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ENERGY BUDGETS AND A CLIMATE SPACE DIAGRAM FOR THE TURTLE, CHRYSEMYS SCRIPTA

THESIS

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts at the State University College at Buffalo

By

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ABSTRACT OF THESIS

ENERGY BUDGETS AND A CLIMATE SPACE DIAGRAM FOR THE TURTLE, CHRYSEMYS SCRIPTA

Heat energy budgets were computed and a steady state climate space was generated for a 1000 g red-eared turtle (*Chrysemys scripta*). Evaporative water loss (EWL) was measured from *C. scripta* at three wind speeds (10 - 400 cm sec^{-1}) and at four air temperatures (5 - 35°C) in a wind tunnel. EWL increased as air temperature and wind speed increased. Smaller turtles dehydrated at a faster rate than large turtles. Heat transfer by convection was measured from aluminum castings of *C. scripta* at three temperature differences between casting and air (ΔT 15°, 10° and 5°C) for three windspeeds (10 - 400 cm sec^{-1}). Convective heat transfer coefficients increased as wind speed and ΔT increased.

Wind speed has a large effect on the shape of the climate space. At high wind speeds, heat loss by evaporation and convection are greatly increased. In still air (10 cm sec^{-1}), a turtle cannot remain exposed to full sunlight when air temperatures exceed 19°C. When wind speed increases to 400 cm sec^{-1}, the turtle can bask for long periods of time at temperatures as high as 32°C. Basking patterns of *C. scripta* probably shift from a unimodal pattern in the spring to a bimodal pattern in summer and return to a unimodal pattern in fall. Terrestrial activity may be extensive in the spring and fall but is limited during the hot summer months to periods of rainfall. Nesting activities cannot

occur around solar noon because increased metabolic heat loading and high solar radiation intensity could cause death.

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INTRODUCTION

Chrysemys scripta (changed from Pseudemys scripta, Conant 1975) is an aquatic turtle inhabiting slow-moving bodies of water that have abundant aquatic vegetation, basking sites and occasional cleared areas along the banks for nesting. The species is widely dispersed, having the greatest latitudinal distribution (from southern Michigan to Argentina) of any freshwater chelonian (Moll and Legler 1971). Through the efforts of Cagle (1937, 1939, 1944, 1946, 1948, 1950) and Legler (1958, 1960a, b, c, 1970), the ecology and life history of this species are fairly complete in the North Temperate Zone of the New World.

Aquatic turtles represent a group of reptiles which have more contiguous relations with water than any other family or order with the exception of the Crocodilians and the water snakes. Turtles of the genus Chrysemys live primarily in water throughout their lives, emerging onto land to lay their eggs and to migrate to other bodies of water. Terrestrial activity is not limited by sex, maturity or reproductive condition. During June and July, most movement is restricted to aquatic environments which serve as refuges from high temperatures (Boyer 1965). C. scripta in Panama are considered almost completely aquatic except for limited basking and nesting excursions (Moll and Legler 1971).

Several studies have shown that turtles can exert some control over body temperature by physiological and behavioral mechanisms. Webb and Johnson (1972) confirmed that considerable physiological control of head temperature is exhibited by Chelodina

longicollis heated radiantly. Spray and May (1972) reported significant differences in the heating rates of C. scripta but no differences in their cooling rates. Lucey (1974) suggested that changes in heating and cooling rates of C. scripta may be due to changes in heart rate and blood flow to the skin and carapace. He found that initially the head heats faster than the body. When head temperature reaches 30°C, the body heating rate becomes greater and could be associated with a change in heart rate. Hutton et al. (1960) and Jackson (1971) demonstrated that changes in ventilation, heart rate and oxygen consumption of C. scripta were proportional to changes in body temperature. Weathers and White (1971) stated that peripheral vascular responses to heating and cooling in Chrysemys floridana appear to represent a means of changing functional insulation and may contribute to the thermoregulatory capacities of this turtle.

Evaporative water loss is an important factor in the thermoregulatory capacities of turtles. Turtles inhabiting arid environments have a lower rate of evaporative water loss than those living in mesic or aquatic habitats (Bentley and Schmidt-Nielsen 1966). Many mechanisms have evolved that act to minimize water loss in desert turtles (Minnich 1970). However, when placed under high temperature stress, turtles often increase their rates of evaporative water loss. Terrapene ornata spreads saliva over its head and forelimbs and urine over its tail and hind legs when subjected to temperatures greater than 40°C (Riedesel et al. 1971).

Basking appears to be an effective thermoregulatory activity. This term refers to the common behavioral activity of emerging

from the water and lying quiescent on some object for variable periods of time. By crawling out of the water during the day, turtles may absorb large amounts of solar radiation and quickly raise their body temperatures (Cagle 1946). Physical factors such as size and shape of turtle, light intensity, wind speed and air temperature greatly affect the rate of heat gain (Boyer 1965). Behavior also affects the final body temperature attained by the ectotherms since time of day and orientation towards the sun alter the amount of radiation absorbed (Porter et al. 1973). The basking habit may dry the skin and retard parasitic infestations (Cagle 1950). Further, Cagle (1944) hypothesized that production of vitamin D is enhanced by exposure to UV rays from the sun. However, C. scripta in tropical areas rarely bask. They are exposed to a narrow range of environmental temperatures and thermoregulate by vertical movements through the water (Moll and Legler 1971). Therefore, it is not clear whether dessication of parasites and production of vitamin D are important factors in the basking habit.

While C. scripta does have the ability to thermoregulate by means of physiological and behavioral mechanisms, the efficiency with which it does so depends upon the constraints imposed on it by its environment. The physical environment affects a turtle through the exchange of heat energy. Understanding the mechanisms of heat energy exchange between a turtle and its environment enables us to define the microclimate requirements of this animal and obtain a better understanding of its thermoregulatory capacities. With an accurate quantification of these relations, we can

predict the effects of environmental perturbations on its behavior.

The transfer of heat energy occurs by a variety of physical processes that can be described by laws of heat transfer (Kreith 1973). In the case of a turtle underwater, the predominant modes of energy exchange are convection and conduction (see Erskine, 1976 for application of underwater heat transfer to biological systems). In the aerial environment, a turtle encounters a more complex energy exchange due to additional modes of heat transfer. When turtles emerge into the atmosphere, they are subjected to evaporative water loss, to the effects of wind, to conduction and to thermal loading from the sun, the atmosphere and its surroundings. Detailed descriptions of animal energy budgets have been given by Birkebak (1966), Porter and Gates (1969) and used or modified by Heller and Gates (1971), Spotila *et al*. (1972), Hillman (1974), Henwood (1975) and others. The objective of this study was to analyze the heat energy exchange between the turtle *Chrysemys scripta* and its environment in order to evaluate the relative importance of the various avenues of heat exchange in the ecology of the turtle. Rates of heat loss by convection and evaporation were determined and a climate space for this turtle was formulated.

Theory

The turtle-environment energy interaction can be defined by use of an energy budget equation that accounts for each mode of heat transfer between the turtle and its environment. As a good

first approximation, we can assume that the turtle is in a steady state energy balance with the environment. C. scripta are small (50 cm) and have a relatively low capacity for heat storage so that they are very close to energy equilibrium with the environment. In steady state, net energy flow between the turtle and its environment is zero so that

$$\text{Energy}_{in} = \text{Energy}_{out}$$

The animal receives energy in the form of radiation from the environment and heat from metabolic activity. Energy leaves the animal in the form of radiation to the environment, convection to the atmosphere, evaporation and conduction to the substrate. These factors are combined into an energy budget equation:

$$Q_{abs} + M = \epsilon\sigma(T_r + 273)^4 + h_c(T_r - T_a) + E_t + C \qquad (1)$$

where Q_{abs} = radiation absorbed (cal cm^{-2} min^{-1})

M = heat produced by metabolism (cal cm^{-2} min^{-1})

ϵ = surface emissivity of animal (0.95)

σ = Stefan-Boltzmann constant (8.13×10^{-11} cal cm^{-2} $^{o}k^{-4}$ min^{-1})

T_a = air temperature (^{o}C)

T_r = radiant surface temperature (^{o}C)

h_c = convective heat transfer coefficient (cal cm^{-2} min^{-1} $^{o}C^{-1}$)

E_t = total evaporative water loss (cal cm^{-2} min^{-1})

C = conduction (cal cm^{-2} min^{-1})

Radiant surface temperature (T_r) is a function of body temperature, the thickness and quality of the animal's insulation and the net heat production inside the turtle. This relationship is expressed as:

$$T_r = T_b - \frac{d_s}{k_s} (M - E_r) \qquad (2)$$

where, d_s = thickness of shell (cm)

k_s = conductivity of bone (cal cm^{-1} min^{-1} $^oC^{-1}$)

E_r = respiratory evaporative water loss (cal cm^{-2} min^{-1})

Insulation is dependent upon the average thickness and conductivity of the bony shell covering its body. The value reported for the conductivity of beef bone (0.0717 cal cm^{-2} min^{-1} $^oC^{-1}$) will be used (Chato 1969). Bentley and Schmidt-Nielsen (1966) reported that C. scripta loses 22% of its evaporative water losses from the respiratory surfaces, thus $E_r = 0.22\ E_t$.

