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22

Thermoregulation and Climate Space of the Slider Turtle

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Abstract

Trachemys scripta has a selected temperature of 28°–29° C, and its greatest capacity for activity is between 25° and 30° C. Temperature tolerance ranges from 2° to 44.5° C, although the critical thermal maximum is 41.0°–41.7° C. In general, freshwater turtles are 7 to 25 times more tolerant to anoxia than are other reptiles; however, mechanisms of winter survival of *T. scripta* remain to be determined. The climate space indicates that in full sun this turtle can withstand 32° C in wind of 400 cm/sec and 19° C in still air. Under a clear night sky it can survive a low of 9° C in still air and 3° C at 400 cm/sec. It can live in water between 1° and 40° C. The climate space predicts the opportunistic behavioral thermoregulatory response reported for *T. scripta* in Par Pond.

Introduction

The pond slider turtle (*Trachemys scripta*) is an aquatic turtle inhabiting ponds, lakes, and slow-moving bodies of water that have abundant aquatic vegetation, basking sites, and occasional cleared areas nearby for nesting (Morreale and Gibbons, 1986). On the Savannah River Plant (SRP) in South Carolina, *T. scripta* inhabit a variety

of habitats ranging from Carolina bays to the Par Pond Reservoir system (Gibbons, 1970b). They live primarily in water throughout their lives, emerging onto land to lay their eggs and to migrate to other bodies of water (Morreale et al., 1984; Gibbons, 1970d, 1986). Like other turtles, they have the ability to regulate their body temperature by means of physiology and behavior within the constraints imposed on them by biophysical interactions with the physical environment (Spotila et al., 1984).

For the past several years researchers in our laboratory have been studying the thermal ecology of *T. scripta*, especially related to the environment of the SRP. The thermal biology of reptiles has been reviewed by Avery (1982), Bartholomew (1982), and Huey (1982), and thermoregulation of turtles has been discussed by Hutchison (1979). Recently we (Spotila and Standora, 1985b) discussed the effect of body size on the thermal energetics of turtles. In this chapter we review our past studies and those of others on the thermoregulation of *T. scripta* and discuss the role of heat energy exchange in determining the constraints of the physical environment on the thermoregulation of this turtle. A climate space diagram is developed for *T. scripta*, and the behavioral thermoregulation of this species in Par Pond is discussed in terms of the limits imposed by its biophysical ecology.

Physiological Thermoregulation

Several studies have shown that turtles can exert some control over body temperature (T_b) by physiological 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 that *T. scripta* and *Chrysemys picta* heated faster than they cooled and that the heating rates of dead turtles were the same as cooling rates of live turtles. Lucey (1974) suggested that changes in heating and cooling rates of *T. 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 is 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 *T. scripta* were proportional to changes in body temperature. Weathers and White (1971) stated that peripheral vascular responses to heating and cooling in *Pseudemys floridana* appear to represent a means of changing functional insulation and may contribute to the thermoregulatory capacities of this turtle. Thus, these turtles have considerable physiological control over their T_b .

The integument of *T. scripta*, like that of other reptiles, is not specialized to retain internally generated heat but rather has an important effect in modifying heat flow to

and from the environment (Cena et al., 1986). The conductivity of reptile skin lies between 392 and 502 mW/m·K (Gates, 1980; Drane, 1981). Because most substrates have a greater conductivity than animal tissue, the rate-limiting step in conduction is usually within the skin (Spotila et al., 1972; Monteith, 1973; Tracy, 1976). Changes in blood flow can greatly affect heat loss or gain (Morgareidge and White, 1969; Grigg and Alchin, 1976; Smith et al., 1978) because blood shunted to the skin rapidly transfers heat between the body core and surface. Under this circumstance, heat transfer between the surface and the environment then becomes the limiting step in warming or cooling the turtle.

Blood flow to the skin of the turtles *T. scripta* and *Chelydra serpentina*, crocodilians, and several lizards appears to be controlled by a reflex response such that warm skin is perfused with more blood than is cold skin. Flows are similar during heating, cooling, and steady-state body temperatures at the same skin temperature in the alligator *Alligator mississippiensis* (Weinheimer et al., 1982). In the Australian lizard (*Tiliqua scincoides*), this local effect of heat on skin perfusion appears to act through changes in the arterioles and venules of the inner surface component of the superficial dermis (Drane and Webb, 1980). We expect that the same is true for turtles. In *Trachemys scripta*, changes in blood flow should affect heat loss and gain from the soft skin of the legs and neck and, to a lesser extent, the heat transfer through the skin on the shell. This may explain the commonly observed behavior of basking turtles in which they extend their head and limbs during basking. Heat loss from the green turtle (*Chelonia mydas*) also occurs through the soft tissues of the neck and the proximal area of the flippers (Heath and McGinnis, 1980). Thus, local changes in blood flow to the skin would tend to increase the rate of heat absorption when the skin warmed during basking and would tend to decrease the rate of heat loss when the skin cooled upon the turtle's reentry into the water. This involuntary mechanism should maximize the time *T. scripta* spends at physiologically and behaviorally optimal temperatures.

Metabolism

In addition to the physiological changes that affect T_b and heat transfer in *T. scripta*, the turtle generates some heat through metabolism. The standard metabolic rate (SMR) of *T. scripta* increases with body temperature (T_b) according to the equation

$$\log \text{SMR} = -2.8780 + 0.0458(T_b) \quad (22.1)$$

where SMR is measured as oxygen consumption in $\text{cm}^3 \text{O}_2/\text{g}\cdot\text{h}$ at standard temperature and pressure, dry air (Fig. 22.1). Active metabolic rate (AMR) in *T. scripta* that are stimulated to activity increases with increasing T_b

