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BEHAVIORAL ECOLOGY OF BASKING IN THE YELLOW-BELLIED TURTLE, CHRYSEMYS SCRIPTA SCRIPTA (SCHOEPFF)

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GAINESVILLE

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BEHAVIORAL ECOLOGY OF BASKING IN THE YELLOW-BELLIED TURTLE, CHRYSEMYS SCRIPTA SCRIPTA (SCHOEPFF)

DAVID L. AUTH!

Synopsis: The purpose of this study is to determine if basking in turtles is thermoregulatory and to describe the attendant behavior. Observations were made from a blind on a marked population of *Chrysemys scripta scripta* (Schoepff) and an unmarked population of *Chrysemys floridana peninsularis* Carr at a north Florida sinkhole pond. The study was conducted between August and December, 1968, thus providing a wide range of environmental temperatures and sunshine in which to observe any variations in basking behavior.

The number of atmospherically-basking C. s. scripta and C. f. peninsularis per day, as well as the number of times individual C. s. scripta basked per day, reached a peak at a daily mean water temperature of 28.5°C. Basking decreased during overcast periods. Aquatic basking in C. s. scripta and C. f. peninsularis increased as water temperature approached 31.5°C, the maximum mean water temperature recorded during the experimental period. Temperature-telemetry revealed that an adult basking scripta could elevate its body temperature at least 10°C above near-surface water temperatures.

Because of decreased sunshine and air and water temperatures from August to December, and the resultant slower rate of body temperature rise, mean basking duration in C. s. scripta increased during those months. Basking duration is also directly related to body size.

Basking does not appear to be a daily requirement, even under optimum weather conditions. Some C. s. scripta basked up to five times a day in favorable weather; however, a considerable percentage of the population did not bask every day.

Basking activity started about 0800 and reached a daily maximum between 1000 and 1100 each clear day in August and September. The time at which activity started and the time it reached a daily maximum shifted to a later part of the day during October and November.

Thermoregulation appears to be the primary function of the basking act in C. s. scripta and C. f. peninsularis. This conclusion is based on the following basking behavioral patterns:

- 1) body orientation, head and leg extension and retraction, leg kicking, and rear-foot digit spreading;
- remaining on a site for considerable periods of time after it becomes shaded and the turtle's body temperature has increased, but rarely emerging at an already shaded site;
- varying frequency and inversely varying duration with decreasing air and water temperatures and sunshine (shown for C. s. scripta only); and
- 4) sitting on submerged basking sites or floating in warm surface water.

The author is currently a graduate student in the Department of Zoology, University of Florida. This paper in an altered form was submitted as partial fulfillment of the requirements for the degree of Master of Science at the University of Florida.

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Introduction

Basking is a characteristic habit of aquatic turtles. Moll and Legler (1971) listed two forms of this behavior in Panamanian Chrysemys scripta: "aquatic basking," or floating in warm surface water, and "atmospheric basking," or basking in air. Chelydra serpentina and Sternotherus odoratus (Cagle 1944) are two species that characteristically practice the former. Unless otherwise stated, the term "basking," as used in the present paper, refers to atmospheric basking.

McDowell (1964) and Weaver and Rose (1967) will be followed in this paper, placing *floridana*, nelsoni, and scripta in the genus Chrysemys rather than Pseudemys.

The yellow-bellied turtle (Chrysemys scripta scripta) periodically leaves the relative thermal stability of water to bask atmospherically. Several people have reviewed the possible functions of this activity in turtles (Boyer 1965, Moll and Legler 1971, Spray and May 1972) and have offered several possible explanations: (1) the increased temperature differential between the turtle's body and the surrounding medium may expedite some discontinuous process such as digestion (Cagle 1950); (2) drying of the integument; (3) removal of algae and parasites; (4) synthesis of vitamin D in the skin; (5) increased ease of respiration; and (6) allowing the turtle to rest, especially in flowing water habitats. As Spray and May (1972) suggested, these explanations are probably not mutually exclusive.

Field observation is one approach to answering the question of why turtles bask. Boyer (1965) watched a population of *Chrysemys scripta elegans* under

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a variety of environmental conditions, but did not trap and mark individuals. During the present study individual turtles were marked so that I could determine where a turtle basked, the number of times it basked, and the duration of each appearance. I could then ask the question whether the turtles were behaviorally thermoregulating by varying their basking movements, frequency, and duration in correlation with daily and seasonal changes in solar and thermal radiation fluxes and air and water temperatures.

