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A FIELD-TESTED THERMOREGULATION MODEL FOR TWO
DIURNAL NAMIB DESERT TENEBRIONID BEETLES¹

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Abstract. The thermoregulatory strategies of two Namib Desert tenebrionid beetles were studied to determine the methods used to attain relatively high and constant body temperatures for several hours each day. In the field thermoregulatory behavior observations were made simultaneously with microclimate data collection and measurement of body temperatures in free-ranging beetles.

A thermal model was developed using beetle heat exchange parameters and combined with microclimate data to predict the range of body temperatures available to the insects in their different environments. The accuracy of the model was validated against measurements of body temperature in the population of free-ranging beetles.

Observations of thermoregulatory behavior, when coupled with the effect of such behavior on modeled body temperatures, make it possible to evaluate quantitatively the efficacy of various thermal strategies and the degree of habitat selection practiced by the insects to maintain preferred temperatures. Thermoregulation methods include squatting, stiling, exposure of lighter-colored body surfaces, climbing and burrowing. These methods, when combined with the ability to seek out and move to unique microenvironments, enable the beetles to maximize thermoregulatory control and achieve greater independence from thermal variations in their habitat. Both beetle species were living maxithermal strategies in which body temperatures were maintained at high levels for a maximum time each day.

Key words: Beetles, tenebrionid; behavioral thermoregulation; energy balance model; Namib Desert.

INTRODUCTION

On the Namib Desert in South West Africa there are a number of tenebrionid beetles that have divided available habitats primarily through behavioral (Hamilton 1971, Holm and Edney 1973), physiological (Louw and Hamilton 1972), and morphological (Koch 1962a, 1962b) adaptations to specialized portions of the microclimate mosaic occurring on the desert. The purpose of this paper is to analyze quantitatively the behavioral and morphological methods that two of these tenebrionid species use to maintain high sublethal body temperatures for several hours each day.

Onymacris plana is a large, shiny black tenebrionid with a round, pancake-shaped body ranging from 1.0-2.5 cm in diameter. *Stenocara phalangium* is much smaller (0.75-1.0 cm in length) with a distinctly pear-shaped body and possessing the longest leg-to-body size ratio of any known tenebrionid. In the early fall upon first emergence, *Stenocara* has a white, downy coating on the sides and posterior of the abdomen that wears off in 1-2 mo leaving the insect totally black. Both species stand 1.0-1.5 cm high and are small enough so that their heat storage capacity is minimal; they must be in thermal equilibrium with their environment most of the time. They are highly mobile, and it is primarily the ability

to rapidly seek out proper thermal microhabitats that allows them to stabilize their body temperatures at high levels for much of the day. This strategy of maintaining maximum temperatures for maximum intervals during the day has been called "maxithermy" by Hamilton (1973). This tactic appears to be practiced by many of the tenebrionids on the Namib. The reasons for maintaining high body temperatures are complex, but the possibility that they help the animal achieve a higher metabolic rate and/or reproductive rate has been suggested by Bullock (1955), Odum and Pinkerton (1955), Bursell (1964), Odum (1971), and others.

Animals in the field exhibit a wide range of behavior patterns and it is not always obvious which parts of the observed behavior are thermoregulatory, reproductive, foraging, or combinations of these and other activities. Even when a behavior type can be definitely identified as thermoregulatory the observer cannot judge the efficacy of that strategy, but can only note that it occurred under a given set of measured or unmeasured physical conditions. To make the connection between observed behavior and its quantitative value to the animal in a thermoregulatory context requires a logical construct that can relate measurements of the environmental parameters as well as physical properties of the animal to the animal's body temperature. An energy balance model can fill this need.

Collection of micrometeorological data simulta-

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neously with field observations of behavior at the same site made it possible to construct an energy balance model of these Namib Desert animals that could be solved iteratively for the equilibrium body temperature of the beetles. The model was validated against the body temperatures of many free-roaming beetles captured concurrently with the micrometeorological and behavioral observations. Using the tested model the different thermoregulatory behavior patterns observed in the field can be separated and evaluated quantitatively for their effect on the animal's energy budget and thereby its body temperature. The thermal usefulness of different morphological adaptations such as color and shape can also be quantitatively evaluated in this manner separate from and in combination with the behavior patterns that employ them to maintain constant body temperatures in these poikilotherms.

The concept of mathematically evaluating the energy relationships between an animal and its environment has been of interest to many authors (Parry 1951, Pepper and Hastings 1952, Digby 1955, Bolwig 1957), but it was not until 1962 that Gates put the concept into a coherent conceptual framework in his book, *Energy Exchange in the Biosphere*. Birkebak (1966) further refined a complete list of energy exchange equations defining the different ways an animal is thermally related to its physical environment. Since then, heat transfer equations that balance heat gained with heat lost have been developed by many investigators (Norris 1967, Bartlett and Gates 1967, Porter and Gates 1969, Heller and Gates 1971) for several different types and classes of animals. All have used estimates or approximations of microclimate variables in their models.

In studying fiddler crabs, Smith and Miller (1973) have followed Hadley's (1970) work on the tenebrionids and scorpions by integrating real time field microclimate information with body temperature and behavioral information to further refine and interpret the output of their energy balance models. Smith and Miller (1973) found their model useful in studying the distribution and thermal behavior of two species of fiddler crabs in relation to the slightly different microclimates they occupied.

Until recently most work on the Namib Desert arthropod fauna had been concerned with its richness and diversity (Lawrence 1959, 1962; Koch 1961, 1962a, 1962b; Holm 1970; Edney 1974). The Namib Desert Research Station at Gobabeb, located well into the desert with a relatively undisturbed ecosystem surrounding it, has been the center of much of this work. The research station also maintains a weather station which supplies climatological data (reviewed by Schulze 1969).

Recent work on the arthropods of the Namib has shifted from description to analysis of the unique ways in which these animals relate to their physical environment. Hamilton (1971) and Louw and Hamilton (1972) have studied the thermal ecology and activity rhythms of one diurnal and one nocturnal beetle species, respectively. Holm and Edney (1973) investigated activity rhythms in several of the diurnal species as well as two nocturnal species. Edney (1971) has also worked on the relationships between color and body temperatures in three species of diurnal beetles.

There are two broad classes of thermal strategies employed by animals on the Namib Desert. Almost all of the diurnal forms so far studied are living a maxithermal strategy while the nocturnal forms operate in a thermal environment that is 10°–20°C cooler. It is the relationship of the diurnal forms to their environment and especially a quantitative analysis of their ability to maintain high but sublethal body temperatures throughout the day that is the focus of this study.

THE DESERT BEETLE ENERGY BALANCE MODEL

At steady state an organism's temperature is dependent on the rate of heat gain from and loss to the environment, plus any metabolic contribution. Numerous authors (Birkebak 1966, Porter and Gates 1969, Beckman et al. 1973, etc.) have developed similar generalized energy balance equations expressing for a steady state condition

$$\text{Energy in} - \text{Energy out} = 0. \quad (1)$$

Expanded, the equation takes the form

$$M + S + \text{IRin} = \text{IRout} + K + E_w + C \quad (2)$$

where M is heat produced metabolically, S is absorbed solar radiation, IRin is longwave thermal radiation from the sky and ground, IRout is re-radiated long-wave radiation, C is convectional heat loss or gain, K is conductive heat loss or gain, and E_w is heat loss by evaporating water either by respiration or sweating. The units of all terms are in calories per square centimeter of body surface per minute.