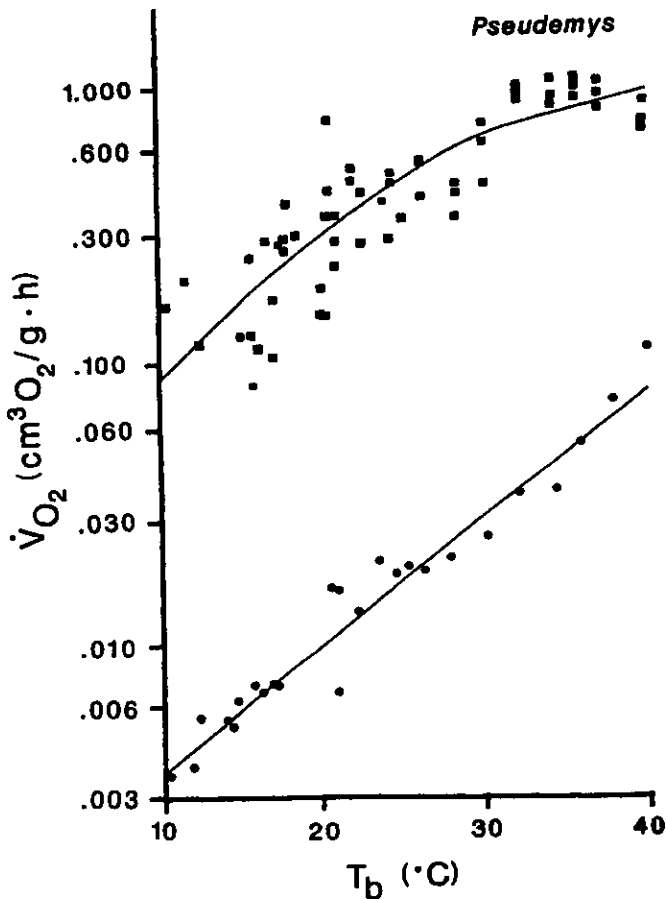


FIGURE 22.1. Standard and active metabolic rates (\dot{V}_{O_2}) in *T. scripta*. Each circle is the mean of approximately 10 hours of measurement of standard metabolic rate of an individual at a given temperature; squares represent individual determinations of active metabolic rate. Regression lines were constructed on the basis of equations 22.1 and 22.2. From Gatten (1974b) with permission.

from 10° to 32° C, remains constant from 32° to 38° C, and decreases slightly at 40° C. This is described as

$$\log \text{AMR} = -1.7541 + 0.0754(T_b) - 0.00078(T_b)^2 \quad (22.2)$$

The aerobic metabolic scope (AMR - SMR) for activity is 1.75 times greater in *T. scripta* than in the more sluggish box turtle (*Terrapene ornata*) at 30° C (Gatten, 1974b). Heart rate also increases with T_b in both resting and active slider turtles and is described as

$$\log \text{SHR} = 0.4557 + 0.0286(T_b)$$

where SHR is standard heart rate (beats/min), and as

$$\log \text{AHR} = 0.5461 + 0.0624(T_b) - 0.00067(T_b)^2$$

where AHR is active heart rate (beats/min). Heart rate increases in activity by a factor of 3.3 at 25° C and by a factor of 2.3 at 10° and 40° C (Gatten, 1974b). An increase in heart rate is not sufficient to provide the increased oxygen needed for aerobic metabolism during warming and exercise. The increase in oxygen pulse must be provided by an increase in stroke volume or arterial-venous oxygen difference. The relative contribution of these mechanisms is unknown (Gatten, 1974c), but unpublished data on *Chelydra serpentina* indicate that it probably changes with temperature (Gatten, pers. com.). These data and those for metabolism suggest that the capacity for activity in *T. scripta* is greatest at T_b between 25° and 30° C and is reduced at lower and higher temperatures.

Temperature Tolerance

Trachemys scripta can tolerate temperatures between 2° C (Schubauer and Parmenter, 1981) and 40° C. Boyer (1965) and Moll and Legler (1971) reported lethal temperatures (LT) of 44.4° to 44.5° C for *T. scripta* in rapid-heating experiments. However, their turtles were showing signs of severe heat stress at temperatures below 40° C. The LT₅₀ is probably no higher than 40° C. The critical thermal maximum (CTM) is 41.0° to 41.7° C for turtles from Georgia and Oklahoma (Hutchison et al., 1966). Values for related turtles range from 39.4° C for *Pseudemys rubriventris* to 40.4° C for *P. nelsoni*, 40.8° C for *P. floridana*, and 41.8° C for *P. concinna*. *Chrysemys picta* from Rhode Island and Minnesota have a CTM of 40.9° C, whereas those from Michigan have a CTM of 42.2° C, and the same species from Nova Scotia, Wisconsin, and Louisiana have intermediate values. In general, the semiaquatic emydid turtles have intermediate tolerances to high temperatures ($\bar{x} = 41.6^\circ \text{C}$), the more aquatic Chelydridae (*Chelydra*, $\bar{x} = 39.4^\circ \text{C}$) and Trionychidae ($\bar{x} = 40.0^\circ \text{C}$) have low CTMs, and the terrestrial Testudinidae (*Gopherus* and *Testudo*) have high CTMs ($\bar{x} = 43.3^\circ \text{C}$; Hutchison et al., 1966). Body size and age do not affect the CTM of *Chelydra serpentina* (Williamson et al., 1989). There are differences in CTM with body size in *Chrysemys picta* (Hutchison et al., 1966), but it is not clear if this is due to differences between juveniles and adults or due to head-body temperature differences related to heating rates (Webb and Witten, 1973). Additional research is needed on the molecular adaptations to temperature in turtles that may be reflected in ontogenetic changes in thermal tolerance (Prosser, 1986).

Selected Temperature

The mean selected temperature of *T. scripta* is 28°–29° C as measured in the laboratory and field. Gatten (1974a) reported that recently fed *T. scripta* tested in a laboratory temperature gradient had a mean body temperature of

29.1° C, with a range of 19°–39° C and with 50% of the observations ranging between 26° and 32° C. The mean selected temperature of nonfed *T. scripta* was 24.6° C. Turtles provided with artificial basking sites in the laboratory had a mean T_b of 30.6° C, with a range of 27.2° to 38.0° C (Boyer, 1965). Cagle (1946) found this species active in the field at a T_b of 10°–37° C, with a “preferred activity temperature range” of 18°–30° C. In Panama, actively feeding *T. scripta* had a T_b of 26.0°–34.4° C (\bar{x} = 29.1° C), and basking turtles had a T_b of 29.0°–34.0° C (\bar{x} = 31.9° C; Moll and Legler, 1971).

