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Behavioral Implications of Mechanistic Ecology
Thermal and Behavioral Modeling of Desert Ectotherms and Their Microenvironment

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Summary. Mechanistic principles from engineering, meteorology, and soil physics are integrated with ecology and physiology to develop models for prediction of animal behavior. The Mojave Desert biome and the desert iguana are used to illustrate these principles.

A transient energy balance model for animals in an outdoor environment is presented. The concepts and relationships have been tested in a wind tunnel, in a simulated desert, and in the field. The animal model requires anatomical information and knowledge of the thermoregulatory responses of the animal. The micrometeorological model requires only basic meteorological parameters and two soil physical properties as inputs. Tests of the model in the field show agreement between predicted and measured temperatures above and below the surface of about 2 to 3° C.

The animal and micrometeorological models are combined to predict daily and seasonal activity patterns, available times for predator-prey interaction, and daily, seasonal and annual requirements for food and water. It is shown that food, water and the thermal environment can limit animal activity, and furthermore, the controlling limit changes with season. Actual observations of activity patterns and our predictions show close agreement, in many cases, and pose intriguing questions in those situations where agreement does not exist. This type of modeling can be used to further study predator-prey interactions, to study how changes in the environment might affect animal behavior, and to answer other important ecological and physiological questions.

I. Introduction

The purpose of this paper is to demonstrate how mechanistic principles from engineering, meteorology and soil physics can be integrated with ecology and physiology to develop models that will predict animal behavior and permit broad assessments of ecologically important factors in

a biome. We show how it is possible to determine the behavioral constraints imposed on animals by the thermal environment and by vegetation type and quantity. We have used a Mojave Desert biome and the desert iguana (*Dipsosaurus d. dorsalis*, Baird and Girard) to illustrate these principles.

Mechanistic modeling of the energy flows between an animal and its environment is a powerful tool in the study of ecology. Such models can be used to give insight into the reasons for observed animal behavior. For example, our predictions indicate that the desert iguana must hibernate from about November 1 to March 1. These predictions are borne out by observations. It is possible that modeling may point out behavior patterns for animals not as well studied as the desert iguana that have not yet been observed.

Modeling can also be used to pinpoint new data needs and to ascertain the accuracy required of experimental data. We recognize that some of the data used in our model are inadequate or incomplete, but they are the best data available at present. For example, plant water content is necessary for the determination of a behavioral limit resulting from evaporative water loss. At present, seasonal plant water content is not well known and must be determined.

Finally, modeling can be used to predict the consequence of man's influence on the environment. It is possible to vary any parameter in the model to determine its influence on animal behavior. It is possible, for example, to assume that an increase in atmospheric particulates reduces the sun's intensity and to ascertain the influence of this change on the desert iguana's average behavior.

This modeling would have been impossible without the large behavioral, physiological and ecological literature that we could draw on for ideas and data. Assessments of steady state physiological and temperature responses of lower animals to different physical environments are numerous and include work by many investigators such as Kendeigh (1939), Lee et al. (1941), Cowles and Bogert (1944), Scholander et al. (1950), Norris (1953), Edney (1954), Dawson and Bartholomew (1958), Prosser and Brown (1962), Lasiewski (1963), McNab and Morrison (1963), Heath (1964), Cloudsley-Thompson (1965), Schmidt-Nielsen et al. (1965), Whitford and Hutchinson (1967), and Regal (1967).

Models for the temperature and behavior of animals during part of a day have been developed by Bartlett and Gates (1967) and by Norris (1967). A more general attempt at the prediction of the behavior and environmental limits has been presented by Porter and Gates (1969). These studies have all considered the animal and the environment to be in thermal steady state and have thus been unable to readily evaluate behavioral patterns in a changing environment.

We have formulated a transient model for both the animal and the environment (Beckman *et al.*, 1973). A detailed microclimate model has been developed for predicting soil and air temperatures as functions of time of day and time of year. A transient model for the lizard is developed based on physiological principles. The lizard and microclimate models are combined to predict lizard temperature and consequent behavior over the course of the year. These predictions are verified through comparison with field observations. The model predictions are extended to consider food and water requirements and the interaction between predator and prey.

II. The Desert Environment

Knowledge of the desert microclimate is necessary if we are to utilize animal energy balance models to predict where animals will be in the physical environment and relate their location to interactions with other species. The climatic data generally available are insufficient to describe the environment completely enough for predictions of animal behavior. Consequently, it was necessary to either make our own micrometeorological measurements for extended periods of time at various locations or to develop a micrometeorological model augmented by standard weather measurements. Considering the quantity of measurements that would be required to describe the desert microclimate, it was decided that mathematical modeling of the environment would be a much simpler approach. Modeling has the added advantage in that we can force the environment to change in any desired manner and investigate the influence of climatic changes on animal behavior.

As shown in Fig. 1 and discussed in subsequent sections, the microclimate variables that are necessary for animal energy balances are: the solar radiation, the infrared radiation from the sky, the wind speed, the air temperature, and the soil temperature. The method used for determining each of these quantities will now be described.

The solar radiation reaching the outer atmosphere is a function of the day of the year, time of day and the latitude. This solar radiation is reduced before it reaches the earth's surface by clouds and various components in the atmosphere that absorb and scatter radiation. For clear days, McCullough and Porter (1971) have developed a program to calculate the radiation reaching the earth's surface. For cloudy days, it is necessary to have meteorological observations of the incident solar radiation. In this paper, cloudy day solar radiation has been obtained from local measurements while on field trips to the desert.

The long wavelength radiation emitted by the atmosphere is not measured in standard weather bureau practice. However, for clear days and for conditions existing over a desert, Swinbank (1963) has developed
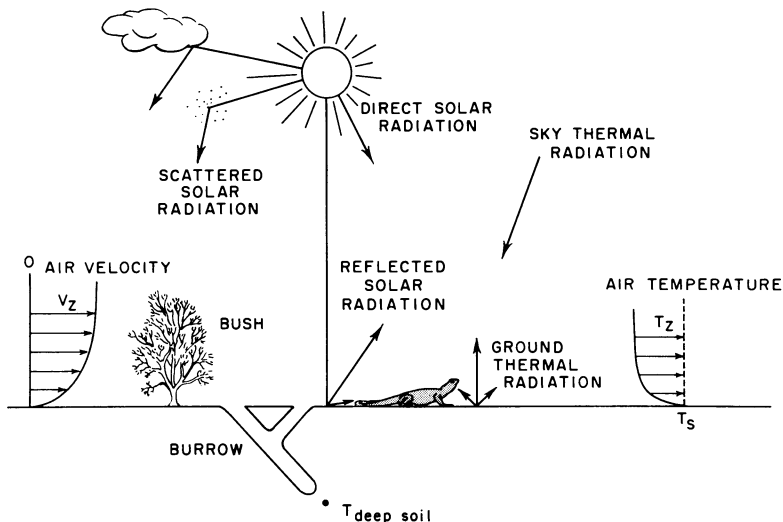
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Fig. 1. Schematic of the desert environment showing the energy flows to the desert surface and to a lizard

an empirical equation relating the equivalent black body sky temperature to the screen temperature[1]

$$T_{sky} = 0.0522 \ (T_{screen})^{1.5}. \tag{1}$$

The equivalent black body sky temperature is a fictitious temperature that treats the sky as a black body radiator to yield the correct value for the total infrared sky radiation.

At present, it is impossible to predict the local wind speed from general climate information. Consequently, in various sections of this paper, we have either assumed a representative wind speed of 200 cm/sec at 200 cm or we have used actual velocity measurements obtained during field trips. Using either the assumed wind velocity or actual measured values at one height, it is possible to predict variation of wind velocity with height.

In the desert, the wind is usually blowing and a turbulent, atmospheric boundary layer exists near the desert surface. This layer near the ground is relatively unaffected by adiabatic or diabatic conditions, and the velocity profile is the neutral profile described by Sellers (1965)

$$V_z = (V^*/k) \ln(z/z_0 + 1). \tag{2}$$

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1 The screen temperature is the temperature measured in a Stevenson screen located 200 cm above the surface.

In order to evaluate the velocity at any height, the shear velocity $V*$ and the surface roughness z_0 are needed. For our assumed velocity of 200 cm/sec at a height of 200 cm, and with an assumed surface roughness[2] of 0.05 cm, $V*$ is equal to 9.6 cm/sec. With $V*$ known, Eq. (2) may be used to determine the velocity at any height.

The air temperatures used in the micrometeorological model were either measured during our field trips or approximated using reported 10-year averages of the maximum and minimum screen temperature from the nearest weather station (Palm Springs, California). For general predictions, we assumed the minimum air temperature occurred one hour before sunrise and that the maximum occurred two hours after solar noon. Curves similar in shape to those in Geiger (1965) for diurnal desert air temperature were constructed for each 24-hour period.

In order to predict the air temperatures at other heights, we utilized the similarity between the transport of heat and momentum for turbulent boundary layers. The temperature and velocity profiles for neutral conditions are given by (Sellers, 1965)

$$\frac{V_z}{V_r} = \frac{T_z - T_s}{T_r - T_s} = \frac{\ln(z/z_0 + 1)}{\ln(z_r/z_0 + 1)} \, . \tag{3}$$

During midday, there are strong free convection currents set up that change the profile shapes from that given in Eq. (3). For the predictions of lizard behavior at Palm Springs, we felt that Eq. (3) was sufficiently accurate in view of the lack of detailed meteorological data.

The final micrometeorological variable that must be determined is the soil temperature. The only soil temperature an animal on the surface can respond to is the surface temperature. However, in order to calculate the surface temperature, it is necessary to calculate the soil temperature below the surface. As discussed later, the soil temperature below the surface is also important in describing animal behavior.

The soil temperature is described by the one-dimensional partial differential equation (Carslaw and Jaeger, 1959)

$$\frac{\partial T}{\partial t} = \frac{k_{so}}{\varrho_{so} c_{so}} \frac{\partial^2 T}{\partial z^2} \tag{4}$$

In order to solve this equation, two boundary conditions and one initial condition are necessary. In this paper, two types of initial conditions are used. Whenever predictions are compared with field observations, measured soil temperature profiles are used as the initial condition. These measurements are described in a later section. Whenever we attempt to make general predictions for an average day, an arbitrary initial con-

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2 Values for z_0 range from 0.01 cm to 0.1 cm for smooth surfaces (Sellers, 1965, p. 150; Van Wijk, 1963, p. 252; Stearns, 1967).

dition is used to find the steady periodic solution. In this steady periodic solution, the temperature at each location repeats itself every 24 hours and is thus independent of the initial condition.

One of the boundary conditions was obtained by assuming that the soil temperature at 60 cm does not change diurnally. The temperature at this depth is taken to be the average screen temperature for the month (Van Wijk, p. 109, 131, 1963). The remaining boundary condition at the soil surface is obtained by equating the energy conducted to the soil surface to the net heat transfer to the surface by solar radiation, infrared radiation and convection. Very little water is evaporated from the desert surface except for short periods after rains, and for our model we have assumed the energy transport associated with surface evaporation is negligible. The surface boundary condition then mathematically expresses an energy balance for the soil surface

$$Q_{s,cond} = -k_{so} \frac{\partial T}{\partial z}\Big|_{z=0} = Q_{s,solar} + Q_{s,IR} + Q_{s,conv}. \tag{5}$$

The solar energy absorbed by the desert surface is given by

$$Q_{s,solar} = \alpha_{so} Q_{solar}. \tag{6}$$

The infrared radiation to the soil surface $Q_{s,IR}$ is the net exchange between the surface and the sky. The radiation emitted by the soil surface, which is assumed to be black (Van Wijk, 1963, p. 91, gives $\varepsilon_{so} = 0.95$ to 0.98), is given by

$$Q_{s,rad} = \sigma T_s^4. \tag{7}$$

The radiation emitted by the sky and absorbed by the soil is given by

$$Q_{sky} = \sigma T_{sky}^4. \tag{8}$$

The net infrared radiation to the soil surface is then given by

$$Q_{s,IR} = \sigma (T_{sky}^4 - T_s^4). \tag{9}$$

The convection heat flow occurs between the ground surface and the air flowing over it, and is given by

$$Q_{s,conv} = h_s (T_r - T_s) \tag{10}$$

where h_s is the surface heat transfer coefficient and is a function of the wind velocity profile, air temperature profile and surface roughness. In the turbulent atmospheric boundary layer, heat is transferred by the eddying motion of the air in the same manner as momentum. Consideration of these mechanisms leads to an expression for the surface heat transfer coefficient during neutral conditions (Sellers, 1965).

$$h_s = (\varrho_a c_{p,a} k^2 V_r)/[\ln(z_r/z_0 + 1)]^2. \tag{11}$$

As with the velocity and temperature profiles given by Eq. (3), free convection currents alter the surface heat transfer coefficient from that given by Eq. (11). However, we used Eq. (11) for predictions of the Palm Springs microclimate, and the relations derived by Beckman *et al.* (1973) when comparing predictions with our field data. For the predictions, the value of h_s is 0.008 cal/min-cm^2-C for a 200 cm/sec velocity at 200 cm and a surface roughness of 0.05 cm.

Eq. (4), subject to the deep soil and soil surface boundary conditions, was solved by finite difference on a digital computer. (These finite difference calculations are described in detail by Holman, p. 98, 1968.)

To test the accuracy of the micrometeorological modeling, we went to a flat area in the Mojave Desert approximately five miles from the Kelso Dunes and monitored the micrometeorological parameters. Soil surface temperatures were measured with thermocouples and a portable radiometer manufactured by the TE Company of Santa Barbara. Solar radiation was monitored by a temperature compensated Eppley pyrheliometer. Wind speed was measured with a Hastings hot wire anemometer and cup anemometers. Air temperatures were measured with thermocouples shielded with aluminum foil. Soil temperatures were measured with copper-constantan thermocouples buried in the sand. The thermocouples were left embedded in the sand and have been reused in subsequent visits to the site. Table 1 lists data measured. The only data used as inputs to the micrometeorological model are the solar heat flux, air temperature at 40 cm, air velocity at 40 cm, and deep soil temperature (60 cm). These data, together with the physical properties of the environment, are used to predict temperatures at any position in the soil or air. The remaining data listed in Table 1 are used in the verification of the micrometeorological model.

The physical properties of the environment that are needed for the model are the roughness length z_0, the soil conductivity k_{so}, and the solar absorptivity of the soil surface α_{so}. The roughness length near the Kelso dunes was determined from velocity measurements at 20, 40 and 200 cm made in October 1971 to be $z_0 = 0.1$ cm. This value is twice that used in the Palm Springs predictions but within the range of values reported in the literature.

The temperature profiles in the soil were analyzed to yield the best values for thermal properties. A value of 0.042 cal/cm-min-C was determined for thermal conductivity and a value of 0.084 cm^2/min for the thermal diffusion $(k/\varrho c)$. These are in the range of tabulated values for dry sand (Van Wijk, p. 228, 1963).

The solar reflectance of the surface was determined by field measurements of the direct and reflected solar radiation using the pyrheliometer and in the laboratory with a Beckman DK-2A spectroreflectometer. The

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Table 1. Micrometeorological variables

Variable	Location
Solar radiation	Ground level[a]
Air temperature	200 cm[b]
	40 cm[a]
	5 cm[b]
	2.5 cm[b]
Air velocity	200 cm[b]
	40 cm[a]
	20 cm[b]
Soil surface temperature	0 cm[b]
Soil temperature	2.5 cm[b]
	5 cm[b]
	10 cm[b]
	60 cm[a]

[a] Data used as input to the model.
[b] Data used in verification of the model.

solar reflectance was determined to be 0.33, and the solar absorptivity is then 0.67. The value for reflectance is consistent with that given by Van Wijk (1963, p. 87) of 0.35 for quartz sand.