Chrysemys scripta scripta was selected because intensive study of its basking behavior had not been attempted, and because it is relatively easy to trap, mark, and observe in one of its preferred habitats, sinkhole ponds. A group of Chrysemys floridana peninsularis was also present at the study site but was not marked. Some information on the basking behavior of this species is included.

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MATÉRIALS AND METHODS

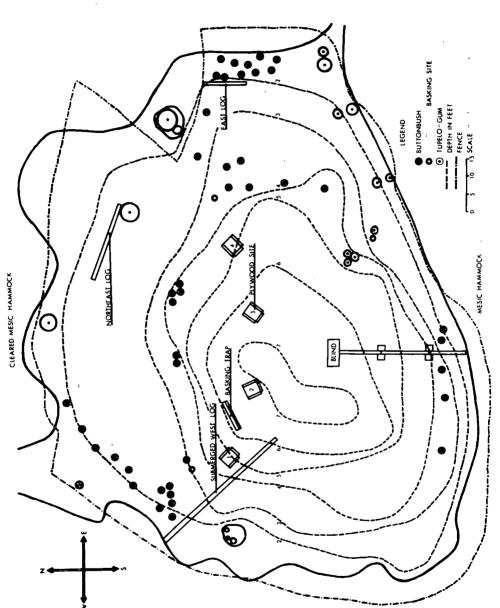
The study was conducted between 4 August and 4 December, 1968, at a single dystrophic sinkhole pond, located seven miles northwest of Gainesville, Alachua County, Florida (Fig. 1). The pond surface area was estimated to be 14,000 sq. ft., but varied seasonally by fluctuating water levels. The pond, surrounded by a mesophytic hardwood forest, was covered with duckweed (Lemnaceae): Lemna minor L., Wolffia columbiana Karst, and Wolfiella floridana (J. D. Smith) C. H. Thompson. The two major woody plants in the water were buttonbush (Cephalanthus occidentalis L.) and tupelo-gum (Nyssa aquatica L.).

The natural turtle population consisted of Chrysemys scripta scripta (Schoepff) (yellow-bellied turtle), Chrysemys floridana peninsularis Carr (peninsular turtle), and Stemotherus odoratus (Latreille) (common musk turtle). The latter species was never seen basking atmospherically.

I caught Chrysemys s. scripta in standard hoop net traps (Lagler 1943), using smelt as bait. Chrysemys f. peninsularis could not be trapped in this way. A basking trap, consisting of a 10-foot cypress plank with a chicken wire basket submerged on one side and a ramp on the other side, was installed in the pond to catch C. f. peninsularis. Because of the time required to catch a significant sample and the amount of the disturbance required to scare turtles into the basket, I soon discontinued using this kind of trap.

Six dimensions for each turtle (Jackson 1964) were measured with a metal caliper. Carapace area was approximated using aluminum foil. The foil was pressed onto the surface of the carapace and the form cut along the outside edge of the marginals. Excess foil folded on itself was then removed from the form. The weight of the foil form divided by the weight per unit area gave the approximate carapace area.

Chrysemys scripta scripta individuals were marked in two ways: (1) by drilling holes in the carapace marginals; and (2) by painting Arabic numerals on the carapace (Cagle 1944), with a marine epoxy paint. Four numbers were painted on larger turtles: one anteriorally, two laterally, and one posteriorly. Turtles having a carapace less than 10 cm in length received only two lateral numbers. Only one adult turtle lost its numbers during the experimental period; this occurred as a result of laminal shedding. Small turtles lost numbers more readily than adults, because of paint chipping from the small turtle's smooth carapace. Of the marked turtles 99 percent could be identified from the blind during basking periods, the remaining one percent was small turtles.



The natural population in the pond was estimated at 47 Chrysemys s. scripta and 18 Chrysemys f. peninsularis, of which 30 C. scripta were marked. In order to increase the number of marked turtles, 24 C. s. scripta, one C. f. peninsularis, and three C. nelsoni Carr (Florida redbellied turtle) were trapped in two other duckweed-covered ponds near Gainesville and added to the study pond. The total number of turtles studied was approximately 93; this comprised 54 marked and 17 unmarked C. s. scripta, one marked and 18 unmarked C. f. peninsularis, and three marked C. nelsoni. The number of unmarked turtles was estimated from the basking frequency of the marked turtles. It is assumed that 13.2 percent of the marked C. s. scripta either escaped from the pond or died, since these adults disappeared from the basking sites early in the experimental period.

