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MICROMETEOROLOGY AND ENERGY EXCHANGE IN TWO DESERT ARTHROPODS¹

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Abstract. Incoming solar, net, and reflected radiation, wind velocity, relative humidity, and temperatures at various levels above and below an open desert surface were recorded simultaneously at 30-minute intervals for a 3-day period. Concurrent measurements were also made of arthropod burrow temperatures and relative humidities, scorpion body temperatures, and body and subelytral temperatures of tenebrionid beetles.

The burrowing habit enabled arthropods to escape the hot, desiccating conditions recorded on the desert surface during the day. Temperatures and humidities to which scorpions were subjected while in their subterranean retreats depended upon the burrow's depth and subsequent movements in the burrow. Vertical movements between the surface and maximum burrow depths during a 24-hour period provided arthropods with a wide choice of micro-environments.

Tenebrionid beetles on the surface were able to achieve a temperature equilibrium only under low temperature and radiation loads. Subelytral cavity temperatures in black *Eleodes armata* were generally 2–7°C warmer than body temperatures after exposure to direct sunlight. Temperature differences between subelytral cavities of black beetles and beetles with their elytra painted white were small, but suggested that a white dorsal surface was, at least, partially effective in reducing absorption of solar radiation. The subelytral cavity, in addition to reducing transpiratory water loss, apparently provides a mechanism for increasing convective cooling, and may serve as a temperature "buffer zone" against heat conduction resulting from high intensity solar radiation.

A heat exchange budget was estimated for *E. armata* on the desert surface. Major contributing factors were heat gained from incoming radiation versus heat lost from convection and reradiation. Contributions from evaporation and metabolism, as determined by laboratory experiments, were very small in comparison, while the role of conduction in energy exchange was assumed to be negligible. Inherent problems in the estimation of contributing factors to net energy exchange, and comparison of similar budgets for mesic arthropods are discussed.

It has long been known that animals living in burrows, crevices, or beneath some form of cover experience climatic conditions quite different from those of the macroenvironment. Exploitation of such habitats is particularly critical for many desert organisms that require this temporary escape from climatic extremes which otherwise would be lethal. Sinclair (1922), Buxton (1924), Guild (1950), and Williams (1954) have reported on the severity of the desert climate on or near the ground, and general discussions of arid-zone microclimate and arthropod fauna are contained in two UNESCO symposia (1958, 1962). A comprehensive review of microclimate and arthropod distribution by Cloudsley-Thompson (1962) includes several references to studies concerning desert species as well as investigations applicable to desert regions (Parry 1951, Edney 1953). Recent interest in vertebrate adaptations to hot, dry environments has also resulted in an accumulation of valuable micrometeorological data.

This study was designed to (i) provide continuous micrometeorological data over a sufficiently long period to establish definite patterns for several climatic parameters in a desert area, (ii) test

new techniques for recording physical conditions in small enclosed spaces, and (iii) correlate micrometeorological data with surface occurrence, burrow movements, and thermoregulatory activities of two desert arthropods.

MATERIALS AND METHODS

The desert site selected for study (Fig. 1) is located approximately 2½ miles southwest of Guadalupe, Arizona on the Ahwatukee Ranch (el. 424 m). The area has an extremely rich arthropod fauna, and weather and arthropod activity data are available from the adjacent South Mountain Park desert. Vegetation here consists predominately of creosotebush (*Larrea tridentata*) with a few scattered bur-sage (*Franseria deltoidea*), saguaro (*Cereus giganteus*), and palo-verde (*Cercidium microphyllum*). Soil is quite sandy and generally is covered by a thin layer of fine gravel. Extensive burrowing activities of rodents, lizards, and arthropods, particularly at creosote bases, are evident throughout the area.

Micrometeorological measurements

Physical parameters measured during June 24–27, 1969 included air and soil temperature, rel-

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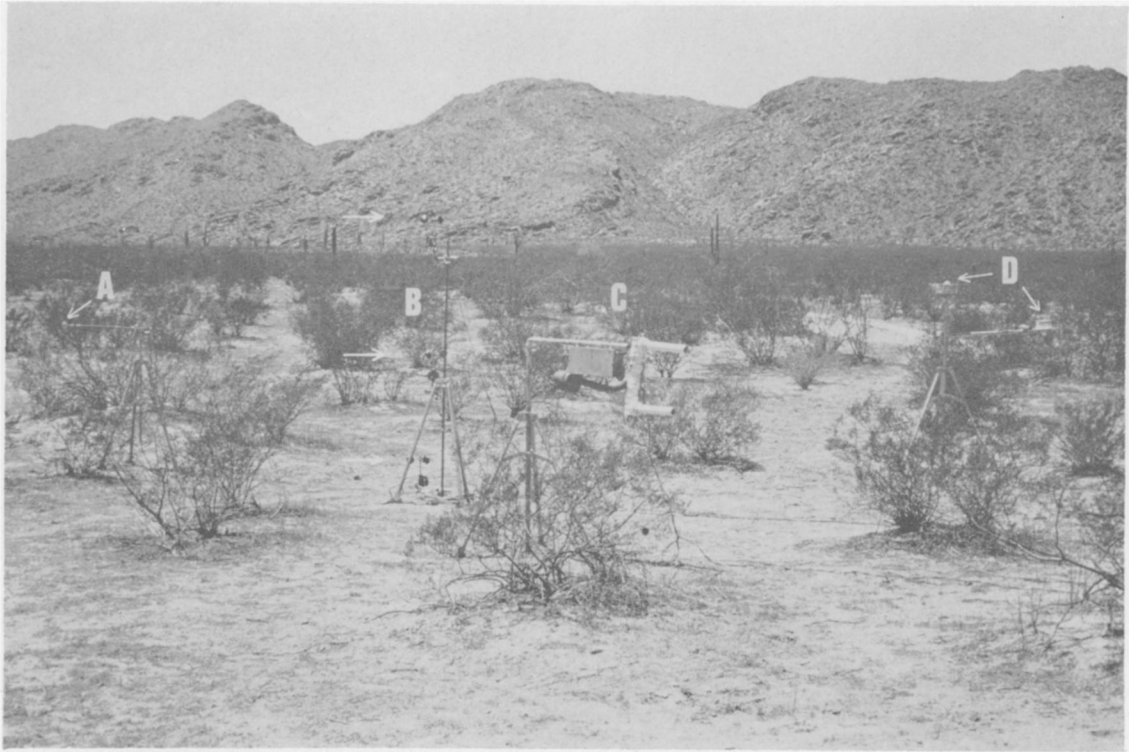