Substituting equation (2) into equation (1), we have:

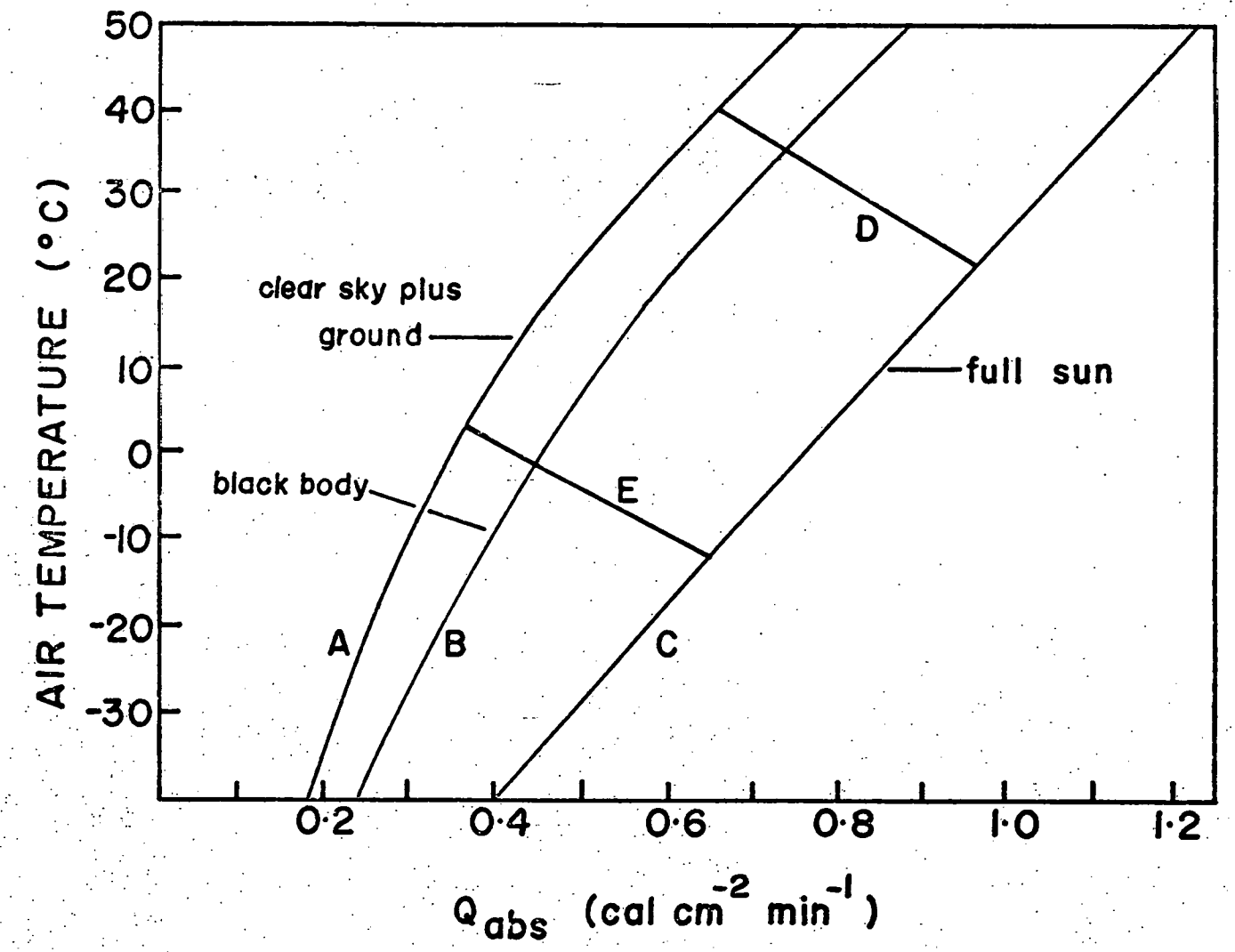
$$Q_{abs} + M = \epsilon\sigma[T_b - \frac{d_s}{k_s} (M - E_r) + 273]^4 +$$

$$h_c\ [(T_b - \frac{d_s}{k_s} (M - E_r) - T_a] + E_t + C \qquad (3)$$

This equation defines the heat energy balance between a turtle and its environment. Using this equation, we can predict the microclimate within which a turtle must live. This microclimate can be visualized as a two dimensional climate space (Fig. 1). The boundaries of this climate space are fixed in part by the interaction of the turtle's physical properties (size, shape, absorptivity to solar radiation) and those of its environment (Fig. 1, lines A, B, C). The other limits are defined by equation (3). To set these limits (Fig. 1, lines D, E) equation (3) is solved for two cases. First for a body temperature (T_b) equal to the upper lethal temperature of the turtle and then for a T_b equal to the lower lethal temperature. For a more detailed discussion of the derivation of a climate space, see Porter and Gates (1969).

A turtle must restrict its activities to those microclimates contained within its climate space. It can exceed these limits for short periods of time depending upon its heat storage capacity. But it cannot exceed these limits for extended periods without altering its energy equilibrium and risking death.

Figure 1. A conceptualized climate space showing the relationships between air temperature and absorbed radiation. The lines bounding the climate space on the left (A) and on the right (C) represent the average radiation absorbed by a turtle. A line of reference (B), shows radiation absorbed by the turtle in a blackbody cavity. Lines D and E are plotted by solving the energy budget equation (3).


AIR TEMPERATURE (°C)
50
40
30
20
10
0
-10
-20
-30
clear sky plus
ground
black body
full sun
A
B
C
D
E
0·2
0·4
0·6
0·8
1·0
1·2
Q_{abs} (cal cm^{-2} min^{-1})

METHODS AND MATERIALS

Chrysemys scripta used for this experiment were obtained from Aiken, South Carolina and Gainesville, Florida. Forty-seven *C. scripta* were maintained in an aquatic animal facility with a photoperiod (LD 13:11) centered at 1200 EST and water temperature of 23°C (±1.0°C). Areas were available for the animals to crawl out of the water and bask under 125 watt incandescent lamps. The animals were fed a diet of freshly killed rats, dog food supplemented with vitamins, cod liver oil, vegetables and fresh fish. A sample of ten turtles was selected that represented the entire range of sizes found in this population (10.6 - 25.6 cm, carapace length). These ten turtles were used throughout evaporative water loss determinations and six of these also served as subjects during the preparation of aluminum castings.

Shell thickness (d_s) was measured at a series of points on plastra of fresh-killed turtles using a Helios vernier caliper (± 0.05 mm). Average plastron thickness was determined and related to plastron length by regression analysis. Plastron thickness as a function of plastron length can be described by regression equation: $y = 0.72\ x - 2.98$.

Evaporative Water Loss

Evaporative water loss measurements were taken in a wind tunnel designed to closely approximate blackbody conditions. Air was drawn thru the test section (122 x 122 x 180 cm) by a fan 104

cm in diameter powered by an electric motor. A variable rheostat allowed accurate control of wind velocity. Laminar air flow (turbulence less than $\pm$ 3%) of any desired velocity between 0 and 400 cm sec^{-1} could be selected. Room air temperature was controlled ($\pm$1.0°C) by an air conditioner and a thermostatically controlled heat source. Ambient temperature in a wind tunnel was measured with 24 gauge copper-constantan thermocouples ($\pm$ 0.5°C) and a Kaye Multipoint recorder (model 8000). Relative humidity was determined ($\pm$ 1.5%) with an electronic hygrometer (Hygrodynamics Inc. model 15-3050) using narrow range sensing elements. A Hastings Air Meter (model RM1R4S) with four hot wire omnidirectional sensors was employed to monitor wind speeds.

Evaporative water loss tests were performed on ten turtles at three wind speeds (10, 100 and 400 cm sec^{-1}) and three temperatures (15°, 25° and 35°C) in the wind tunnel and at 160 cm sec^{-1} at 5°C in a modified environmental chamber. Animals were held for a minimum of 12 hours at test temperature before being tested. Turtles were allowed to rehydrate for at least twenty-four hours before being tested again. Before each test condition, a turtle was blotted dry with paper towels and allowed to air dry for 5 - 10 minutes to eliminate surface water remaining on the skin. After the turtle's bladder was evacuated using a cotton swab, the animal was weighed to $\pm$0.005 g. using a Mettler top-loading balance (model P-120). It was then placed into a wide mesh restraining cage positioned on the center of the test section. The effects of the animal's orientation to air flow were minimized by placing all turtles facing into the direction of air flow. The

animal was dehydrated for periods of up to two hours and reweighed. Evaporative water loss was measured as the change in body weight. Data were not used if an animal urinated or defecated during the experiment. Partitioning of weight loss due to respiration of CO_2 was not performed.

Convection

Six turtles (12.2 - 25.6 cm in length) served as subjects for the construction of aluminum castings. A negative cast of each turtle was prepared using Jeltrate alginate impression material, a fast-setting dental molding compound. The live animal was removed unharmed and hot wax was poured into the mold to produce a replica of the turtle. The wax turtle was placed in a cylindrical metal collet and imbedded in grey investment plaster. The wax mold was melted from within the plaster-filled collet which was then dried and cured at 482°C for 15 - 20 hours. Molten aluminum was poured into the plaster mold before it cooled to produce a solid aluminum replica of the original turtle. This technique provided aluminum castings which were accurate representations of the size, shape and surface characteristics of each turtle.

Each aluminum turtle was provided with three, 38 gauge copper-constantan thermocouples, secured with epoxy cement. One was implanted at the center of mass through a 0.838 mm drilled hole, one was attached at the surface of the anterior edge of the carapace and the third was attached at the posterior edge of the carapace. Casting temperatures were monitored throughout the

course of experimentation by a Kaye multipoint recorder. The casting was heated in an oven above 65°C and placed perpendicular to wind flow in the wind tunnel on a polystyrene pad (61 x 56 x 2.5 cm). The time-temperature responses of the casting were measured between 65°C and equilibrium. Temperatures of the polystyrene were monitored at six points by 38 ga. copper-constantan thermocouples. Three thermocouples measured internal polystyrene temperatures 5 mm below the surface directly beneath the casting. Two thermocouples were placed on the surface beneath the turtle and the remaining thermocouple was positioned at the polystyrene surface, 1 cm from the lateral edge of the casting. In this way the temperature regime of the test substrate could be monitored throughout cooling curve experiments. Temperatures of the polystyrene, air stream, walls and ceiling of the wind tunnel were continuously monitored throughout each cooling period. Castings were cooled to equilibrium with air temperature. This procedure was repeated for the six castings at three different wind speeds (10, 100 and 400 cm sec^{-1}).