Using multichannel telemetry, Standora (1982) found that free-ranging *T. scripta* in a pond on the SRP had deep body temperatures, throughout the year, from 4.6° to 38.2° C, with a selected (preferred) temperature in summer of 28° C. These turtles had a diel cycle in T_b , with mean daily excursions of 4.2° to 10.4° C, depending on the season. Body temperatures peaked during the afternoon and were lowest at night. The highest temperature recorded was 40.0° C for the carapace surface. During winter the most frequently recorded deep body temperature class ($\pm 1^\circ$ C) was 6° C. This changed to 26° C in spring, 28° C in summer, and 14° C in autumn. Thus, there appears to be a seasonal shift in T_b accepted for activity by this species. Standora observed turtles swimming and initiating basking at T_b below 6° C during winter. Likewise, Schubauer and Parmenter (1981) reported that *T. scripta* move sluggishly in Par Pond at water temperatures between 5° and 11° C and bask out of the water at air temperatures as low as 2° C. These seasonal differences are probably related to differences in nutritional status (Hammond et al., 1988), ambient temperature, photoperiod (Graham and Hutchison, 1979), age, and reproductive condition.

Winter Survival

Aquatic turtles overwinter at the bottom of a lake or river and may be buried in mud. The use of the term “hibernation” to describe the behavioral and physiological events accompanying winter dormancy in reptiles has been questioned by Mayhew (1965), Whittow (1973), and Hutchison (1979). However, Gatten (1987) stated that winter-dormant reptiles undergo profound physiological changes parallel to those in winter-dormant mammals and agreed with Gregory (1982) that the term “hibernation” is clearly applicable to reptiles.

During hibernation, anaerobic metabolism is very important because oxygen may be limited in the bottom mud. Freshwater turtles are well adapted to anoxia. They can survive several hours in a nitrogen atmosphere and can survive days of forced submergence (Belkin, 1963; Ultsch et al., 1984). Diving turtles exhibit bradycardia and redistribution of cardiac output (White and Ross, 1966). They are 7 to 25 times more tolerant to anoxia than

are lizards, snakes, crocodylians, and marine turtles. Their ability to survive hypoxia is due primarily to their capacity to rely on glycolysis and endure the buildup of lactate (Millen et al., 1964; Robin et al., 1964; Jackson, 1968; Seymour, 1982; Gatten, 1985, 1987).

When the soft-shelled turtle (*Trionyx spiniferus*), musk turtle (*Sternotherus odoratus*), *Chelydra serpentina*, and *Chrysemys picta* were forcibly submerged at 10° C under anoxic conditions, lactate concentrations rose and blood pH and HCO_3^- levels fell continuously in all species (Ultsch et al., 1984). Survival times were 2.6 days for *Trionyx*, 5.2 days for *Sternotherus*, 8.5 days for *Chelydra*, and 17.0 days for *Chrysemys*. In another experiment *Chrysemys picta* accumulated up to 3,000 μg per gram of total body lactate in two weeks when forcibly submerged at 5° C, without becoming comatose (Gatten, 1981). *Chrysemys picta* resting in air or freely diving at 5° C have low lactate levels (\bar{x} = 870 $\mu\text{g/g}$). They build up high lactate levels (5,580 $\mu\text{g/g}$) while overwintering but can survive at 0° to 8° C in the field at least 67 days without breathing. At 3° C they can survive anoxia under water for up to 168 days (Ultsch and Jackson, 1982a,b). Thus, at low temperatures their metabolic rate is reduced enough to permit survival in ice-covered northern ponds by anaerobic metabolism without a buildup of lethal levels of lactate.

Trachemys scripta may have a similar capacity for anaerobic metabolism under cold conditions. However, in many parts of their geographic range they are not restricted to the bottom mud for the entire winter. In Par Pond and other aquatic habitats on the SRP, *T. scripta* spend much of their time on the bottom but occasionally swim through the water column and even bask out of water on clear sunny days (Schubauer and Parmenter, 1981; Standora, 1982; Spotila et al., 1984). During these periods body temperatures rise to as high as 28.1° C (\bar{x} = 10.8° C; Standora, 1982), and the turtles can eliminate CO_2 , take up O_2 , and reduce the levels of lactate in their tissues and blood. These periods of aquatic and aerial activity may be crucial in allowing *T. scripta* to survive long periods of submergence during winter in the southern part of their range. Sexton (1959b) and Gibbons (1967a) reported that *C. picta* were active under ice in Michigan lakes in December and February. These turtles probably used aquatic gas exchange to supply the oxygen needed to sustain their activity metabolism during these periods when aerial exchange was generally unavailable.

Climate Space

Like all other animals, *T. scripta* obeys the laws of physics and is intimately connected to the physical environment by heat energy exchange as described by the laws of thermodynamics (Gates, 1962). Heat energy exchange determines the turtle's body temperature and thus affects biochemical, physiological, and behavioral processes.

The transfer of heat energy occurs by a variety of physical processes (Kreith, 1973). In the case of a turtle under water, the predominant modes of energy exchange are convection and conduction (see Erskine and Spotila, 1977, for application of underwater heat transfer to biological systems). In the aerial environment, a turtle encounters a more complex energy exchange because of 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 direct, scattered, and diffuse solar radiation and from thermal radiation from the atmosphere and its surroundings. Detailed descriptions of animal heat-energy budgets have been given by Birkebak (1966) and Porter and Gates (1969) and used or modified by Heller and Gates (1971), Spotila et al. (1972, 1973), Porter et al. (1973), Tracy (1976), Porter and James (1979), Bakken (1981), Scott et al. (1982), and Christian et al. (1983) among others. Gates (1980) described biophysical ecology in detail, and Tracy (1982) reviewed the application of biophysical modeling to reptiles. We discussed heat and food energy budgets of ectothermic vertebrates (Spotila and Standora, 1985a) and environmental constraints on the thermal energetics of sea turtles (Spotila and Standora, 1985b). Derivation of a climate space diagram for *T. scripta* now allows us to consider the role of heat energy exchange in the thermoregulation of this turtle.