The experimental results for a 52 hr test are presented in Fig. 2 in comparison with the predictions. The first period, April 12, was sunny throughout the day. For April 13, there was sunshine in the morning followed by heavy cloud cover beginning at 1 300 and continuing throughout the night. The predicted and measured values at 2.5 cm above the soil surface, at the soil surface, and at depths of 2.5, 5, and 10 cm into the soil are shown. The measurements used as inputs to the model (solar heat flux, velocity and temperature at 40 cm, and deep soil temperature) are also shown. The results for the other two days studied in April are similar to these.

The predictions for the entire period in April were started using as initial values the temperatures, solar radiation, and wind speed that were measured at 1 100 on April 11, 1971. During periods (usually nighttime) when measurements were not made, we estimated the wind speed and temperature from similar periods for which data are available, and utilized these values in our predictions. The estimated values are shown in Fig. 2 for the night of April 12 as dashed lines. It is important to note that our model predictions are continuous and are not restarted each day.

The data and predictions for the air temperature at 2.5 cm agree within 3° C during the day, and 1° C at night. The predicted value is
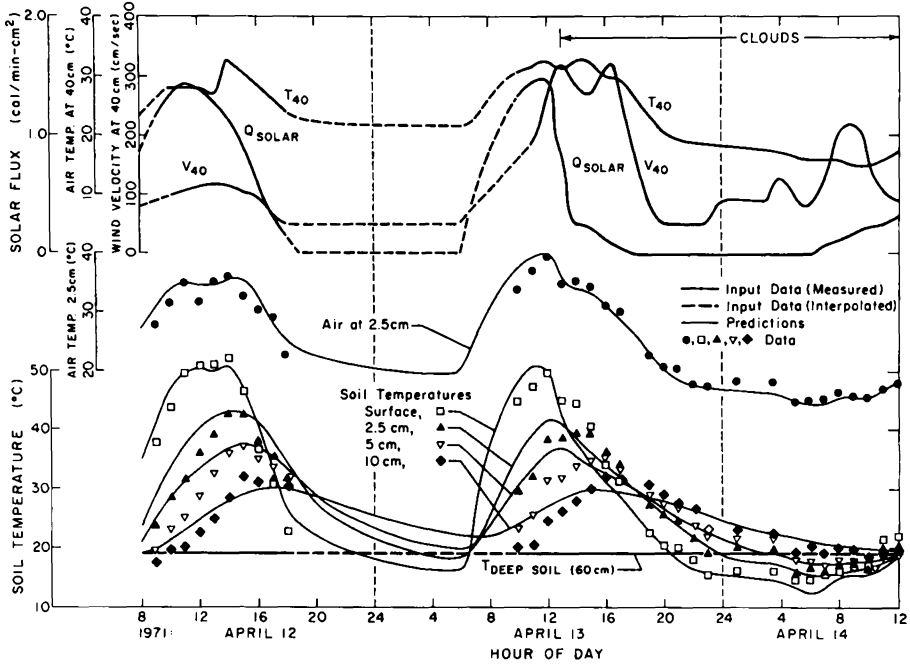
Fig. 2. Comparison of experimentally determined temperatures with the micro-
meteorological model predictions for the period, April 12-14, 1971

generally higher than the observed during the day. The temperature
profile in the air at midday is quite steep; the profile changes about
1° C per 0.2 cm change in height near the ground. The predicted soil
surface temperature is within 2 to 3° C of the observed value during the
day, and within about 1° C at night. The differences do not appear to be
systematic. The soil temperatures generally agree within about 2° C,
although systematic differences (for one day) of up to 5° C occur. It is
felt that the movement of water and the change in thermal properties
with depth may account for these discrepancies. We feel that the model is
sufficiently accurate for predicting the gross desert environment.

III. Environment-Lizard Thermal Interactions

The thermal energy flows from the environment that influence the
lizard are solar radiation, infrared radiation, convection and conduction.
We assumed negligible conduction between the lizard and the sand, which,
except for the early warming stage after emergence from the burrow,
appears reasonable (Norris, 1953; DeWitt, 1967). The net environmental
heat flow to the lizard, Q_e, is

$$Q_e = Q_{L,solar} + Q_{L,IR} + Q_{L,conv}. \tag{12}$$

In the open, the solar energy incident on the lizard is the sum of the direct plus scattered solar energy and the energy reflected from the ground to the lizard. Of this energy, the fraction α_L is absorbed by the lizard

$$Q_{L,solar} = \alpha_L (A_{p,d} \, Q_{solar} + A_{p,r} (1 - \alpha_{so}) \, Q_{solar}). \qquad (13)$$

The solar radiation incident on the sand is assumed to be diffusely reflected and is calculated as $(1 - \alpha_{so}) \, Q_{solar}$. In evaluating the solar absorptivity of the lizard, we assumed maximum absorption by the skin $(\alpha_L = 0.8)$ until a body temperature of 38° C was reached, minimum absorption $(\alpha_L = 0.6)$ above a body temperature of 43° C, and a linear variation between these limits (Norris, 1967; Porter, 1967). The projected area of the lizard for direct plus scattered solar radiation, $A_{p,d}$, varies with the relative orientation between the lizard and the sun. For our calculations, we assumed this projected area was a constant and equal to the vertical projected area. The projected area of the lizard for the reflected solar radiation, $A_{p,r}$, was assumed to be 0.4 times the total lizard area.

The net infrared radiation is the sum of the net exchange to the lizard from the sky and the ground. The lizard and sand infrared emissivities are both assumed to be unity (Norris, 1967). Thus

$$Q_{L,IR} = A_L \, F_{L-s} \, \sigma (T_s^4 - T_{sk}^4) + A_L \, F_{L-hky} \, \sigma (T_{sky}^4 - T_{sk}^4). \qquad (14)$$

The radiation shape factor from a lizard to the whole environment has been determined by Bartlett and Gates (1967) to be approximately 0.8. We assumed that one-half of the radiation from the lizard reaches the ground and one-half reaches the sky. Consequently, F_{L-s} and F_{L-sky} are both equal to 0.4. The convection heat transfer between the lizard and air is given by:

$$Q_{L,conv} = h_L \, A_L (T_z - T_{sk}). \qquad (15)$$

To evaluate the convection heat transfer, the air velocity and temperature in the vicinity of the lizard are needed. We assumed that the velocity and temperature varied with height according to Eq. (3), and that when the lizard was on the ground, it was at an elevation of 1 cm. We assumed that the lizard could climb to various elevations in a bush, and used the corresponding local air temperature and velocity to determine the convection heat transfer. The only parameter that is not known is the heat transfer coefficient h_L, and this quantity must be determined experimentally.

We developed a technique for casting a live specimen of *Dipsosaurus dorsalis* without destroying the animal. The animal was first inactivated by cooling, covered with freshly mixed dental investment compound, and after two minutes recovered from the flexible mold. A wax casting was

Fig. 3. *Dipsosaurus dorsalis* and a gold-plated casting of the same individual

made using this mold, then a plaster cast was made from the wax casting, and finally an aluminum casting was made in the plaster cast. Fig. 3 compares the casting detail and the live lizard used to make the casting.

The aluminum casting of the desert iguana was gold-plated to minimize thermal radiation exchange and to give maximum accuracy in determining the convection coefficient. A copper-constantan thermocouple was soldered into the casting. The casting was placed on a sandy board in a low speed wind tunnel (50–300 cm/sec with 70 cm × 70 cm dimensions at the test section), heated 10 to 15° C above the ambient temperature and allowed to cool. The heat transfer coefficient h_L was determined from the transient temperature response (London *et al.*, 1941; Wathen *et al.*, 1971). In calculating the lizard heat transfer coefficient from the cooling curves, the lizard surface area must be known. We used the casting to obtain the surface area by a modified electrolytic bath technique (Tibbals *et al.*, 1965).

The heat transfer results for the castings are shown in Fig. 4 for parallel and transverse orientations to the air flow. The transverse orientation, which was used in all predictions, gives about 25% higher heat transfer due to the shorter flow lengths and consequently thinner boundary layers.

In Fig. 5, the heat transfer results of Fig. 4 are presented in nondimensional form. Nusselt number, $Nu = h_L L/k_a$, is plotted as a function of Reynolds number, $Re = V_z L/\nu_a$, where L is the snout-vent length, k_a is the air thermal conductivity, and ν_a is the air kinematic viscosity. Also given are least squares relations for the transverse and parallel orientations. Heat transfer coefficients deduced from the data of Weathers (1970) for heating of live lizards are also presented. These data are compared with results using our casting placed in the wind tunnel in the same orientation as were Weathers' lizards. There is excellent agreement between our casting results and the live animal tests of Weathers. In addition, the data for 20, 50 and 100 g lizards are correlated by the use of the Nu and Re parameters. Thus Fig. 5 establishes the use of castings to determine live animal heat transfer characteristics, and also shows that the heat transfer coefficient for any size *Dipsosaurus dorsalis* can be determined from Fig. 5 using Nu and Re.
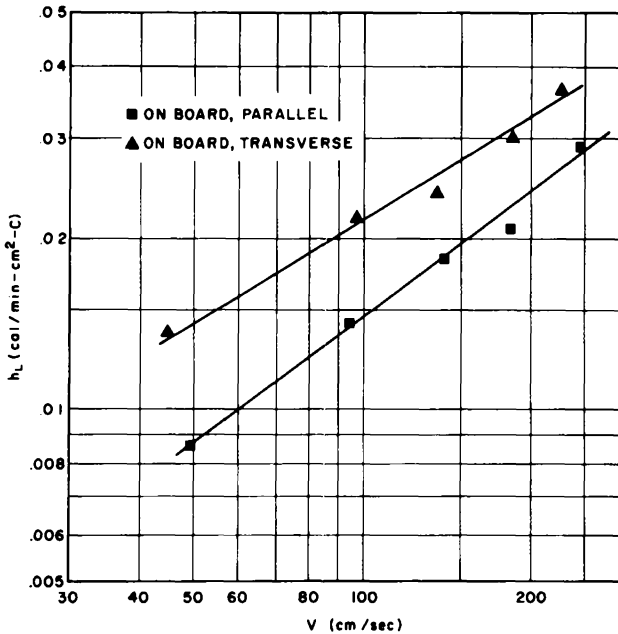

Fig. 4. Heat transfer coefficient as a function of air velocity for the lizard casting in a wind tunnel
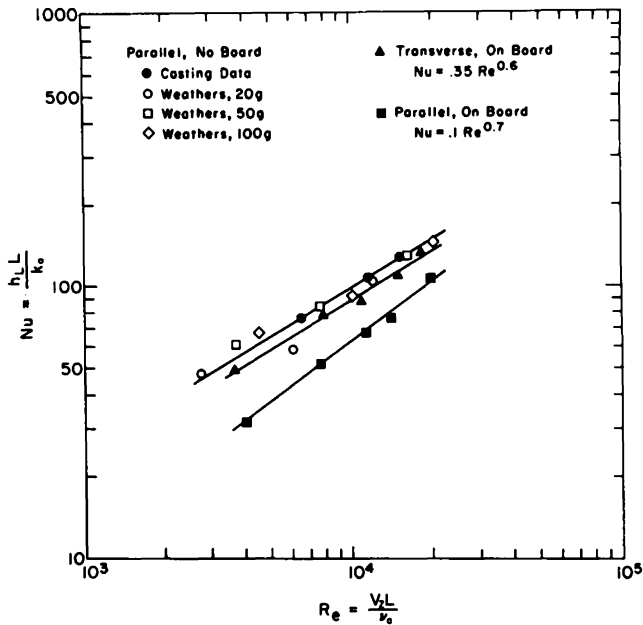
Fig. 5. Nusselt number as a function of Reynolds number for lizard castings (solid symbols) and comparison with results from live lizards (open symbols, Weathers, 1971)

Measurements of heat transfer coefficients in outdoor environments are 50 to 100 % higher than corresponding values obtained in wind tunnels (Pearman *et al.*, 1971; and some unpublished results we have obtained in the desert). For all field predictions, the wind tunnel relations given in Figs. 4 and 5 were increased by 50 % to simulate field conditions.

IV. Model for Physiological Temperature Regulation in the Lizard

The behavioral response of lizards is dependent on internal temperature (Templeton, 1970). Internal temperature is determined in part by the skin temperature, which in turn depends upon the environmental heat flows. Thus, the relations between skin and internal temperatures need to be determined. We modeled the internal thermal processes inside the lizard using the two-layer core-shell concept of Crosbie *et al.* (1961). We feel that this approach includes the known physiological processes in the lizard, and yet is not so complex to require data that is not avaialble.

The model for internal heat transfer is depicted schematically in Fig. 6. The thermal circuit is a representation of the heat flows in the animal, and facilitates an order of magnitude comparison of the various

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SKIN
AND
FAT

CORE
•
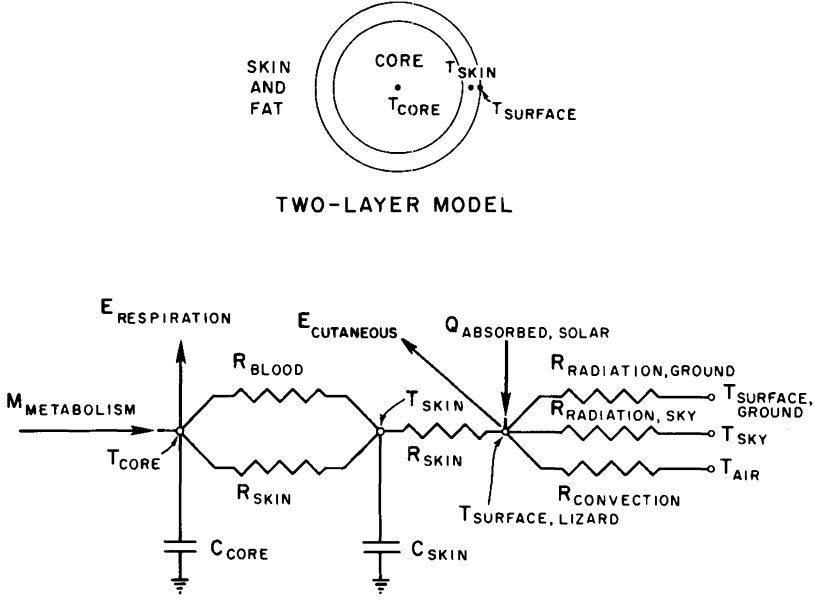T_{CORE}
T_{SKIN}
$T_{SURFACE}$

TWO-LAYER MODEL

Fig. 6. Core-shell (two-layer) model for the lizard and a schematic representation of the thermal energy flows

energy flow terms. A thermal resistance is the ratio of the temperature difference producing a heat flow to a heat flow. With a thermal resistance known, the corresponding heat flow can be obtained by dividing the temperature difference by the thermal resistance. A thermal capacitance represents the capacity of any isothermal region to store thermal energy, and is the product of mass and specific heat.

The core, which includes the central portion of the appendages, has a uniform temperature T_c due to blood flow and a thermal capacitance C_c. Energy M due to metabolism enters the core, and energy $E_{respiration}$ leaves due to breathing. The thermal energy transported to the skin at temperature T_{sk} from the core by blood flow is given by:

$$Q_b = (\dot{m}c)_b (T_c - T_{sk}). \tag{16}$$

The corresponding thermal resistance for blood flow is

$$R_b = 1/(\dot{m}c)_b. \tag{17}$$

The heat conducted from the core to the center of the skin layer is given by

$$Q_{cond} = k_{sk} A_L (T_c - T_{sk})/(\delta/2). \tag{18}$$

The corresponding skin thermal resistance is

$$R_{sk} = \delta/2\,k_{sk}\,A_L. \tag{19}$$

The skin layer is at temperature T_{sk} and has a thermal capacitance C_{sk}. Heat is conducted from the skin layer to the surface through resistance R_{sk}. Energy due to evaporation $E_{\text{cutaneous}}$ leaves from the skin surface.