Determination of the Convection Coefficient

The data from cooling curve experiments were used to calculate heat transfer coefficients according to Wathen et al. (1971). An equation describing energy flow between a heated casting and its environment can be written as a simple energy balance:

$$Heat_{in} = Heat_{out} + Heat_{stored} \quad (4)$$

a. Total Heat Transfer Coefficient

Since a metal casting does not produce heat metabolically and because of the high absorptivity of the blackbody test conditions in the wind tunnel, heat input to the casting becomes negligible. Also, the high thermal conductivity of aluminum (33.9 cal cm^{-1} min^{-1} $^oC^{-1}$) allows rapid exchange of heat between the center and the surface of the casting. Thus the change in internal heat energy of the casting must equal the net heat flow from the casting to the environment and can be described as:

$$h_t A (T - T_e) = - mc \frac{dT}{dt} \tag{5}$$

where, h_t = total heat transfer coefficient (cal cm^{-2} min^{-1} $^oC^{-1}$)

A = total surface area (cm^2)

T = casting surface temperature (^oC)

T_e = environmental temperature (^oK)

m = mass of casting (gm)

c = specific heat of aluminum (cal g^{-1} $^oC^{-1}$)

t = time (min)

Rearranging equation (5) to solve for h_t gives:

$$h_t = - \frac{mc}{A} \left(\ln \frac{T - T_e}{T_i - T_e}\right) \frac{1}{t - t_i} \tag{6}$$

where, T_i = casting temperature at an initial time (t_i)

However, total heat flow to the environment must be partitioned into convection and radiative heat flow before the convection coefficient can be determined. The total heat transfer can be expressed as:

$$h_t(A) = h_r(A) + h_c(A) \tag{7}$$

I assumed that available surface area of each mode of heat exchange is the same, so that total heat transfer coefficient can be simplified to:

$$h_t = h_r + h_c \tag{8}$$

b. Radiative Heat Transfer Coefficient

The radiative heat transfer coefficient (h_r) can be defined according to the net radiative heat loss as:

$$h_r = \frac{Rad_{net}}{A\ (T - T_r)} \tag{9}$$

The equation for net thermal radiation (Rad_{net}) is

$$Rad_{net} = A\ (T^4 - T_r{}^4) \tag{10}$$

Substituting equation (10) into equation (9) results in:

$$h_r = A\ (T^2 + T_{rad}{}^2)\ (T + T_r) \tag{11}$$

By substracting h_r from h_t, we may determine the convection coefficient (h_c).

RESULTS

Evaporative Water Loss

Evaporative water loss of *Chrysemys scripta* was determined at 5°, 15°, 25° and 35°C. The effect of size, air temperature and wind speed on rates of evaporative water loss was clarified by regression analysis using the method of least squares (all statistical procedures used in this study are described by Sokal and Rohlf 1969). At 5°C, size had no statistically significant effect on the rate of water loss. The coefficient of determination (r^2) was 0.1. Weight losses at this temperature ranged from 0.10 to 0.24 mg g^{-1} hr^{-1}. Evaporative water loss increased with increasing temperature and wind speed (Table I). Variation in rates of evaporative water loss (EWL) at 15°, 25° and 35°C was primarily due to differences in the sizes of turtles tested. At these temperatures, large turtles lost water at a slower rate than small turtles. There was an exponential relationship between evaporative water loss and body weight for these conditions. A representative case is seen in Figure 2. Relatively high coefficients of determination were found in all but one experimental condition. At 15°C, 400 cm sec^{-1}, water loss from two test animals was much less than the water loss of the remaining eight animals. However, no discernable differences in the environment of the test apparatus between turtles was noted during these tests.

Interaction between body size and air temperature affected EWL at wind speeds of 10, 100 and 400 cm sec^{-1}. The effect of

increases in air temperature on EWL is shown for one wind speed (400 cm sec^{-1}) in Fig. 3. Temperature increases EWL in a similar manner for all body sizes. Confidence limits for the regression lines of water loss at 15° and 35° indicated that these were significantly different ($P < 0.05$).

Regression equations of rates of evaporative water loss on body size at $15^{o}C$ show the effect of increasing wind speed on water loss (Fig. 4). There was an increase in evaporative water loss when wind speed increased from 10 to 100 cm sec^{-1}. Another, smaller increase in the rate of EWL was produced when wind speed was increased to 400 cm sec^{-1}. Also, there was a difference in the increase in EWL as wind speed increased between small and large turtles. This interactive effect of body size and wind speed on EWL was greatest in large turtles ($>$ 1000 g).

Convection

Convection coefficients (h_c) were calculated for six solid aluminum castings of turtles at three wind speeds (10, 100 and 400 cm sec^{-1}). The effects of size, wind speed and temperature differential between casting and air (ΔT) were assessed with linear regression analysis. A summary of all equations produced by this regression analysis is provided in Table III. The significance of these effects on h_c were tested by an analysis of variance of the partitioned sum of squares. This procedure is discussed by Sokal and Rohlf (1969, pg 419-423). A model ANOVA table for linear regression is seen in Table IV.

In still air, differences in h_c cannot be attributed to change in size of turtle (Table V a, $P > 0.05$). At wind speeds of 100 and 400 cm sec^{-1}, size has a significant effect on h_c (Table V b, c, $P < 0.05$). However, the slopes of the regression lines for these test conditions are opposite in sign (Fig. 4) indicating that the relationship between size and convective heat loss at 100 cm sec^{-1} is inverse of the relationship at 400 cm sec^{-1}.

Temperature differential between castings and air (ΔT) had a statistically significant effect on h_c in still air Table VI a, ($P < 0.05$). ΔT had no effect on h_c at windspeeds of 100 and 400 cm sec^{-1}. Wind speed also had a highly significant effect on the convection coefficient Table VII, ($P < 0.01$). At all test conditions, changing wind speed produced a significant change in the amount of heat loss from the castings. The lines produced by regression of h_c on wind speed for each casting were in close agreement with each other at 10 and 100 cm sec^{-1} (Fig. 6). The confidence intervals of regression lines for all sizes of casts at these wind speeds overlap ($P > 0.05$). However, at 400 cm sec^{-1}, confidence intervals for castings a, c, d and e do not overlap each other ($P < 0.05$). Casting b is significantly different from castings a and c and casting f is significantly different from all other castings except b ($P < 0.05$).

The Climate Space

The climate space represents the interaction between the physical and physiological properties of the turtle and the physi-

cal factors of the environment including radiation, ambient temperature, wind speed and humidity (Porter and Gates 1969). Several climate spaces were constructed for different sizes of Chrysemys scripta. This group of climate spaces were almost identical in size and shape. Therefore, a typical climate space is presented for a turtle weighing 1000 g (Fig. 7). Standard metabolic rates were taken from Gatten (1974), heat loss due to respiratory evaporative water loss (E_r) was calculated according to Bentley and Schmidt-Nielsen (1966) using my total evaporative water loss measurements. A caloric conversion factor of 580 cal gm^{-1} was used to convert water loss into energy loss. Convection coefficients (h_c) and shell thickness (d_s) were determined in this study. Only 4 - 8% of the total surface area of a turtle (unpublished data) is in contact with the substrate when the turtle is out of the water and its limbs are retracted. Since rates of heat energy exchange by conduction would be minimal, they have not been included in this first order approximation.

The line marked sun (Fig. 7) represents the radiation absorbed by a turtle at different air temperatures on a cloudless day when body orientation provides maximum exposure to direct sunlight. This sets the right side of the climate space. Absorptivity to solar radiation (a) was assumed to be 0.9 because of the dark coloration of this species' skin and carapace (Porter and Gates 1969). The line labeled clear sky + ground represents radiation absorbed by the turtle at night from outer space, the atmosphere and ground. This sets the boundary for the left side of the climate space. The blackbody line is a reference line indi-

cating the amount of energy received by a turtle in a blackbody cavity where energy flux is equal from all sides e.g. an underground burrow. The upper boundary was determined by solving equation (3) for Q_{abs} using a body temperature of 40°C, a corresponding metabolic rate and evaporative water loss and the convection coefficient for a given wind speed. Substrate temperature was assumed to be equal to air temperature. This procedure was repeated for several air temperatures and the upper lines plotted as air temperature vs. Q_{abs}. Lower lines were computed for a body temperature of 1°C (Musacchia and Sievers 1956) following the above procedures. Upper and lower boundaries were determined for wind speeds of 10, 100 and 400 cm sec^{-1}.

From the climate space (Fig. 7), we can determine various limitations which are imposed on the turtle by the environment. In full sunlight, a turtle could withstand higher air temperatures (32°C) when it is subjected to wind speeds of 400 cm sec^{-1} then while it is in still air (19°C). A turtle could withstand ambient temperatures equal to its upper lethal temperature when sheltered in a blackbody cavity. At night, air temperatures as high as 48°C could be tolerated in still air, however, these are conditions which never occur in this turtle's habitat.