The equation is greatly simplified in desert tenebrionids since both conduction and water loss terms can be neglected. Edney (1967) and Louw and Hamilton (1972) have shown that these beetles are extremely resistant to desiccation (even at low humidities) to the extent that heat lost in the evaporation of water is effectively zero. Conduction of heat between the substrate and the insects is also negligible since they carry their bodies well above the surface on thin legs that do not have significant circulation below the femur. Equation (2) expanded to include variables

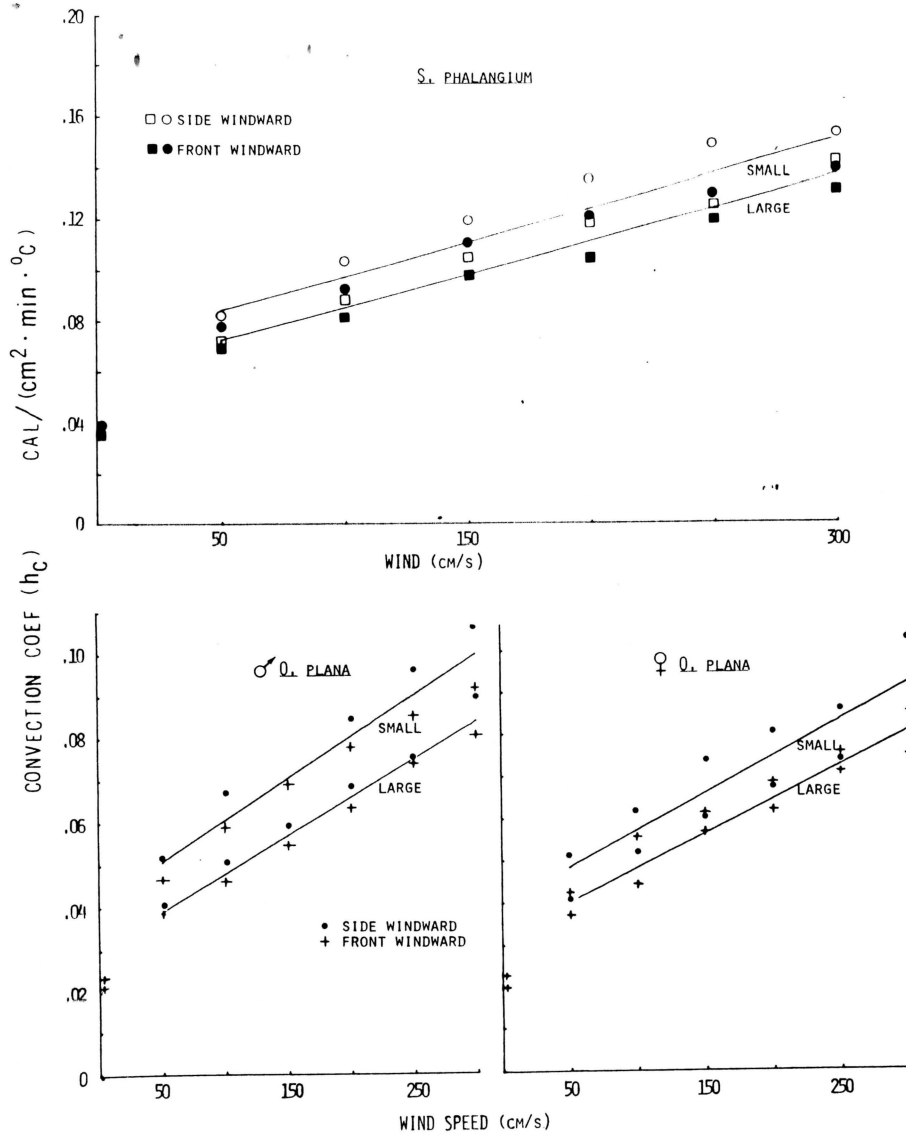


FIG. 1. Convection coefficients for *S. phalangium* and ♂ and ♀ *O. plana* for both the front and side windward conditions. Regression lines are fit to the front and side windward points for large and small beetles to show the range of convection coefficients between large and small specimens.

determined by the desert insect and the environment then becomes

$$\begin{aligned}
 &M + a_D S_D A_D + a_R S_R A_R \\
 &+ a_{IR} IR_A A_{IR_A} + a_{IR} IR_G A_{IR_G} \\
 &= \epsilon_S \sigma T_b^4 A_{IR_b} + h_c (T_b - T_a) A_c, \quad (3)
 \end{aligned}$$

where A_D, A_R and A_c are the respective animal surface areas for absorbing direct and diffuse solar radiation (S_D), reflected solar radiation (S_R) and for convective heat transfer; A_{IR_A} and A_{IR_G} and A_{IR_b} are, respectively, the beetle surface areas for absorbing atmospheric long-wave infrared radiation (IR_A), long-wave infrared radiation from the ground (IR_G) and the surface area for reradiation of long-wave

energy from the beetle (IR_b). Absorptivities to direct and diffuse solar radiation, reflected solar radiation, and infrared radiation are shown as a_D , a_R , and a_{IR} , respectively, while the emissivity of the beetle surface is given by ϵ_S , σ is the Stefan-Boltzmann constant, h_c is the convection coefficient, T_b is body temperature and T_a is the 1-cm air temperature.

Further expansion of the terms involving long-wave infrared radiation from the atmosphere and the ground show IR radiation from the atmosphere and the ground determined by $\epsilon_G \sigma T_G^4$ where ϵ_G is the emissivity of the desert sand. Infrared radiation from the atmosphere (IR_A) is represented by $c \sigma T_a^6$ (Swinbank 1963) where T_a is the 1-m air temperature in °Kelvin

and c is an empirically derived constant (7.6109×10^{-16}). All temperatures in long-wave radiation terms are in °Kelvin, but T_a and T_b in the convection term are in °Celsius for ease of input and output.

Once derived the energy balance model can be used to determine the data that must be gathered to enable the equation to be solved for T_b . Since there is but one equation, all terms must be defined if a solution for the unknown T_b is to be determined. The field micrometeorological measurement program monitored all the environmental parameters that affect the heat transfer to or from the insect. Direct and reflected solar radiation, air temperature, and wind velocity were the principal environmental variables measured during the field work.

Properties of the insect that determine the impact of the environmental variables on body temperature are mainly reflectivity, convective properties, body shape, and surface area. These parameters were evaluated in the laboratory according to the manner in which the beetles responded to them in the wild state. The surface area absorbing direct solar radiation is the principal variable that the animals can readily alter and it was measured for the different postures observed in the field.

METHODS AND MEASUREMENTS

Convection coefficients

Convection coefficients (h_c) for the two beetle species were determined from cooling curves of gold-plated, cast silver models. The models were made using conventional lost-wax techniques with dead beetle exoskeletons as patterns. Gold plating was applied with a high vacuum sputter coating process. The unique infrared spectral qualities of gold (long-wave emissivity = 0.02, reflectivity = 0.98) allow long-wave radiation to be neglected in determination of the convection coefficient.