FIG. 1. View of creosote-flat study area and meteorological instruments as follows: A, Fritschen net radiometer; B, Casella cup anemometers; C, Honeywell dew probe enclosed in ventilated housing; D, Kipp solarimeters. The height of radiometer sensor (A) is 1 meter.

ative humidity, wind velocity, and incoming solar, net, and reflected radiation. Copper-constantan thermocouples (30 ga.) were used to record temperatures for both an open surface and the base of a creosote bush at the following levels: -20 cm, -15 cm, -10 cm, -5 cm, surface, 1 cm, 5 cm, 10 cm, and 1 m. Subsurface placement of thermocouples with minimal soil disturbance was achieved by vertically penetrating the soil with a small cylindrical rod to the proper depth, inserting the thermocouples, and then filling with soil. Thermocouple junctions were shielded with aluminum foil for measurements made above ground. Relative humidity at 1 m was measured with a Honeywell dew probe enclosed in a specially built ventilated housing. Measurements of relative humidity near the ground were made with a thermistor psychrometer (Atkins Tech., Gainesville, Fla.) or estimated from general purpose humidity indicators (Humidial Co., Colton, Calif.). Wind velocity at 25 cm, 1 m, and 2 m was recorded using Casella cup-type anemometers. Kipp solarimeters provided data on total incoming solar radiation and reflected radiation over an open surface. Net radiation for both an open area and beneath a creosote was measured by Fritschen net radiometers (Fritschen 1963, 1965) constructed at the

U.S. Water Conservation Laboratory, Phoenix, Arizona.

Acquisition and analysis of data

All meteorological data were fed into a mobile micrometeorological laboratory (U.S. Water Cons. Lab) via 30- or 60-m cables and connected to a Vidar data acquisition system. Components of this particular system model included a digital time clock, a built-in thermocouple reference junction, a maximum combination of 50-thermocouple and/or EMF junctions, eight separate counters for wind speed or any event with a pulse count, a visual display window, and a paper tape system onto which coded data were punched and later read on an ITT teletype reader. The system was programed to cycle automatically and record all meteorological factors every 30 min during the 3-day study; however, it could also be operated manually as often as every 15 sec without interfering with the established program.

Burrow microenvironment and arthropod body temperatures

The inflexibility of thermocouple wire or thermister leads makes it extremely difficult to follow complex arthropod burrows and record temper-

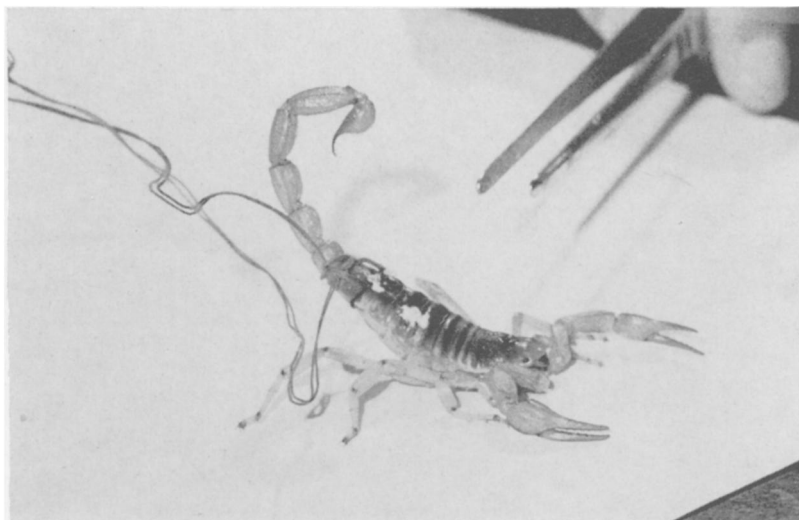


FIG. 2. *Hadrurus arizonensis* carrying two thermocouples. The junction of one was projected anteriorly over the metasoma; the second junction was inserted beneath the dorsal surface into the body cavity.

atures at deeper levels. To overcome this problem, thermocouples (30 ga.) were secured to scorpions by tying them to the base of their tails, projecting the junction forward over the body, and allowing the scorpion to carry the thermocouple down into the burrow (Fig. 2). Adult hairy scorpions, *Hadrurus arizonensis*, were selected because of their size (7–10 cm). Thermocouples did not appear to hinder their movement down burrows in spite of frequent turns. Penetration distance into a burrow was noted by marking pre-measured thermocouple leads with tape at the burrow opening. This technique did not provide information as to penetration depth without actually excavating the burrowed scorpion, but did indicate if any further movements into the burrow occurred after initial penetration.