The primary basking areas were (1) four floating plywood sites, (2) the trap, (3) three large logs, and (4) three buttonbush trunks. The plywood sites measured 3' wide × 4' long × 1' deep. These were made by nailing a piece of marine plywood to a rectangular wooden frame, to form a five-sided box which was inverted in the water and held in place by anchor ropes. Two partially inflated tire inner tubes were inserted under the plywood in order to keep it floating when crowded with basking turtles. Ramps were nailed to three sides of the raft at an angle of 45 degrees. It was found that large turtles had difficulty ascending the ramps, repeatedly slipping back into the water; hardware cloth nailed to the ramp surfaces solved this problem. The plywood sites were arranged in a row from east to west (Fig. 1). As the sun increased its seasonal southward declination and an increasing percentage of the pond surface was shaded by surrounding trees, this row was moved periodically northward in order to provide more-or-less constant exposure to the sun.

The blind, supported by two 50 gallon oil drums and pilings driven in the pond bottom, floated on the pond and could be approached via a floating pier (ca. 35 feet long). After removing a few buttonbushes, the entire pond could be seen from the blind. The blind was equipped with a Yellow Springs 12 channel telethermometer to record air and water temperatures at two-hour intervals during the day. Air temperatures were taken in the shade at a height of 15 cm, and water temperatures were taken in the duckweed at a depth of less than a centimeter and below the duckweed at a depth of 5 cm. Wind velocity was measured at a height of 25 cm with a three-cup anemometer. A daily record was kept of basking appearances and included identification of the turtle, time of emergence, time of departure, and site chosen. A short time lag was unavoidable, especially when 20 or more turtles were basking at once. Observations were made using binoculars, and a portable tape recorder and stop watch were used to record the timing of a turtle's movements.

In addition to the above field study, temperature telemetry was used to record a turtle's changing body temperature during basking in a small concrete-lined pond, by implanting the probe of a frequency-modulated, temperature-telemetering radio transmitter in a 1901 g female C. s. scripta. The receiver used was a Biotronics Model 90 module plus Model 133 Receiver-Converter. The squegging transmitter, set at 88 megacycles, was accurate to within 1°C. Audible signals were received approximately 3 m from the turtle, without the use of a transmitting antenna. The transmitter probe was implanted interpleurally through a hole drilled in the carapace at the junction of the first and second lateral and the second central laminae, and the probe wire was glued to the top of a plastic dropper bottle affixed to the carapace with epoxy glue and four small brass screws. The transmitter, sealed in a plastic cylinder measuring 1½ cm wide by 3½ cm long, was attached to the posterior carapace with wires running through holes drilled in the 11th marginal and a postcentral. The turtle basked the same day she was released. No postoperative abnormalities were noted. Interpleural temperature, air and water temperatures, and notes on basking behavior were recorded on five consecutive days, starting 49 days after implantation.

RESULTS

BASKING AND THE PHYSICAL ENVIRONMENT

Light.—Light intensity is one factor that determines whether turtles bask. C. s. scripta and C. f. peninsularis respond to at least two characteristics of the

sun's electromagnetic radiation: the intensity of visible light and the transfer of heat energy. The former is probably more important in determining frequency and the latter more important in determining duration. Air and water temperatures also influence basking frequency and duration. With so many variables involved, an environmental room study is required to quantify the control of basking frequency and duration; however, some insight into the relative importance of the environmental factors can be obtained from field observations.

The influence of three factors (minutes of direct sunlight per day, mean water temperature, and mean air temperature) on the number of turtles basking per day is shown in Figure 2. Within the mean water temperature range of 21-29°C, the number of basking individuals increased in direct proportion to the length of time the sites were exposed to the sun. Outside this water temperature range, longer exposure to sunlight was required to attract the same number of turtles. In other words, low or high environmental temperatures and overcast skies reduced the arrival rate at otherwise satisfactory basking sites.

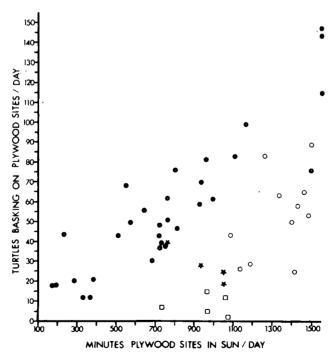


FIGURE 2.—Influence of light on number of turtles basking per day. Mean water temperature 30.0°C or above (open circles), 21.0-29.9°C (solid circles), 15-20.9°C (stars), 14.5°C or less (open squares). Water temperature mean was calculated from readings taken at two hour intervals each day in the surface duckweed and at a depth of five cm.