The cast models were instrumented with both external and internal fine wire thermocouples (Cu/Con), heated and allowed to cool in a wind tunnel at seven different wind velocities (0, 50, 100, 150, 200, 250, 300 cm/s) while model and air temperatures were monitored simultaneously on strip chart recorders. The convection coefficient is given by:

$$h_c = mc/A_T[\ln(T - T_a/T_i - T_a)][1/(t - t_i)]$$

(Wathen et al. 1971) where m is the mass of the model (in grams); c is the specific heat of silver; A is surface area of model (in square centimeters); T_a is air temperature in the tunnel. T_i and T are the initial and final model temperature (°C); and t_i and t are the initial and final times (in minutes). Each casting was placed first with the head windward, and then sideways to the wind. A convection

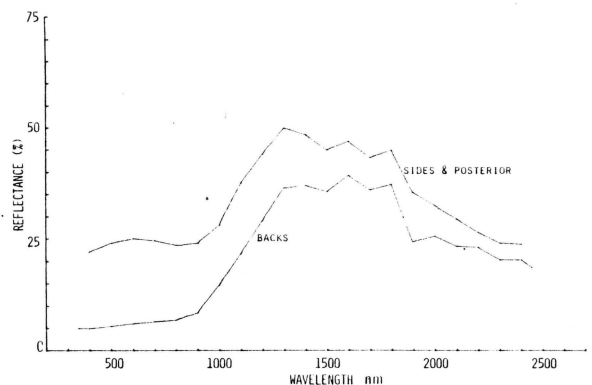


FIG. 2. Spectral distribution of reflectance for the backs and whiter sides of *S. phalangium*.

coefficient was calculated for both orientations at each wind velocity for eight beetles (two *S. phalangium*, and three male and three female *O. plana*) then a least-squares regression line was fit to the convection coefficients for the head-on and the sideways orientations for each beetle (Fig. 1). The composite regression equation was programmed into the model to give an average convection coefficient at any wind speed for a given beetle size and species.

An error analysis was run on the convection coefficient equation using the method of partial differentials (Beers 1957) and predicted errors in h_c on the order of $\pm 4\%$ – 5% for *O. plana* and $\pm 3\%$ – 4% for *S. phalangium*. The values used in each term of the equation for determining the error were averaged for all models of that species so the predicted uncertainty is an average for h_c at all wind velocities.

Reflectance

Reflectance was measured at two locations on both species of beetles. On *O. plana* properties of both the dorsal and ventral sides of the thorax and abdomen were examined, while on *S. phalangium* reflectance was determined for the back and for the side and posterior which are shaded white. Reflectance was measured ($\pm 2\%$) between 350 and 2500 nm with a Beckman™ DK-2A spectrophotometer. Mean reflectance for these wavelengths was determined by multiplying the average absorptance (absorptance = $1 - \text{reflectance}$) at each wavelength by the solar energy available at that wavelength for clear skies at noon, and dividing the area under the absorptance curve by the total area under the sea level solar irradiance curve (Gates 1965).

The whitish sides and posterior of *S. phalangium* have an average reflectance of 35% while the blacker back averages only 23% (Fig. 2). The lighter-colored portions of the beetles may have reflectances as high

as 50%–60% since the animals were so small that the spectrophotometer beam overlapped black portions of the beetle when measuring reflectance on the white sides.

Onymacris plana is black in the visible spectrum, but has slightly elevated reflectances and greatly elevated elytral transmissivities in near-infrared wavelengths (see Henwood 1975). For live specimens the average reflectivity to noontime reflectance was 7.4%. Dead pinned specimens used in the original reflectance determinations were found to have significantly altered reflectance properties. Whole body reflectances averaged 8%–15% higher than for live specimens and showed sexual differences that were not measured in live samples.

Future investigators working with insects must be extremely cautious in assuming that the pinned specimen has not changed in its reflectance characteristics due to desiccation and/or other effects. Accurate reflectance measurements can only be obtained by the use of live specimens. If dead specimens must be used, the results should be checked against a minimum number of live specimens to verify that they accurately represent the animals' true spectral characteristics.

Effective absorbing areas

The effective absorbing area of the beetles for direct solar radiation (A_D) and IR radiation from the ground (A_{IR_g}) was measured by the method of Bartlett and Gates (1967). The shadow produced by the casting when exposed to a point source of light (placed across the room) was traced and the area of the tracing subsequently determined with a planimeter to the nearest 0.05 cm². Castings were oriented with their sides, dorsal surfaces, and in the case of *Stenocara*, posterior surfaces perpendicular to the light rays to determine absorbing areas for all observed postures. The area absorbing reflected solar radiation (A_R) was considered to be the same as that absorbing direct radiation for the tall, cylindrically shaped *S. phalangium*. For the squat, pancake-shaped *O. plana* A_R was assumed to be one-third of A_D , due to the effect of the beetle's shadow in reducing reflected radiation. The effective absorbing area for long-wave atmospheric radiation and convectional heating or cooling were considered to include the entire surface area of the beetle (A_T). Body surface areas were measured by coating the model beetles with plastic and skinning them. The plastic skin was then pasted onto paper backing and the area determined by planimeter (± 0.1 cm²).

Metabolic rates

Metabolic rates were measured in a Gilson Respirometer™ at 30°, 35°, and 40°C. With a conversion factor of 5 cal/cm³ O₂ consumed, metabolic heat production is only 0.017 cal/(min·cm²) at 40°C (the highest rate measured) and is insignificant when compared to other energy sources. Metabolic heat production was therefore ignored in the energy balance equation.

Field sites

All field observations of the two species of beetles were made in April and May 1973, near the Namib Desert Research Station in South West Africa at 23°34'S, 15°03'E. Behavioral, body temperature, and microclimatic data were obtained simultaneously for *O. plana* while only behavioral and microclimatic data were collected for *S. phalangium* because of their small body size and heat capacity. Handling such small beetles for the 1–2 s necessary to insert a thermistor probe can alter the body temperature to an undetermined degree and thus render temperature data from the population unreliable.

Microclimate and behavioral observations were tailored to the special conditions presented by the widely different habitats the two species occupy in the respective interdune valleys selected for study. The *O. plana* study site was a north-south oriented interdune valley about 2 km wide and 5 km long, with dunes ranging from 200–300 m high to the east and west. Numerous Naras clumps, small dunes formed by sand collecting around a growing Naras bush (*Acanthasicyos horridus*), from 1–10 m tall were scattered along the valley floor. *Onymacris plana* live on and between these small, conical sand dunes. The Naras bushes supply the beetle population with food, in the form of blossoms and the remnants of melons broken open by larger animals, and a mosaic of microclimates on the small, complex dune that forms around each living bush.

The *S. phalangium* site was a vegetationless interdune valley about 1 km wide and 3 km long, 13 km east of the *O. plana* site. The flat floor of the dune street consisted of fine sand with quartz gravel from 0.25 cm to 5.0 cm diam distributed over it. Microclimatically the *S. phalangium* habitat provided less variability than the *O. plana* habitat and the food of these beetles consisted solely of the dried root crowns of ephemeral desert grasses that had appeared after the last rains in the area 3 yr previously. The insects were able to find and excavate these tussocks for food during their daily activity period.