In several scorpions, a second thermocouple was inserted beneath the dorsal surface of the metasoma into the body cavity and its junction sealed with nail polish. Taping lead wires together reduced the problem of carrying down two thermocouples into burrows. Few problems were encountered during the recording of air and scorpion temperatures on the surface at night because of their stationary behavior (Hadley and Williams 1968).

Relative humidity inside burrows was determined by tethering individual scorpions with nylon thread to which thin strips of humidity indicator paper were tied immediately above the scorpion's tail. Scorpions were then allowed to enter burrows and sufficient time given for exposure of the humidity paper to the burrow air. The relative humidity for any specific time during

a 24-hour period could be obtained by simply pulling the scorpion out of the burrow and quickly reading the humidity paper.

Body temperatures were also recorded from desert tenebrionid beetles (*Eleodes armata*) in sunlight. Thermocouples were placed into either (1) the body cavity, entering above the coxa of the second walking leg and/or (2) the subelytral cavity, an air-filled space which lies beneath the thick, fused elytra and into which the spiracles open. Thermocouples were sealed into place with nail polish and secured with nylon thread. Test beetles were able to walk, stilt, feed, and generally behave much like normal beetles.

RESULTS

Mean hourly values of radiation flux and wind velocity for a 24-hour period, based on data acquired from June 24–27, 1969, are shown in Figure 3. Mean daily sums of incoming solar, net, and reflected radiation are also given. Skies during the entire 75-hour study were clear and all weather conditions, except for slightly cooler air temperatures, were typical for this 3-day period of the year (Green and Sellers 1964).

As would be expected for clear days, the plot of incoming solar radiation is smooth and symmetrical, reaching its maximum shortly after 1200. The daily mean solar radiation sum (723 ly) compares favorably with radiation levels recorded at Sky Harbor Airport, Phoenix (726 ly day⁻¹) for this time of year. Blowing dust in the afternoon probably prevented higher radiation values. The plot of surface reflectivity is also smooth and symmetrical. The high albedo (24% of incom-

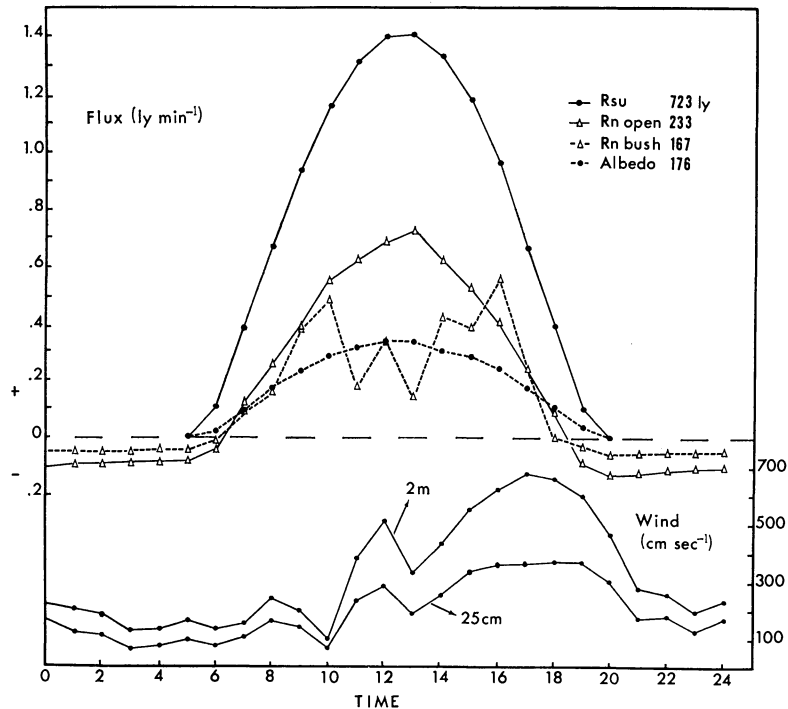


FIG. 3. Mean hourly distribution of radiation flux ($1\text{y} = \text{cal}/\text{cm}^2$) over an open desert surface during June 24–27, 1969. Mean daily sums of incoming solar radiation (R_{su}), net radiation over an open surface (R_n open), net radiation beneath a creosotebush (R_n bush), and reflected radiation (albedo) are also given. Mean hourly wind velocity for the same period is plotted for 25 cm and 2 m heights.

ing solar radiation) is typical of dry, light desert soils (Sellers 1965).

Net radiation values were slightly negative for approximately an hour before sunset to 1 hour following sunrise during which time effective outgoing long-wave radiation predominated. With sunrise and the changeover to incoming short-wave radiation, net radiation values quickly reverted to positive and rose rapidly to a maximum at 1230. The high albedo of the desert surface, plus clear skies and high surface temperatures resulted in considerable energy being radiated back to the atmosphere. As a result, the mean net radiation sum over an open surface (233 ly day^{-1}) was less than sums observed in nondesert areas at the same latitude (Sellers 1965).

The mean net radiation value for a 24-hour period beneath the creosote was 31% less than the mean daily sum recorded over an open surface. During the night the surface beneath the creosote was partially shielded from the sky, resulting in slightly higher net radiation values, although still negative. The plot of net radiation beneath the creosote during the day fluctuated depending on the position of the sensor in reference to shading provided by leaves and branches.

At 1600 creosote net radiation values surpassed those over an open surface because of the direct illumination of the sloping surface beneath the creosote at this time.