Three wind speeds were used to determine the lower limit of the climate space. When exposed to a clear night sky, a turtle could not survive an air temperature less than 9°C in still air or less than 3°C at wind speeds of 400 cm sec^{-1}. During cold weather, a blackbody cavity could provide a tolerable habitat to temperatures as low as 1°C. In full sunlight, a turtle would with-

stand air temperatures as low as $-17^{o}C$ when wind speed is 10 cm sec^{-1}. An air temperature of $-5^{o}C$ can be endured at 400 cm sec^{-1}.

DISCUSSION

Evaporative Water Loss

Evaporative water loss determinations indicate that Chrysemys scripta loses water at an increasing rate as wind speed and air temperature increase. In addition, smaller individuals lose water at a faster rate than larger individuals except at low air temperatures. Several authors have discussed the physical processes which partially account for these changes in evaporative water loss in animals (see Leighley 1937, Martin 1943, Machin 1964, Spotila 1972 and Spotila and Berman 1976 for application of evaporation theory to biological systems). These physical processes include changes in the amount of water vapor per unit volume of air, changes in wind speed, boundary layer thickness, air turbulence and orientation to air flow.

The amount of water vapor per unit volume of air is in part a function of air temperature. As air temperature increases, the capacity of air to hold water increases. Vapor pressure deficit (VPD) is the difference between the amount of water vapor in the air at saturation and that actually present at a given relative humidity. Spotila (1972) and Spotila and Berman (1976) have demonstrated that the difference in moisture content between the skin and the air is the driving force of EWL from the surface of animals. The larger the VPD, the larger this difference. In these experiments, VPD increased as temperature increased (Table I). Therefore, a large part of the temperature effect on EWL was related to increase in the steepness of the moisture gradient from

the turtle to the air as VPD increased.

Changes in wind speed and size of turtle also affected evaporative water loss (Fig. 4). Leighley (1937) hypothesized that changes in boundary layer thickness were inversely related to wind speed and size of an evaporator up to a maximum size approximately four meters in diameter. Martin (1943) successfully applied Leighley's theory to evaporators as small as 1 mm in length. Therefore, the relationship between boundary layer thickness, wind speed and size applies over the range of dimensions of most moist-skinned animals. Figures 2, 3, and 4 illustrate the effect of size and wind speed on evaporative water loss in turtles. An increase in wind speed changes boundary layer thickness by decreasing the distance through which water must diffuse before being swept away by mass transport in the free air stream. There is a great increase in the rate of EWL when wind speed is increased from 10 to 100 cm sec^{-1} (Fig. 4). This can be attributed to a decrease in the thickness of the boundary layer. The effect of increasing wind speed further, to 400 cm sec^{-1} is less marked because a large part of the boundary layer has already been stripped away at 100 cm sec^{-1}.

Although the physical environment has a dominant effect on evaporative cooling in this animal, physiological factors can contribute to evaporative water losses in C. scripta. Bentley and Schmidt-Nielsen (1966) demonstrated that about 22% of total evaporative water losses occur thru the respiratory surfaces of C. scripta. Changes in an ectotherm's body temperature affect the metabolic and oxygen consumption rates and indirectly alter the

rate of EWL (Prosser 1973). Jackson (1971) and Jackson et al. (1974) noted that frequency of respiratory ventilation in turtles was proportionate to body temperature as a result of increased metabolic oxygen consumption. Since aerobic passages in the lungs are free water surfaces, any increase in the rate of exchange of air between the lungs and atmosphere will cause an increase in water loss. Therefore, some part of the increase in EWL at higher body temperatures may have been due to increases in respiratory rate.

Convection

Wind speed, size and ΔT have significant effects on convective heat transfer between a turtle shaped object and its environment. Wind speed causes the greatest variation in the convection coefficient regardless of interaction with ΔT and size. In still air, when the effects of wind speed are minimized, h_c varies as a function of ΔT. Also, at higher wind speeds (100 and 400 cm sec^{-1}), the size of the turtle causes differences in h_c.

Convective heat transfer is dependent upon the thickness of the boundary layer of air, air velocity and the temperature differential between the animal's surface and ambient air. Boundary layer thickness is proportionate to fluid velocity, size of the animal, surface characteristics such as a shape and texture, orientation to flow and fluid densities (Kreith 1973). Within the boundary layer heat is conducted away from the heated casting to the free air stream where it is carried away by mass transport.

The driving force for convection in still air is the temperature difference between an object and the air. ΔT affects the rate of conduction through the boundary layer by changing the steepness of the gradient of heat loss from the castings as ΔT increases. The effect of ΔT on convective heat transfer is greatest at 10 cm sec^{-1} when boundary layer thickness is greatest. At this wind speed, heat loss is more dependent upon density differences within the boundary layer than mass transport outside the boundary layer. As wind speed increases, heat transfer by conduction diminishes and mass transport becomes the major avenue of heat exchange. More heat transfer occurs directly to air in motion rather than through the motionless boundary layer. Thus heat transfer is greatest at 400 cm sec^{-1} because much of the boundary layer has been removed enhancing convection by mass transfer.

The effect of an object's size on its convection coefficient has been reviewed in Kreith (1973) and can be defined using dimensionless analysis. These relationships were simplified by Gates (1968) when he applied heat transfer theory to biological systems. He calculated h_c as a ratio of wind speed divided by the characteristic dimension of an animal. Convection coefficients for turtles compared according to their characteristic dimensions do not agree with Gate's calculations at 10 or 100 cm sec^{-1} (Fig. 5). At these wind speeds, there are no significant differences between different size turtles. At the higher wind speed, 400 cm sec^{-1}, h_c for some sizes of turtle are significantly different but cannot be correlated with Gate's assumption. The reasons for this are unknown but may be due to changes in the shape of the boundary layer

around turtle shaped objects or to differences in the internal structure of the solid aluminum casts.

The Climate Space

Energy budget analysis clearly demonstrates the combined effects of wind speed and absorbed radiation on the physiological limits of Chrysemys scripta. Limits of the climate space are shifted by wind speed because heat exchange by convection and evaporation is directly affected by changes in wind velocity (Fig. 7). At high temperatures, in full sunlight, the turtle would be restricted to a lower air temperature when exposed to still air than at wind speeds of 100 or 400 cm sec^{-1}. Still air reduces the rate of convective and evaporative heat loss so that these factors cannot compensate for the high radiation load absorbed. Convective heat loss is reduced at 10 cm sec^{-1} because a thick boundary layer of air surrounds and insulates the turtle. Increasing wind speed decreased the boundary layer thickness and allowed more heat by convection and evaporation. Thus the animal can withstand higher air temperatures in full sunlight. Therefore, an increase in wind speed increases heat transfer between the turtle and the air which couples the animal more closely to environmental temperatures.

Under clear sky and ground conditions, the turtle is losing large amounts of heat via radiation, therefore, survival at cold night temperatures (in the lower left portion of the climate space) is dependent upon air temperature and windspeed. In still air, a turtle receives less heat via convection which reduces its ability

to tolerate cold conditions. As wind speed increases, convective heat transfer to the turtle increases and the animal would be able to survive colder air temperatures.

During cold sunny days, the turtle can survive at lower air temperatures because it is receiving large amounts of solar radiation. In still air, the turtle loses less heat by convection and can survive lower air temperatures (-17°C). Higher wind speeds remove heat and shift the lower survival temperature upward (-3°C).

From this type of energy budget analysis, we can predict interaction between this species of turtle and its environment. A turtle's activity would be limited to microclimate conditions which are bounded by the climate space. We can predict that periods which would be energetically stressful to C. scripta in a terrestrial environment include the hot summer months, cold winter months and portions of the spring and fall when changeable weather conditions produce large and potentially lethal temperature fluctuations. From late fall to early spring throughout most of its range in the U.S., the turtle would be forced to live along the blackbody line of its climate space because of stressful environmental conditions. During this portion of the year, C. scripta must live in protective cavities or in water (a blackbody substitute) where microclimate variations are minimal. In water, this turtle could be active throughout the year. Seasons which favor terrestrial activity include spring, summer and fall when environmental factors are within the limits of the climate space. These periods of the year vary according to maximum and minimum air temperature and solar radiation which is a function of the day of

the year, time of day and latitude.

Some evidence is available in the literature to support these predictions. Terrestrial activity of C. scripta is not limited by sex or maturity and can be related to seasons and precipitation in South Carolina (Gibbons 1969). He noted that terrestrial movement occurred in March, April and May but from June to October, turtles left the water only after periods of precipitation. During these periods, decreased VPD may be a stimulus for turtles to emerge from water to feed, lay eggs or move to adjacent bodies of water. After October, no level of precipitation provided sufficient stimulus for overland activity. Energy budget analysis indicates that terrestrial movement after rainfall is probably in response to periods of lower evaporative stress during or immediately after rainfall in hot weather. However, after diurnal temperatures begin to decrease in October, decreased evaporative stress was not a significantly strong stimulus for initiating overland movement.