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. *Trachemys scripta* are small and have a relatively low capacity for heat storage, so that they are very close to heat energy equilibrium with the environment. In steady state, net energy flow between the turtle and its environment is zero, so that

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

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

$$Q_{\text{abs}} + M = \epsilon\sigma(T_r + 273)^4 + h_c(T_r - T_a) + E_t + C \quad (22.3)$$

where Q_{abs} is the radiation absorbed (W/m^2), M is the heat produced by metabolism (W/m^2), ϵ is the surface emissivity of the animal (1.0), σ is the Stefan-Boltzmann constant ($5.673 \times 10^{-8} \text{ W}/\text{m}^2 \cdot \text{K}^4$), T_r is the radiant sur-

face temperature ($^{\circ}\text{C}$), h_c is the convective heat transfer coefficient ($\text{W}/\text{m}^2 \cdot ^{\circ}\text{C}$), T_a is the air temperature ($^{\circ}\text{C}$), E_t is the total evaporative water loss (W/m^2), and C is the conduction (W/m^2). Radiant surface temperature (T_r) is a function of T_b , the thickness and quality of the animal's insulation, and the net heat production inside the turtle. This relationship is expressed as

$$T_r = T_b - \frac{d_s}{k_s}(M - E_r) \quad (22.4)$$

where d_s is the thickness of the shell (cm), k_s is the conductivity of bone ($\text{W}/\text{m} \cdot ^{\circ}\text{C}$), and E_r is the respiratory evaporative water loss (W/m^2). Insulation is dependent upon the average thickness and conductivity of the bony shell covering the turtle's body. We used the value for conductivity of bone ($0.5004 \text{ W}/\text{m} \cdot ^{\circ}\text{C}$) computed from Chato (1969). Bentley and Schmidt-Nielsen (1966) reported that 22% of *T. scripta*'s evaporative water loss is from the respiratory surfaces; thus, $E_r = 0.22E_t$.

Substituting equation 22.4 into 22.3, we have

$$Q_{\text{abs}} + M = [T_b - \frac{d_s}{k_s}(M - E_r) + 273]^4 + h_c[T_b - \frac{d_s}{k_s}(M - E_r) - T_a] + E_t + C \quad (22.5)$$

This equation defines the heat energy balance between a turtle and its environment. We determined shell thickness, evaporative water loss, and convection coefficients in the laboratory and used these data to solve the energy budget equation 22.5 and to formulate a climate space for *T. scripta*.

We measured shell thickness (d_s) at a series of points on plastrons of fresh-killed turtles using a Helios vernier caliper ($\pm 0.05 \text{ mm}$). Average plastron thickness (y , in mm) was related to plastron length (x , in mm) as described by the regression equation

$$y = 0.072x - 2.98$$

We also measured the percentage of the plastron surface area in contact with the substrate and found that it was minimal. Only 4% to 8% of the total surface area of a turtle is in contact with the substrate when the turtle is basking or resting on land or on a log out of the water. Because rates of heat exchange by conduction would be minimal, we have not included conduction in this first-order approximation.

We (Foley and Spotila, 1978) determined evaporative water loss (EWL) for a range of sizes of *T. scripta* at 15 $^{\circ}$, 25 $^{\circ}$, and 35 $^{\circ}$ C and wind speeds of 10, 100, and 400 cm/sec. Rates of water loss increased as wind speed and air temperature increased but were inversely propor-

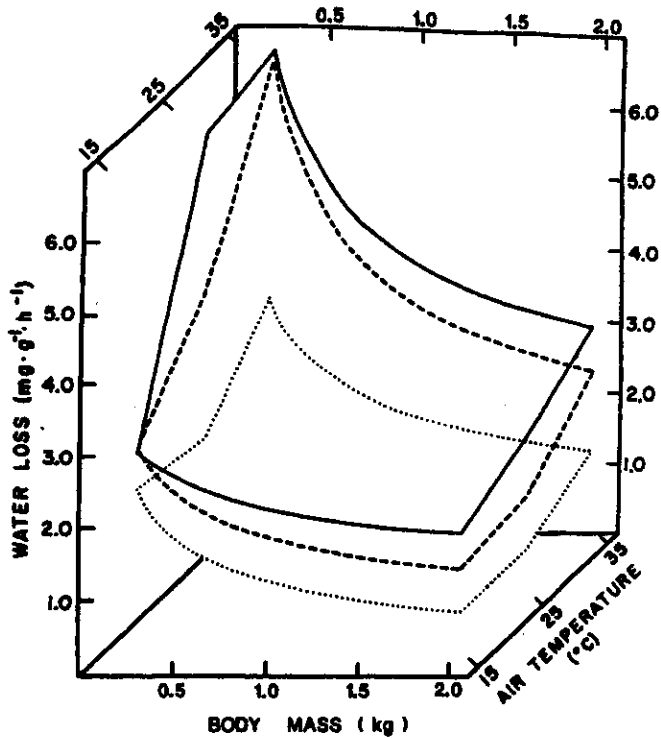


FIGURE 22.2. Three-dimensional plot of evaporative water loss from *Trachemys scripta* as a function of body mass, air temperature, and wind speed. The plane outlined with dotted lines is water loss in still air (10 cm/sec), the plane outlined with dashed lines is water loss at 100 cm/sec, and the plane outlined with solid lines is water loss at 400 cm/sec. The multiple regression equation to define evaporative water loss as a function of air temperature, wind speed, and body size is given by Foley and Spotila (1978). Used with permission.

tional to body size (Fig. 22.2). An increase in wind speed from 10 to 100 cm/sec caused a large initial decrease in boundary layer thickness and a large increase in EWL. A further increase in wind speed up to 400 cm/sec had a relatively smaller effect on EWL because much of the boundary layer was already removed at 100 cm/sec. We used regression equations to compute water loss rates for various sizes of turtles at different air temperatures and wind speeds.

