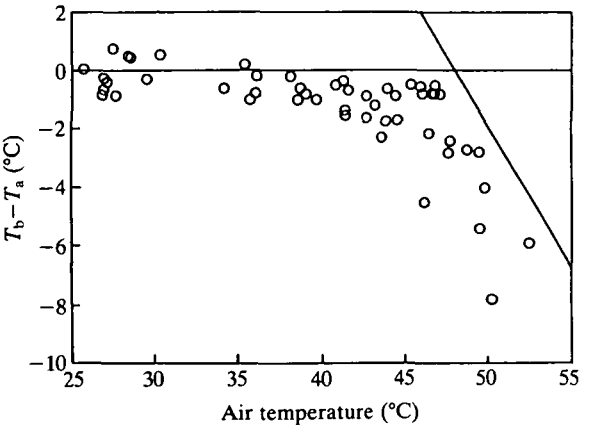

Fig. 1. Difference between air temperatures (T_a) and body temperatures (T_b) of *Schistocerca nitens*, *Locusta migratoria* and *Tmethis pulchripennis*. The diagonal line indicates the difference that must be maintained to keep the internal temperature below the observed lethal temperature of 48°C.

internal temperature significantly below air temperature does not appear to occur below an air temperature of about 45°C. Grasshoppers usually died if their internal temperature exceeded 48°C. In most cases they were able to avoid this limit in air temperatures as high as 52–53°C.

Ventilation and heart rates at different temperatures

Data were obtained only for *L. migratoria* and *T. pulchripennis* and are shown in Figs 2 and 3, for ventilation, and Figs 4 and 5 for heart rate, respectively. Although the trends are less distinct in the case of *T. pulchripennis*, the maximum ventilatory rate for both species was about $3\,s^{-1}$ but remained within a range of

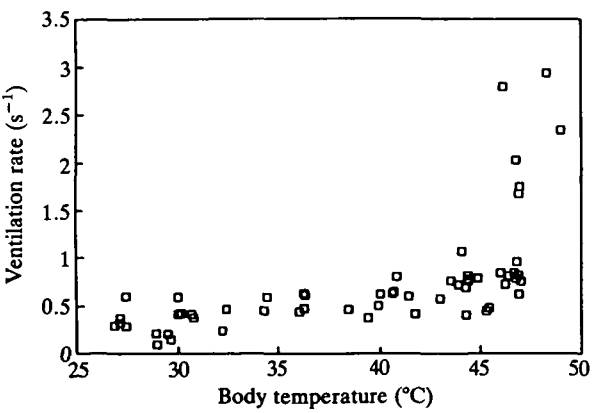

Fig. 2. Ventilation rates at different internal temperatures for *L. migratoria*. Seven locusts were tested, each at several temperatures.

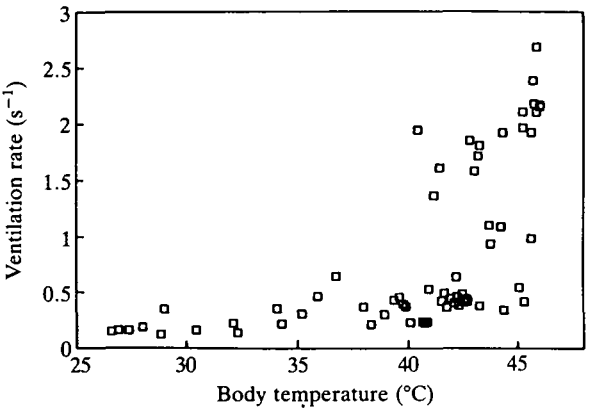

Fig. 3. Ventilation rates at different internal temperatures for *T. pulchripennis*. Six locusts were tested, each at several temperatures.