All thermal interactions between the lizard and the environment occur at the skin surface as shown on Fig. 6 and described by Eq. (12). The convection resistance from the skin to the environment is

$$R_{conv} = (T_z - T_{sk})/Q_{L,conv} = 1/h_L\,A_L. \tag{20}$$

Radiation heat transfer occurs between the lizard skin and both the sky and ground. The two radiation resistances, which are dependent on the lizard surface temperature, are given by:

$$\begin{aligned}R_{rad,sky} &= (T_{sky} - T_{sk})/Q_{rad,sky}\\ &= 1/A_L\,F_{L-sky}\,\sigma\,(T_{sky}^2 + T_{sk}^2)\,(T_{sky} + T_{sk})\end{aligned} \tag{21}$$

$$\begin{aligned}R_{rad,s} &= (T_s - T_{sk})/Q_{rad,s}\\ &= 1/A_L\,F_{L-s}\,\sigma\,(T_s^2 + T_{sk}^2)\,(T_s + T_{sk}).\end{aligned} \tag{22}$$

The general model represented by Fig. 6 was simplified for the lizard by considering the relative values of the resistances and capacitances. A 40 g lizard with a surface area of 140 cm², a snout-vent length of 13 cm, and a skin thickness of 1 mm was selected as representative. For the desert iguana, the total cardiac output is about 3.5 g/min–100 g over the range of 20 to 40° C (Templeton, 1970), and this value was also assumed for the skin blood flow. The value of thermal conductivity of the skin was taken to be 0.072 cal/min-cm-C (Chato, 1966).

In order to draw some general conclusions about the model, the three environmental resistors, R_{conv}, $R_{rad,sky}$ and $R_{rad,s}$, were combined into a single equivalent environmental resistance. For the purpose of calculating this environmental resistance, the lizard skin, the sky and the ground temperatures were all assumed to be at 300° K[3]. The lizard convection coefficient was calculated using a 200 cm/sec air velocity which, from Fig. 4, gives $h_L = 0.033$ cal/min-cm²-C. The three resistances described by Eqs. (20), (21) and (22) are then 0.216, 2.87 and 2.87 min-C/cal, respectively. If a single effective environmental temperature is used in place of the three environmental temperatures, then the single environmental resistance can be found as the equivalent resistance resulting from

3 The choice of 300° K was somewhat arbitrary, but the arguments to follow would not be changed for any reasonable choice.

three parallel resistors. The thermal resistance and capacitance values for this representative animal subjected to a representative environment are:

Core capacitance	$C_c = 23.4$ cal/C
Skin capacidance	$C_{sk} = 12.6$ cal/C
Skin resistance	$R_{sk} = 0.0046$ min C/cal
Blood flow resistance	$R_b = 2.5$ min C/cal
Environmental resistance	$R_e = 0.19$ min C/cal

The blood flow and skin resistances act in parallel to facilitate heat transfer from the core to the skin. Since the skin resistance is three orders of magnitude less than the blood flow resistance, the majority of the heat flow occurs by conduction, and the skin blood flow can be neglected. However, the blood flow is important for maintaining the core at a uniform temperature.

For *Dipsosaurus dorsalis*, the values of the resistances are such that we will be able to treat the animal as being uniform in temperature. We will show this by estimating the temperature differences in both transient and steady state conditions. In steady state, the temperature difference between the core and skin is due to the flow of heat $(M - E_{\text{respiration}})$ through the internal resistance. The total water loss from *Dipsosaurus dorsalis* in dry air has been measured by Templeton (1960). Of the total loss, at low temperatures approximately 30% is respiratory loss. As temperature increases, the respiratory percentage increases (Templeton, 1970). The data of Templeton plot as straight lines on semilog coordinates, and we fitted the data by eye with exponential relations. The energy flow corresponding to water loss was obtained by multiplying water loss by the latent heat of vaporization for water. The evaporative water loss per g of body weight is given by:

$T_L < 20°$ C:

$$E = 0.39 \text{ cal/min-100 g} \tag{23a}$$

$20° \text{ C} < T_L < 36° \text{ C}$

$$E = 0.12 \, e^{0.0586 \, T_L} \text{ cal/min-100 g} \tag{23b}$$

$T_L \leqq 36°$ C

$$E = 4.25 \times 10^{-3} \, e^{0.1516 \, T_L} \text{ cal/min-100 g} \tag{23c}$$

Other water loss data for resting desert iguanas is available. Minnich (1970a) found values somewhat lower than Templeton's values. The values from Templeton were used in our study as an upper bound for our water loss calculations.

The oxygen consumption values obtained by Dawson and Bartholomew (1958) for *Dipsosaurus dorsalis* were used throughout this paper to estimate the metabolic heat generated. We assumed that 5 cal of heat

were produced for each cc of oxygen consumed. The relation for meta-
bolism M per 100 g of body weight is given by

$$M = 0.37\ e^{T_L/10}\ \text{cal/min-100 g.} \tag{24}$$

To estimate the maximum core-skin temperature difference in steady
state, we assumed that all of the metabolism occurs at the core, and all
water loss occurs at the skin. Over the range of core temperature 20–43° C,
we find that the core-skin temperature difference is less than 0.1° C, and
that respiratory water loss would reduce this difference further. Thus in
the steady state, the lizard is essentially at a uniform temperature.

Under transient or nonsteady state conditions, a system may be con-
sidered as being at a uniform temperature if the Biot number (the ratio
of internal to external resistance) is less than 0.1 (Holman, p. 78, 1968).
For this value of Biot number, the maximum temperature difference
inside the animal is about 5% of the temperature difference between the
core and the environment. For *Dipsosaurus dorsalis* under typical
environmental conditions, the Biot number is about 0.025, and the
maximum temperature difference is about 3%. Thus, for both steady
state and transient conditions, the desert iguana can be treated as a single
node (i.e., at a uniform temperature T_L throughout). The skin and core
capacitances are combined into a single capacitance $C = (C_{sk} + C_c)$.

The thermal energy balance equation for the lizard becomes:

$$Q_e + M = E + C\ dT_L/dt. \tag{25}$$

Rearranging,

$$\frac{dT_L}{dt} = \frac{Q_e}{C} + \frac{(M-E)}{C}. \tag{26}$$

We found that including the term $(M-E)/C$ in Eq. (26) affected the
computed core temperatures by less than 0.4° C over the range of lizard
temperatures of 20 to 45° C. Under exercise conditions, metabolism may
increase up to four times (Templeton, 1970), but evaporation may be
expected to increase proportionately due to the increased ventilation
rate needed to supply the additional oxygen. Thus we can neglect the
contribution of the metabolism and water loss to the energy balance for
all conditions, and Eq. (26) can be simplified to:

$$\frac{dT_L}{dt} = \frac{Q_e}{C}. \tag{27}$$

It is important to realize that these simplifications are not a necessary
part of the model. For lizards of larger size or thicker skin, or for other
animals, these simplifications may not be valid and all of the terms of
Fig. 6 may have to be included. For very large animals, even the two-
layer model may not be adequate. For example, Stolwijk (1971) utilizes

25 nodes to model the thermal response of man, and Wissler (1971) has extended this to 250 nodes.

The lizard model developed in this section was verified through a comparison between actual and predicted response of a live lizard. An animal was heated 10–14° C above the air temperature and allowed to cool in the wind tunnel. Its temperature was measured by a copper-constantan thermocouple inserted 3 to 4 cm into the cloaca. During these test conditions, there was no solar energy incident on the animal and air and radiant temperatures were all equal. The environmental heat flow, Q_e, under these conditions becomes

$$Q_e = h_L A_L (T_z - T_L) + (F_{L-s} + F_{L-sky}) A_L \sigma (T_z^4 - T_L^4) \qquad (28)$$

which can be written using the environmental resistance introduced earlier

$$Q_e = (T_z - T_L)/R_e \qquad (29)$$

where

$$R_e = 1/[|h_L A_L + (F_{L-s} + F_{L-sky}) A_L \sigma (T_z + T_L) (T_z^2 + T_L^2)]. \qquad (30)$$

Eq. (27) can be written in terms of R_e as:

$$\frac{dT_L}{dt} = \frac{(T_z - T_L)}{R_e C} . \qquad (31)$$

The temperatures in Eq. (30) are degrees absolute and thus do not change significantly during the tests. Therefore, R_e is essentially a constant and Eq. (31) can be integrated to give

$$T_L = T_z + (T_{L, i} - T_z) e^{-t/R_e C} \qquad (32)$$

where $T_{L, i}$ is the lizard initial temperature (i.e., at the start of cooling).

Two of the eight cooling curves obtained are shown in Fig. 7 in comparison with the predicted relation Eq. (32). The lizard cools slightly slower than predicted; the difference between heating and cooling has been noted previously (Templeton, 1970; Weathers, 1970). A vasoconstriction of the skin alone would require an increase in skin thickness of about 0.3 cm to produce these differences. The desert iguana has an anatomical skin thickness of about 0.1 cm, and thus restriction of skin blood flow would not be sufficient to account for these differences. An alternative mechanism would be vasoconstriction in the appendages. Evidence on another species of lizard (Brattstrom, 1972) supports the idea of circulatory shutdown only in the appendages during cooling. There is no difference between the predictions and the heating results, and the data for the heating of live lizards (Weathers, 1970) agrees with the castings which are uniform in temperature. These observations are sufficient to account for the difference between heating and cooling.
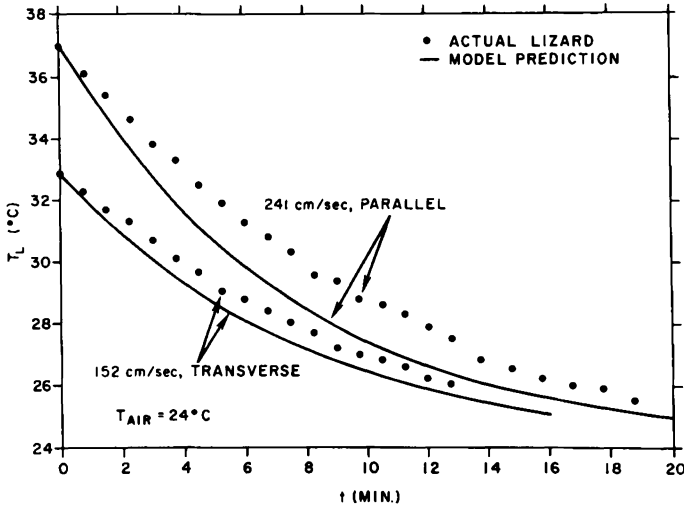
Fig. 7. Comparison of predicted and experimental cooling curves for live *Dipsosaurus dorsalis* in a wind tunnel

Such questions about blood flow changes, however, tend to obscure the point that even ignoring the physiological capabilities of the animal and assuming the animal to be uniform in temperature, the simplified model, Eq. (27), predicts the time at which a lizard reaches a given temperature to within about three minutes. For this and other small species, it is questionable whether finer resolution is wanted for predictive purposes. In the following section, the model represented by Eq. (27) is used to predict the gross behavioral response of the desert iguana in the field.

V. Predicted Behavior of *Dipsosaurus dorsalis* in the Field

The prediction of the behavior of *Dipsosaurus dorsalis* in the field requires combining the environmental microclimate model and the physiological model for the animal developed earlier with physiological data on preferred temperature ranges for activity. In laboratory experiments, the thermoregulatory behavior of *Dipsosaurus dorsalis* results in a maintenance of body temperature near a preferred level of 38.5° C with the central 95% of all body temperatures ranging between 33.2 to 41.8° C, respectively (DeWitt, 1967). However, a temperature of 38° C appears to be a minimum preferred temperature for activity (Kluger, 1973). Similar levels of body temperature are observed in the field (McGinnis and Dickson, 1967; Mayhew, 1971). Voluntary hyperthermia may occur up to a level of 43–44° C (Norris, 1953; DeWitt, 1967). Under naturally

2*

or experimentally imposed high temperatures, panting is also employed, and this serves to prevent head and trunk temperatures from rising above 43 and 47° C, respectively (DeWitt, 1967). In the field, panting is a temporary emergency defense only since it results in excessive loss of water reserves. In view of these observations, we have chosen a minimum activity temperature of 38° C, and a maximum temperature of 43° C for our predictions.

Fig. 8 shows the predicted environmental temperatures and core temperature for the desert iguana for the average 15th of July in Palm Springs, California. For the purpose of this calculation, the animal is assumed to be standing on the surface the entire day[4]. We assume that when the predicted desert iguana temperature is below 38° C, the animal would actually be in its burrow. This is indicated by the vertically hatched line extending to 07:30. After emergence at 07:30, the animal warms rapidly and reaches 43° C by about 08:15. Since the maximum temperature of the animal is 43° C, we allow the animal to step into and out of the shade until 08:45. After 08:45, however, the lizard temperature even in the shade exceeds 43° C. Without bushes to climb, the animal would have to retreat to its burrow or overheat and die. In the afternoon the temperatures fall and the pattern would be reversed with the animal,
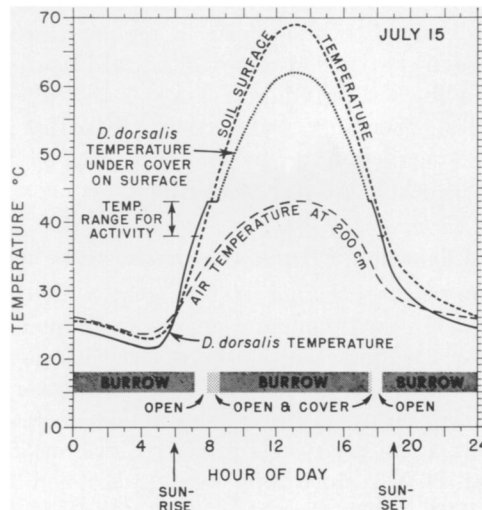

Fig. 8. Predicted environmental and lizard temperatures for July 15 in Palm Springs, California

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4 For these predictions, the following lizard parameters were used: $A_L = 150$ cm², $A_{p,d} = 31$ cm², $A_{p,r} = 60$ cm², $L = 13$ cm.

re-emerging, moving in and out of the shade, remaining in the open for a short time and finally retreating to the burrow.

We have performed similar calculations for the average 15th of every month of the year. The predicted behavioral pattern as a function of time of day and day of the year is shown in Fig. 9. The predicted activity pattern at the bottom of Fig. 8 is displayed vertically in Fig. 9 for July 15. In the early spring, the desert iguana should be active in the middle of the day. This pattern progresses to a morning and afternoon pattern in the middle of the summer with the animal becoming active again in the middle of the day in the fall.

The earliest possible yearly emergence using the criterion stated above is seen to be about the 1st of February, and activity is possible only for a very short time. However, we predict the soil surface temperature will not reach 38° C for the average year until about the first of March. Since the desert iguana emerges by lying at the burrow entrance on the sand surface before emerging completely and becoming active, we predict that animals would not be active before the first of March. Similarly, after the first of November, the surface under average conditions would not reach 38° C. Thus, we predict surface activity would be restricted to between March 1 and November 1.