Data from cooling curve experiments were used to calculate convection coefficients according to Wathen et al. (1971). 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 an alginate 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 gray investment plaster. The wax mold was melted from within the plaster-filled collet, which was then dried and cured at 482° C for 15 to 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 that 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 0.84-millimeter 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 to above 65° C and placed perpendicular to wind flow in the center of a wind tunnel (test section of 122 × 122 × 180 cm) on a polystyrene pad (61 × 56 × 2.5 cm). The time-temperature responses of the casting were measured between 65° C and equilibrium. 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). Details of these experiments were provided by Foley (1976). As wind speed increased, h_c increased. There was a clear effect of body size at a wind speed of 400 cm/sec, but at 100 cm/sec and 10 cm/sec there were no significant differences in h_c between different-sized turtles. A larger range of body sizes does result in differences in h_c (Spotila and Standora, 1985b). Convection coefficients were used to solve equation 22.5.

Several climate spaces were constructed for different sizes of *T. scripta*. Unlike those for alligators (Spotila et al., 1972), these climate spaces were almost identical in size and shape. Therefore, a typical climate space is presented for a turtle weighing 1,000 g (Fig. 22.3). Standard metabolic rates were taken from Gatten (1974b), and heat loss due to respiratory evaporative water loss (E_r) was calculated according to Bentley and Schmidt-Nielsen (1966), using our total evaporative water loss measurements. Evaporative water loss was multiplied by 2.430×10^6 J·K/g (latent heat of vaporization of water) to convert it to heat loss.

The boundaries of the 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. 22.3). The line marked "full sun" 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 determined by measuring the reflectances of the carapace of a preserved *T. scripta* with a Beckman DK-2A spectrophotometer in the laboratory

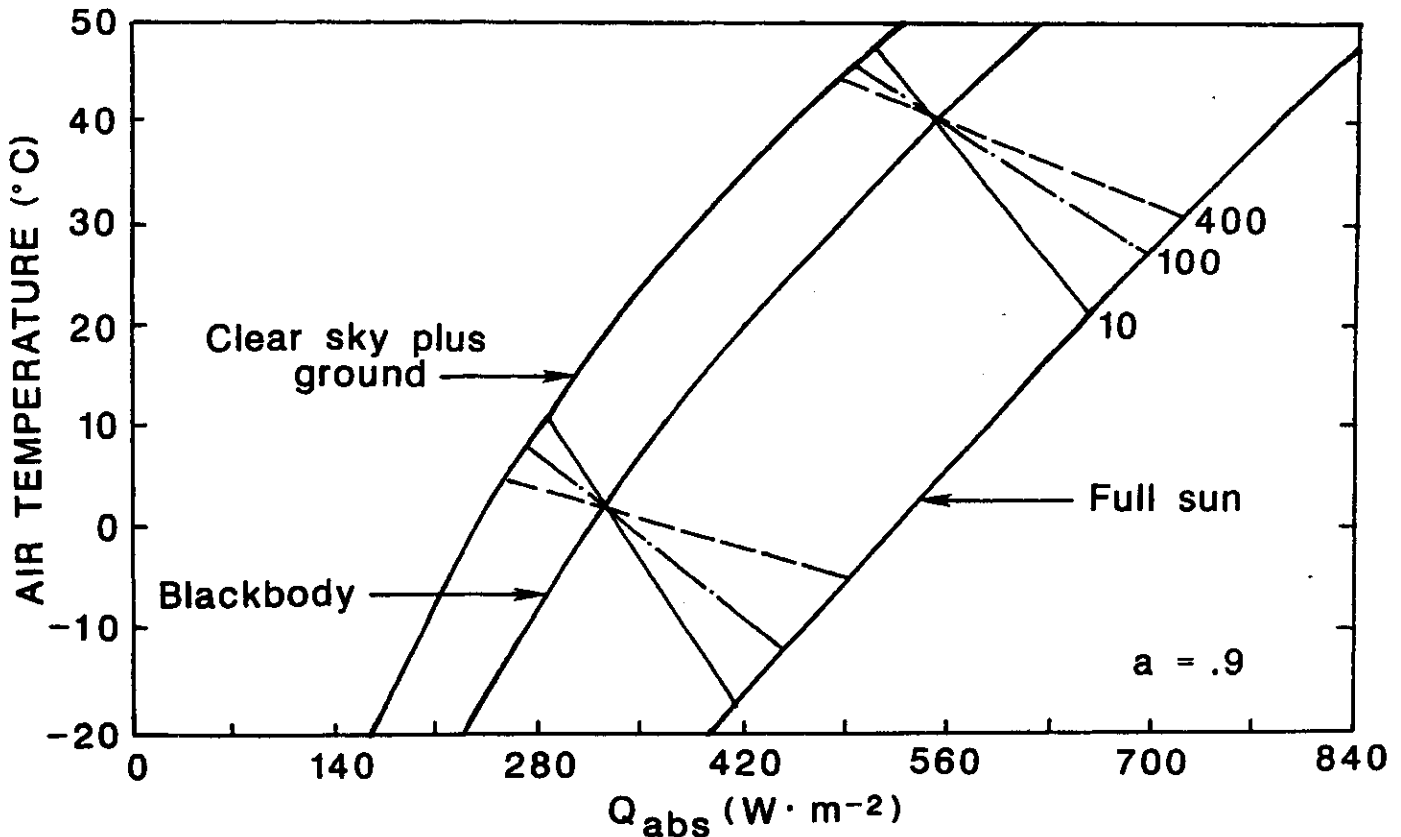


FIGURE 22.3. A climate space diagram for an adult *T. scripta* of average size (1,000 g) showing the effects of solar and thermal radiation, air temperature, and wind speed under steady-state conditions. The solid, dashed, and dot-dashed lines in each set were calculated for wind speeds of 10, 100, and 400 cm/sec, respectively. Upper limits were calculated from equation 22.5 at a body temperature of 40° C, using corresponding values of metabolism = 0.0899 ml O₂/g·h, and heat loss from evaporative water loss = 19.54 W/m². Lower limits were drawn according to the same procedures at a body temperature of 1° C; metabolism = 0.0012 ml O₂/g·h, and heat loss from evaporative water loss = 14.65 W/m².

of W. P. Porter (University of Wisconsin—Madison). The average reflectances (\bar{r}) of various portions of the carapace were computed by integrating the reflectance spectrum over the normal solar spectrum with the computer program SOLRAD (McCullough and Porter, 1971). The absorptivity was calculated as $a = 1 - \bar{r}$. Light-colored areas of the carapace with yellow streaks had an a of .81; darker areas had an a of .86 to .89. Because the preserved animal appeared to be lighter in color than living *T. scripta* from the SRP, we assumed that a was .9 for these calculations. The absorptivity of the turtle's surface to long-wave radiation was assumed to be 1.0 (Gates, 1980).