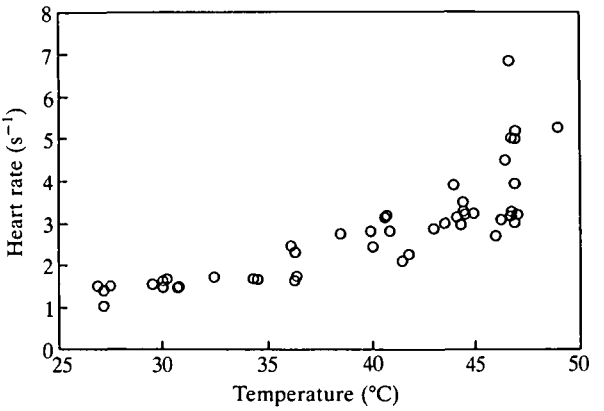

Fig. 4. Heart rate at different internal temperatures for *L. migratoria*. Six locusts were tested, each at several temperatures.

0.2–0.6 s^{-1} until an internal temperature of about 42–46°C. In contrast to the abrupt change in ventilation rates, heart rates tended to show a more gradual increase with temperature. A regression analysis of the relationship of heart rates of both species to temperature gives a Q_{10} of about 2.4.

These data were collected at steady state or during temperature increases. When grasshoppers were removed from the hot chamber and subjected to rapid cooling in room temperature air, their ventilatory movements usually ceased entirely for several minutes. Heart contractions did not cease abruptly during rapid cooling.

Evaporative water loss at different temperatures

Data for the total evaporative water loss of *L. migratoria* and *T. pulchripennis* as

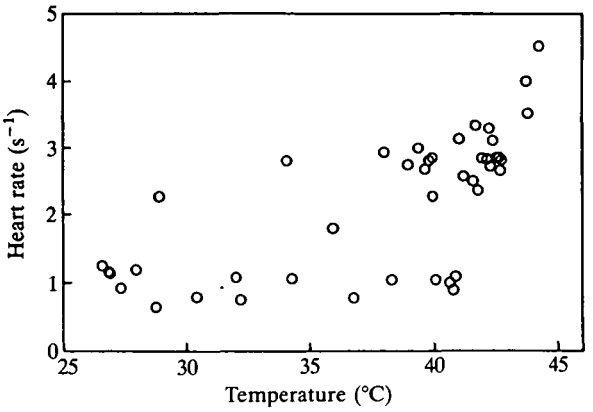

Fig. 5. Heart rate at different internal temperatures for *T. pulchripennis*. Seven locusts were tested, each at several temperatures.

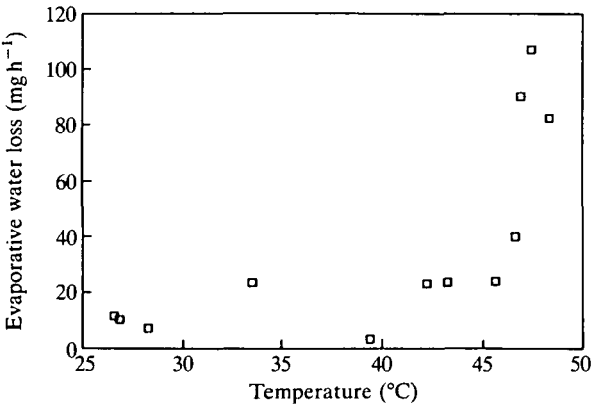

Fig. 6. Total evaporation for *L. migratoria* at different temperatures. Five locusts were tested, most at more than one temperature.

a function of temperature are shown in Figs 6 and 7, respectively. As for ventilation rate, total evaporation tended to remain at a nearly constant level, less than 20 mg h^{-1}, until the air temperature was about 45 °C and then rose rapidly to rates as high as 100 mg h^{-1} at higher temperatures.