The natural environment of the desert iguana has different bushes of varying heights, and these allow the desert iguana to extend its activity times. As indicated in Fig. 1, both temperature and wind speed vary depending on the height above the ground. By climbing up into bushes,
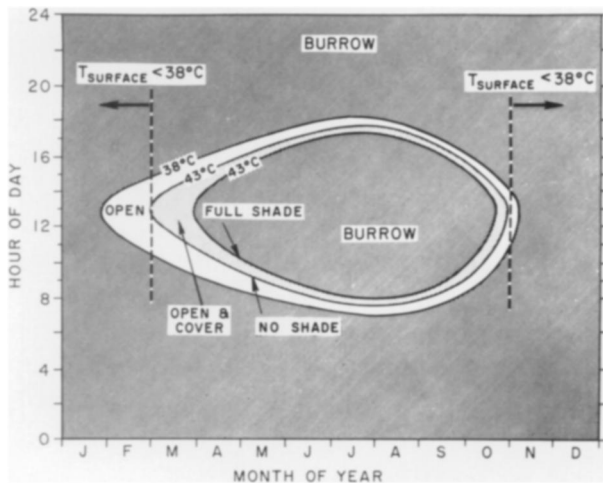

Fig. 9. Predicted seasonal behavioral pattern for *Dipsosaurus dorsalis*

animals reach not only lower air temperatures but higher wind speeds which increase convective heat transfer. We modeled these conditions by employing the logarithmic velocity and temperature profiles, Eq. (3) to compute the local velocity and temperature for a lizard at any height, z, in a bush. We also assumed that the lizard in the bush is shielded from solar radiation and that the infrared radiation exchange is between the lizard and the local surrounding vegetation which is assumed to be at local air temperature.

The activity pattern for a lizard able to climb to different heights is shown in Fig. 10. The presence of bushes allows a considerable extension of the time available for outside activity. If the animal could climb to 200 cm and still be in deep shade, it could stay out all day even in August.

Because of uncertainty about the lower temperature limit for activity, particularly for emergence at early times of the year, other body temperature contours have also been added to Fig. 10. This graph also shows that emergence criteria would be more easily resolved in the middle of April or in October when the constant core temperature lines are spaced farther apart than in July and August when temperatures rise rapidly and the temperature contours are close together. Fig. 10 also demonstrates that if the animals could be active at a core temperature of 20° C, they could be nocturnal in the middle of the summer.
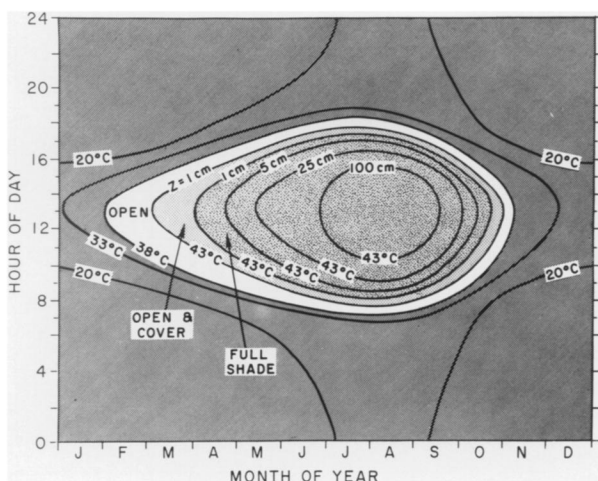

Fig. 10. Influence of bush height on the seasonal behavioral pattern for the desert iguana

VI. Comparison of Behavior Predictions with Field Observation

1. General Studies

Johnson *et al.* (1948) reported that near Kelso, California on June 20, 1940, the desert iguanas were first observed at 8 a. m. and remained out until 1 p. m. Norris (1953) reported that "Early in the year (March and early April), the lizard is active throughout the middle of the day, and in midsummer, temperatures are usually so high that the lizard remains above ground for only 3 or 4 hrs in the morning". The general behavioral sequence of animals throughout a day described by Norris was that of emergence, warming, feeding, climbing, seeking shade in hummocks of creosote bushes, and finally retreat into burrows.

2. Studies by W. W. Mayhew

The behavioral sequence in time is present in W. W. Mayhew's (1971) accumulation of body temperature and location data collected over more than ten years on the desert iguana at Palm Springs, California. The data comes from individuals he found while walking or driving on the desert, as opposed to continuous observation of specific individuals.

Fig. 11 summarizes all of Mayhew's data for desert iguanas captured at Palm Springs[5]. We do not know how much earlier or later than the
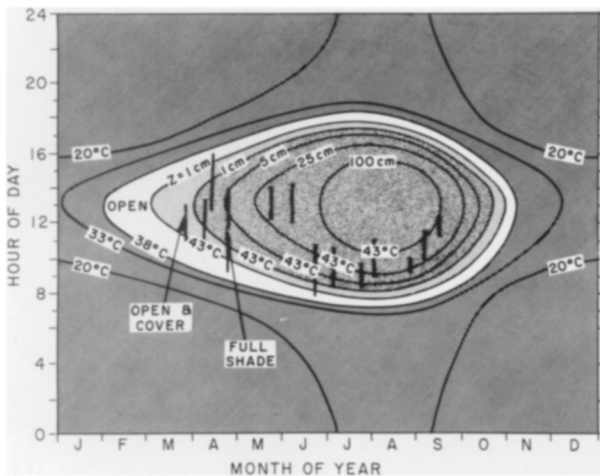

Fig. 11. Comparison of behavioral observations of Mayhew (1971) with model predictions. Data of Mayhew shown as solid bars

5 Mayhew (1965) published similar data for *Uma inornata* which has a lower temperature range for activity. The general behavior pattern looks similar to that shown on Fig. 11, except that afternoon activity patterns are clearly present and there is no activity in the middle of the day.

time of the observation that lizards were present. Thus exact emergence and retreat times are uncertain. The predictions are based on the average thermal environment for the month, while the data of Mayhew are taken on specific days which may differ from the average. For example, the two days with late observed activity (May 26 and June 9) were each unusually cool days with the air temperature never exceeding 38° C.

Probably the most intriguing discrepancy between Mayhew's observations and our predictions is the lack of afternoon activity in the summer and the much reduced activity in the fall. The midsummer pattern agrees with our more detailed field observations described later which shows that the majority of a desert iguana population apparently does not emerge in the afternoon. One possible explanation for this is the high temperature wave in the sand that might drive the animal deeper into its burrow (Fig. 2). Another possibility is that there might be a total daily water loss that would be too costly. This possible water limitation is discussed below in section VII on predictions of water and food requirements.

The lizard temperatures measured by Mayhew in July are higher than those measured in March, as shown in Fig. 12. This would seem to indicate a seasonal change in temperature preference. However, the rate of temperature increase is more rapid in July than March (Fig. 9), and in July an animal would have to be located, captured, and measured within 15 minutes of the time it emerged (assuming 38° C emergence temperature)
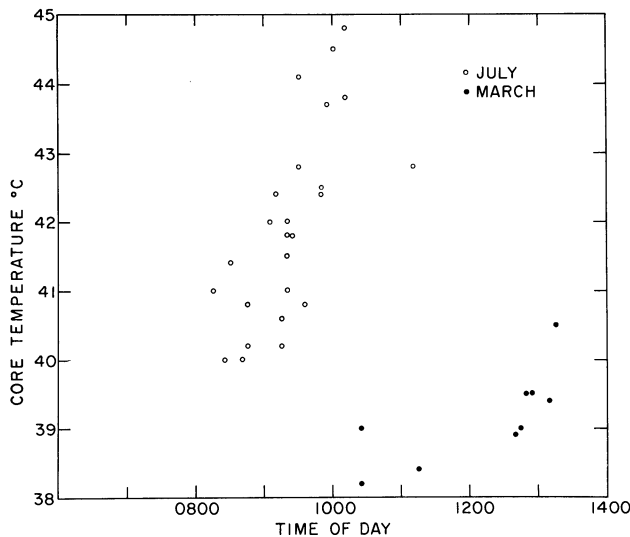

Fig. 12. Variation with season of measured lizard core temperature in the field from Mayhew (1971)

to obtain the lowest temperatures (40° C) shown in Fig. 12. In March, on the other hand, desert iguanas would never have to reach 43° C at all by utilization of shade and could easily remain at lower temperatures. Thus, inferences on temperature preference from field data must be scrutinized with care, especially if the data are obtained by sampling animals encountered by chance (also see DeWitt, 1967, Fig. 12).

3. Palm Desert Field Studies

In an extensive study of these animals throughout July and August, 1961, one of us (C. B. D.) conducted a series of experiments on physiological and behavioral problems of the desert iguana on a flat, 45 by 80 m site in Palm Desert, Riverside County, California. Forty-seven of the estimated population of 58 desert iguanas inhabiting the site were individually marked by various combinations of colored tape wrapped around the base of the tail. On July 11, 12, 25 and 27, observations were made continually from sunrise to sunset by a stationary observer and by a second observer walking through the site. Observations were made throughout the night at about 3-hr intervals. Locations of all observed animals were recorded on a map.

The daily patterns of environmental temperatures were similar to that in Fig. 8. The pattern of activity for the iguanas is shown in Fig. 13 in relation to the times for sunrise, sunset, peak solar radiation, and predicted emergence. Emergence first occurs at about 07:00, peak activity occurs from 08:00 to 10:00, and activity terminates at about 12:00 to 14:00. Deviations from this pattern sometimes occur, as on July 12 when emergence was delayed about 1.25 hrs as a consequence of cloudy skies from 05:00 to 10:00. The predicted emergence times compare favorably with those observed for clear days.

Additional evidence that actual emergence times correspond closely with the time at which the preferred body temperature can be maintained outside the burrow is supported by an experiment in which four desert iguanas were tethered out on the desert one hour before the first natural emergence. At the time of the first observed natural emergence, these lizards had attained body temperatures of 37.5, 38, 39 and 40° C which are all within 2° C of the lower level of 38° C used in our predictions.

After emerging, the lizards first occupy open areas, often orienting their bodies perpendicular to solar radiation. Tethered animals with implanted thermocouples show a rapid rise in body temperature under these conditions (about 6° C per hr). Utilization of shade begins soon after emergence and increases until nearly all lizards are observed in the shade of bushes. Data on these observed patterns of activity for a typical summer day are summarized in Fig. 14. The first peak of activity in bushes shown in this figure is largely due to arboreal feeding on leaves
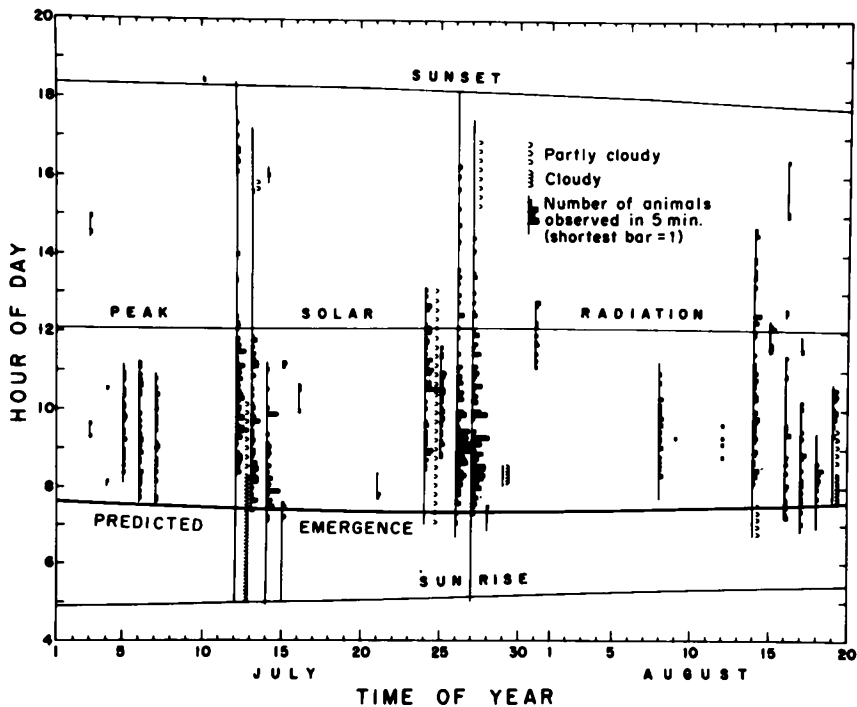
Fig. 13. Behavioral observations in Palm Desert, California in comparison with
model predictions

and *Petalonyx* flowers. This early peak of activity in bushes is not pre-
dicted from our thermal analysis, and is an example of the importance
of including both engineering and biological data in an analysis of
animal-environment interactions.

Since the density and height of bushes varies from one lizard territory
to another, variability in times of retreat to burrows is expected. A desert
iguana would be able to remain out all day if it could climb to 200 cm
in a bush and be completely shaded (Fig. 10); however, the bush height
on the test site was about 100 cm. It would also be possible for a cooled
lizard to re-emerge and make a brief excursion throughout the hottest
parts of the day. Such a sortie would be severely restricted due to the
rapid heating of desert iguanas. Consequently, there is a gradual drop
in the numbers of animals active after peak activity as shown in Figs. 13
and 14.

Throughout midsummer, parts of burrows usually have temperatures
of 37–40° C, and thus afford temperatures which at all times are in the
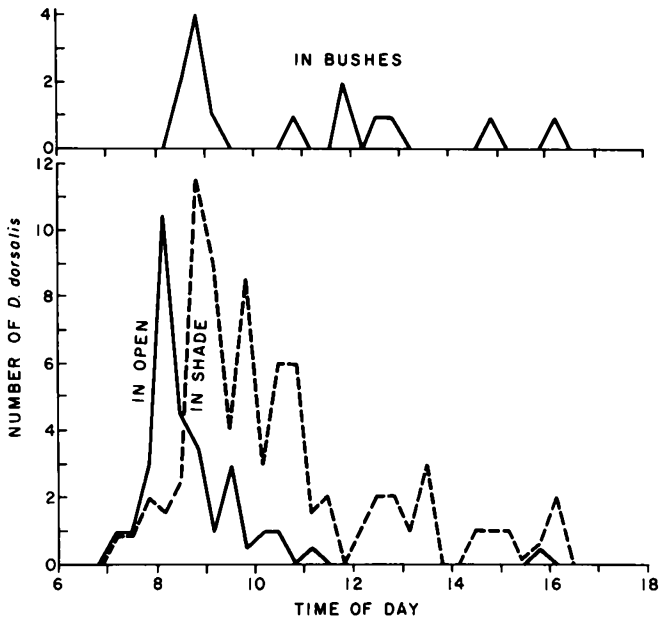preferred body temperature range. Temperatures at the ground surface

Fig. 14. Activity pattern for the desert iguana during a typical day in July

as well as beneath the surface down to about 32 cm daily exceed 38° C. We expect and find that burrows are at least 32 cm deep if continually exposed to the sun in midsummer.

4. Kelso, California Field Studies

A series of studies on the behavior of the desert iguana was initiated at two sites near the Kelso dunes, Kelso, California, beginning in June 1970. From June 15 to July 7, 1970, we observed the stereotyped daily summer activity pattern described by Norris (1953), Johnson (1948), and DeWitt (previous section). The animal emerges over a 10–15 min period and then begins to browse and sample various vegetation, sand, twigs, and fecal pellets. The animal roams about, which during this time of year lasts about an hour and covers about 70 to 100 m. The lizard originally spends most of its time in the sun moving from bush to bush with progressively faster traverses from one bush to the next as the temperature increases. During the period April 11 to April 15, 1971, additional behavioral observations were made. These were supplemented by meteorological instrumentation in order to verify the behavioral predictions.