Predictions can be made concerning the nesting activities of C. scripta from the climate space. When females are reproductively ripe, the immediate stimuli for females to nest are air temperature, Q_{abs}, wind speed and humidity. Seasons such as late spring thru early fall are best because females would not encounter adverse terrestrial conditions while nesting. Combinations of these parameters vary daily during these seasons but it is evident from the climate space that C. scripta would not nest during midday in full sunlight. During the afternoon and evening, nesting could occur without the possibility of the turtle exceeding its climate space. If temperatures are moderate, nesting could con-

tinue at night when metabolic heat produced by the exertion of digging a nest would be eliminated most efficiently. Temperatures during early morning might be too low for nesting to occur and there is the chance that turtles remaining out of water after sunrise could be adversely affected by solar radiation and increasing air temperatures. Nesting activity by C. scripta in Panama occurs during the dry season (from January to April). This appears to be contradictory because of increased evaporative stress during the dry seasons, however, this is the only period when available nesting areas are not covered by water. Nesting begins in the afternoon and continues until approximately 12:30 a.m. but most of it (78%) occurs after dark, from 6:00 p.m. to 12:30 a.m. (Moll and Legler 1971). Nesting activity was not observed when air temperature fell below 22°C which usually occurs in the early morning during the dry season in Panama. Heat loss by radiation to the night sky and decreasing air temperatures probably stimulated the turtles to return to water. Energy budget analysis indicates that levels of Q_{abs} around solar noon would place an animal at or beyond the upper limit of the climate space during periods of nesting. The addition of metabolic heat produced by these activities could be sufficient to cause death from excessive heating. Moll and Legler (1971) noted that nesting requires approximately 1-1/2 hours of strenuous activity which if it occurred in direct sunlight or at midday could result in body temperature exceeding the turtle's CTM.

Basking is another activity which lends itself to predictions based upon energy budget analysis. Turtles may bask under conditions that are found outside of the climate space, however, they

must return to a less adverse environment within the climate space to prevent overheating. Duration of excursions beyond the climate space are limited by the heat storage capacity of these turtles. During the spring and fall, turtles could bask for long periods of time because they would have a lower body temperature at initiation of basking and solar radiation would be at relatively low intensities. When temperatures and radiation levels are higher in summer, the time spent basking by turtles would be reduced. Cold conditions during the winter would greatly restrict basking. A daily basking pattern for C. scripta should be as follows. Cool environmental conditions during early spring influence the turtle to bask in a unimodal activity pattern or during the middle of the day. Water and body temperatures are low but air temperatures and solar radiation during the middle of the day should stimulate basking. If weather conditions are favorable, basking may continue for long periods of time because Q_{abs} during this time of year would not increase the turtle's body temperature to lethal levels. As the seasons progress, air temperature and solar radiation intensity increase and influence the turtle to bask predominantly in a bimodal activity pattern. Morning and late afternoon or evening become the most favorable portions of the day for the turtle to emerge from the water. Basking around solar noon during the summer would cause the turtle to exceed the limits of the climate space, therefore it should not occur. When fall conditions prevail, turtles would return to a unimodal pattern of basking.

Limited information is available in the literature on the daily basking activity of C. scripta through an annual cycle. On

clear sunny days, basking is limited by high body temperatures (Cagle 1944 and Moll and Legler 1971). Cagle (1950) noted that turtles cannot bask for long periods in direct sunlight because of rapid increases in body temperature, however, when the sun is obscured, basking is prolonged. Moll and Legler (1971) in a description of the seasonal basking activities of C. scripta in Panama concluded that basking frequency is greatest during the coolest portion of the year especially after several days of rain or cloudiness. During this type of weather, on clear sunny days, all available basking sites were occupied. Basking was most intense on sunny days during the latter part of the rainy season when fewest sunny days occurred. They also indicated that the greatest numbers of turtles engaged in atmospheric basking occurred at 9:00 a.m. and at 2:00 p.m. Reliable data demonstrating basking activities during the middle of the day is unavailable.

Porter et al. (1973) have demonstrated that the desert lizard Dipsosaurus dorsalis has a daily activity pattern very similar to that predicted for C. scripta. In spring, it was predicted that the lizard should be active outside of its burrow in the middle of the day. As the seasons progress, the summer activity pattern shifts to morning and afternoon. In the fall, noon day activity resumes.

The similarities in the activity patterns of the desert lizard and aquatic turtle indicate the importance of microclimate conditions on the behavior of small reptiles. Similar responses by these two organisms to basic cyclic changes which are common to all environments tie together thermal relations between these distinctly different reptiles. Physiological and structural adapta-

tions and thermal tolerances may differ between turtles and lizards because of evolutionary responses to different environments but the similarity of their behavioral responses to comparable environmental situations is striking. The predictions for the turtle cannot be successfully validated with existing data in the literature. There is a need for extensive field studies combined with microclimatological measurements to provide supportive data for this model.

Table I. A summary of results of evaporative water loss determinations for *Chrysemys scripta*. Surface temperature (T_r) was continuously monitored and body temperature (T_b) was measured at the end of each condition. Vapor pressure deficit was calculated from measurements of relative humidity and air temperature.

Air Temperature (°C)	Wind Speed (cm sec^{-1})	Turtle Temperature T_b (cloacal)	Turtle Temperature T_r (surface)	Sample Size	Vapor Pressure Deficit	Evaporative Water Loss Rate (mg g^{-1} hr^{-1}) Mean	Evaporative Water Loss Rate (mg g^{-1} hr^{-1}) Range
5	160	7.6	6.2	9	4.74	0.161	0.102 - 0.245
15	10	12.1	13.8	10	10.37	0.142	0.080 - 0.355
	100	13.4	14.5	10	9.64	0.197	0.120 - 0.379
	400	12.5	14.3	9	11.39	0.200	0.112 - 0.348
25	10	24.0	24.4	10	20.86	0.126	0.063 - 0.207
	100	23.9	24.8	10	21.48	0.212	0.121 - 0.381
	400	23.2	25.3	10	22.77	0.232	0.166 - 0.374
35	10	29.6	30.8	10	34.17	0.207	0.098 - 0.369
	100	31.0	31.2	10	35.97	0.363	0.228 - 0.596
	400	31.4	32.1	10	41.10	0.392	0.274 - 0.599

Table II. Regression equations for calculating evaporative water loss (mg g^{-1} hr^{-1}) from body weight (g) for *Chrysemys scripta*. A coefficient of determination is included for each equation.

Air Temperature (°C)	Wind Speed (cm sec^{-1})	Equation of Regression Line y = EWL, x = Body Weight (g)	Coefficient of Determination (r^2)
15	10	$y = 5.60x^{-.57}$	0.87
15	100	$y = 2.73x^{-.40}$	0.86
15	400	$y = 0.82x^{-.21}$	0.46
25	10	$y = 4.10x^{-.53}$	0.76
25	100	$y = 6.71x^{-.50}$	0.95
25	400	$y = 2.24x^{-.31}$	0.62
35	10	$y = 4.57x^{-.47}$	0.60
35	100	$y = 10.0x^{-.49}$	0.84
35	400	$y = 2.95x^{-.30}$	0.58

Table III. Regression equations describing the relationship between the convection coefficient (h_c) and size of turtle (in IIIa), ΔT (in IIIb) and wind speed (in IIIc). Equations in IIIa describe $h_c = y$ according to body weight = x at three different wind speeds. Equations in IIIb describe h_c according to $\Delta T = x$ at three wind speeds. Equations in IIIc describe h_c according to wind speed = x for turtles of different size. Size was determined by measuring the significant dimension of the turtle in the direction of the wind flow.

a. Regression of h_c on size at three wind speeds

Test Variable	Regression Equation	r^2
10 cm sec^{-1}	$y = (7.3 \times 10^{-5})x + 0.0075$	0.23
100 cm sec^{-1}	$y = (-2.9 \times 10^{-6})x + 0.0180$	-0.80
400 cm sec^{-1}	$y = (7.1 \times 10^{-6})x + 0.0414$	0.49

b. Regression of h_c on ΔT at three wind speeds

Test Variable	Regression Equation	r^2
10 cm sec^{-1}	$y = (1.4 \times 10^{-4})x + 0.0065$	0.67
100 cm sec^{-1}	$y = (1.7 \times 10^{-5})x + 0.0160$	0.07
400 cm sec^{-1}	$y = (-5.1 \times 10^{-4})x + 0.0484$	-0.20

Continued on next page

c. Regression of h_c on v at six body sizes

Test Variable (cm)	Regression Equation	r^2
9.8	$y = (8.98 \times 10^{-5})x + 0.0075$	0.99
10.6	$y = (1.04 \times 10^{-4})x + 0.0061$	0.99
12.7	$y = (8.64 \times 10^{-5})x + 0.0078$	0.99
14.0	$y = (9.53 \times 10^{-5})x + 0.0068$	0.99
17.1	$y = (9.27 \times 10^{-5})x + 0.0068$	0.99
18.6	$y = (1.18 \times 10^{-4})x + 0.0053$	0.99

Table IV. A model ANOVA table used to test significance by linear regression. The source of variation of the dependent variable, Y, can be assessed in terms of the variation of the independent variable, X. This variation can be partitioned to show the amount of variation in Y accounted for by variation of X (explained error) and the residual variation (unexplained error), a quantity that is part of all standard error in regression (Sokal and Rohlf, 1969 p. 421).