Daily wind pattern during the 3-day study consisted of relatively calm mornings with increasing wind velocity and gusts during afternoon. Following sunset, wind speed decreased to approximate morning levels. Peak wind velocities of $600\text{--}675 \text{ cm sec}^{-1}$ were reached around 1600–1700. As expected, wind movement was always less closer to the ground. The lull observed at 1000 is typical of the general wind pattern at this time of year and reflects a change in wind direction from southeast to southwest.

The daily temperature sequence at various levels above and below an open desert surface are shown for selected intervals in Figure 4. Plotted points at a particular height or depth represent the mean temperature recorded for that hour over the 3-day period.

In general, the tautochrones reflect expected patterns. The greatest daily temperature variation occurred on the desert surface with decreasing temperature fluctuation recorded with increased height above and depth below the surface. During

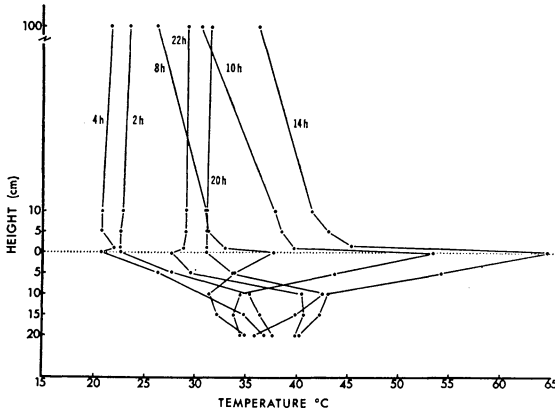


FIG. 4. The daily temperature sequence at various levels above and below an open desert surface. Plotted points represent mean values for that particular hour during the 3-day study.

the day, the positive radiation balance resulted in maximum surface temperatures at 1400, 1½ to 2 hours following peak solar radiation values. The warmest temperature at -20 cm, however, was not reached until 2000, indicating a significant lag in conductive heat penetration during the day.

At night when heat flow in the soil was directed upward and outgoing radiation produced a negative radiation balance, the soil surface cooled rapidly producing minimum temperatures. Temperatures now generally increased with depth into the ground, although patterns at certain times (2200) were sometimes complicated by differences in direction of heat flow at various levels. Temperatures at the lowest recorded depth (20 cm) still fluctuated 6°C during a 24-hour period. Earlier studies reported that a depth of 45 cm must be reached before temperature fluctuations become negligible (Sinclair 1922; Guild 1950).

A similar temperature gradient occurred above the desert surface, although during hotter portions of the day a very small increase in height above the surface (1 cm) resulted in a greater decrease in temperature than observed for an equivalent depth below the surface. Strong wind activity in the afternoons prevented the establishment of sharper temperature gradients and kept surface temperatures somewhat lower by increasing convective heat loss. Air (1 m) and soil surface temperatures of 46°C and 80.5°C, respectively, were recorded in July at the study site in mid-

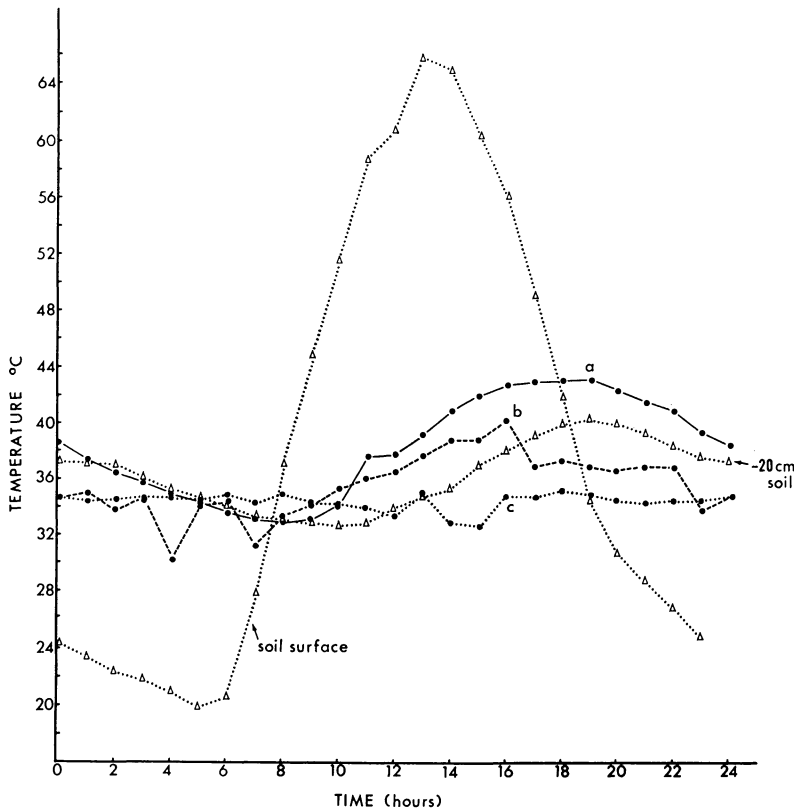


FIG. 5. Burrow temperatures experienced by three scorpions (a, b, c) at various depths over a 24-hour period. Surface and -20 cm soil temperatures during the same period are included. All scorpions remained in the burrows throughout the 24 hours.

afternoon during a day when wind activity was minimal.

Patterns (not shown) of the temperature sequence beneath the creosote at the same levels were very similar, although temperature extremes at most levels were reduced. One noticeable difference was the occurrence of slightly cooler nighttime temperatures at 1 and 5 cm above the ground rather than on the surface as observed over the open area (see Ramdas 1958).