W. P. Porter *et al.*:

In Fig. 15, the observed emergence and retreat of several lizards are shown in comparison with the activity time predicted by the model. Only those lizards which were actually observed to emerge from a burrow or retreat into a burrow are shown. The two observed emergence times lag by 2 to 3 hrs the predicted emergence time. The predictions were made
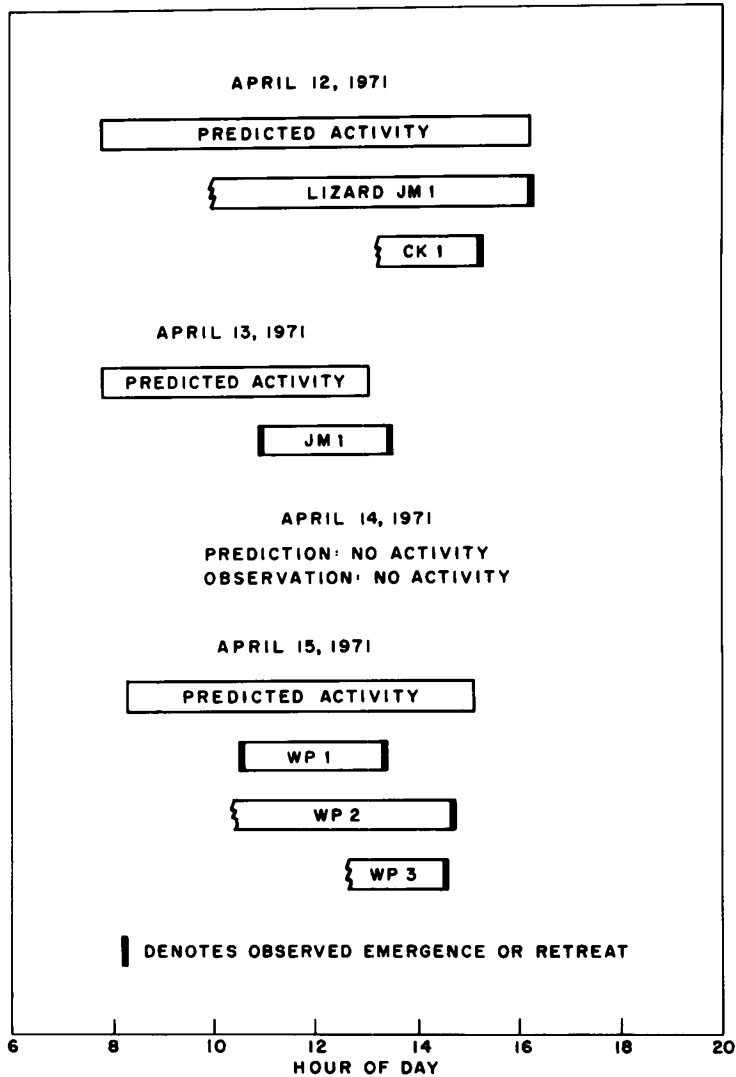

APRIL 12, 1971

PREDICTED ACTIVITY

LIZARD JM 1

CK 1

APRIL 13, 1971

PREDICTED ACTIVITY

JM 1

APRIL 14, 1971

PREDICTION: NO ACTIVITY
OBSERVATION: NO ACTIVITY

APRIL 15, 1971

PREDICTED ACTIVITY

WP 1

WP 2

WP 3

▌ DENOTES OBSERVED EMERGENCE OR RETREAT

6   8   10   12   14   16   18   20
HOUR OF DAY

Fig. 15. Comparison of behavioral observations with model predictions for April 12–15, 1971

for flat terrain while the burrows of these two lizards were on the western slope of hummocks. The observed retreat times generally agree with the predicted times. The animals are typically moving about in the open prior to retreat. On April 12 and 15, the sun shown all day and the observed retreat occurred close to the predicted times. April 15 was a colder day than April 12, and both the observed and predicted retreats occur 1 to 1.5 hrs earlier than April 12. April 13 was initially sunny, with heavy cloud cover beginning at 13:00 hrs. The one lizard observed to retreat entered its burrow 2.5 hrs earlier than it had on the previous day, consistent with the predictions. The heavy cloud cover on April 14 gave rise to a maximum predicted lizard temperature of 20° C, and there were no observations of emergences or activity.

In addition to the observations of activity patterns of free ranging animals and measurements of their physical environment, we set up a series of field experiments with castings of the desert iguana on the surface of the sand in April, 1971 (Fig. 16). We are able to predict temperatures of the casting in the wind tunnel, but had not done so for the field and so these tests were undertaken to further evaluate the model. Two identical castings were fitted with thermocouples to monitor their
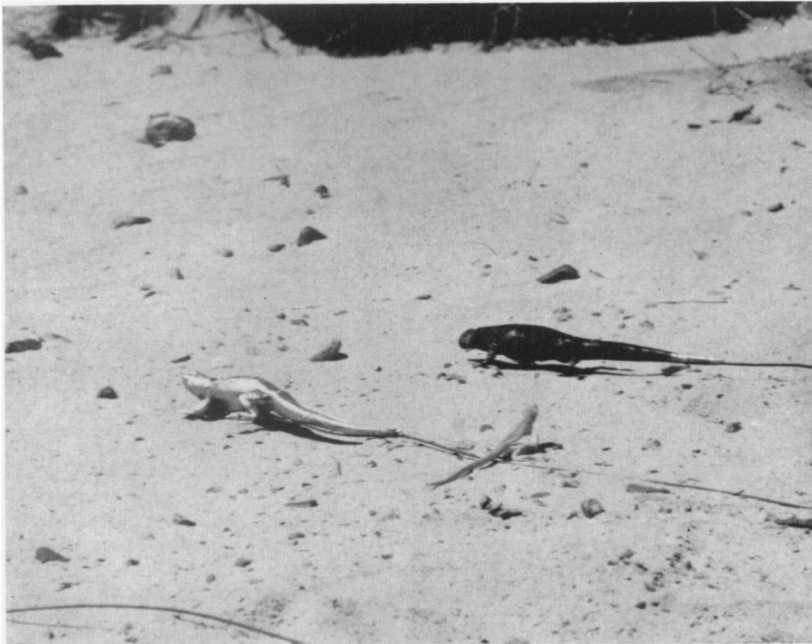

Fig. 16. Field experiments showing live lizard, gold-plated and blackened lizard castings (April, 1971)

Fig. 17. Mojave Desert field site showing terrain and micrometeorological instrumentation
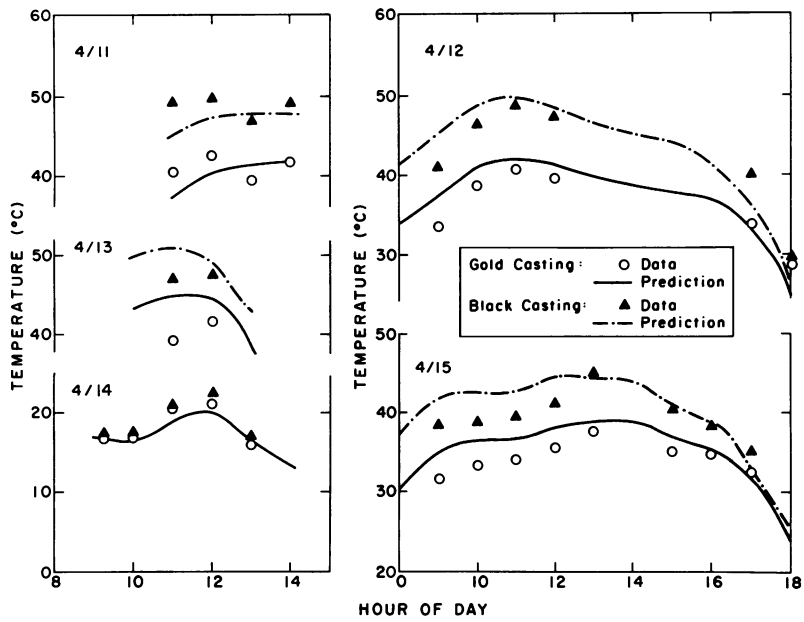

Fig. 18. Comparison of predicted and measured lizard casting temperatures in the field

temperature. One of the castings was gold-plated and had a solar absorptivity of 0.36 and a long wavelength emissivity of 0.1. The other casting was covered with soot from a paraffin candle and had a solar absorptivity and long wavelength emissivity of about 0.99. These surfaces were chosen to test the model at the limits of absorbed radiation and thus bracket the radiation absorbed by a live animal. The two castings were placed about 1 mm off of the sand surface with tiny pebbles under each foot to minimize conduction to the substrate. The test area is a flat sandy wash with creosote bushes around the perimeter (Fig. 17) and typical of lizard habitat.

The experimentally determined temperatures for the castings are presented in Fig. 18 in comparison with the predictions. The data and predictions agree within about 3° C for the sunny days. During the day with heavy cloud cover, April 14, the gold and black castings are essentially at the same temperatures, and these temperatures agree within about 2° C of the predictions. We feel that these results further substantiate the micrometeorological model developed here.

5. Biotron Laboratory Results

Our predictions of activity patterns were investigated further in a miniature desert setup in the Biotron (a controlled environment facility) at Madison, Wisconsin (Fig. 19). The room is $8^1/_2 \times 12$ feet and contains
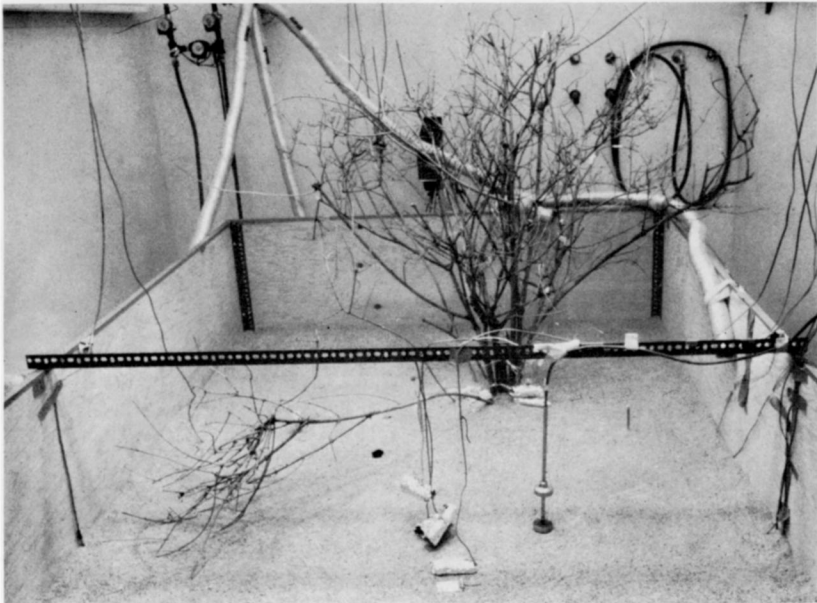

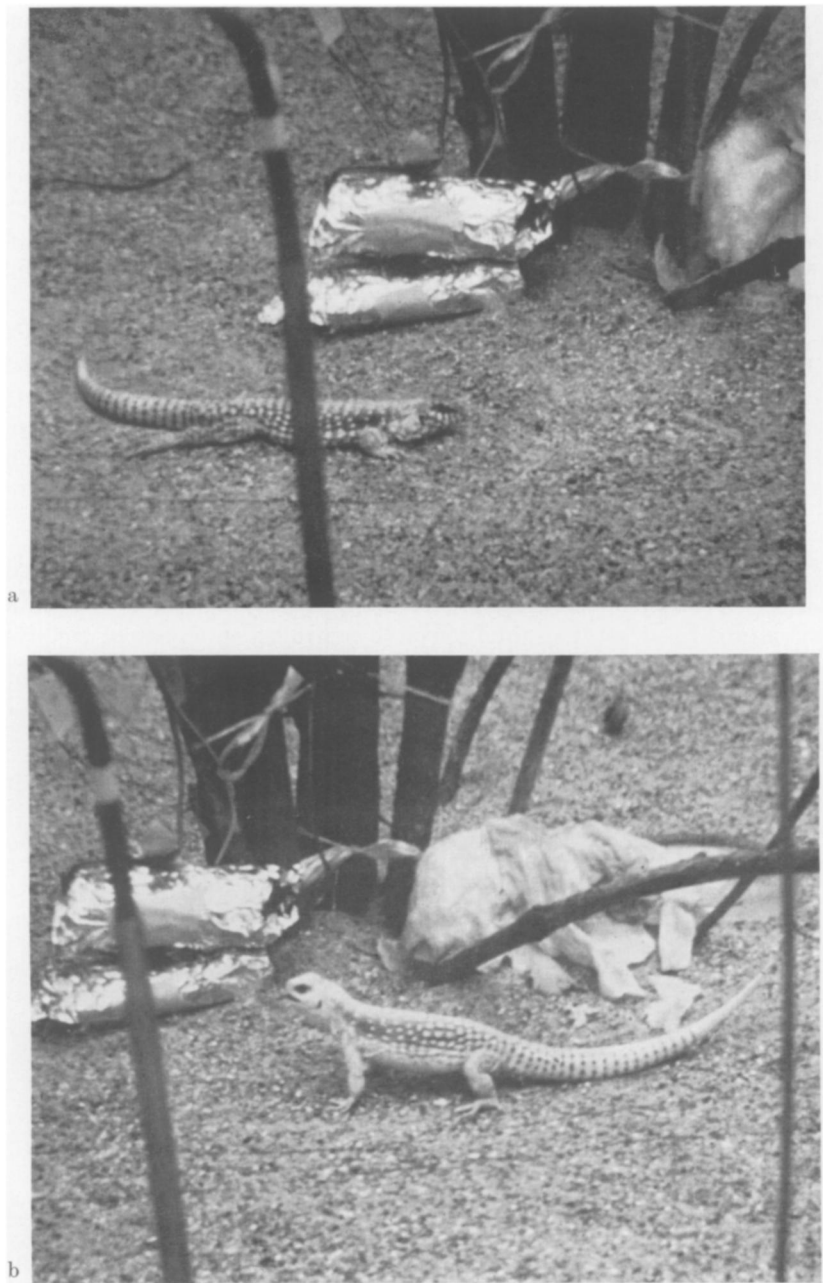Fig. 19. Simulation of the desert in the Biotron facility, Madison, Wisconsin

Fig. 20a—d. Behavior of the lizard in the Biotron: a Shortly after emergence;
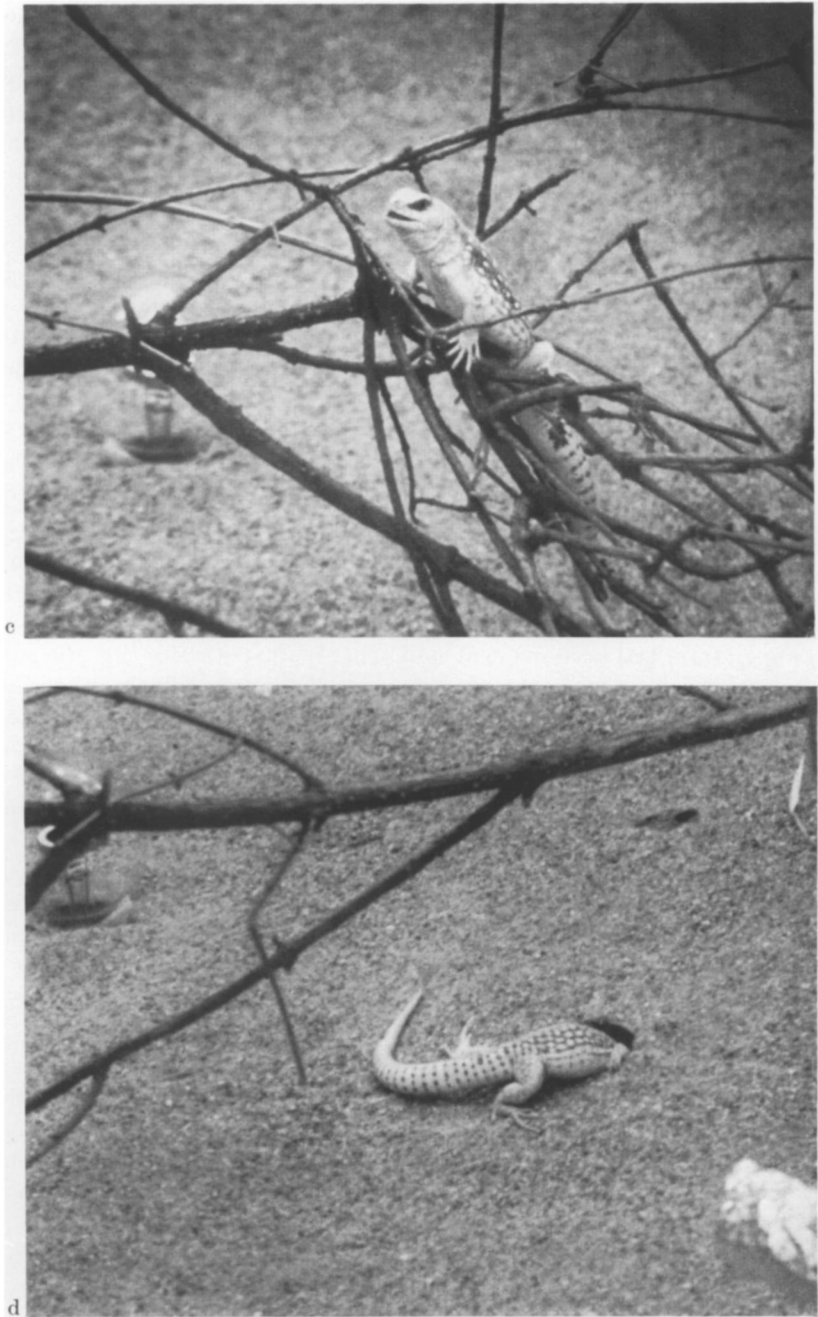b midday behavior; c climbing a bush; d retreat

Fig. 20c and d

7000 pounds of sand approximately 65 cm deep. At the bottom of the sand is a bed of copper tubing through which hot or cold fluid passes to control deep sand temperature. A bank of tungsten iodide and fluorescent lamps are in the ceiling to allow simulation of desert sunlight. However, the magnitude of the thermal radiation from the lamps has a large uncertainty. Air temperature, humidity, and wind speed can also be controlled to duplicate desert conditions at any time of the year.