Source	df	SS	MS	F
Explained due to linear regression	1	y^2	s^2_y	
Unexplained due to error around regression line	n - 2	$d^2_{Y \cdot X}$	$s^2_{Y \cdot X}$	
Total	n-1	y^2	s^2_Y	

Table V. Results of ANOVA of regression analysis of h_c on size (body weight) at three wind speeds. Variation of predicted h_c is assessed according to variation in body weight. A significant F value indicates that body weight is a suitable parameter for predicting h_c at a particular wind speed.

a. 10 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by size	1	7.26×10^{-7}	7.26×10^{-7}	0.935
Variation unaccounted for	16	1.24×10^{-5}	7.76×10^{-7}	
Total	17			

b. 100 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by size	1	1.16×10^{-5}	1.16×10^{-5}	28.6**
Variation unaccounted for	16	6.52×10^{-6}	4.07×10^{-7}	
Total	17			

c. 400 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by size	1	6.88×10^{-5}	6.88×10^{-5}	5.07*
Variation unaccounted for	16	2.17×10^{-4}	1.36×10^{-5}	
Total	17			

* P 0.05
** P 0.01

Table VI. Results of ANOVA from regression analysis of h_c on ΔT at three wind speeds. Variation of predicted h_c is assessed according to variation of ΔT. A significant F value indicates that ΔT is a suitable parameter for predicting h_c at a particular wind speed.

a. 10 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by ΔT	1	5.82×10^{-6}	5.82×10^{-6}	12.7*
Variation unaccounted for	16	7.32×10^{-6}	4.85×10^{-7}	
Total	17	1.31×10^{-5}		

b. 100 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by ΔT	1	8.33×10^{-8}	8.33×10^{-8}	0.068
Variation unaccounted for	16	1.81×10^{-5}	1.13×10^{-6}	
Total	17	1.82×10^{-5}		

c. 400 cm sec^{-1}

Source	df	SS	MS	F
Variation accounted for by ΔT	1	7.61×10^{-5}	7.61×10^{-5}	0.694
Variation unaccounted for	16	1.75×10^{-3}	1.10×10^{-4}	
Total	17	1.83×10^{-3}		

* P 0.05
** P 0.01

Table VII. Results of ANOVA from regression analysis of h_c on wind speed for six sizes of turtle. Variation of predicted h_c is assessed according to variation in size. A significant F value indicates that wind speed is a suitable parameter for predicting h_c at a particular size.

a. 9.8 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	2.02×10^{-3}	2.02×10^{-3}	286.3**
Variation unaccounted for	7	4.94×10^{-6}	7.05×10^{-7}	
Total	8	2.03×10^{-3}		

b. 10.6 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	2.69×10^{-3}	2.69×10^{-3}	165.1**
Variation unaccounted for	7	1.14×10^{-5}	1.63×10^{-6}	
Total	8	2.70×10^{-3}		

c. 12.7 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	1.87×10^{-3}	1.87×10^{-3}	167.47**
Variation unaccounted for	7	7.81×10^{-6}	1.11×10^{-6}	
Total	8	1.87×10^{-3}		

Continued on next page

d. 14.0 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	2.27×10^{-3}	2.27×10^{-3}	404.5**
Variation unaccounted for	7	3.93×10^{-6}	5.62×10^{-7}	
Total	8	2.28×10^{-3}		

e. 17.1 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	2.15×10^{-3}	2.15×10^{-3}	124.8**
Variation unaccounted for	7	1.21×10^{-5}	1.72×10^{-6}	
Total	8	2.16×10^{-3}		

f. 18.6 cm

Source	df	SS	MS	F
Variation accounted for by wind speed	1	3.48×10^{-3}	3.48×10^{-3}	393.5**
Variation unaccounted for	7	6.19×10^{-5}	8.84×10^{-6}	
Total	8	3.54×10^{-3}		

* P 0.05
** P 0.01

Figure 2. The effect of body size on the rate of evaporative water loss of the turtle Chrysemys scripta tested under blackbody conditions at 25°C with a wind speed of 100 cm sec^{-1}. The line was drawn from a regression equation computed using the method of least squares. The coefficient of determination was 0.95.

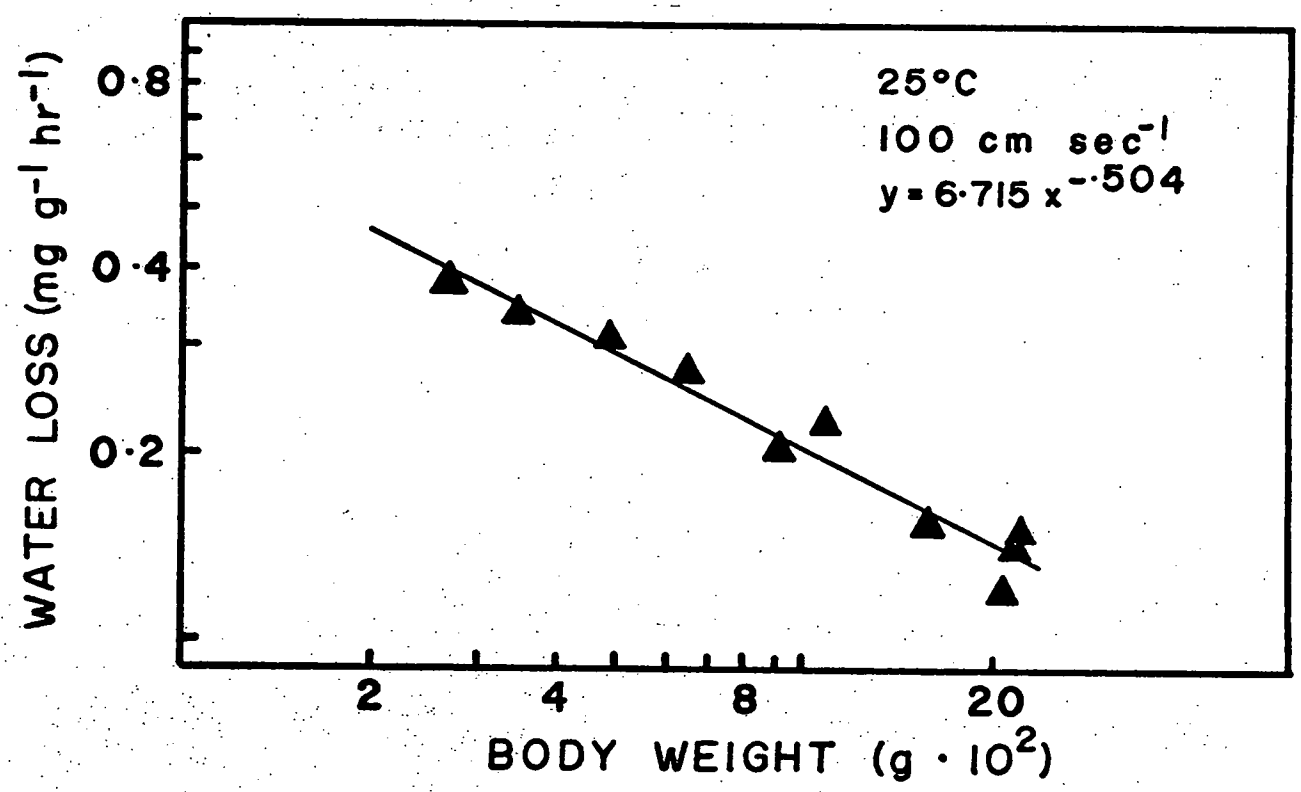

25°C
100 cm sec⁻¹
y = 6·715 x^-·504
WATER LOSS (mg g⁻¹ hr⁻¹)
0·8
0·4
0·2
2
4
8
20
BODY WEIGHT (g · 10²)

Figure 3. The effect of body size and temperature on the rate of evaporative water loss of C. scripta tested with a wind speed of 400 cm sec^{-1}. Lines are drawn from regression equations computed using the method of least squares. The lines at 15° and $35^{o}C$ are significantly different ($P < 0.05$). Equations of these lines can be found in Table II.