Burrow microenvironment

Temperatures experienced by scorpions occupying burrows at various depths for a 24-hour period are shown in Figure 5. These three temperature records, which illustrate various patterns observed, were selected from eight such recordings made during the 3-day study. Scorpions which also carried a body thermocouple exhibited body temperatures equal to or slightly below ($< 0.5^{\circ}\text{C}$) burrow air temperatures.

The diurnal fluctuation in temperature to which scorpions were subjected was largely dependent on the depth of penetration and subsequent movement once inside the burrow. Scorpion "a" occupied a very shallow terminal burrow and experienced temperatures in the afternoon which approached 44°C . The scorpion died sometime while in the burrow, quite likely from heat death since this temperature can be lethal over a 2-hour period (Hadley unpubl.). Scorpion "b" entered a burrow which permitted movement to deeper levels. Such movements were apparent during the early morning hours and particularly at 1400 when continued occupation at this depth might also have resulted in heat death. The deepest penetration depth (40 cm), plus relatively stationary behavior in the burrow, enabled scorpion "c" to experience the smallest diurnal temperature fluctuation. From 1600 to 0830, burrow air temperature did not fluctuate over 1°C ; total variation over the 24 hours was only 3.6°C .

Spot checks of relative humidity at depths of 20–35 cm indicated a daily range of 55–70% compared to relative humidities of less than 5% on the surface during the day and approaching saturation during the night. At 1 m height, mean hourly relative humidity for the 3-day period ranged from 19.4% at 1400 to 54.0% at 0500.

Figure 6 illustrates a more abrupt and marked temperature change brought about by vertical movements associated with feeding behavior. This particular scorpion stationed itself at the base of a burrow's first turn (–16 cm) and remained in this position until approximately 0200 at which time it moved out onto the surface. Movement

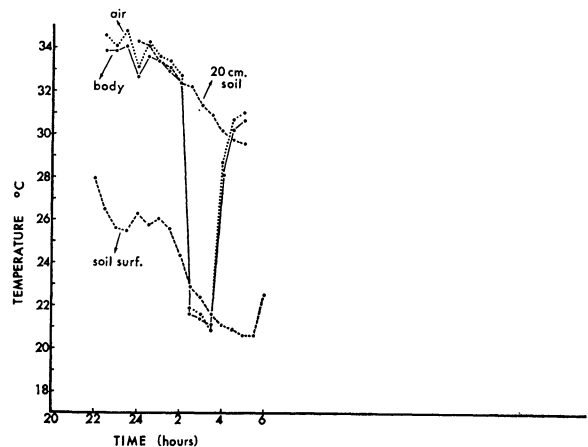


FIG. 6. Temperature changes experienced by a scorpion moving from a burrow to the surface and returning to the burrow during the night. The scorpion carried both a thermocouple over its dorsal surface (air) and one inserted into the body cavity (body). Substrate and –20 cm soil temperatures are included for reference.

over this relatively small distance resulted in a temperature change of over 10°C . At some time between 0330 and 0400, the scorpion returned to the burrow and this time experienced a sharp rise in temperature. Thus, the burrow which provided the scorpion with protection from extreme daytime temperature also offered a retreat from suboptimal temperatures which resulted from the rapidly cooling desert surface during the early morning hours.

Body versus subelytral temperatures in black beetles

Body and subelytral temperatures were recorded for 11 black tenebrionid beetles (*Eleodes armata*) on the desert surface during the study. In Figure 7, typical temperature data and patterns obtained are illustrated for two black *Eleodes* subjected to increasing temperature and radiation loads as the morning progressed. Animals were maintained in shade until body and subelytral temperatures coincided and then transferred to direct sunlight on the desert surface.

For both individuals the body temperature rose well above ambient. The rate of increase was less during the first run under reduced heat and radiation loads and eventually reached an equilibrium temperature. Later runs (1112 and 1131) resulted in more rapid temperature increases and the inability of the beetles to maintain an equilibrium temperature. Continued exposure to these extremes would have resulted in paralysis and eventual death.

During the three runs, the subelytral temperature was always higher than the body temper-