Population census and thermoregulatory behavior

Visual census techniques were employed to gather the principal information on population activity

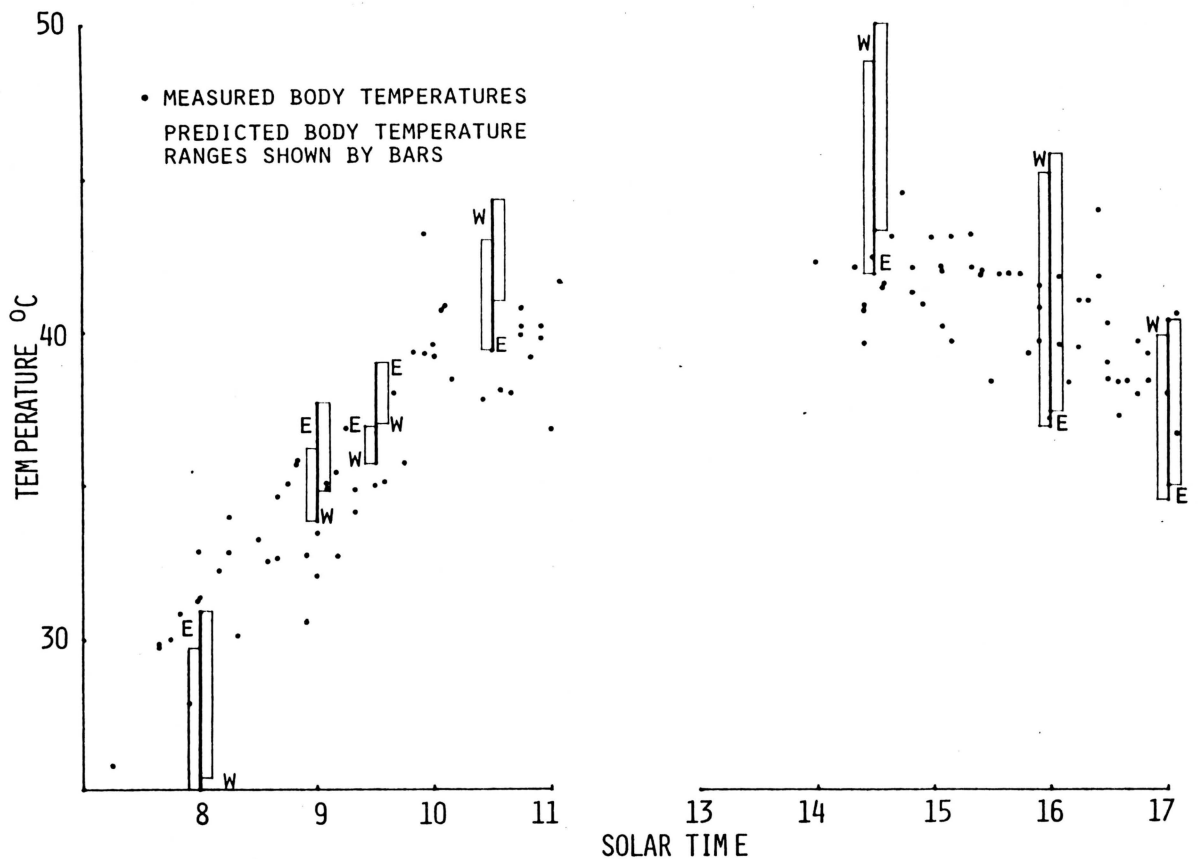


FIG. 3. Distribution of body temperatures for the population of *O. plana* sampled on 26 April 1973. Predicted range of body temperatures available to *O. plana* on east and west slopes of the Naras dunes are shown by bars for two different conditions at seven times during the day. Left-hand bars denote body temperature ranges using microclimate data for 26 April 1973 while body temperature ranges denoted by right-hand bars show the change in available body temperatures if wind speeds measured on 26 April are reduced by $\frac{1}{2}$.

periods with a route retraced every 15–60 min depending on the species being studied. Due to their large size, rich habitat, and obvious sexual dimorphism, *O. plana* were more intensely studied. Hourly data were gathered along a 10-Naras-dune census route. Data taken included orientation of the beetle on the dune (N, E, S, W), activity, sex, and time of copulation whenever a mating was observed. The census taker walked around each isolated Naras dune on the route and made a visual count using binoculars. On 26 April 1973, another team in another area measured the body temperature of individuals in the population concurrently with the census (Fig. 3). Active beetles observed on the surface were caught, and a fast response thermistor probe immediately inserted into the mid-body between the head and thorax. This technique was checked against beetles ($n = 38$) with chronic implants and found to produce an average low error of only $0.16^{\circ}\text{C} \pm 0.7^{\circ}\text{C}$.

Activity information on *S. phalangium* was ob-

tained by laying out a rectangular grid over the study area, with five routes 30 m apart and extending the full 1-km width of the dune street. Censuses were made by walking the grid and counting the number of beetles observed in a band extending approximately 2 m on either side of the path. Simultaneously with the activity counts, feeding and thermoregulatory behavior observations were made by following and watching a succession of individual beetles with binoculars.

Microclimate information

Two days of microclimate information are shown in Figs. 4–7 for each of the study sites. For the *O. plana* study site, two temperature profiles were made, on east and west sides of a 3-m-high Naras dune with a slope of 15%–20%. Wind velocity and radiation were measured on the flat sand next to this dune. Two temperature profiles were run ≈ 20 m apart at the extremely uniform *S. phalangium* site to get an average profile and for redundancy in case

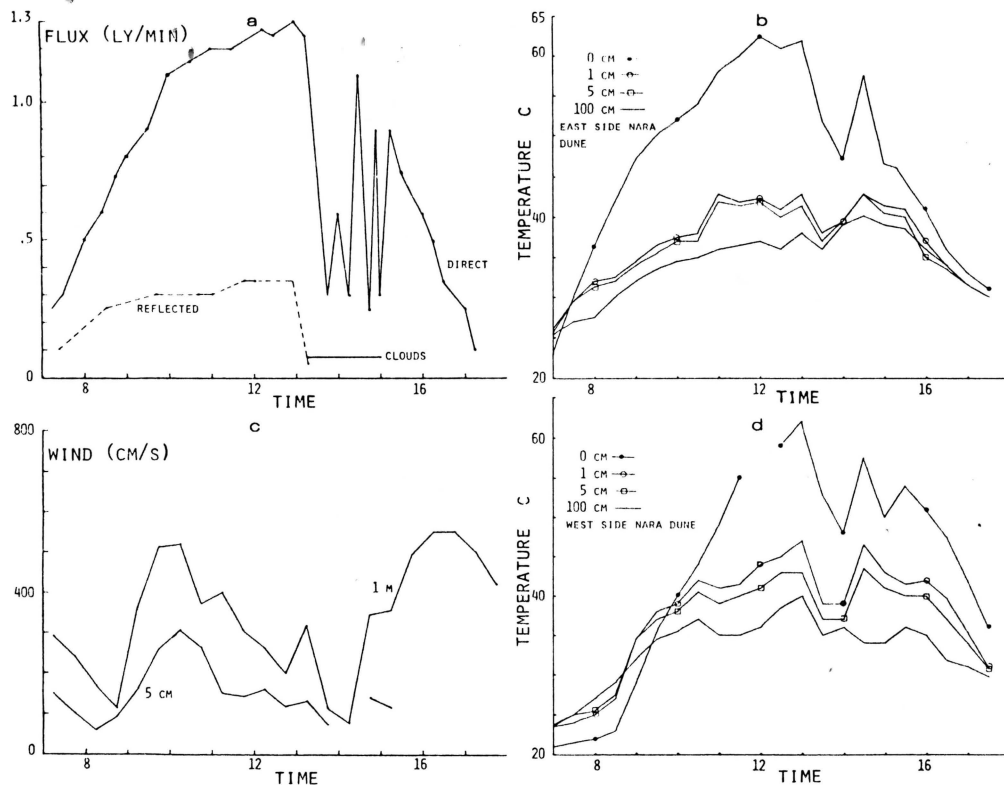


FIG. 4. Microclimate data for the *O. plana* study site on 23 April 1973 plotted against local sun time. Direct and reflected solar radiation (a), and wind velocity (c) at two heights are shown. The temperature regimes at four heights on the east (b) and west (d) sides of the Nara dunes illustrate the difference in microclimate on the two slopes. The lag in the time of peak temperatures on the west slope is masked by the effect of the clouds that appeared between 1315 and 1500.

of instrumentation problems. The 2 days shown in Fig. 6 and Fig. 7 were selected because of their wide divergence in conditions and their effect on the behavior of *S. phalangium*. May 1 was cooler than average, while 6 May was 0.1°C hotter than the highest temperature in 5 yr of record at Gobabeb (Schulze 1969).