Turtles were much more likely to emerge at sites located in direct sunlight than at those in the shade. During eight warm clear days in September (mean air temperature=29.2°C) only 57 of a possible 973 turtles emerged (5.9%) on shaded basking sites. At lower air temperatures the percentage decreased still more. On eight clear days with a mean air temperature of 16.8°C, only one of 153 turtles emerged (0.65%) in the shade.

Both C. s. scripta and C. f. peninsularis rapidly decreased their rates of emergence when a cloud blocked the sunlight on partially cloudy days (Fig. 3). The emergence rate dropped almost to zero during cloudy periods. The departure rate did not increase as much as the emergence rate decreased, although if the overcast period lasted very long many turtles returned to the water. The increase in emergence rate with clearing skies could be quite dramatic, especially in the morning. At 1100 (EST) on August 31, when the sky had partially cleared, two turtles were basking. After 85 minutes of partially cloudy skies, the number of emerged turtles had risen to 35.

Basking turtles were not randomly distributed over the pond on clear days. The distribution of emergences was skewed toward the west side of the pond in the morning and toward the east in the afternoon. The basking sites

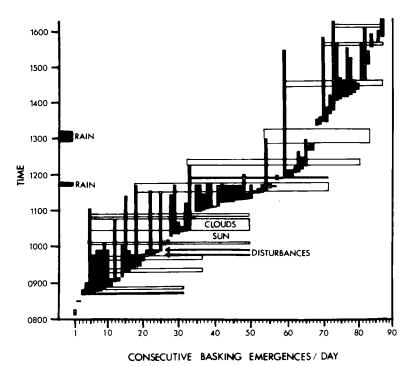


FIGURE 3.—Effect of intermittent cloud cover on the rate of turtle basking emergence. Each vertical bar represents the basking time of one turtle on September 20.

on the west side of the pond received direct sunlight first. As time progressed the forest canopy shaded fewer and fewer basking sites, until almost the entire pond was in direct sunlight. As the western sites became shaded in the early afternoon, the turtles progressively shifted to the more eastern basking sites. Since turtles clearly preferred basking sites located in direct sunlight, pond shading may be the only reason for the daily shift in sites of emergence. However, there is some indication that turtles were changing sites of emergence in direct response to the changing position of the sun (Fig. 4). Sites were arranged in a row, numbered consecutively from west to east. All four sites were in direct sunlight between 1000 and 1400. Turtles emerged more frequently on the western sites between 1000 and 1200, distributed more equally between 1200 and 1300, and emerged more frequently on the eastern site in the early afternoon. The low emergence rates at sites two and three may be due to their close proximity to the blind. One way to determine the influence of the sun's position on basking site choice would be to observe the distribution of emergences in a pasture pond, free of forest canopy shading.

The shift of activity from east to west during the day was also seen in the distribution of surface-floating turtles (Fig. 5). The number of turtle heads

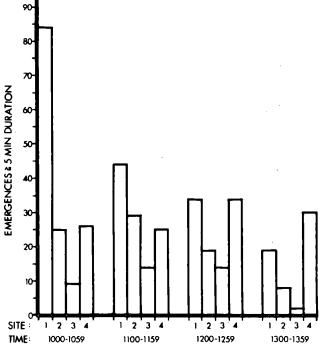


FIGURE 4.—Influence of the position of the sun in the sky on the turtle's choice of basking site. Each bar represents the sum of emergences at one plywood site for 10 days in late August and early September. Sites arranged and numbered as in Figure 1.

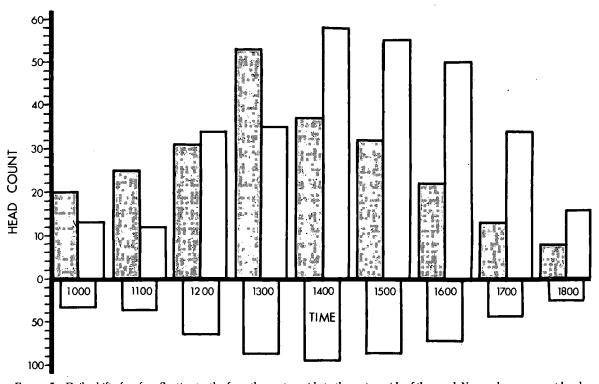


FIGURE 5.—Daily shift of surface floating turtles from the western side to the eastern side of the pond. Narrow bars represent heads counted at one hour intervals west (shaded bars) and east (open bars) of site three, located in the center of the pond. Wide bars are sums for the entire pond. Bars are sums of data collected on eight clear warm days in September through November.

seen east and west of the site three, which was located in the middle of the pond, was counted each hour during eight warm clear days. In the morning and early afternoon, more heads were seen west of the site; later in the afternoon, more heads were seen east of the site.