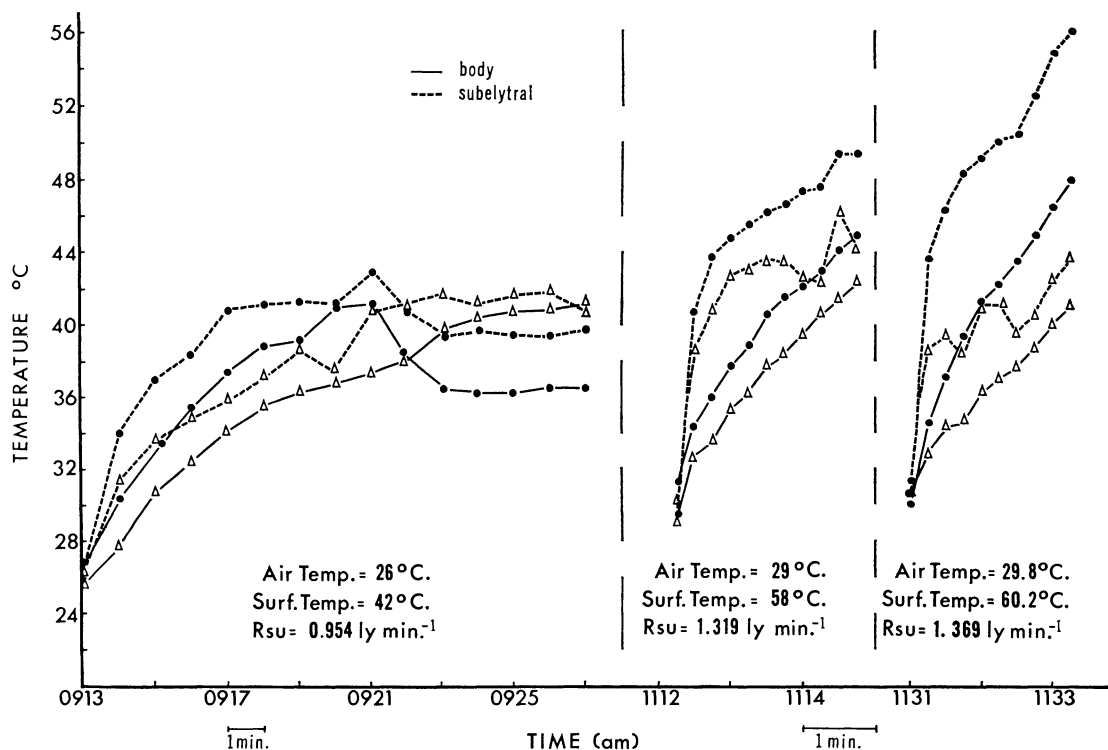


FIG. 7. Body and subelytral temperatures of two black tenebrionid beetles, *Eleodes armata*, recorded on the desert surface under increasing radiation and temperature loads. Mean air temperature (1 m), soil surface temperature, and incoming solar radiation during the three test runs are given below that particular testing period. Equilibrium conditions achieved during the first testing period (0913) continued until 0935 at which time the experiment was terminated.

ature. Differences between body and subelytral temperatures increased with increased radiation loads, reaching a maximum of 8°C in the one beetle examined at 1131. Both body and subelytral temperatures dropped rapidly when beetles were removed to shade.

Differences in body size, shape, and orientation made temperature comparisons between beetles tested simultaneously difficult. Often the body temperature of one beetle was equal to or even higher than the subelytral temperature of another beetle even though the usual relationship between body and subelytra for both individual beetles persisted.

Temperatures in black versus white beetles

Further information concerning the effect of black coloration on radiation absorption and resultant heat load was obtained by comparing black *Eleodes* with individuals whose dorsal surfaces were painted white (Fig. 8). The results shown here are generally typical of data obtained from simultaneous comparisons of six white and black beetles tested under several climatic conditions.

In almost all comparisons the temperature of

the subelytral cavity beneath the black elytra was higher. The magnitude of temperature difference was not great, however, particularly under low radiation levels. These data support the hypothesis that the white surface is at least partially effective in increasing the percentage of reflected light and, thus, reducing or delaying temperature increase of the subelytral cavity due to radiation absorption. Temperature differences between the subelytral cavity and body in white beetles was not as marked as those observed for black beetles.

No consistent relationship was noted between the body temperature of white versus black beetles. The majority of experiments showed body temperatures of black beetles to be the same or slightly higher ($< 1.0^{\circ}\text{C}$); however, during the 0946 run (Fig. 8) the body temperature of the white beetle was actually higher than the black beetle. These data seem contradictory in view of the significant temperature difference between the black and white subelytral cavities. Possible factors responsible for this result were differences in the beetles' positions in relation to incoming radiation and/or their heights above the substrate due to tilting behavior.

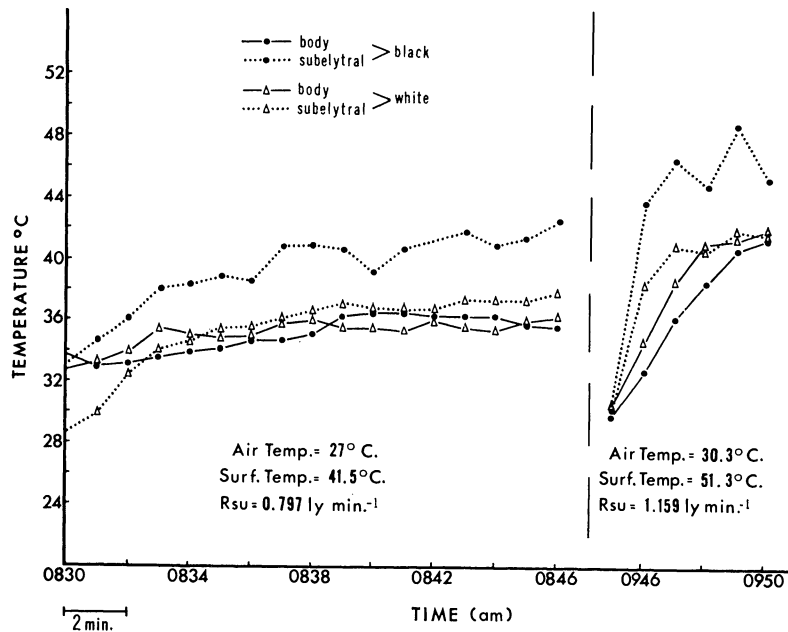


FIG. 8. Temperature differences between the body and subelytral cavity of black beetles and beetles whose elytra were painted white. Mean air temperature (1 m), surface temperature, and solar radiation for both test periods are included.

Body temperatures in beetles with elytra removed

Comparison of body temperatures of normal black beetles with beetles which had the elytra completely removed provided some information on the adaptive function of the subelytral cavity. Under shaded conditions, elytra-less beetles had 1–2°C lower body temperatures. When both groups were transferred to sunlight on the desert surface, the elytra-less individuals heated up more slowly, their body temperatures being 4–6°C lower than normal beetles. The reduced body temperatures no doubt resulted from the rapid evaporation of water from the exposed abdominal tissues which became severely dehydrated under the test conditions.