Soil and air temperatures were measured with silvered thermistor probes shaded and affixed to rods at 0, 1, 5, and 100 cm above the surface and running into a 10-channel monitor. Temperatures on all 10 channels were monitored every $\frac{1}{2}$ hour throughout the day as was relative humidity at 5 cm and 1 m with a psychrometer. Wind velocity was measured at 5 cm and 100 cm with hot wire and cup anemometers respectively while radiation was monitored with an Eppley pyranometer. The anemometer and radiometer outputs were recorded continuously for 30 s every 3 min with a battery-powered strip chart recorder.

Mathematical model

Using the available microclimate and behavioral information, body temperatures were calculated using

a programmable calculator with extended memory to solve iteratively the energy balance equation (Eq. 3) for T_b to the nearest 0.1°C . Body temperatures calculated for *O. plana* on 26 April (Fig. 3) were used to check the reliability of the model against actual population body temperatures. The utility of thermoregulatory behavior observed in the populations of *O. plana* and *S. phalangium* was readily checked at different hours of the day by solving the energy balance equation for T_b , given different body orientations to the sun and microclimate parameters for locations on either Nara dunes in the case of *O. plana*, or on rocks in the case of *S. phalangium*. Table 1 shows the beetle parameters for *Stenocara* and *O. plana* that were used in the model to predict body temperature.

DISCUSSION

Thermal ecology

Figure 8 shows *O. plana* activity curves for 23 and 26 April 1973 and illustrates the typical bimodal activity rhythm of the population. The beetles cannot behaviorally maintain tolerable body temperature

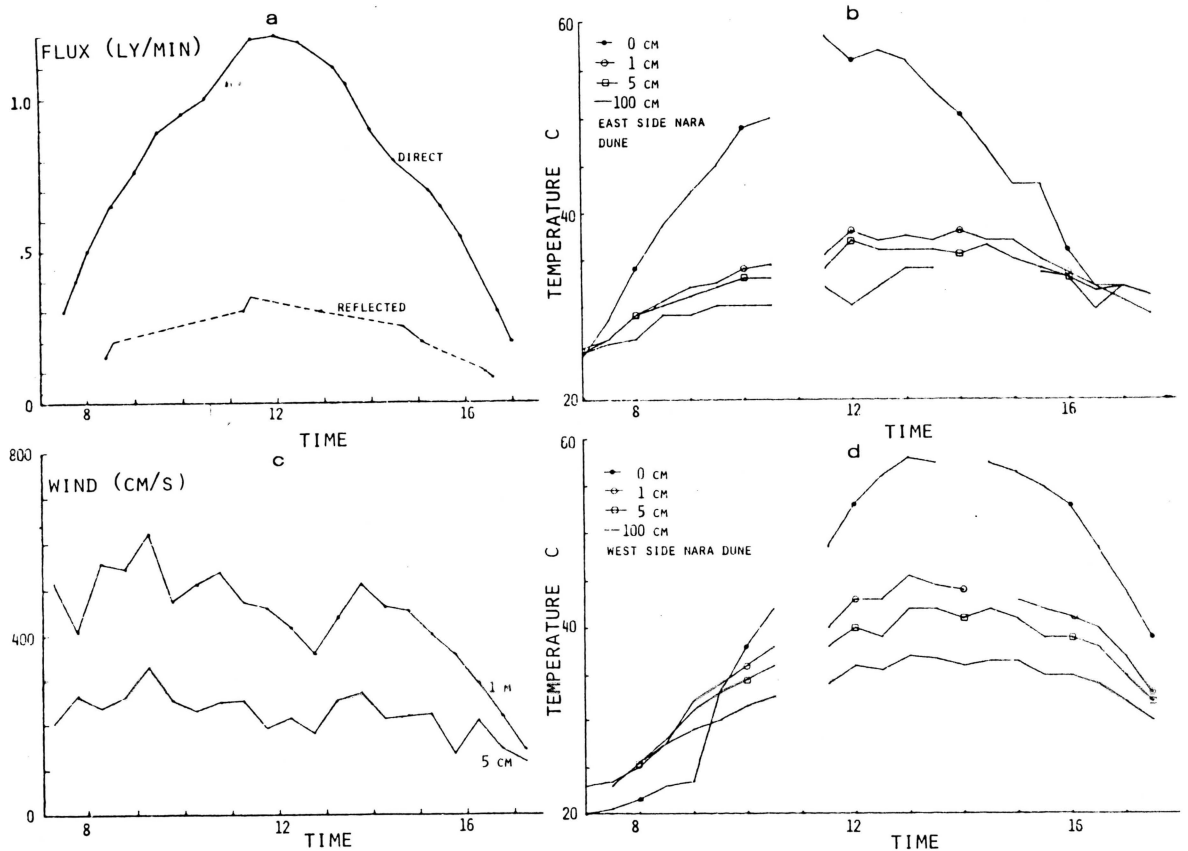


FIG. 5. Microclimate data for the *O. plana* study site on 26 April 1973 plotted against local sun time. Direct and reflected solar radiation (a), and wind velocity (c) at two heights are shown. The temperature regimes at four heights on the east (b) and west (d) slopes of the Naras dune illustrate the difference in microclimate on the two slopes. Without the effect of clouds the lag in the time of maximum temperatures on the west slope of the dune is readily seen in (b) and (d).

during the midday period because of high temperatures and radiation loads. Temporary subsurface thermal refuge is taken on the steep slip faces on the Naras dunes where digging is facilitated by the loose sand.

Figure 9 shows the manner in which slope selection is used to thermoregulate behaviorally. Slope selection allows regulation of both radiative heat gain and, to a lesser degree, ambient (at beetle level) air temperature. Beetles emerge in the morning and concentrate their activities on east slopes to take advantage of maximum radiation absorption and thereby force rapid warming. In late morning southerly slopes are preferred since these slopes have the least radiation load during these hours. Early afternoon finds higher numbers of beetles on east slopes due to the reduction in radiation load, air and sand surface temperatures. By late evening the active population has moved to westerly slopes to catch the last rays of sun and permit maintenance of maximum body temperatures during the last hours of the day.

The effectiveness of the behavioral thermoregulation strategies employed by *O. plana* can be seen

from Fig. 3. The temperature ranges denoted by the left-hand bars are derived from the model using actual climate data for 26 April. The scatter diagram of body temperatures from free-roaming beetles that were caught and probed wherever they were sighted shows the degree of microhabitat selection practiced by *O. plana*. Until about 1000 the beetles select habitats that allow temperatures to rise as rapidly as possible. Since any given beetle has a body temperature dependent on its immediate thermal history, points that lie well below the range of body temperatures available on either an east or west slope probably are from beetles that were captured just subsequent to emergence from the cool sand where they spent the night. A warm *O. plana* is highly mobile and adept at avoiding capture so it is likely that these cool individuals are overrepresented in the sample.