The line labeled "clear sky plus ground" represents radiation absorbed by the turtle at night from the sky, the atmosphere, and the substrate. This sets the boundary for the left side of the climate space. The "blackbody" line is a reference line indicating 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). This also represents a turtle when it is under water. In water, heat

transfer occurs by conduction-convection because thermal radiation does not penetrate water. Solar radiation may add heat to a turtle that is at or just below the surface, but in general a turtle submerged more than a few centimeters below the surface will be in a unithermal environment where heat transfer is rapid.

The upper boundary was determined by solving equation 22.5 for Q_{abs} , using a body temperature of 40° C (a temperature causing extreme behavioral and physiological stress and assumed to be the LT₅₀ value), 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 were plotted as air temperature versus Q_{abs} . Lower lines were computed for a body temperature of 1° C following the above procedures. Upper and lower boundaries were determined for wind speeds of 10, 100, and 400 cm/sec.

From the climate space (Fig. 22.3), we can determine various limitations that are imposed on the turtle by the

environment. 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. However, it cannot exceed these limits for extended periods without altering its energy equilibrium and risking death. In full sunlight, a turtle can withstand higher air temperatures (32° C) when subjected to wind speeds of 400 cm/sec than it can in still air (19° C). Still air reduces the rate of convective and evaporative heat loss, so these factors cannot compensate for the high radiation load absorbed. Convective heat loss is reduced at 10 cm/sec because a thick boundary layer of air surrounds and insulates the turtle (Foley and Spotila, 1978; Spotila and Standora, 1985b). Increasing wind speed decreases the boundary layer thickness and allows more heat transfer by convection and evaporation. Thus, the animal can withstand higher air temperatures in full sunlight because an increase in wind speed couples the animal more closely to environmental temperatures and reduces the effect of solar heating. A turtle can withstand ambient temperatures equal to its upper lethal temperature when sheltered in a blackbody cavity. At night, air temperatures as high as 48° C can be tolerated in still air under a clear sky; however, these are conditions that never occur in this turtle's habitat.

Under clear sky and ground conditions, the turtle loses large amounts of heat via thermal radiation; therefore, survival at cold night temperatures (in the lower left portion of the climate space) is dependent upon air temperature and wind speed. When exposed to a clear night sky, a turtle cannot survive an air temperature less than 9° C in still air or less than 3° C at a wind speed of 400 cm/sec. In still air, a turtle receives less heat via convection, thus reducing its ability to tolerate cold conditions while radiating heat away to the cold sky. Convective heat transfer to the turtle increases with wind speed, and the animal can survive colder temperatures because it is more effectively coupled to air temperature and less to the radiative environment. During cold weather, a blackbody cavity or water provides a tolerable habitat to temperatures as low as 1° C.

On cold sunny days, the turtle can survive at lower air temperatures than on cold nights because it is receiving large amounts of solar radiation. In still air, the turtle loses less of the heat gained from the sun by convection than at high wind speed and can survive at lower air temperatures. Higher wind speeds remove heat and shift the lower survival temperature upward because heat gained from the sun is lost to the wind.

From this type of energy budget analysis, Foley (1976) predicted interactions between this species of turtle and its environment. Periods that are energetically stressful to *T. scripta* in a terrestrial environment include the hot summer months, cold winter months, and portions of the spring and fall when changeable weather conditions pro-

duce large and potentially lethal temperature fluctuations. From late fall to early spring, throughout most of its range in the United States, *T. scripta* must spend most of its time in protective cavities or in water (a blackbody substitute), where microclimate variations are minimal and potentially stressful environmental conditions can be avoided. In water, this turtle could be active throughout the year.

Basking, a commonly observed behavior in *T. scripta* and related species, can be predicted using energy budget analysis. Turtles may bask under conditions that are found outside 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 is limited by the heat storage capacity of these turtles. During spring and fall, turtles can bask for long periods of time because they have a lower body temperature at initiation of basking, and solar radiation is at relatively low intensities. When temperatures and radiation levels are higher in summer, the time spent basking by turtles is reduced. Cold conditions during the winter greatly restrict basking except on calm sunny days. Under these conditions a turtle could bask out of the water and gain a considerable thermal advantage. For example, a turtle's body temperature could reach 20° C if it basked in full sun, with still air, at an air temperature of 0° C.

Based on our data and those in the literature, the daily basking pattern for *T. scripta* can be predicted as follows: Cool environmental conditions during early spring should influence the turtle to bask in a unimodal activity pattern 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 its climate space; therefore, this should seldom occur. When fall conditions prevail, turtles should return to a unimodal pattern of basking.

Behavioral Response to Biophysical Constraints of the Par Pond Environment

We tested the predictions of the climate space model in a series of experiments on *T. scripta* in Par Pond and Dick's Pond, a 0.8-hectare abandoned farm pond on the SRP. Crawford et al. (1983) measured the operative environmental temperatures (T_e) for basking *T. scripta* at these

two locations. Operative environmental temperature has been developed as a thermal index of microclimate and is defined as the temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal exposed to the same microclimate. It represents the temperature along the blackbody line of the climate space that corresponds to the point the turtle occupies on the full-sun line when basking, assuming wind speed is the same. T_e can be calculated following equation 12 of Bakken (1976) as modified by Crawford et al. (1983). We measured T_e with hollow copper replicas of *T. scripta* painted with flat black paint with $\alpha = .9 - .95$ and $\epsilon = 1.0$.