Discussion

Internal temperature at different air temperatures

The grasshoppers exposed to high air temperatures in this study avoided exceeding a lethal internal temperature by maintenance of internal temperatures

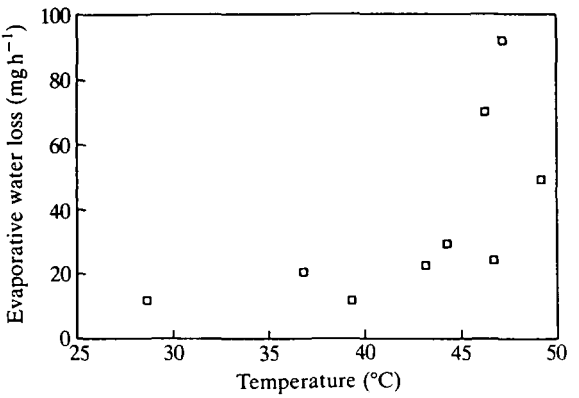

Fig. 7. Total evaporation for *T. pulchripennis* at different temperatures. Five locusts were tested, most at more than one temperature.

just below the apparent lethal temperature of 48 °C. Although they cannot regulate their internal temperature in the sense that a true homeotherm would, they are able, with a physiological response, to maintain their internal temperature within the range necessary to avoid thermal death. The diagonal line in Fig. 1 indicates the minimum difference between air and internal temperature that will allow the grasshopper to survive. It appears that the grasshoppers can detect their approach to this limit and respond by controlling their evaporative cooling accordingly.

Ventilation and heart rates at different temperatures

The ventilation rate shows little response to temperature below internal temperatures of about 45 °C and then increases markedly. There are two possible interpretations that can account for the observed change in this rate. First, the increase in internal temperature will increase the metabolic rate and, hence, the demand for increased gas exchange will stimulate an increase in ventilation as a simple Q_{10} effect. Second, the change in ventilation may be due primarily to the need to increase evaporative water loss as the upper lethal internal temperature is approached.

One way to test the Q_{10} effect hypothesis is to compare ventilation and heart rates. Because of the extensive tracheal system that carries out gas exchange and the lack of directed flow within the open circulatory system of an insect, the circulation has no obvious involvement in the temperature regulation of the animals studied. The rate of heart contraction can be reasonably assumed to be a function of the overall metabolic rate. This conclusion is supported by the data that show (Figs 5 and 6) an increase in rate with temperature consistent with a Q_{10} effect.

In contrast, the ventilation rates (Figs 3 and 4) change abruptly as the lethal temperature is approached. This direct departure of the ventilation rate from the gradual increase at lower temperatures suggests that the onset of hyperpnea

augments evaporation rather than satisfying a dramatic increase in the need for respiratory gas exchange at that critical temperature.

Evaporative water loss at different temperatures

A second confirmation that the increase in ventilation rate primarily serves the function of evaporative cooling can be made by comparing changes in total evaporation with changes in temperature. As can be seen comparing Figs 6 and 7 with Figs 4 and 5, the rates of ventilation and evaporation change with nearly identical relationships to temperature. A similar relationship has been reported by Loveridge (1968*b*) for *L. migratoria*.

Because my measurements do not separate cuticular from respiratory water loss, it is important to consider the contribution of non-respiratory evaporation. Loveridge (1968*a*) measured cuticular water loss in *L. migratoria* and reported rates generally less than $10\,mg\,h^{-1}$, much less than the approximately $100\,mg\,h^{-1}$ I have found. Although a temperature-dependent transition in cuticular transpiration of *L. migratoria* was shown by Loveridge (1968*a*), the magnitude of the increased loss was still much less than the values I measured and did not occur appreciably below 50°C. Thus, the transition of cuticular permeability is presumed to be a parallel but unimportant contributor to the increase in total evaporation. No previous work on the cutaneous water loss of *T. pulchripennis* could be found, but the similarity in the data to those for *L. migratoria* suggests that there is a similar relationship between ventilation and evaporation in this species.

At a temperature somewhat too low to lead to hyperpnea, say 30°C, the density of saturated water vapor in air is approximately $0.03\,g\,cm^{-3}$ (Weast, 1964). By subtracting the cuticular loss for *L. migratoria* measured by Loveridge (1968*a*) from the total evaporation, one can calculate the approximate volume of air moved through the spiracles by this species. Using appropriate values from Fig. 6 for the calculation, the total evaporation is about $10\,mg\,h^{-1}$, from which $5\,mg\,h^{-1}$ is subtracted as the cuticular portion (Loveridge, 1968*a*). Assuming the inhaled dry air becomes saturated in the tracheal system, the ventilation necessary to account for the rate of water loss is slightly less than $0.05\,cm^3\,s^{-1}$, a minute volume of $2.8\,cm^3$. At a ventilatory rate (from Fig. 2) of about $0.4\,s^{-1}$ the resulting tidal volume is about $0.11\,cm^3$.