With the approach of midday, body temperatures have risen to desired levels near 40°C, and the cooler parts (S and W slopes) of the microenvironment are used, allowing the beetles to avoid further temperature increases. Body temperatures are clustered along

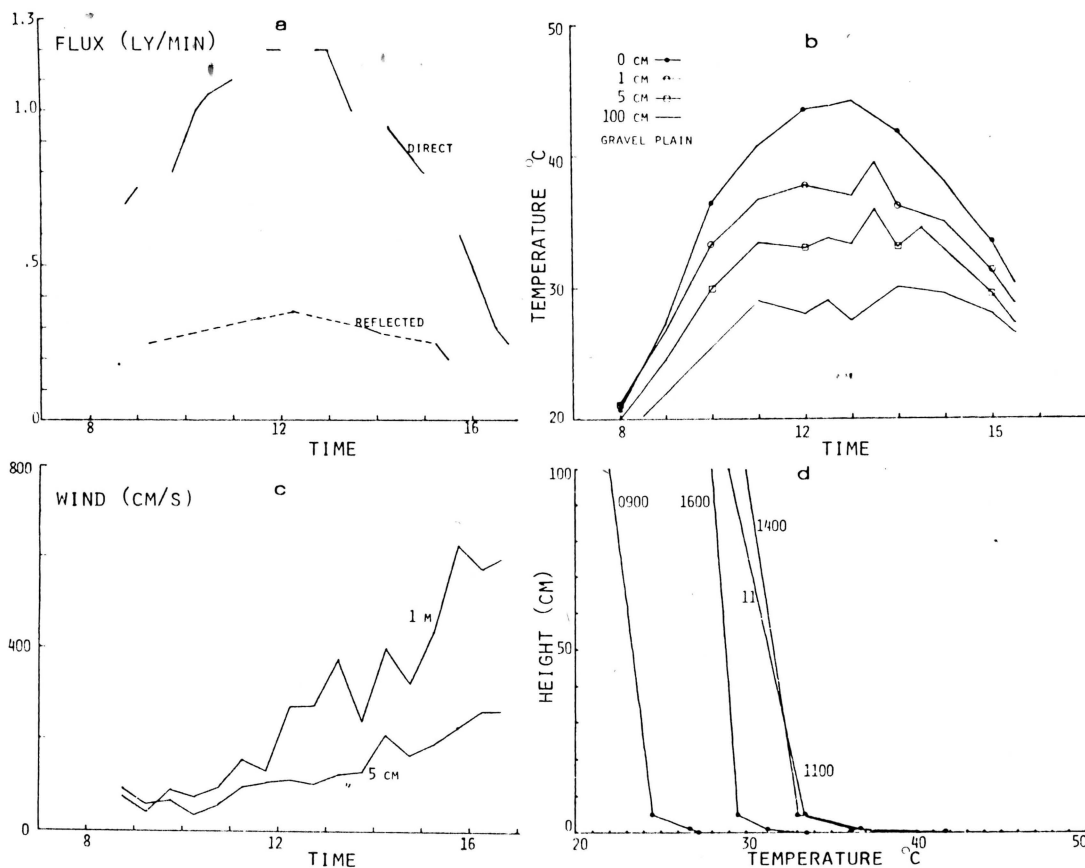


FIG. 6. Microclimate data for the *S. phalangium* study site on 1 May 1973. Direct and reflected solar radiation (a), wind velocity at two heights (c), and the temperature regime (b) are shown plotted against local sun time. The temperature gradient above the gravel plain is shown in (d).

the lower edge of the range of available body temperatures and remain there after emergence in the afternoon until about 1600. From 1600 to 1700, when the population once again digs underground

for the night, the whole of the environment is habitable and body temperatures remain regulated near 40°C. The effect of the east wind on 26 April is readily apparent in the increased numbers of active

TABLE 1. Animal and soil parameters used in the beetle energy-balance model

	Mean radiation absorptance (%)			Emissivity (ε)		Convection coefficient (h _c) (cal/cm ² · min · °C) [†] [h _c = m(wind vel.) + b] m b h _c			Areas (cm ²)			
	Direct	Reflected	IR ^a	Beetles ^a	Sand ^b	(× 10 ⁻⁴)	(× 10 ⁻²)	(free conv.)	A _D	A _R	A _T	A _{TR}
	<i>O. plana</i>											
♂♂	0.784	0.774	0.97	0.97	0.90	1.85	3.39	0.0211	2.05	1.025	5.95	2.05
♀♀	0.846	0.851	0.97	0.97	0.90	1.91	4.01	0.0224	2.00	1.00	5.45	2.00
<i>S. phalangium</i>												
Normal posture	0.775	0.648	0.97	0.97	0.90	2.66	7.13	0.0382	0.325	0.325	1.30	0.325
Thermoregulatory posture	0.648	0.648	0.97	0.97	0.90	2.66	7.13	0.0382	0.150	0.325	1.30	0.325

^a Bartlett and Gates 1967.

^b Sellers 1965.

[†] To convert calories per square centimeter per minute per °C into watts/m² per °C, multiply by 4.184/60.

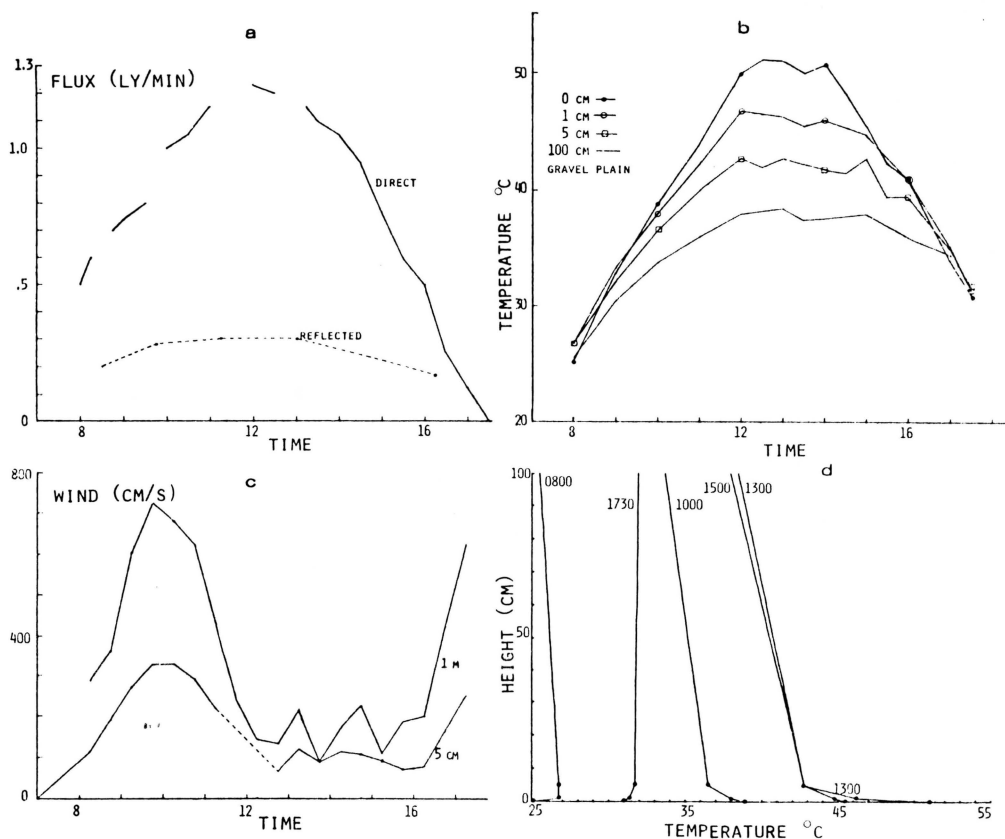


FIG. 7. Microclimate data for the *S. phalangium* study site on 6 May 1973. Direct and reflected solar radiation (a), wind velocity at two heights (c), and the temperature regime (b) are shown plotted against local sun time. The temperature gradient above the gravel plain is shown in (d).

beetles through the day (Fig. 8) as a result of the increased convective cooling rate. Strong wind is also effective in uncovering food and blowing *Naras* blossoms off the thorn bushes. Wind thus contributes motivation for, and makes thermally possible, the increased activity measured in the population that day.