Operative environmental temperature was a good predictor of basking behavior of *T. scripta*. In general, turtles did not bask until T_e reached or exceeded their selected temperature of 28° C (Fig. 22.4). More than 98% of the turtles basking did so at T_e greater than or equal to 28° C. This was not an artifact of the analysis, because we often measured T_e of less than 28° C and only a few turtles basked at low T_e . This suggests that basking is not a random behavior but is primarily thermoregulatory. Operative environmental temperature was positively related to shortwave and total solar radiation as well as to air and substrate temperature. Regression equations that define these relationships were provided by Crawford et al. (1983). Schwarzkopf and Brooks (1985) used the equations to compute T_e for *Chrysemys picta* in Algonquin Park, Ontario, Canada, and found that *C. picta* basked most often in the morning when T_e was close to the selected T_b for this species (21.4° C). They also calculated T_e for *Chelydra serpentina*, using data from Obbard and Brooks (1979, 1981b) and found that the peak in basking activity for this species occurred with T_e at 28° C, which was close to the selected temperature (28.1° C) measured by Schuett and Gatten (1980). Movement of the sun through the day results in spatial variation in T_e 's available to the turtles and influences their location and basking behavior (Crawford et al., 1983). At midday on a sunny summer day at Dick's Pond, *T. scripta* in deep water would experience a T_e of 24° C, while a turtle basking on a log near the center of the pond would experience a temperature of 45° C (Fig. 22.5). In the morning when the sun was low on the horizon, a turtle basking near the southwest shore would experience a T_e of 40° C, and a turtle along the northeast shore would experience a T_e of 26° C. Turtles in Dick's Pond and Par Pond responded to these types of differences and chose basking sites with T_e 's of 28° C and higher, changing basking sites as the day progressed. Auth (1975) noted similar shifts in the location of basking turtles in a Florida pond. Thus, measurements of T_e of basking turtles are consistent with our predictions from the climate space of *T. scripta* and indicate that basking is a thermoregulatory behavior.

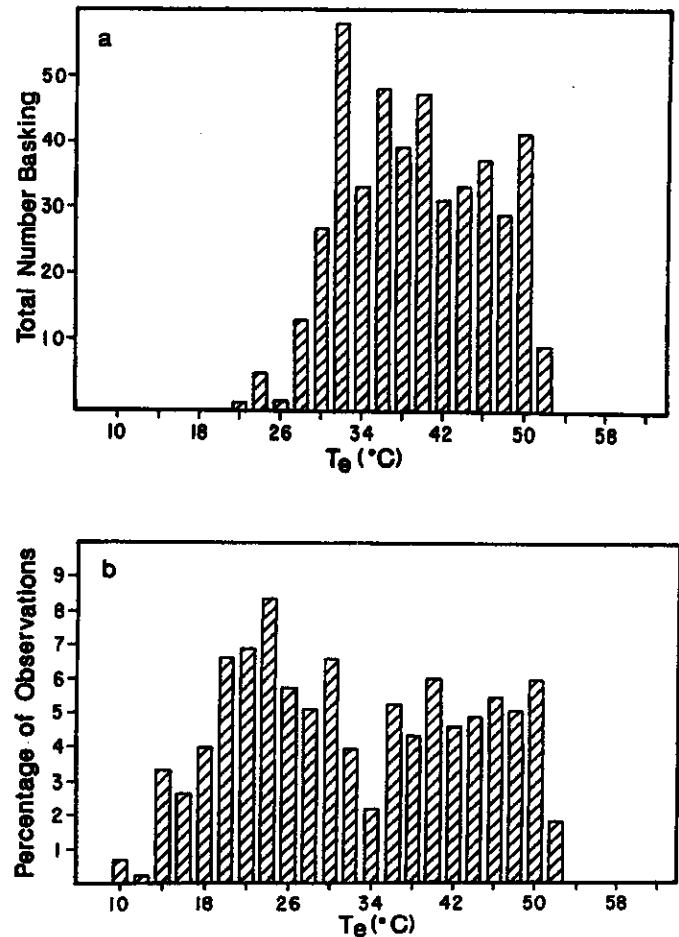


FIGURE 22.4. *a*, histogram of the total number of turtles (*T. scripta*) observed basking at Dick's Pond in 1979 and 1980, and their associated operative environmental temperatures (T_e , grouped by 2° C intervals). *b*, histogram of the frequencies of observed operative environmental temperatures (T_e) measured for hollow copper models of turtles at Dick's Pond on the SRP in 1979 and 1980 (temperatures are grouped by 2° C intervals). From Crawford et al. (1983) with permission.

Trachemys scripta in Par Pond used an opportunistic strategy of thermoregulation (Spotila et al., 1984) consistent with the constraints of their climate space. No *T. scripta* resided at the point of thermal discharge. Turtles in heated areas basked aquatically. Body temperatures telemetered from unrestrained individuals were within the selected temperature range. In the normothermic portions of the reservoir, turtles underwent atmospheric basking on sunny days throughout the year. In summer, basking during the day showed a bimodal curve (Fig. 22.6). On hot days, no turtles basked. In spring and fall, basking intensity showed a unimodal pattern. Schubauer and Parmenter (1981) reported turtles in normothermic areas of Par Pond basking on sunny, calm days at air temperatures as low as 2° C. These data support the