A desert iguana was placed in the room, and the conditions for the 15th of March and the 15th of July were duplicated. The animal each day goes through the behavior patterns observed in the desert. On any given day, the darkened lizard emerges slowly and lies on the substrate (Fig. 20a). As the day progresses, the lizard becomes lighter in color, moves faster, and carries its body higher (Fig. 20b). Finally, it seeks shade at the base of its bush and also climbs up into the bush (Fig. 20c). It also uses its burrow to cool off (Fig. 20d) and then reemerges with the length of stay in the burrow before reemergence increasing as the day becomes hotter.

When the "day" programmed for the room was changed from spring (March 15) to summer (July 15), the animal emerged nearly an hour earlier as predicted, though all thermal changes (including deep sand temperature) had been made at midnight. We hypothesize that the animal only emerges when the sand surface temperature is higher than the burrow temperature, for then the emerging animal gains a thermal advantage and is assured of continued warming. To investigate the cue(s) used for emergence, the environment was "split" at the sand surface into "top" and "bottom" halves. The air temperature, humidity and sunlight simulated one season, while the deep soil temperature simulated the same or a different season. The sequence of experiments was as follows: a) Spring on top and bottom to serve as a frame of reference; b) Summer on top and spring below; c) Summer on top and bottom; and d) Spring on top and summer below.

Results of the experiments in the Biotron are shown in Fig. 21. Behavior for both spring and summer days appeared consistent with spring and summer field observations. When spring/spring suddenly switched to summer/spring at midnight on November 27, emergence time rapidly advanced. However, the first of the two days showed an emergence almost an hour later than the second day. The reason for this is uncertain. Possibly the cool deep soil and/or a circadian rhythm caused the animal to ignore temperature cues from above.

A midnight switch from summer/summer to spring/summer on 2 December resulted in the animal arriving at the burrow entrance at the appropriate emergence time for summer on top, but apparently because
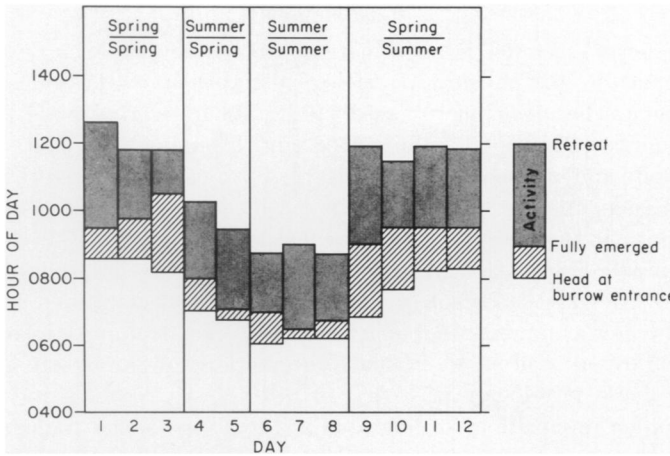
Fig. 21. Influence of controlled seasonal alterations on lizard behavior in the Biotron

it was cool on top, emergence was delayed until 09:00 hours. This emergence was apparently still too early because the animal kept returning to the burrow to warm up the first half hour after emergence. The desert iguana's use of the burrow to warm up was an activity we have never observed in the field. On the second day of spring/summer, the animal remained in the burrow 45 min longer than the first day before emerging, and on the third day emergence was an additional half hour later. Possibly, the animal was beginning to ignore the warm deep burrow temperature as an indication that the day above would be "expected" to be a warm summer day rather than a cool spring day. Kavanau and Norris (1961) have shown that for a burrowing shovelnosed sand snake, *Chionactis occipitalis*, circadian rhythms determined positioning near the surface in anticipation of emergence, while sand surface temperatures determined the actual emergence. Whether subsurface temperatures entrain those rhythms in the desert iguana is unresolved at present.

A failure of the dimmer system on the third day of spring/spring suggested that temperature, not light, is the final emergence cue for the desert iguana. At 08:30 hours the tungsten iodide bulbs stopped increasing in intensity. At 09:30 hours the dimmer was fixed and the lights brought to proper intensity without any disturbance to the room. The delay in temperature rise of the soil surface temperature coincided with the delay in emergence of the animal. Since light intensity at anticipated emergence time was normal, the delay in emergence suggests soil or animal temperature as the final emergence cue for the desert iguana.

3*

6. Summary

A general mechanistic micrometeorology model has been developed, and a model for the physical, physiological and behavioral response of the desert iguana has been incorporated with it. The integrated model predicts field emergence times to within 15–30 min throughout the course of the year. Daily and seasonal activity patterns have been predicted that agree with the general field descriptions in the literature. Predicted length of time active in the spring and fall agree with observations of Mayhew and with our own observations. However, the predicted activity period in the summer, which is based solely on temperature considerations, is longer than Mayhew's and our observations indicate. To attempt to resolve this discrepancy, as well as to evaluate interactions of the desert iguana's anatomy and physiology with that of other desert animals and plants, we examine implications of food quality, food and water requirements, and predator-prey interactions in the next sections.

VII. Implications Concerning Water Loss and Metabolism

The thermal environment provides an outside limit on the time available for the desert iguana to engage in surface activity (Fig. 10). This activity requires an increased energy expenditure and water loss over that for an inactive animal in a burrow. The activity times determined from the behavioral model can be combined with metabolism and water loss measurements to estimate food and water requirements. Botanical information on the food value, water content, and leaf density of the various desert species can be incorporated to estimate the time required to obtain food and water. These considerations provide additional insight into the behavior of the desert iguana.

Metabolic rate and water loss are functions of body temperature as given by Eqs. (23) and (24). The data on which these equations are based has been obtained from laboratory experiments, and may not accurately reflect metabolic rate and water loss in the field. Nevertheless, these data do provide a basis for estimating field food and water requirements, and allow us to quantify the concepts discussed here[6].

The instantaneous values for metabolism and water loss for the lizard from Eqs. (23) and (24) were integrated over each day. Fig. 22 shows the contour pattern for cumulative daily energy expenditure of a lizard resting on the surface at any time of the year. For example, on July 15 there is little energy expenditure before 07:30. After activity begins, as represented by the dotted contour for $T_L = 38°$ C, metabolism rapidly increases. For these calculations, we have assumed that the animal tem-

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6 Water loss quantities in the following figures are based on Templeton's data (1960). If Minnich's data (1970) had been used, all values would be slightly reduced.
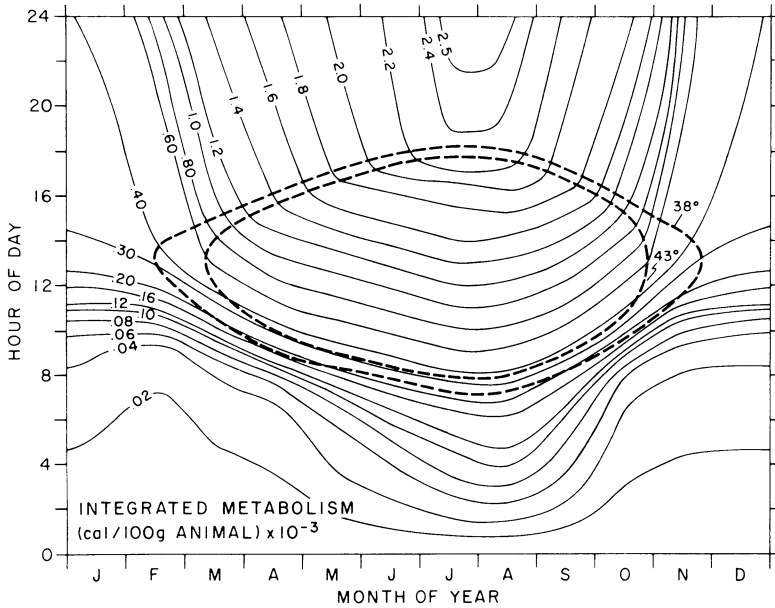
Fig. 22. Integrated daily metabolism for the desert iguana on the surface as a function
of time of year

perature does not exceed 43° C, which accounts for the even spacing of
the lines within the 43° C contour. As the lizard temperature drops late
in the day, there is a reduced rate of energy expenditure. The correspond-
ing water loss for this activity pattern, Fig. 23, is similar to that for the
metabolic expenditure.

We have chosen several behavioral alternatives to obtain upper and
lower bounds for food and water requirements. The cumulative daily met-
abolic requirements for a lizard on the surface at rest, active with a
metabolic rate twice that of the resting value, and active with a meta-
bolic rate five times that at rest are shown in Fig. 24. Also shown are
two estimates for metabolism of the animal in the burrow. For the lower
curve, we assumed that the animal was at deep soil temperature, and for
the other, that it moved in the burrow to seek the highest temperature
not exceeding 38° C. The metabolic scopes were chosen from data (Bar-
tholomew and Tucker, 1963; Templeton, 1970) which show a maximum
value for activity of about five times the resting value. The maximum
metabolic rate of five times the resting value is unrealistic for activity
all day, but represents an upper limit for computations of food require-
ments. For these calculations, it was assumed that metabolic rates higher
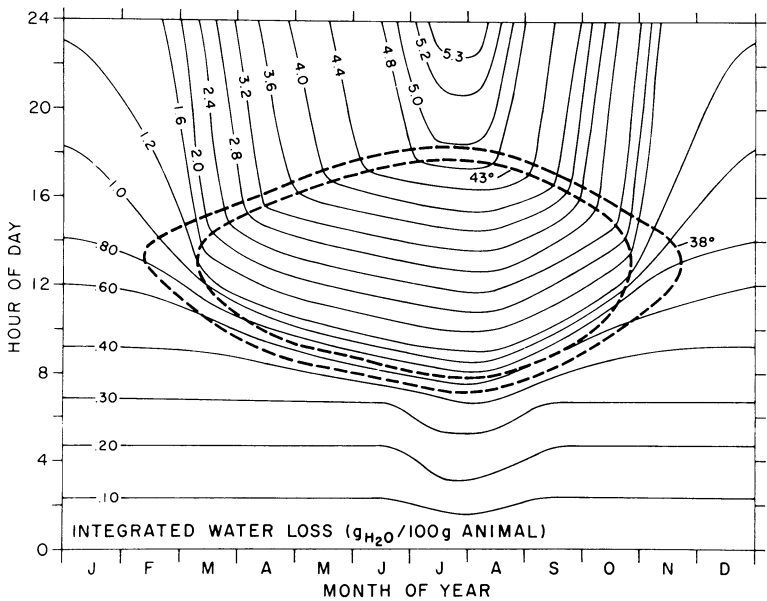than resting values occur only within the 38° C contour.

Fig. 23. Integrated daily water loss for the desert iguana on the surface as a function of time of year
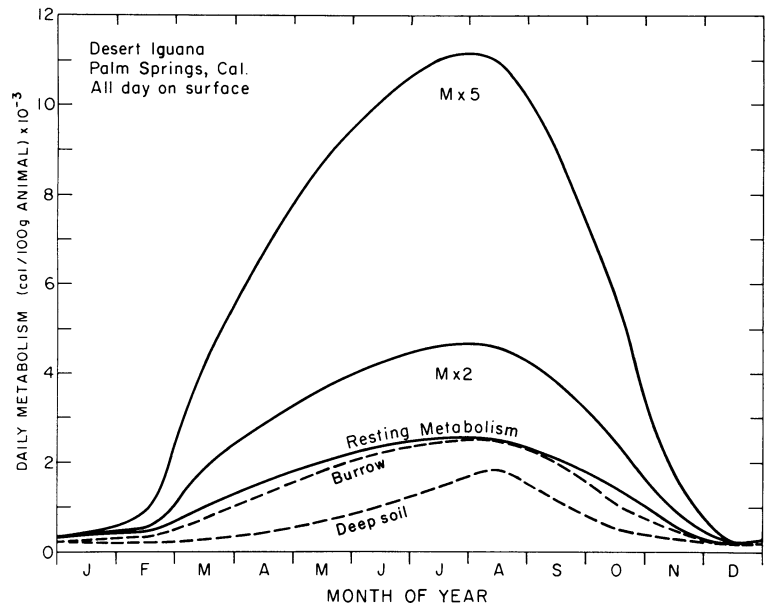

Fig. 24. Daily total metabolic expenditure for a lizard under various behavioral alternatives

The water losses for the behavioral assumptions corresponding to those used to obtain Fig. 24 are shown in Fig. 25 and are similar in shape to the metabolic curves. A total of 5 g/100 g per day are evaporated from a resting lizard and a maximum of 24 g/100 g per day from an active animal during July. This amounts to about 5 to 24% of the total body weight of any animal, and must be made up daily.

A comparison of water losses with metabolic caloric requirements has additional implications regarding behavior. The grams of food needed to meet the metabolic requirements may be estimated using a representative caloric equivalent of food consumed for a carbohydrate-fat mixture $(4.7 \times 10^3$ cal./g) and a digestive efficiency (30–50%, Minnich and Shoemaker, 1970). For example, on the 15th of July a 100 g desert iguana requires 1.0–9.0 g of food (fresh weight) to be active on the surface. Minnich and Shoemaker (1970) report approximately 5 g fresh weight/100 g per day for the desert iguana in the field. For all activity levels, the grams of water required is five times higher than the grams of food. Therefore, if the desert iguana is to engage in prolonged activity in the dry environment, additional water must be obtained.