DISCUSSION

Hot, dry desert conditions are intensified many times as the ground surface is approached. Most arthropods cannot tolerate the high temperatures and desiccating atmosphere at the surface and must rely on burrowing activities to at least temporarily escape these harsh extremes. Occupation of subterranean retreats can provide a relatively constant, moderate environment, particularly if burrow depths reach levels which do not experience diurnal temperature fluctuation (Fig. 5). For those species which do not restrict their surface activity to nighttime hours, behavioral patterns such as burrowing are supplemented by morpho-

logical and physiological adaptations. Combined, these adaptations confer rather remarkable abilities for keeping cool and reducing water loss.

The burrowing habit presents some interesting points when considered in terms of the animal's daily behavior pattern. The time lag in daytime penetration of heat from the surface downward, plus rapid radiative surface cooling after sunset, results in the warmest temperatures at 2000 occurring between 5 and 15 cm, with cooler temperatures being found above and below this level (Fig. 4). Thus, scorpions which move from deep-set daytime retreats directly to the surface after sunset actually move through several different temperature regimes. Evidence suggests, however, that this movement is not direct, but that scorpions approach the surface gradually, perhaps remaining at certain levels in response to decreasing illumination. Scorpions located 10–15 cm below the burrow opening or at the burrow's mouth following sunset can experience temperatures 3–10°C higher than substrate temperature (Figs. 4 and 6). Prolonged occupation of these warmer regions could sharply increase evaporative water loss, but at the same time may also facilitate locomotor and digestive functions associated with predation. Tolerance of high temperatures at these levels may be enhanced by a "stilt-ing" behavior observed in *Opisthophthalmus latimanus* in which the scorpion raises its body off

the substrate by straightening its legs (Alexander and Ewer 1958).

Field observations indicate a strong homing behavior for many scorpion species. Marking and redetection methods show that many individuals confine their surface activities to areas immediately surrounding the burrow (< 1 m) and return to the same burrow on successive nights (Hadley and Williams 1968). Such homing behavior provides the animal with a certain degree of familiarity with the area which may be important in thermoregulation. A scorpion might escape a potential predator by entering a burrow only to succumb to heat because the burrow selected was too shallow to provide protection from high temperatures encountered during the following day (Fig. 5). Returning to the surface and reentering a new burrow is only practical during hours of darkness, for surface temperatures increase rapidly with sunrise and scorpions appear to function very poorly under high solar radiation intensity. Thus, the scorpion must either remain at the present level and tolerate the subsequent high temperatures or increase the burrow's depth by digging. The latter activity would require considerable energy expenditure and result in increased water loss even if the increased depth proved to be satisfactory.

Disagreement exists regarding the effect of color on heat absorption by arthropods exposed to direct sunlight. Some investigators present evidence that the heat load is reduced in light-colored arthropods (Uvarov 1948; Parry 1951); however, Pepper and Hastings (1952) found no appreciable differences in temperature response to solar radiation between black- and buff-colored forms of the grasshopper, *Melanoplus differentialis*. Bursell (1964) states that color is probably relatively unimportant because a high proportion of energy is transmitted at infrared-wave lengths.

Beetles whose elytra were painted white had somewhat lower subelytral cavity temperatures than normal black beetles under the same radiation load (Fig. 8). On the basis of these temperature differences, it appears that light-colored beetles reflect a greater percentage of the incident solar radiation. Bolwig (1957) obtained similar results when he compared subelytral temperatures of black African tenebrionid beetles with another species which had naturally occurring white elytra, although the temperature difference was small. In the present study, body temperatures of the same beetles recorded simultaneously did not always follow the same pattern observed for white versus black subelytral cavities. Reflected radiation from the desert substrate may be an important contributing factor here since the ventral

surfaces of all beetles were black. Bolwig (1957) found body temperatures of beetles with white elytra to be somewhat lower than black beetles, but his experiments were conducted on beetles suspended dorsal side up 25 cm above the surface under laboratory conditions. Thus, the importance of reflected and surface radiation would be very much reduced.

The functional significance of the subelytral cavity has been the subject of several investigations. Cloudsley-Thompson (1964) reviewed earlier studies and concluded the major function of this structure was to reduce transpiratory water loss. Recent water balance studies (Ahearn and Hadley 1969) of two desert tenebrionid beetles, plus field observations of *E. armata* with its elytra removed, support this finding. Thermal advantages provided by the cavity are not as clearly demonstrated. It seems doubtful that air used for respiration is first cooled and moistened in the subelytral cavity in view of the high temperatures recorded (Fig. 7). However, ventilation of this air space apparently increases convective cooling rates (Bolwig 1957) and enables these beetles to achieve an equilibrium temperature under mild thermal stress.

One possible thermal advantage provided by the subelytral cavity involves high intensity solar radiation. In the absence of this cavity, heat resulting from absorbed incident solar radiation would be quickly conducted from the dark surface to the body cavity. By separating the two with an air-filled pocket, a temperature "buffer zone" is created which delays the heat transfer to the beetle's internal structures. With this added protection against heat build-up, the beetle is quite capable of making short jaunts across the hot desert sand in spite of its black coloration.