The sensitivity of body temperature to wind velocity can also be seen from the right-hand bars in Fig. 3 where wind velocity was reduced by a factor of two. The bars denoting body temperature ranges show the increases in body temperature that result solely from a reduction in wind speed while holding all other environmental factors constant. The reduction in wind speed brings the microclimate for 26 April very close to an average day for late April and helps explain why the behavior data for the population of *O. plana* show an increase in numbers of active beetles on 26 April.

The atypical high winds made it possible for *O. plana* to cool convectively and avoid overheating in late morning and early afternoon, thereby permitting more beetles to remain active and reducing the more

typical extreme bimodality of activity seen in the data from 23 April.

The results show *O. plana* to be a maxithermic species in which high body temperatures are chosen and maintained for the longest possible times each day through microhabitat selection. The model coupled with the behavior data indicates that the preferred body temperature range is near 40°C, and the attempt to spend the maximum time at these temperatures forces body temperatures near lethal levels for a short period after emergence in the afternoon. The range of microhabitats that will allow selection of sublethal temperatures is very narrow at this time but expands rapidly to include practically the entire environment by 1530–1600 in the afternoon.

Stenocara phalangium present an interesting contrast to *O. plana* because their environment so effectively limits the thermoregulatory strategies that can be employed to maintain relatively constant body temperatures. Figures 6, 7, and 10, showing microclimate and population activity information for 1 and 6 May 1973, indicate how limited activity times

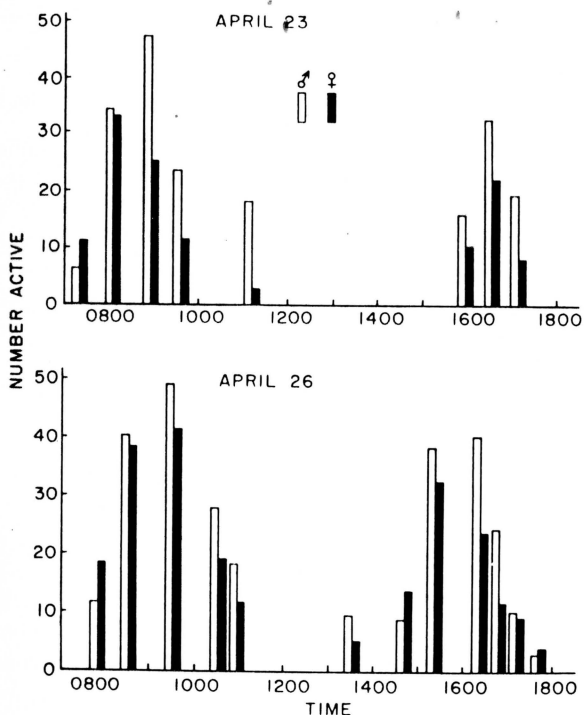


FIG. 8. Population activity data for *O. plana* on 23 and 26 April 1973 shown on the mean hour of the census. Male and female data are shown separately to illustrate the divergence in activity time between the sexes.

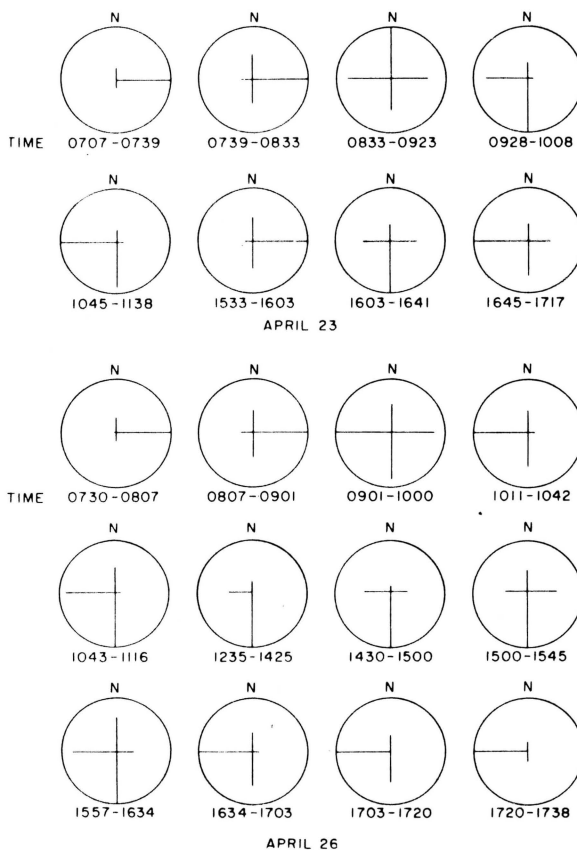


FIG. 9. Population slope selection data for *O. plana* for 23 and 26 April 1973. In each case the mode value of the census period is shown as 100% of scale and numbers of insects observed on other slopes scaled accordingly.

are for *S. phalangium*. This is primarily a result of their small size and the lack of microclimatic variation in the habitat. Small size couples *S. phalangium* body temperature more closely to air temperature than is the case for *O. plana* while environmental uniformity reduces the range of air temperatures available.

Since large differentials between body and air temperatures are not possible, *S. phalangium* must wait until later in the morning when surface air temperatures are higher before beginning its daily activities which last throughout the midday hours (Fig. 10). Beetles appear on the surface of the gravel plain as the 1-cm air temperature reaches 34°C which allows maintenance of a predicted 36°C body temperature. Once active, the entire population is subject to an equal microclimate which leads to the rapid increase in activity and uniformity in thermal behavior observed in the field. Beetles will remain active on the surface until body temperatures reach 40°-42°C at which time temperature-reducing behavioral strategies appear throughout the population.

The range of thermoregulatory behaviors available to *S. phalangium* can promote both heat gain or loss depending on conditions. On cool mornings (such as 1 May) beetles will warm themselves by standing

with the body depressed on bent legs and oriented perpendicular to the sun's rays. This behavior will maximize heat gain while an opposite strategy involving minimization of further heat gain (or maximization of heat loss) uses small rocks to take advantage of the steep surface temperature profile (Fig. 7b and 7d). These rocks serve as thermal refuges during extremely hot days and their value is corroborated by observations of vigorous territorial defense employed by resident beetles against intruders.

The dip in afternoon activity data for 6 May is a result of this extreme thermoregulatory strategy. Beetles mounted the larger rocks available and "stilted" on the highest available portion of the stone with only the white posterior of the abdomen pointed at the sun. Pointing the abdomen at the sun reduces both the absorptivity of the surface receiving direct radiation as well as its area. The beetles became inactive during this period and would not flee from the rocks even when approached. The refusal

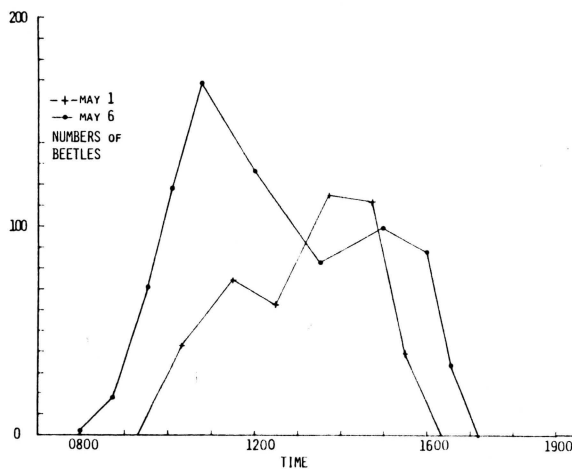


FIG. 10. Numbers of *S. phalangium* sighted by mean hour of census for 1 and 6 May 1973.

to flee accounts for the drop in active beetles between 1100 and 1330.