An additional source is the water that might condense from the air in the sealed burrow. As an upper limit, we assume that burrow air is saturated at all times and that the desert iguana can take in all of the condensate. A typical burrow is about 30–50 cm deep and 3–5 cm in
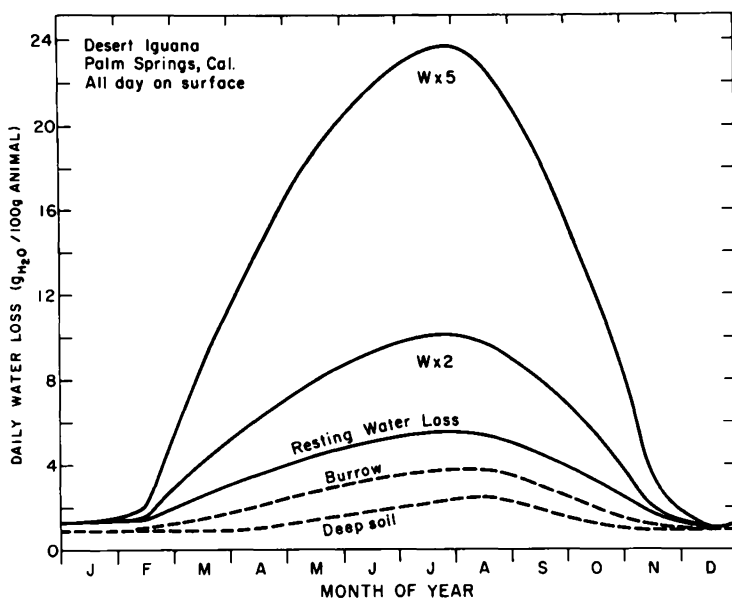

Fig. 25. Daily total water loss for a lizard under various behavioral alternatives

diameter with an air volume of 200 to 1000 cm³. The highest average
subsurface temperatures for these depths are about 40° C during the day,
and the lowest are about 25° C. During the day, the air in the burrow, if
saturated, would contain 0.01–0.05 g water, and at night would contain
0.004–0.02 g water. Thus 0.01–0.03 g water might condense in a burrow.
This is about two orders of magnitude lower than that lost by the lizard
during the day and is insufficient to supply the animal with the necessary
water even if replaced hourly.

As an alternative to additional water sources, the desert iguana might
consume approximately 5 times as much food as needed to obtain suffi-
cient water. Metabolic water may contribute 10–20% to the free water
available, but it alone is insufficient to meet the need. However, there
may not be sufficient time available to obtain the necessary food and
water.

There are several constraints on the animal that limit its activity
period and thus the time available for obtaining food and water. The
maximum daily activity period is determined by the "thermal time
limit" (Fig. 10), which set limits on the time available for obtaining food
and water. The other constraints are the limits on eating time, metabolic
reserve, and water reserve. The "eating time limit" is the time permitted
for the animal to engage in surface activity using one stomachful of
food. The "water time limit" is the time permitted for the animal to
engage in surface activity from the water available from one stomachful
of food.

Stomach volume and leaf density determine daily ingestible mass (the
number of leaves that can be ingested) and form the basis for computing
time limits. Eating rate, together with leaf density and stomach volume,
determines how long it takes to fill the stomach. Leaf caloric value and
digestive efficiency determine how many calories are available for a given
day. Leaf water content and digestive efficiency determine the free and
metabolic water available from a stomachful of food. Total water available
from the food in a full stomach determines the amount of time available
for surface activity. In similar fashion, the calories available for surface
activity will be those available from a full stomach that are not utilized
while the animal is in its burrow. The equations for performing these
calculations are given below, and the data used in these equations are
given in Table 2. Fig. 26 displays four time limits of the desert iguana:
eating time limit, thermal time limit, metabolic time limit, and water time
limit.

The eating time limit is computed by

Eating time limit [min] = stomach volume [cm³] × stomach fullness [%] ×
leaf density [g/cm³]/(leaf wet weight [g/leaf] × eating rate [leaf/min])   (33)

Table 2. Data used in computation of eating, metabolic and water time limits

Parameter	Stomach volume	Leaf density	Leaf dry weight	Leaf water content	Leaf caloric value	Digestive efficiency
(Units)	(cm³/100 g animal)	(g/cm³)	(smallest–largest) (mg)	(gH$_2$O/100 g wet weight) (%)	(cal/g dry weight)	(assumed) (%)
Stomach volume (100 g animal)	5.3					
Ambrosia dumosa		0.57	1.17–4.36	43–78	4.11×10^3	50–70
Larrea divericata		0.90	1.19–3.54	47–53	4.55×10^3	30–50
Source of data	Dissections by authors, Minnich, pers. comm.	Plants grown under optimum conditions in U. W. Biotron	Plants from Kelso site Aug. 30, 31, 1971 (wet season almost daily rains for 2 weeks prior) plants from Biotron for comparison yield same results ($\pm$ 2%)	Same as previous column; Minnich, pers. comm.	Same as previous column	Minnich (1970b) and pers. comm.

The time to fill a stomach depends upon the leaf volume per bite and the biting rate. We assume one leaf consumed per bite and a 5.3 cm³ stomach volume (100 g animal). Since a smaller animal has a smaller stomach volume yet consumes one leaf per bite, less time is required to fill the stomach at the same biting rate. More specifically, the bites/min depicted on Fig. 26 are (bites/min) for a 100 g animal. To compute the limit for a different size animal, the bites/min should be multiplied by (100 g/body weight). For example, a 100 g lizard eating large *Larrea* leaves at a rate of 4 bites/min will take 2.6 hrs to fill its stomach. On the other hand, a 50 g animal eating at the same rate will take half as long.

In the field, then, we should see very casual, sporadic feeding of small lizards, but the very large animals should be eating at much higher rates and spending a significantly larger portion of their time feeding. On our Mojave site in late August during the rainy season, we observed 50 individuals of widely varying ages. The small hatchlings spend relatively little time feeding. Larger animals, up to about 50 g, were taking about 75
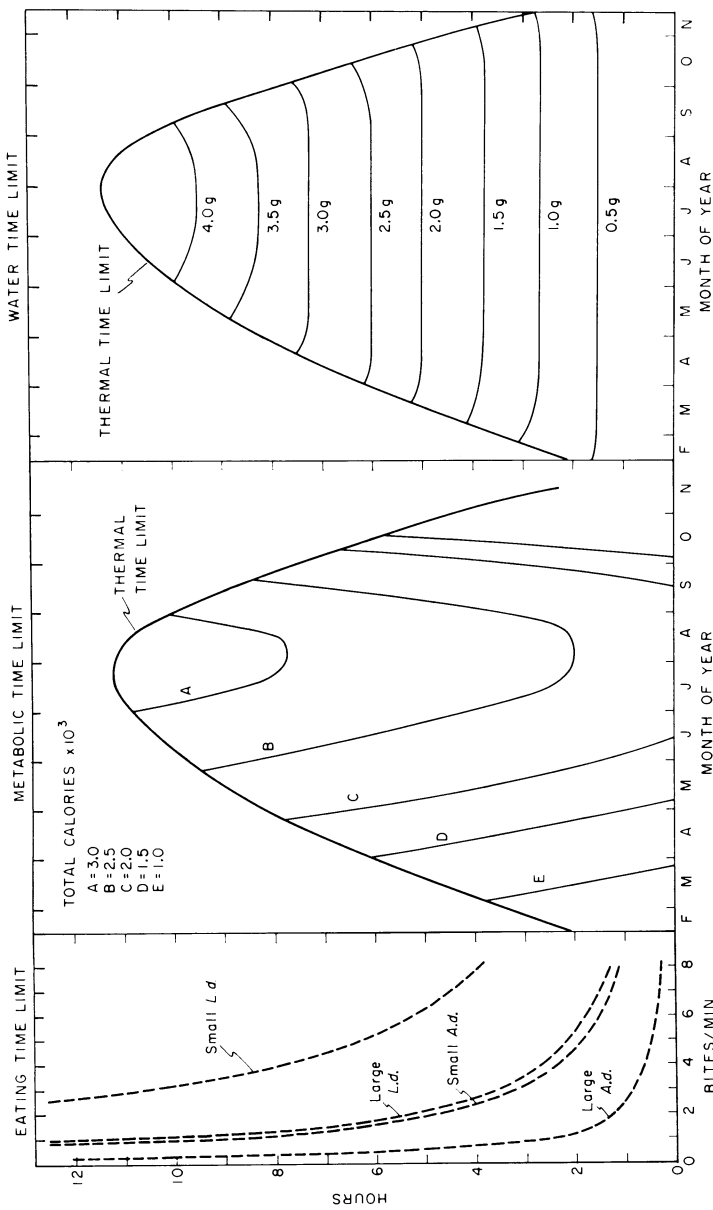
Fig. 26. Hours of activity available to a lizard as limited by the thermal environment, eating time, metabolic reserve, and water reserve

leaves (bites) in a 6-hr day with some animals observed taking as few as 20 and some as many as 100 leaves. The main diet of these animals was *Ambrosia dumosa*. From Fig. 26, a 50 g animal with 6 hrs of eating time

can fill his stomach by eating at a rate of 1 bite per 4 min, or 90 bites in a 6-hr day.

The thermal time limit shown in the center of Fig. 26 is the time within the 38° C contour of Fig. 10. For example, on July 15 the 38° C contour extends from 07:30 to 18:30 for a total time of 11 hrs. It is seen on Fig. 26 that in mid-July the thermal time limit for a desert iguana of any size is 11 hrs.

The metabolic time limit is the time available for surface activity using the calories available for a stomachful of food. The energy available for surface activity is

$$\text{Activity Energy [cal]} = \text{total energy available [cal]} \\ \qquad -\text{energy expenditure in burrow [cal]} \tag{34}$$

where

$$\text{Total Energy Available [cal]} = \text{stomach volume [cm}^3\text{]} \times \\ \text{leaf density [g wet wt/cm}^3\text{]} \times \text{(1-plant water content [%])} \times \tag{35} \\ \text{food energy [cal/g dry wt]} \times \text{digestion efficiency [%]}.$$

The term "energy expenditure in burrow" in Eq. (34) is the energy expended when the animal is underground because of thermal constraints and is the region outside the 38° C contour in Fig. 10. During the time within the 38° contour, the animal spends time on the surface and underground. The energy expenditure for the lizard in the burrow outside the 38° contour was determined by integrating the metabolic rate of a lizard underground. The animal was allowed to seek the maximum possible burrow temperature but not to exceed 38° C. The animal was also assumed to be no closer than 7.5 cm of the surface. The integrated metabolism for these conditions is shown on Fig. 27.

We assume that inside the times defined by the 38° C contour, the desert iguana never exceeds 43° C when on the surface and is at a constant 38° C when underground. The activity energy for a given day is divided up into surface and underground energy expenditures as given by the following relation

$$\text{Activity [cal]} = \text{metabolic rate at 43° C [cal/min]} \times \text{activity time} \\ \text{[min]} + \text{metabolic rate at 38° C [cal/min]} \times \text{(potential activity time} \tag{36} \\ \text{[min]} - \text{activity time [min])}$$

where the potential activity time is the time for any day's activity within the 38° C contour as given in Fig. 10.

The metabolic time limit for a desert iguana of 100 g is shown in the center of Fig. 26 along with the thermal time limit. Each of the lines represents a value of the total energy available from Eq. (35). The same total energy available can be obtained from a given plant species with many different combinations of fullness of stomach, percent plant water and digestive efficiency. For example, a lizard with a digestive efficiency
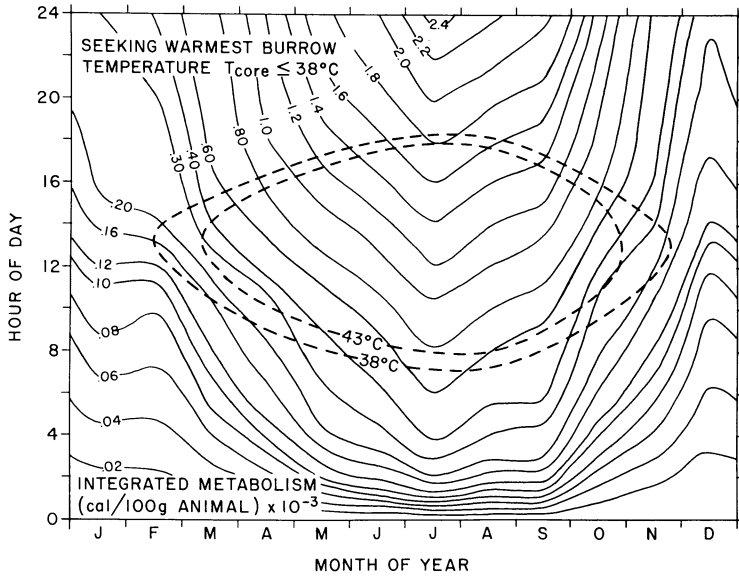
Fig. 27. Integrated daily metabolism for the desert iguana in a burrow seeking 38° C
and remaining below 7.5 cm from the surface

of 80%, a 5.3 cm^3 stomach half full of *Ambrosia* (leaf density of 0.57 g/cm^3
and caloric value of 4.11×10^3 cal/g-dry wt) with a water content of
60% will yield a total energy available, from Eq. (35), of 2000 cal[7]. The
values in this and following examples have been chosen as representative
of desert plants and animals as reported in the literature (e.g., Minnich,
1970a, b; Nagy, 1971; Table 2). Another of the possible combinations that
gives the same value is a full stomach of *Ambrosia* with 20% plant water
at a digestive efficiency of 20%. These relationships are shown on Fig. 28.

These 2000 calories on June 1 will enable a 100 g desert iguana to be
active for about 2 hrs, while a 50 g animal could be active for 4 hrs. On
the other hand, on the same day the thermal limit for both is 9.5 hrs. For
the 100 g lizard to reach the thermal limit, it must obtain about 2500
calories.

If an animal obtains the same amount of energy every day (e.g.,
2500 calories), then during the spring its thermal limit restricts its
surface activity and excess calories may be used for gonad development
and growth. Likewise, in the fall there is excess energy which could be
used for fat deposition. During midsummer, its surface activity would be
restricted considerably below the thermal limit. This metabolic time

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7 $(5.3/2) \times 0.57 \times (1-0.60) \times 4.11 \times 10^3 \times 0.8 = 2 \times 10^3$ cal.
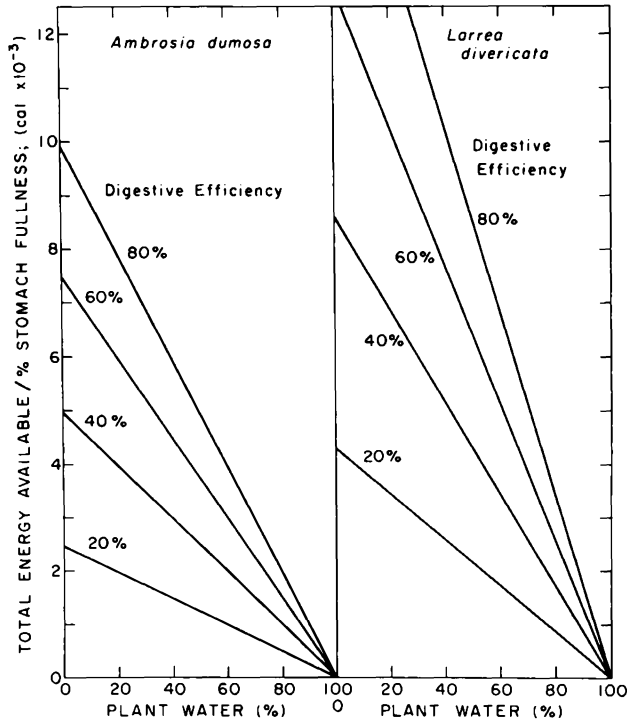
Fig. 28. Total energy available to *Dipsosaurus dorsalis* from desert plants as a function of plant water and digestive efficiency

limit may be one reason for the lack of afternoon activity observed in midsummer.

In order to evaluate fat production for hibernation, we have integrated Fig. 24 between November 1 and March 1 and have computed the metabolic requirement for a 100 g animal. An animal resting deep in the burrow at deep soil temperatures will need 33 000 calories, and one seeking the warmest temperatures not exceeding 38° C will need 45 500 calories. If we assume only fat is used during hibernation, and that the animal gets 9000 calories from a gram of fat, then an animal will need 3.5 to 5.1 g of fat to survive the winter. Moberly (1962) calculated that 5.0 g of fat were needed for hibernation based on measured soil temperatures at hibernating depths and resting metabolic rates.