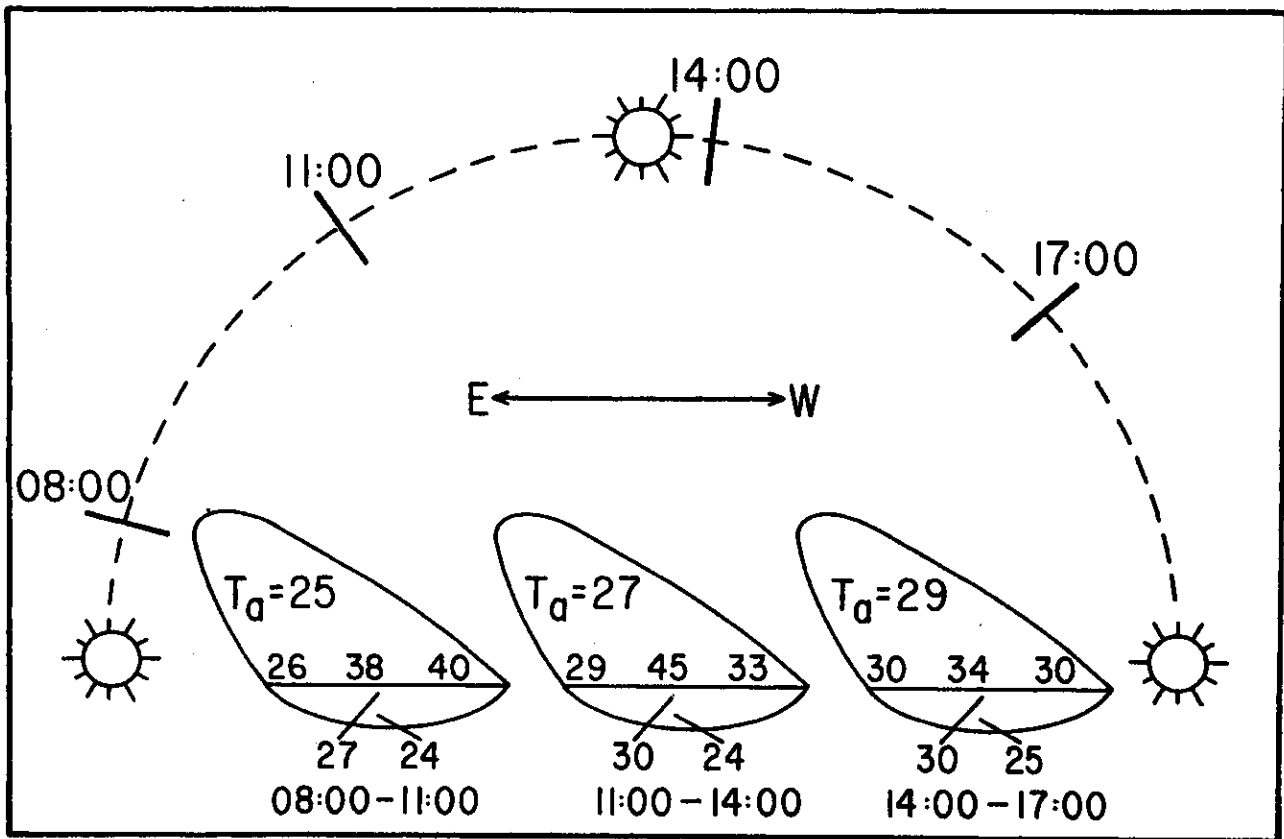


FIGURE 22.5. Operative environmental temperature (T_e) of *T. scripta* as affected by locations on Dick's Pond at different times on a sunny day in July and August. Temperatures on the maps of the pond are average T_e 's for data collected every 30 minutes for the three-hour period indicated below the map. The dashed line indicates the path of the sun; intersecting solid lines represent the position of the sun at particular times. Each temperature indicates T_e for a different location on, in, or near the pond. In the cross-sectional diagram of the pond for 0800-1100 EDT, 26° C is T_e for a turtle basking on the northeast shore; 38° C is T_e for a turtle on a log or basking platform in the center of the pond; 40° C is T_e for a turtle basking on the southwest shore; 27° C is T_e for a turtle aquatically basking in the center of the pond; and 24° C is T_e for a turtle on the bottom. T_a is air temperature. The other cross sections of the pond present average T_e 's for the periods 1100-1400 and 1400-1700. From Crawford et al. (1983) with permission.

predictions presented above and by Foley (1976). Data from other studies are also consistent with these predictions (Cagle, 1944b, 1950; Moll and Legler, 1971; Auth, 1975; Bury et al., 1979). These are discussed by Spotila et al. (1984). More recent data for *C. picta* (Schwarzkopf and Brooks, 1985) indicate that this species also displays unimodal basking patterns on cool days and bimodal basking patterns on warmer days in Algonquin Park.

Thus, *T. scripta* in Par Pond have adjusted to the thermoregulatory constraints imposed on them by this environment. They remain within their climate space and change their behavior as predicted from our heat energy budget analysis. Turtles in other locations respond with similar behavioral thermoregulatory strategies when exposed to similar microclimates. This should be reflected in various aspects of their life histories, including foraging strategies, growth, age and size at maturity, and re-

productive effort. The mechanistic relationships between these aspects of their ecological (heat and food) energetics remain to be determined.

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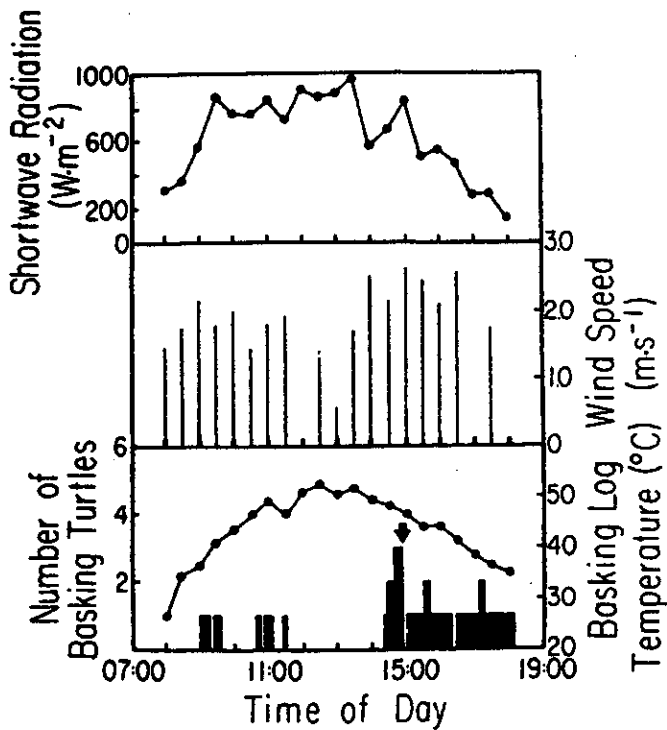


FIGURE 22.6. Basking activity of *Trachemys scripta* and microclimatic conditions for a sunny July day at Susan's Swamp on Par Pond. Shortwave radiation (300–3,000 nm) shows depressions due to periodic cloud cover. Wind speeds are means for 15-minute periods. Basking log temperature is represented by a solid line connecting circles. Lower histogram indicates numbers of turtles basking. Arrow shows a disturbance that caused turtles to enter the water. Data are for 14 July 1976. From Spotila et al. (1984) with permission.

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