It is clear from examination of the location of emergence of individual turtles (Fig. 6) that the shift in basking activity is not necessarily a result of the turtle population swimming across the pond to the east each day returning to the west by the following morning. Some turtles (15 of the sample of $32\ C.\ s.\ scripta$) chose basking sites in the western portion of the pond more than 60 percent of the time with the extreme represented by a turtle emerging $32\ times$ west of site 3 and only 2 times east of the site. A second group of nine regional baskers chose predominantly eastern basking sites. A third group (N=8) emerged a nearly equal number of times in both regions of the pond (diffuse baskers). Unfortunately, I was unable to track individuals when they were in the water. Thus, I do not know how much time regional baskers spent in the portion of the pond where they did not commonly emerge. The small

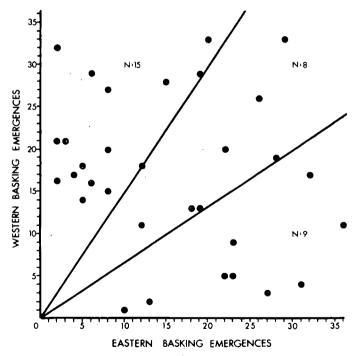


FIGURE 6.—Regional and diffuse basking site choice. Basking emergences east and west of site three were counted for 32 Chrysemys scripta scripta for 33 days of observation. Sites were arranged as in Figure 1. Dots on the upper and lower diagonal lines represent turtles emerging 60 percent of the times west of site three, 40 percent east of site three, and 40 percent west, 60 percent east, respectively.

size of the pond ($125' \times 150'$) and the occasional emergence of even the most regional basker outside its usual region indicate that most $C.\ s.\ scripta$ have the whole pond as their home range. However, some restriction of movement is indicated for the majority of the turtles. One result of turtle preference for one basking region is a partial equalization of numbers among the sites, limiting crowding on any one site.

Water and Air Temperatures.—Water temperature is a second important environmental variable influencing turtle basking. During warm weather both C. s. scripta and C. f. peninsularis spent considerable time floating with heads out of the water. Therefore, except at low water temperature, pond surface water temperature was considered more important in determining basking frequency than bottom temperature. Mean water temperature in this paper is the average of measurements taken at two-hour intervals during the day in the duckweed at a depth of less than a centimeter and below the duckweed at a depth of 5 cm.

Figure 7 is a scatter diagram showing numbers of basking appearances per day of C. s. scripta and C. f. peninsularis vs. mean water temperature. The peak number appeared at about 28.5°C, with a noticeable decline above and below this temperature level (The two highest numbers of C. s. scripta at a mean water temperature near 18°C occurred on two days of a warming trend in early November, when mean air temperature was considerably above mean water temperature [+3.5 and +4.6°C, corresponding respectively to 98 and 114 total baskers per day]. Perhaps turtles were responding to the high air temperatures by increasing basking frequency). Boyer (1965) stated that Chrysemys s. elegans did not bask when the water temperature at 5 cm depth was below 7°C; the same minimum was found for Chrysemys s. scripta in the present study. Chrysemys f. peninsularis stopped such activity at a water temperature of approximately 14°C, seven degrees higher than for Chrysemys s. scripta and C. s. elegans. Perhaps C. f. peninsularis stopped basking at a higher water temperature than C. s. scripta or elegans because it is a more southern form that only narrowly overlaps with C. s. scripta and not at all with C. s. elegans.

In August, surface water temperature reached as high as 37°C during the early afternoon, partly due to the heat absorbing layer of duckweed. During this time, many turtles floated quietly at the surface or basked on submerged sites, with only part of the carapace and head exposed. Basking on submerged sites increased as mean water temperature increased (Fig. 8), with the peak for such activity occurring at approximately 31.5°C (highest mean water temperature recorded during the observational period); this peak was three degrees higher than for individuals both partially submerged and completely out of the water (Fig. 7). The higher the water temperature, the greater the number of turtles that selected a partially submerged site, as opposed to a site completely out of water.