With the winter fat requirements known, some general assessments about the amount of food or leaves necessary to produce that fat can be made. The number of stomachfuls of food needed (assuming the food is only used to produce fat) for a 100 g animal is:

No. of Full Stomachs = energy from fat utilized [cal]/conversion efficiency
of carbohydrate to fat × digestive efficiency × (1-plant water [%] × food
energy [cal/g dry wt] × leaf density [g/cm³] × stomach volume [cm³]   (37)

We have assumed 60% and 50% digestive efficiencies (Minnich, 1970b),
60% and 50% plant water contents for *Ambrosia dumosa* and *Larrea
divaricata*, respectively (Table 2), and a 50% conversion efficiency of
carbohydrate calories to fat calories. We compute 20 to 35 stomachfuls
of food if *Ambrosia* is consumed and 10 to 20 stomachfuls for *Larrea*. The
lower numbers correspond to animals at deep burrow temperatures that
need less fat. These numbers suggest that for one stomachful per day,
a minimum of two weeks and probably more than a month is needed to
acquire sufficient food to produce fat under these conditions.

Impact of the desert iguana on desert vegetation over an entire year
may be evaluated in similar fashion. Integrating the resting metabolism
curve of Fig. 24 from March 1 to November 1 yields about 5×10^5 calories
needed by a 100 g animal. A 50 g animal would require approximately
half that amount of energy. Using the same assumptions as the previous
paragraph, an animal eating *Ambrosia dumosa* would need 160 stomach-
fuls of food, and one eating *Larrea divaricata* would need 90 stomachfuls.
The total annual number of stomachfuls would then be about 200 for an
exclusive diet of *Ambrosia* and about 100 for *Larrea*. These are equivalent
to 600 g wet weight of *Ambrosia* and 480 g wet weight of *Larrea*. De-
pending on whether large or small leaves are consumed, a 100 g animal
would be expected to consume 100000 to 300000 leaves of *Ambrosia* or
60000 to 200000 leaves of *Larrea*.

The water time limit is determined from the water obtained from a
stomachful of food. Assuming no day to day depletion or addition to
water reserves, a water mass balance yields the maximum possible
evaporative water loss [assuming negligible water loss in urine and from
salt gland (Nagy, 1971; Minnich, 1970b)].

Available Evaporative Water = plant water in + water from
metabolism—feces water out   (38)

where

plant water in [g] = stomach vol [cm³] × leaf density
[g/cm³] × plant water content [%]   (39)

water from metabolism [g] = stomach vol [cm³] × leaf density
[g/cm³] × (1-plant water content [%]) × food energy [cal/g dry wt]   (40)
× metabolic water [g H₂O/cal] × digestive efficiency

feces water out [g] = stomach vol [cm³] × leaf density [g/cm³]
× (1-plant water content [%]) × (1-digestive efficiency) ×   (41)
feces water content [%]/feces solids [%].

The water time limit is found from Fig. 23 by starting at 0 hrs and moving
vertically until the integrated water loss equals the available evaporative

water calculated from Eq. (38). In our calculations, to obtain maximum possible activity time available, we have assumed no water loss in the burrow, leaf caloric values from Table 2, and a metabolic water production of 0.00015 g of water per calorie of food utilized (glucose).

The water time limit is shown on the right hand side of Fig. 26. Each of the lines represents a value of the total water available from Eq. (38). For example, a 100 g animal with 2 g of available evaporative water has approximately 5 hrs available for activity, while a 50 g animal would have about 10 hrs. This time limit is essentially independent of season because we have assumed no water loss in the burrow. However, even if we had included water loss in the burrow, the low burrow temperatures combined with the constant low rate of water loss below 20° C and the probable high humidity in the burrow would not significantly change the shape of these curves.

As in the case of the metabolic time limit, many different combinations of plant and animal variables will yield the same water time limit. All combinations, from Eq. (38), are shown on Fig. 29. It should be empha-
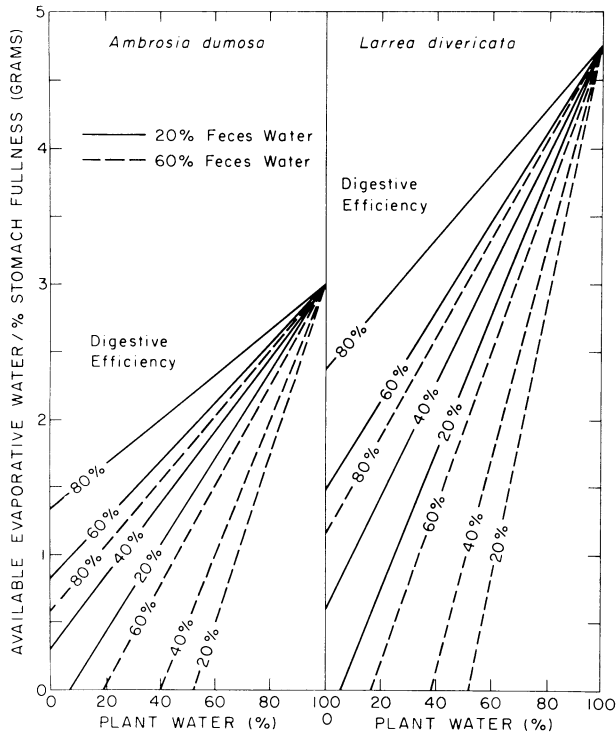

Fig. 29. Water available to *Dipsosaurus dorsalis* from desert plants as a function of plant water, feces water, and digestive efficiency

sized that Figs. 28 and 29 are just graphical representations of Eqs. (35) and (38) and permit visualization of the interactions between the parameters. For example, if we consider the same conditions as described for the metabolic time limit of a half full stomach of *Ambrosia* with a water content of 60% and a lizard digestive efficiency of 80%, the 60% feces water content will yield an available water of 0.9 g. From Fig. 26, 0.9 g of available water will permit about 2 hrs of activity. This is almost the same time for activity as imposed by the metabolic time limit on June 1. However, if the feces water content had been 20%, then the available water would be about 1.7 g with a corresponding water time limit of over 4 hrs.

As already pointed out, the thermal time limit for June 1 is about 9.5 hrs, and an animal could obtain sufficient calories to reach this limit. The amount of water required to reach this limit is about 4.3 g which cannot be obtained by eating *Ambrosia*. If the lizard were to shift to eating *Larrea*, he could obtain 4.3 g of water if the plant water content exceeded 80%. This food could still supply the necessary 2500 calories even with a digestive efficiency of 60%[8]. It appears that in summer the animal is more limited by his ability to obtain water than by either his ability to obtain calories or by his thermal constraints.

Nagy (1971) has measured a significant seasonal variation in water content of desert plants consumed by the chuckwalla and observed a corresponding decrease in activity. It is important to realize that a seasonal variation in activity may be correlated with other limits such as the thermal limit and metabolic limit of Fig. 26. Moreover, from Fig. 29, plant water content alone does not determine the water time limit.

VIII. Predator-Prey Implications

The model developed in this paper is a general one, and can be extended to other animals in the desert biome. Behavioral patterns for animals that might prey or be preyed upon by the desert iguana can also be determined. Then, when the activity patterns of the prey and predator are overlapped, the times available for predation can be ascertained. Such information would serve as a basic input to the types of predator-prey models developed by Holling (1965) and Griffiths and Holling (1969). Data on hunting efficiency and the length of time to stalk, capture, kill, consume and digest a prey before the next meal would be combined with the time available to accomplish these activities. The expected number of prey to be eaten over specified time intervals could then be computed.

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8 If the animal is to obtain significant water from his food during the dry season, there must be a relationship between the water content of the food and the percent of food metabolized ("digestive efficiency"). Thus, if an animal is consuming large quantities of food and "using" it primarily as a source of water, "digestive efficiency" may have little meaning.

With data on initial population densities of predator and prey, population fluctuations through time and environment effects on those fluctuations could be computed.

As an example of how the first stages of these computations can be accomplished, we have computed the activity pattern for a hypothetical ant preferring a relatively low temperature. The temperature range for activity for this hypothetical species of ant is 27–31° C. Fig. 30 shows the predicted behavior pattern of the animal. In the winter months, it should have a single activity period in the middle of the day, in spring and fall a bimodal activity pattern, and in the summer it would be completely nocturnal.

To determine whether the desert iguana might eat ants with this range for temperature preference, the activity patterns of each are overlapped. The hatched area in Fig. 31 is the overlap that occurs and shows when the two might be expected to be in the same part of the physical environment at the same time, and thus when predation might occur. Since the desert iguana would not be expected to be out until about March 1, virtually no ant predation would be anticipated for ants active in this temperature range.

More important than this hypothetical example is the principle it illustrates, namely, that seasonal changes in activity patterns imposed by
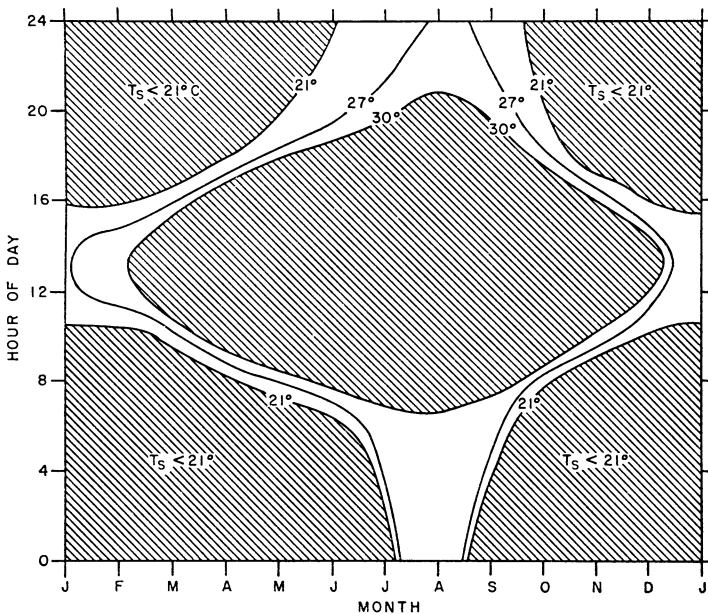

Fig. 30. Predicted seasonal behavioral pattern for an ant
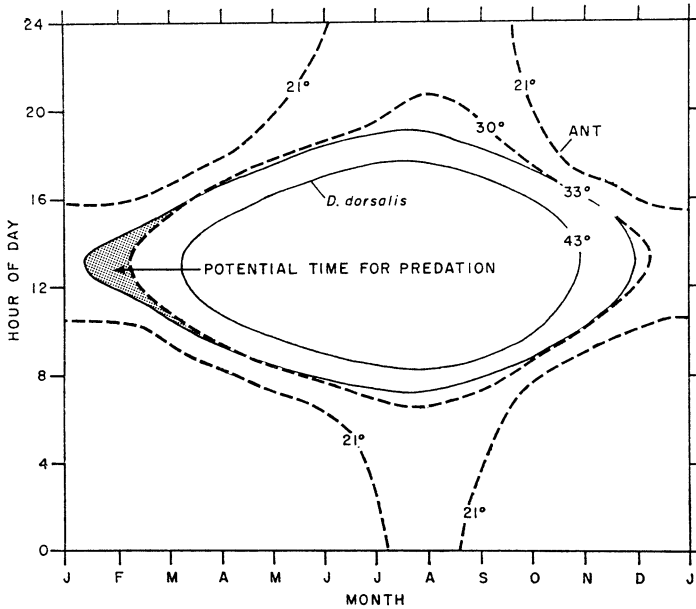
Fig. 31. Overlap of behavioral patterns for a *Dipsosaurus dorsalis* and an ant indicating the potential time for predation

the physical environment and by the animal's physiology can have important influences on the species of prey consumed by a predator at different times of the year.

Nomenclature

Symbol		Units
A_L	Lizard surface area	cm^2
$A_{p,d}$	Projected lizard area for direct plus scattered solar radiation	cm^2
$A_{p,r}$	Projected lizard area for reflected solar radiation	cm^2
$c_{p\,a}$	Specific heat of air	cal/gm-C
c_{so}	Specific heat of soil	cal/gm-C
C	Lizard thermal capacitance $= C_c + C_{sk}$	cal/C
C_c	Lizard core thermal capacitance	cal/C
C_{sk}	Lizard skin thermal capacitance	cal/C
E	Energy loss via evaporation due to breathing	cal/min
F_{L-s}	Shape factor for radiation between lizard and ground	—
F_{L-sky}	Shape factor for radiation between lizard and sky	—
h_L	Lizard convection heat transfer coefficient	cal/cm^2-min-C
h_z	Soil convection heat transfer coefficient	cal/cm^2-min-C
k	Karman constant (0.4)	—
k_a	Thermal conductivity of air	cal/cm-min-C
k_{so}	Thermal conductivity of soil	cal/cm-min-C
k_{sk}	Thermal conductivity of skin	cal/cm-min-C
L	Snout-vent length	cm

Symbol		Units
$(\dot{m}c)_b$	Blood flow rate-specific heat product	cal/min-C
M	Metabolic rate	cal/min-100 g
N_u	Nusselt number, $h_L L/k_a$	—
Q_b	Energy transfer due to blood flow	cal/min
Q_{cond}	Conduction heat flow from core to skin	cal/min
Q_e	Heat flow between lizard and environment	cal/min
$Q_{L,conv}$	Convection heat flow between lizard and air	cal/min
$Q_{L,IR}$	Long wavelength energy exchange between lizard, sky and ground	cal/min
$Q_{L,solar}$	Direct and reflected solar energy absorbed by lizard	cal/min
$Q_{rad,s}$	Thermal radiation exchange between lizard and ground	cal/min
$Q_{rad,sky}$	Thermal radiation exchange between lizard and sky	cal/min
Q_{sky}	Thermal radiation emitted by sky	cal/cm^2-min
Q_{solar}	Solar energy incident on soil	cal/cm^2-min
$Q_{s,cond}$	Conduction heat flux in the soil	cal/cm^2-min
$Q_{s,conv}$	Convection heat flow between ground and air	cal/cm^2-min
$Q_{s,IR}$	Net long wavelength radiation incident on soil	cal/cm^2-min
$Q_{s,rad}$	Thermal radiation emitted by soil surface	cal/cm^2-min
$Q_{s,solar}$	Solar energy absorbed by soil surface	cal/cm^2-min
Re	Reynolds number, $V_z L/\nu_a$	—
R_e	Environmental thermal resistance	min-C/cal
R_b	Blood flow thermal resistance	min-C/cal
R_{conv}	Lizard convection thermal resistance	min-C/cal
$R_{rad,s}$	Lizard-soil surface thermal resistance	min-C/cal
$R_{rad,sky}$	Lizard-sky thermal resistance	min-C/cal
R_{sk}	Lizard skin conduction resistance	min-C/cal
t	Time	min
T	Soil temperature at any depth	C
T_c	Lizard core temperature	C
T_L	Lizard temperature	C, K
T_r	Air temperature at reference height	C
T_s	Soil surface temperature	C, K
T_{sk}	Lizard skin temperature	C, K
T_{sky}	Sky temperature	C, K
T_z	Air temperature at any height	C
V_r	Air velocity at reference height	cm/min
V_z	Air velocity at any height	cm/min
V^*	Shear velocity $= \sqrt{\tau_0/\varrho_a}$	cm/min
z	Height above or depth below ground surface	cm
z_0	Roughness length	cm
z_r	Reference height	cm
α_L	Solar absorptivity of lizard skin	—
α_{so}	Solar absorptivity of soil surface	—
δ	Skin thickness	cm
ε_L	Infrared emissivity of lizard skin	—
ε_{so}	Infrared emissivity for soil	—
ν_a	Kinematic viscosity of air	cm^2/min
ϱ_a	Density of air	g/cm^3
ϱ_{so}	Density of soil	g/cm^3
σ	Stefan-Boltzmann constant	cal/min-cm^2 K^4
τ_0	Air shear stress at ground surface	dynes/cm^2

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