When *L. migratoria* is ventilating vigorously at 46°C, the comparable data are $0.07\,g\,cm^{-3}$ for vapor density, a corrected evaporation rate of approximately $100\,mg\,h^{-1}$ and a ventilation rate of $3\,s^{-1}$. From these data the calculated necessary ventilation rate is $0.40\,cm^3\,s^{-1}$ (eight times greater than the value at 30°C), a minute volume of $23.8\,cm^3$. The calculated approximate tidal volume is $0.13\,cm^3$. These calculations suggest that, because the calculated tidal volume changes little, the increase in ventilation is almost entirely due to an increase in ventilatory frequency.

Loveridge (1968*b*) reported similar values for the change in ventilatory frequency with temperature in *L. migratoria*. Weis-Fogh (1967) measured ventilation by abdominal pumping in the locust *Schistocerca gregaria*. The increase

in ventilation, in comparison to resting level, was slightly less than fivefold for flying locusts but as much as sevenfold for those stimulated with 5% CO_2. The increase in pumping frequency can account for only about half of the increase in ventilation for flying *S. gregaria*. Data for pumping rates are not given for the CO_2-induced ventilation by Weis-Fogh (1967), but data from Miller (1960) on the same species exposed to CO_2 levels of 3–6% show nearly identical rates of about $0.9\,s^{-1}$; in air, the frequency was about $0.4\,s^{-1}$. This dissimilarity in response suggests that, in contrast to *L. migratoria*, *S. gregaria* uses both frequency and tidal volume changes to modify total ventilation: extrapolations from one species to another should therefore be made with caution. Further, ventilatory changes induced by hypercapnia may be different from those induced by hyperthermia.

Weis-Fogh (1967) reported a water loss rate of $8\,g\,kg^{-1}\,h^{-1}$ for continuously flying *S. gregaria*. In terms of those dimensions, the grasshoppers in this study lost water at a much greater rate, more than $60\,g\,kg^{-1}\,h^{-1}$. Weis-Fogh's measurements were made at a higher relative humidity and lower temperature than mine but one might speculate from so large an observed difference that the animals had some control over their water loss rate. The flying locust may be able to dissipate heat adequately by the convection inherent in flight, in which case lowering the body temperature by evaporation would be counterproductive. Perhaps the grasshoppers can alter the pattern of air flow through the tracheal system by a varied order of opening of the spiracles to conserve water when convection is adequate. If the air flow pattern were reciprocating rather than unidirectional, condensation might occur from the outflow, as in the case of some desert mammals (Schmidt-Nielsen *et al.* 1970).

Many insects have air sacs as part of the tracheal system. These have recently been described in detail for the grasshopper *Chrotogonus senegalensis* by Maina (1989). Many functions have been assigned to these organs from acting as bellows to sound resonators or heat insulators (see review in Wigglesworth, 1984). Given the apparent importance of respiratory evaporative cooling to the grasshoppers of this study, the surfaces of the air sacs seem likely sites for evaporation and, hence, to be thermoregulatory organs as well.

Control of ventilation

Miller (1960) found that increased P_{CO_2} stimulated ventilation in grasshoppers, which suggests that respiration and acid–base regulation are linked. In contrast, Harrison (1988) concluded that variation in ventilation relative to metabolic CO_2 production in the grasshopper *Melanoplus bivittatus* did not explain the changes in hemolymph pH with temperature that he observed. Wong *et al.* (1989) suggest that respiratory mechanisms are not of primary importance in the acid–base regulation of the locust *S. gregaria*.