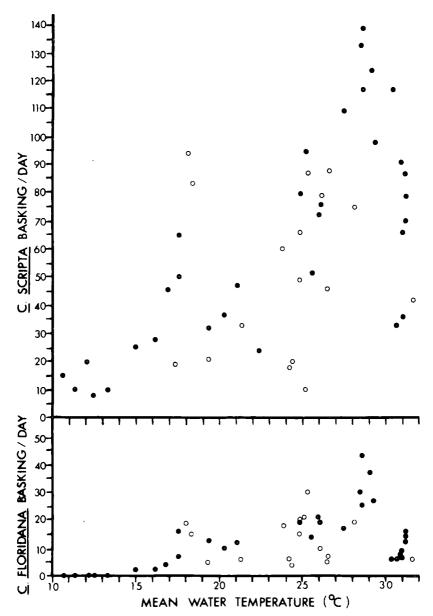


FIGURE 7.—Influence of water temperature on basking emergence in Chrysemys scripta scripta and Chrysemys floridana peninsularis. Plywood basking sites shaded by clouds for 300 minutes or less per day (solid circles), more than 300 minutes per day (open circles). Water temperature is an average of readings taken at two hour intervals in the duckweed and at a depth of five cm.

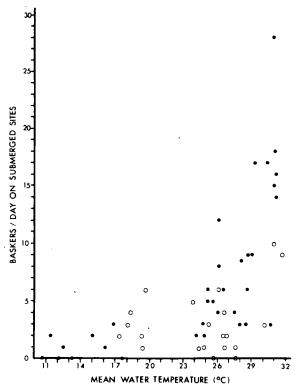


FIGURE 8.—Influence of water temperature on the number of turtles basking on submerged sites. Plywood basking sites shaded by clouds for 300 minutes or less per day (solid circles), more than 300 minutes per day (open circles). Water temperature is an average of readings taken at two hour intervals in the duckweed and at a depth of five cm.

Water temperature may also have influenced the sex ratio of basking Chrysemys s. scripta (Fig. 9). The sample analyzed consisted of 13 males and 13 females, all of which were in the pond for the duration of the study. All turtles selected had carapace lengths greater than 11 cm, since smaller individuals could not be accurately sexed using nail and tail characters. As can be seen from Figure 9, males basked more commonly than females below an approximate mean water temperature of 20°C, and below 14°C no females at all were observed. The number of basking males and females both decreased with decreasing mean water temperature, with the rate of decline in females greater than that in males. As the water temperature rose above 14°C between November 30 and December 3, a number of females reappeared at the basking sites. The male predominance above 30°C possibly resulted from greater female wariness of the sites or the blind early in the experimental period (which began in August). No explanation of male predominance below 20°C can be given.

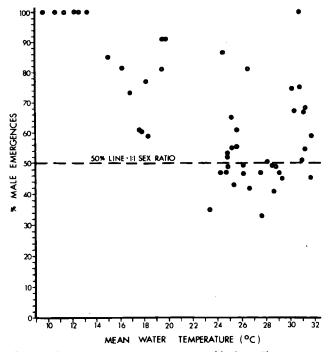


FIGURE 9.—Influence of water temperature on sex ratio of basking Chrysemys scripta scripta. The numbers of turtles in the samples are 13 males and 13 females larger than 11 cm carapace length. Dots falling on the dashed line indicate that equal percentages of the 13 males and 13 females basked that day.

Rain decreased the rate of basking emergence and increased the rate of departure; the rates were dependent on both the duration and strength of the rain. During 25 periods of rainfall totaling over eight hours on 14 different days, only 14 turtles emerged, and 98 of 208 baskers (47%) departed soon after the rain started. The departure rate was greater and the emergence rate less as rainfall per unit time increased. The rapid departure of turtles during a hard rain is illustrated in Figure 3.

The question may be asked whether water or air temperature is more important in influencing a turtle to bask. Body temperature of turtles in the size range of C. s. scripta and C. f. peninsularis is not much higher than the temperature of the surrounding water. Thus, water temperature is probably more important in preventing turtles from emerging. At the experimental pond, the difference between mean air temperature and mean water temperature usually did not exceed 2°C until mid-October, when differences exceeding 2°C became more common due to intermittent cold fronts from the north. Mean water temperature was usually lower than mean air temperature, the largest difference observed being 5.7°C during a warming trend in early No-

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vember. On four clear days when the mean air temperature reached 16.9°C and the mean water temperature 11.9°C, only 56 turtles basked. On four other clear days during which mean air temperature was 17.7°C (0.8°C higher than the first four day sample) and the mean water temperature 16.8°C (4.9°C higher), 133 turtles emerged or almost 2.4 times as many. In this case at least, the warming of the water seemed to be the important inducement for emergence.