Heat exchange

Beetles on the surface were able to establish a temperature equilibrium under mild heat and radiation loads (Figs. 7 and 8). At this time, theoretically, a balance was achieved between heat gained from radiation, conduction, metabolism, and heat lost via convection and evaporation. Knowing the relative contribution of each of these factors, one can construct a heat exchange budget for the beetle. Similar budgets have been estimated for an insect from a theoretical point of view (Parry 1951), for intertidal woodlice (*Ligia*) by Edney (1953), for the desert iguana (*Dipsosaurus dorsalis*) by Norris (1967), and for the spiny lizard (*Sceloporus occidentalis*) by Bartlett and Gates (1967). The absence of simultaneous measurements of incoming solar radiation, long-wave radiation, and wind velocity in some of these

earlier studies, however, permitted the investigators to make only rough estimates of energy exchange. The heat exchange budget for *E. armata* under conditions illustrated in Figure 7 was estimated from the following data:

Temperature.—Relevant temperatures were as follows: air temperature (1 cm) = 32.0°C; substrate temperature = 42.0°C; body temperature = 40.0°C. The subelytral temperature for this particular beetle fluctuated between 40.0 and 42.0°C during the equilibrium period. Elytral surface temperature was estimated to be 42.0°C.

Radiation.—The net radiation load on the beetle was calculated from the following equation in present notation (Sellers 1965):

$$R_n = R_a + R_{su} - \alpha \epsilon T^4 - r R_a - r' R_{su}$$

where R_a = long-wave or atmospheric radiation, R_{su} = solar radiation, α = Stefan-Boltzmann constant, ϵ = emissivity, T = absolute temperature, r = reflectance of atmospheric radiation, and r' = reflectance of solar radiation. Emissivity was estimated to be 0.95 based on values obtained from a hard glossy rubber plate (Brown and Marco 1958), while reflectance was estimated to be approximately 60%.² The latter value, although

² The black carabid beetle, *Calosoma semilaeva*, reflected only 8.6% of the incident energy when subjected to a perpendicular light beam (Porter 1967).

high, may not be unrealistic considering the sun's angle at this hour and the reduction in absorption due to stiling behavior by the beetle (Parry 1951). Solving for R_n , the net radiation load was calculated to be approximately 0.170 cal/cm²/min.

Conduction.—Heat gained from the surface by conduction was not measured. The amount is thought to be very small for arthropods since only a small area is in contact with the surface (Parry 1951). For this reason, conductive heat transfer is often omitted from heat balance equations.

Evaporation.—Water loss in *E. armata* determined in moving air (1 liter/min) at 40.0°C and 0% R.H. (sat. def. = 55.32 mm Hg) was 6.92 mg/g/hr (Ahearn and Hadley 1969). Expressed in terms of surface area this value is equivalent to 0.506 mg/cm²/hr and results in a heat loss of only 0.005 cal/cm²/min.

Metabolism.—Oxygen consumption rates of adult *E. armata* at 40°C were 500 μ l/g/hr (Ahearn unpubl.) or approximately 0.61 μ l/cm²/min. Assuming 4.775 calories produced per ml O₂ consumed, this rate is equivalent to a heat production of .003 cal/cm²/min.

Convection.—Convective heat loss was calculated by considering the beetle to be a cylinder of 0.7 cm diameter in moving air using the following equation (Gates 1962):

$$\text{convection coefficient} = h_c = 6.17 \times 10^{-3} \frac{v^{1/3}}{D^{2/3}}$$

Wind velocity at 1 cm (5 cm/sec) was estimated by extrapolation from a log profile of wind velocity versus height above ground based on recorded values at 25 cm. Multiplication of " h_c " by the body-air temperature difference (10.0°C) resulted in a convective heat loss rate of 0.134 cal/cm²/min.

Substituting values into the heat exchange equation, it now appears as follows (values in cal/cm²/min):

$$\begin{array}{rcl} \text{radiation} + \text{metabolism} + \text{conduction} & & \\ (.170) & (.003) & (x) \\ & & = \text{convection} + \text{evaporation} \\ & & (.134) & (.005) \end{array}$$

Since contributions of metabolism, evaporation, and conduction are so small, they can be discarded and the equation simplified to read heat gained by radiation equals heat lost through convection. This results in an excess of 0.036 cal/cm²/min on the left side.

This discrepancy between calculated values which indicate a small heat gain and the actual observed temperature equilibrium can best be accounted for by modifying the contributions of either radiation or convection. In order to reduce " R_n " to balance the convective heat loss, it is necessary to increase reflectance by slightly more than 3% (if $r' = .63$, $R_n = 0.141$ cal/cm²/min). If the 0.60 value for reflectance is retained, one can balance the resultant heat gain by increasing wind velocity from 5 to 12 cm/sec which increases the convection rate to approximately 0.179 cal/cm²/min. Although such an increase may be unjustified on the basis of observed wind speeds at 25 cm, ventilation of the subelytral cavity may very well increase forced convective cooling rates to this level.

The temperature of insects and other arthropods exposed to direct sunlight on the desert surface is determined by an interaction of many complex factors. For species which possess a waxy cuticle and, therefore, exhibit small water loss rates, the most important factors are those which affect heat gained by radiation or heat lost by convection (Bursell 1964). Heat exchange budgets for arthropods with permeable integuments present a different picture (Edney 1953). The woodlice in his study lost approximately 50% of their total heat load through evaporation. It is possible that evaporation rates determined for tenebrionid beetles in the laboratory do not accurately reflect rates which occur under field conditions and, thus, calculated values for evaporative cooling may indeed be too small. In addition, release of defensive quinones at high temperatures (Ahearn and

Hadley 1969) may supplement cuticular and respiratory water loss. In spite of these considerations, however, the overall contribution of evaporation to heat loss appears to be quite small for desert-adapted arthropods.

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