In this study, grasshoppers that exhibited prolonged hyperpnea under heat stress ceased ventilation almost immediately when the air temperature was reduced, even though their internal temperature was still at a level at which, had the air temperature been high, one would normally observe increased ventilation.

This observation suggests that the thermoregulatory hyperpnea hyperventilates the grasshopper and lowers P_{CO_2} in the hemolymph; when the thermoregulatory drive is removed, ventilation is inhibited by low P_{CO_2}. The abrupt cessation of ventilation as air temperature decreased also suggests that the grasshopper may use a peripheral rather than a core temperature to control its thermoregulatory hyperpnea.

The relationship between P_{CO_2} and ventilation may be different in this study from those of Harrison (1988) and Wong *et al.* (1989) because I used different species, different physiological perturbations and higher temperatures.

If grasshoppers need to maintain an internal temperature lower than air temperature, a physiological mechanism, evaporative cooling, is available to them, despite the common assumption that they can regulate their temperature only by behavioral means. The assumption of such a limitation in their repertory of thermoregulatory responses is especially curious because the phenomenon of insects having internal temperatures lower than that of the air has been reported several times. Pirsch (1923) indicated that honeybees could maintain an internal temperature of 46.4°C in an air temperature of 58°C, a difference of 11.6°C. Necheles (1924) showed that the cockroach (*Periplaneta orientalis*) in dry air could maintain an internal temperature well below air temperatures as high as 50°C but, in saturated air, its internal temperature was above that of the air, a clear implication of the importance of evaporation. Mellanby (1932) showed that a cockroach (species not given), when placed in humid air of 45°C, reached equilibrium with the air temperature. When the humid air was replaced with dry air, the cockroach's internal temperature fell to 39°C. Clarke (1960), in a study of *L. migratoria*, points out that internal temperature is lower than air temperature at high air temperatures if the humidity is low and that '...evaporation of water is a key factor'. Edney and Barrass (1962), Stower and Griffiths (1966), Seymour (1974) and, most recently, Toolson (1987) have implicated evaporative cooling as important for some species of insects. These latter two authors are among the few who have clearly pointed out the phenomenon of insects adaptively making use of this mechanism in response to high ambient temperatures. One may be sure the list is more extensive than those I have cited but these references, along with the findings of this paper, should belie the assumption that evaporative cooling is not of adaptive significance for insects.

The limited effect of evaporative cooling for locusts in tethered flight found by Church (1960) can be accounted for because of the overwhelmingly high heat production of flying insects along with the ready availability of convective cooling. Heinrich (1980*a*,*b*), perhaps explaining the observations of Pirsch (1923), showed that flying honeybees could cool their head and thorax near to and below air temperatures as high as 46°C by regurgitation of crop contents onto the body surface. The grasshoppers in this study were not observed to exude any fluids from their mouths so their evaporation must be primarily internal.

The only basis I can suggest for the notion that quiescent insects cannot use evaporative cooling because of their small body size is a misinterpretation of

Schmidt-Nielsen's (1964) calculations regarding fraction of body water lost and body size of desert-dwelling mammals. Endotherms, such as small mammals, that must deal with a large metabolic heat load in addition to that of a hot environment, must lose too great a fraction of their body water to survive in hot regions by evaporative cooling. But these calculations do not apply to quiescent insects for which metabolic heat production is insignificant. Further, it is unlikely that, even in the desert, day-long exposures to air temperatures as high as 50°C occur. Mammals are generally unable to survive internal temperatures as high as 45°C at which grasshoppers just begin to turn on their evaporative cooling. An insect need only survive its exposure to occasional superlethal environmental temperatures for a few peak hours of the day, whereas the mammalian desert dweller may need to cool itself evaporatively throughout the day to survive. The grasshoppers in this study lost water at a maximum rate of about 8% of their body mass per hour and could tolerate a loss of one-third of their initial mass. At that rate they should be able to avoid superlethal temperatures for at least 4 h. For grasshoppers unable otherwise to escape the extreme heat stress of the hot desert one may conclude that such evaporative cooling is a sufficient, and probably also necessary, mechanism for survival.

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