The model was used with surface and rock microclimate data from the 2 days in May to predict body temperatures (Fig. 11) for a medium-sized *S. phalangium* on the ground, on a 5-cm rock, and standing on the rock posing with the lighter-colored abdomen pointed at the sun. Using the model in this way, the efficacy of various thermoregulatory strategies can be determined. On 6 May 1973, the nearby Gobabeb weather station recorded a Stevenson Screen temperature of 37.1°C, 0.1°C warmer than the hottest day in May for the 5 yr of climatic data reviewed by Schultze (1969). Rock climbing started about 0930 that day, and by 1030 most beetles in the population were defending their particular

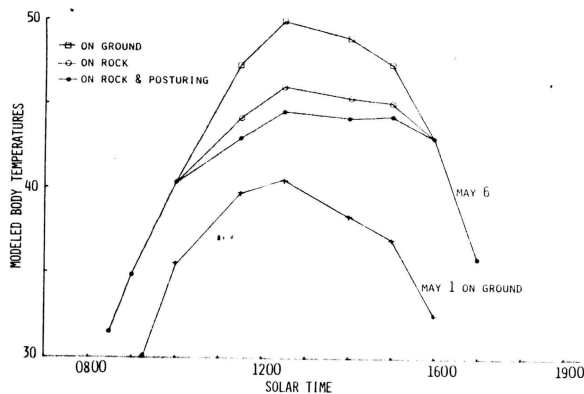


FIG. 11. Body temperatures predicted with the model for the population of *S. phalangium* on 1 May 1973. Also shown is the range of possible body temperatures on 6 May 1973 using different thermoregulatory strategies between 1000 and 1600 h.

rock. At 1030 there is a 2°C difference predicted in body temperatures between a beetle on the ground and one standing on a 5-cm rock. By midday there was nearly a 6°C spread between body temperatures on the ground and those attainable by mounting a 5-cm rock and posing with the abdomen pointed at the sun (Fig. 11). Beetles pushed off their rock at this time made vigorous attempts to get up on another and when denied the opportunity became disoriented and unable to walk after a period of 15–20 min.

May 1 was a more typical winter day, with the census and behavior data showing the normal unimodal activity curve. Predicted body temperatures (Fig. 11) for the day were well below the point where rock climbing started on 6 May ($\approx 40^\circ\text{C}$) and no temperature-reducing behavior was observed. Beetles emerged in the morning, warmed themselves for a short time, and then commenced the feeding and courtship activities that consumed the active hours for the rest of the day.

The 5 yr of records compiled by Schulze (1969) show that the days with measured air temperatures $> 35^\circ\text{C}$ occur on the average 8 times in May, 0 times in June and July, 8 times in August, and 5.6 times in September. However, absolute maximum temperatures in those data had not exceeded 37°C for May or August and 40.3°C for September. Viewed in light of these data the *Stenocara* emerging in May must be exposed to conditions near those observed on 6 May about 25% of the days in that month. After the first of June, conditions on the dune street moderate and *Stenocara* is only faced with the problem of days that are too cool. By the end of July few beetles remain on the gravel plains and these remnants of the population are tattered, nonreproductive individuals.

It appears that *S. phalangium* is living a maxithermic strategy similar to *O. plana* but in a more extreme environment. Long legs, smaller body sizes with correspondingly higher convection coefficients, shorter diurnal activity times, and a winter months activity cycle are necessary to exploit the thermally extreme dune street gravel plains. To explore the possibility that *O. plana* are thermally excluded from the gravel plains habitat the model was used to place an *O. plana* in the *S. phalangium* habitat on 6 May. The theoretical beetles placed on 5-cm rocks had predicted body temperatures $> 53^\circ\text{C}$ for smaller individuals and $> 55^\circ\text{C}$ for larger males and females. From these data it seems apparent that *S. phalangium*'s small size and light, early season coloration are necessary adaptations to life on the gravel plains.

CONCLUSIONS

The beetle energy-balance model validated with population body temperatures taken on free-roaming beetles in the field was combined with field microclimate and behavior data to interpret the thermoregulatory strategy of two Namib Desert beetles, *O. plana* and *S. phalangium*. These animals used only the portion of the habitat available to them that allowed maintenance of the highest possible sublethal temperatures for the maximum number of hours each day. Hot microenvironments were preferred over cooler environments available in the same geographic area solely through a temporal activity shift.

Modeled body temperatures show that a high degree of microenvironmental selection is practiced for short periods each day when major portions of the habitat experience conditions that produce body temperatures very near to or exceeding the thermal damage or death point. When examined with the model, the thermal behavior observed in the field was very effective at such times in limiting further body temperature increases as well as maintaining warm body temperatures in the cooler morning and evening hours. This thermal strategy is maxithermy (Hamilton 1973) and seems to entail certain advantages for these poikilotherms whose adult population is not always limited by food supply.

Bullock (1955), Schmidt-Nielsen (1964), Odum (1971), Hochachka and Somero (1973), Heinrich (1974), and others have recognized that, after correcting for acclimatization temperatures, higher body temperatures allow poikilotherms to have higher metabolic rates. If we assume, as Lotka (1925), Odum and Pinkerton (1955), Bursell (1964), and Odum (1971) have, that a poikilotherm with a higher intraspecific metabolic rate has a higher reproductive rate, the evolution of maxithermic strategies is feasible on the Namib Desert since the beetle that can select, tolerate, and reproduce at a higher body temperature will leave more progeny.

A shortage of food resources can make maxithermy unworkable, but for both species at the time of the field study there were unutilized food resources in the environment, indicating that, for the adult form of *O. plana* and *S. phalangium* at least, maxithermy is a viable strategy.

There are areas on the Namib where *O. plana* and *S. phalangium* occur contiguously. The dune street habitat of *S. phalangium* borders on lower dune slopes that are partially vegetated with spiny grass clumps of *Stipogrostis* sp. around which *O. plana* live. In this situation there is practically no overlap between the two populations. The model shows that *O. plana* is thermally excluded by high body temperatures from the gravel plains where they are unable to dig underground.

It is less clear why *Stenocara* are not found in the *O. plana* habitat but perhaps they cannot compete with the much larger *O. plana* for food or space. In other areas where *O. plana* are not present on the sandy dune shoulders *Stenocara* were observed 20–30 m above the edge of the gravel plain, foraging for windblown detritus.

In a resource-limited situation a maxithermic strategy with its correspondingly high resource utilization rates could be disadvantageous. Such a situation can arise on the desert through an environmental perturbation and/or competition from other animals moving into the environment and exploiting the same food resource. An alternative strategy in such a situation could involve selection of a lower temperature thermal environment with its correspondingly lower metabolic rates. The efficacy of this strategy is doubtful in a competitive situation, but in a situation where environmental conditions can cause temporary food shortages it is a possible alternative. In Angola on the northern Namib such a strategy is possibly in use by the small black *Stenocara desertica* that has relinquished the warm diurnal habitat to two large white *Onymacris* species and is now temporally confined to the cool, crepuscular, early morning and late afternoon hours (W. J. Hamilton III, *personal communication*).

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