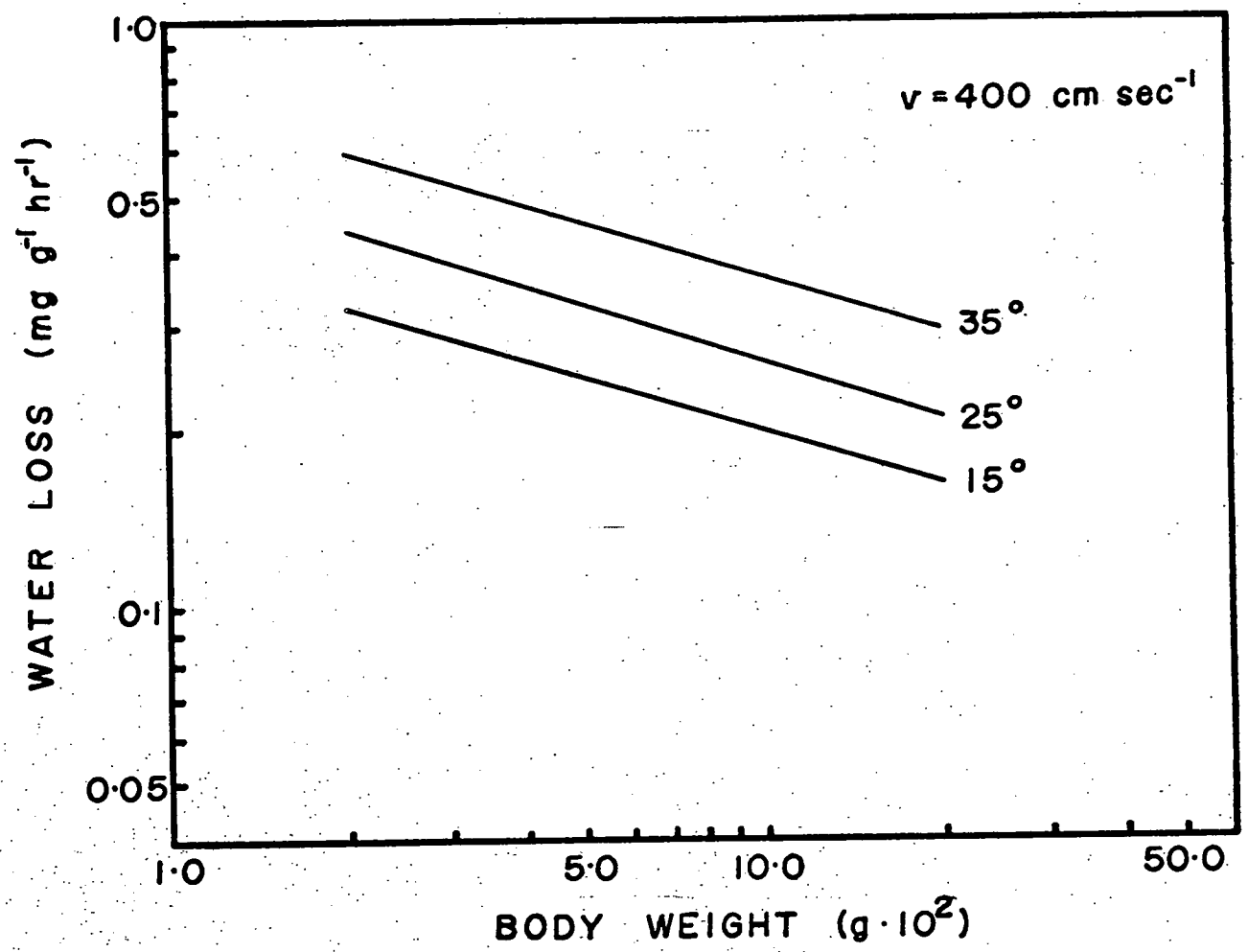

v = 400 cm sec⁻¹
35°
25°
15°
1·0
0·5
0·1
0·05
WATER LOSS (mg g⁻¹ hr⁻¹)
1·0
5·0
10·0
50·0
BODY WEIGHT (g · 10²)

Figure 4. The effect of wind speed and body weight on the rate of evaporative water loss of C. scripta tested at 15°C. Lines were plotted using regression equations computed by the method of least squares. Equations of these lines can be found in Table II.

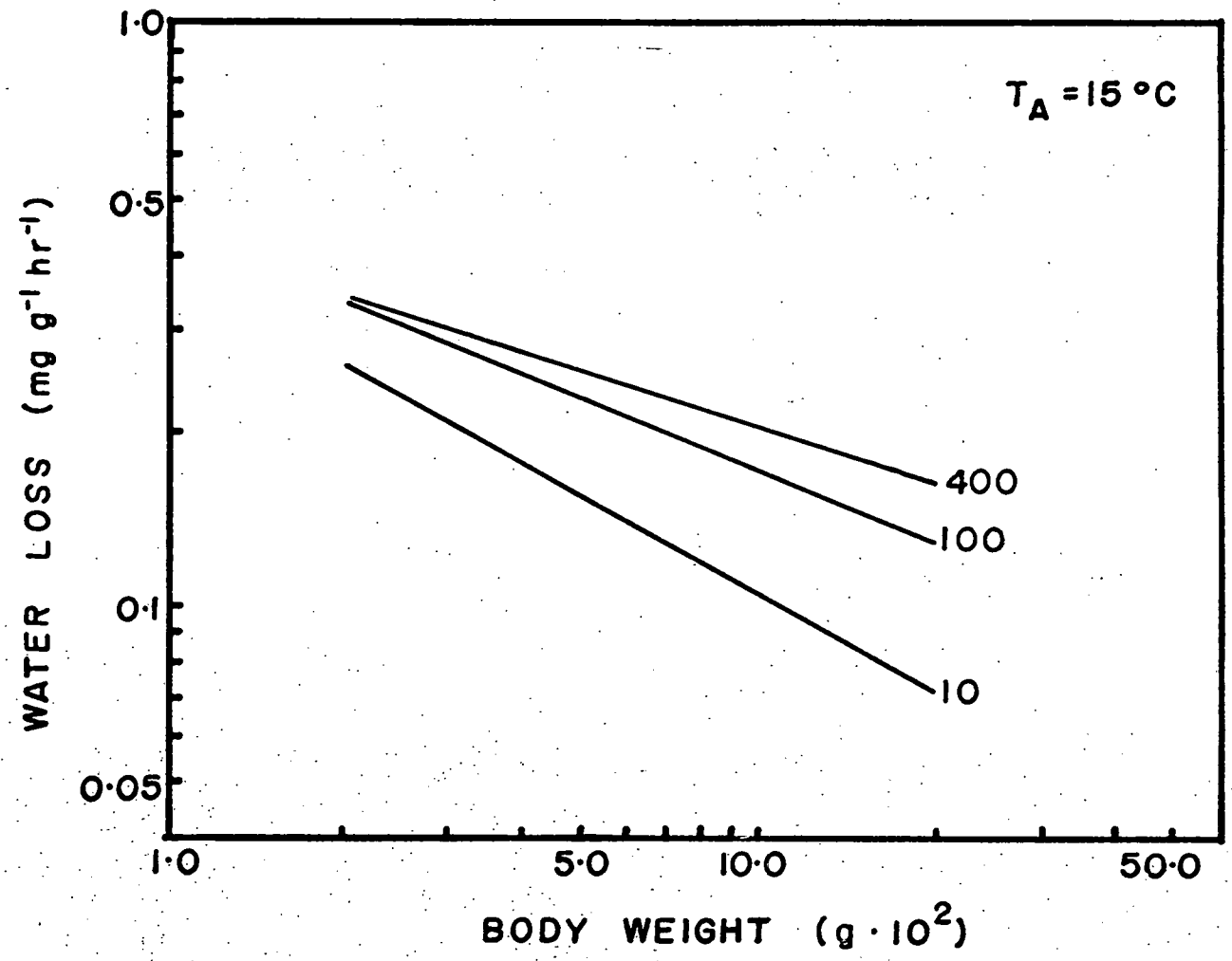

T_A = 15 °C
400
100
10
1·0
0·5
0·1
0·05
WATER LOSS (mg g^{-1} hr^{-1})
1·0
5·0
10·0
50·0
BODY WEIGHT (g · 10^2)

Figure 5. A least squares fit of h_c (n=18) as a function of size for three wind speeds. Equations of these lines can be found in Table IIIa.

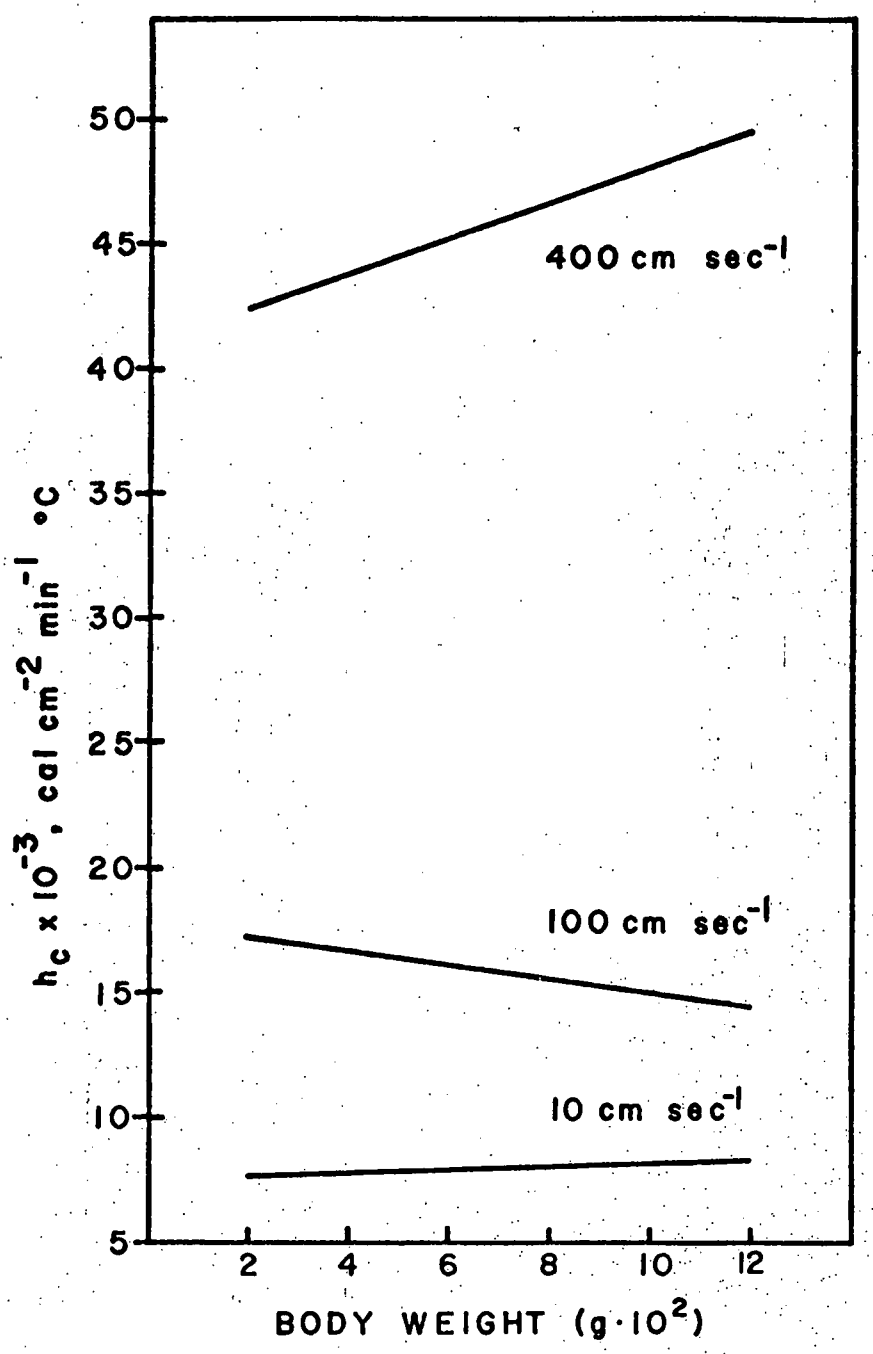

50
45
40
35
30
25
20
15
10
5
$h_c \times 10^{-3}$, cal cm^{-2} min^{-1} °C
400 cm sec^{-1}
100 cm sec^{-1}
10 cm sec^{-1}
2
4
6
8
10
12
BODY WEIGHT (g·10^2)

Figure 6. Least square plots of h_c as a function of wind speed for each size of turtle. Size of each turtle was determined as the significant dimension of carapace in the direction of wind flow. All h_c determinations were performed with turtles perpendicular to wind flow. Equations of these lines can be found in Table IIIc.