In order to determine optimum basking temperatures (both air and water) on clear days, temperatures were analyzed for those days considered to have had "ideal" basking conditions. Such days were arbitrarily considered to be those during which 100 or more basking appearances were recorded; using this criterion 15 of the 65 days of observation qualified. The average of the daily mean air temperatures for these 15 days was 28.7°C (range 25.0-32.4°C, S.D. 1.98), and the average of the daily mean water temperatures 27.9°C (range 22.0-31.2°C, S.D. 2.45). Analysis of the 10 days during which the greatest number of turtles were observed basking at any one time shows a mean of 36.7 individuals (range 33-51, or approximately 35.5-54.8% of the total pond population; S.D. 5.5). The mean time of occurrence was 1109 (0940-1236), the mean air temperature 25.7°C (range 22.0-29.0°C, S.D. 2.5), and the mean water temperature was 24.3°C (range 22.7-26.1°C, S.D. 1.1).

Basking Duration

Basking duration is defined as the time of a single basking appearance. In Chrysemys s. scripta this time was found to increase, on the average, during the clear days of the observational period. Illustrated in Figure 10 are the mean basking duration, mean basking frequency (mean number of basking appearances per turtle for individuals emerging at least once a day), mean air temperature, and mean water temperature for marked C. s. scripta during 22 clear days. Duration increased slowly during August and September and more rapidly during October and November, as mean air and water temperatures fell below 28°C and became more variable. This increase probably was caused primarily by the seasonal decline in daily solar energy flux, decreasing the rate of heating of the basking turtle. The increasing temperature difference between the CTM (critical thermal maximum, defined as the body temperature at which the turtle is no longer able to right itself when placed on its back) and body temperature at emergence probably is also important. Water temperature, which is approximately equal to the body temperature of emerging turtles (Edgren and Edgren 1955), determines the magnitude of difference at emergence. Other factors being equal, the greater the temperature difference between body temperature at emergence and the CTM, the greater the basking duration, assuming that the turtle leaves the site only when the CTM is approached (Boyer 1965). Minor decreases in duration may be expected

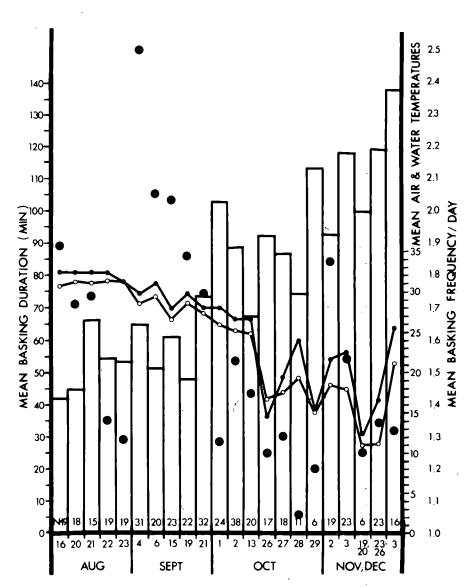


FIGURE 10.—Mean basking duration and mean basking frequency of marked Chrysemys scripta scripta on clear days. Mean basking duration (histogram), mean basking frequency (large solid circles), mean air temperature (small solid circles), and mean water temperature (open circles). The number of turtles used for the duration and frequency means is given at the base of each bar.

from a decrease in the CTM in response to decreasing seasonal water temperature and photoperiod (Hutchison and Kosh 1964). Mean basking frequency generally decreased during the observational period from a peak which occurred during the first half of September. Basking duration appears to be inversely related to atmospheric basking frequency, except during the warm month of August, when aquatic basking was most common.

In C. s. scripta body size was found to be directly related to basking duration, as can be seen in Figure 11. All regression lines show a significant upward trend (0.1% level). As body size increases, the surface to volume ratio decreases, resulting in decreased heating and cooling rates and presumably an increased range of possible basking durations. Data for Figure 11 were carefully selected in order to minimize the influence on basking duration of shading, cloud cover, environmental temperature, time of emergence, and disturbance. Except in four cases in which basking exceeded 200 minutes, turtles were in the sun the full time. Turtles commonly returned to the water before body temperature increased appreciably. This is undoubtedly due in part to increased turtle wariness, caused by trapping and marking.