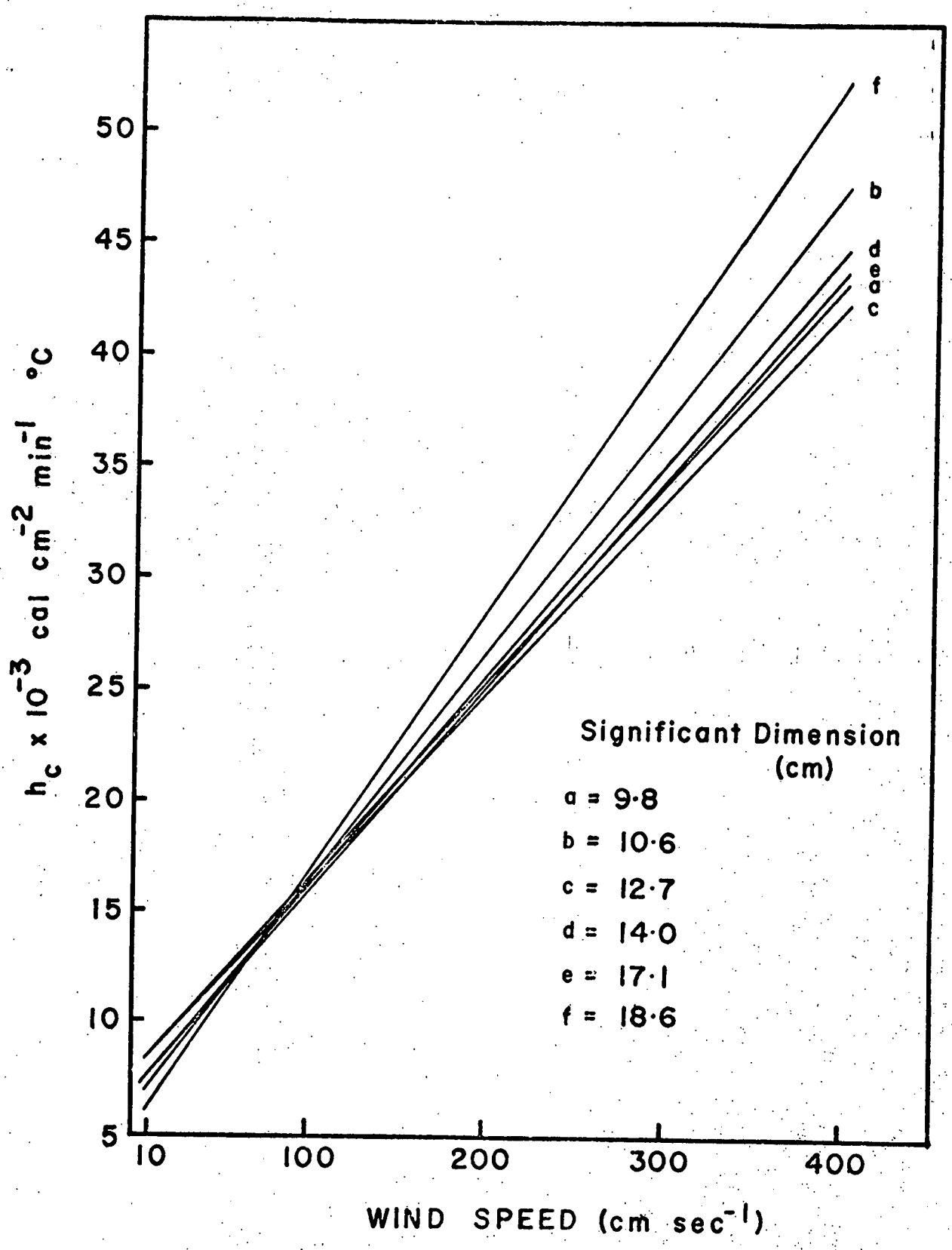
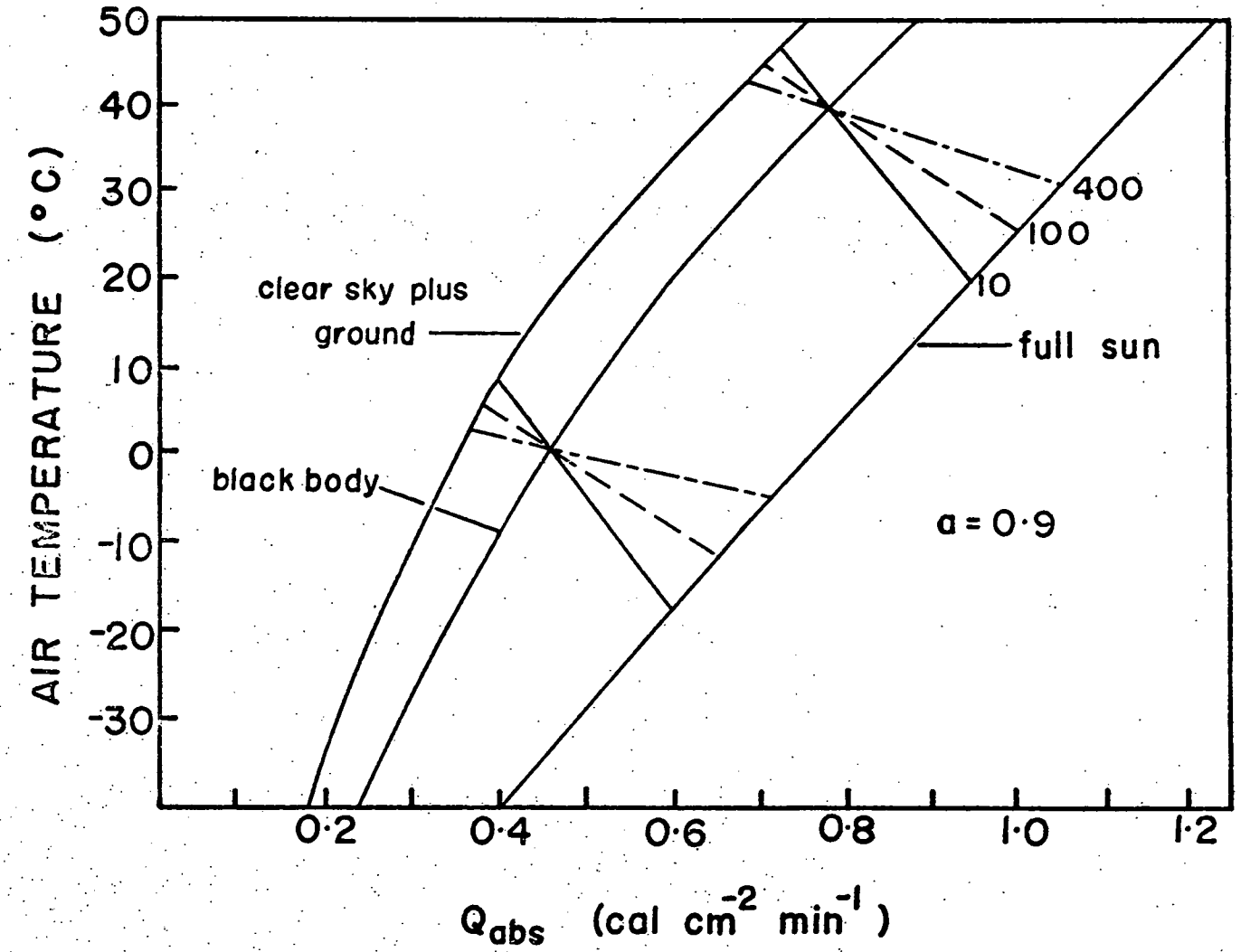

50
45
40
35
30
25
20
15
10
5
$h_c \times 10^{-3}$ cal cm^{-2} min^{-1} °C
10
100
200
300
400
WIND SPEED (cm sec^{-1})
f
b
d
e
a
c
Significant Dimension (cm)
a = 9·8
b = 10·6
c = 12·7
d = 14·0
e = 17·1
f = 18·6

Figure 7. A climate space diagram for an average size C. scripta (1000 g) showing the effects of radiation, air temperature and wind speed under steady state conditions. The solid, dashed and dot-dashed lines in each set were calculated for wind speeds of 10, 100 and 400 cm sec^{-1} respectively. Upper limits were calculated from equation (3) at a body temperature of 40°C using corresponding values of metabolism = 0.0899 ml O_2 g^{-1} hr^{-1} and evaporative water loss = 0.028 cal cm^{-2} min^{-1}. Lower limits were drawn according to the same procedures at a body temperature of 1°C; metabolism = 0.0012 ml O_2 g^{-1} hr^{-1} and evaporative water loss = 0.021 cal cm^{-2} min^{-1}.


50
40
30
20
10
0
-10
-20
-30
AIR TEMPERATURE (°C)
0·2
0·4
0·6
0·8
1·0
1·2
Q_{abs} (cal cm^{-2} min^{-1})
clear sky plus
ground
black body
400
100
10
full sun
a = 0·9

LITERATURE CITED

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