Although large turtles usually basked longer than small ones, this did not always hold true. Of the 102 basking sessions lasting 180 minutes or longer that I observed, turtles smaller than 10 cm carapace length accounted for 27 (26.5%). It is surprising that the body temperature of some of these small turtles did not exceed the CTM. The smallest basking $C.\ s.\ scripta$ caught had a volume to carapace area ratio of 0.35 (carapace length = 3.9 cm). This turtle could not have basked between 1000 and 1400, according to the position of the regression lines of Figure 11.

Some small basking turtles had a large percentage of their carapaces covered with duckweed, whereas in larger turtles only scattered clumps were usually present. Little algal growth was present. Duckweed may decrease the rate of body temperature rise in three ways; (1) by increasing the reflection of sunlight, (2) by increasing insulation, providing a so-called "private zone" (Guyton 1966:992) that must be heated before the shell can be heated, and (3) by increasing heat loss by evaporative cooling. The water holding capacity of duckweed is large, a 744 g wet sample having a dry weight of 35.2 g. In an experiment designed to test the insulating properties of duckweed, 8 g of wet duckweed were evenly distributed on top of a black metal cube, which in turn was exposed to a 150 watt incandescent bulb located directly above. In 40 minutes the surface temperature of the metal had increased from 25 to 40°C. In contrast, when only a thin film of water was initially present on the cube, the same temperature increase required 6.4 minutes. A dry cube required only 4.3 minutes.

The majority of turtles returned to the water before the basking sites on which they were resting became shaded. Some turtles, however, spent as much, or more time on the shaded basking site as on the same exposed one.

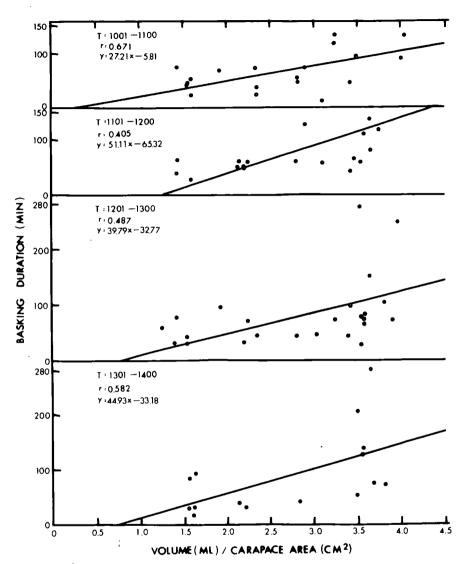


FIGURE 11.—Relation of basking duration to turtle size. Each dot represents the time of a single basking appearance of a *Chrysemys scripta scripta* on one of six warm clear days in September. The time span of 1000 to 1400 is divided into four one hour segments and each segment is graphed separately. T is the time of turtle emergence, r is the coefficient of linear regression. Regression lines were determined by the method of least squares.

Amount of time spent in the shade was related to size of the turtle, time previously spent basking in the sun, and air temperature (Fig. 12). Time spent in the shade, as well as time spent in the sun, increased directly with size of the turtle. For turtles smaller than 1500 ml, longer sun-basking times appear to be correlated positively with time in the shade. For turtles larger than 1500 ml, this does not appear to be the case. However, some of these large turtles were out of water for more than five hours at a time, and thus one may ask if a time limit may be reached beyond which it is no longer profitable to stay on the basking site, even though a temperature difference between the body and the water exists. As might be expected, on cold days turtles quickly returned to the water when the basking sites became shaded. As air temperature fell, the shade times of all turtles decreased, regardless of sun basking time or body size.

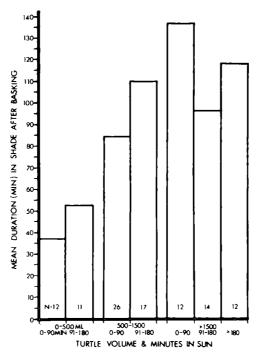


FIGURE 12.—Relation of shade duration to turtle size and sun basking time. The number of turtles used for the mean is given at the base of each bar. Data were collected on 15 clear days with a mean air temperature of 16.1-31.0°C.

BASKING FREQUENCY

Turtle basking frequency is defined as the number of basking appearances per unit time. Basking frequency will be examined in several ways: on the population level by a simple count of baskers per day (Fig. 13) and by mean

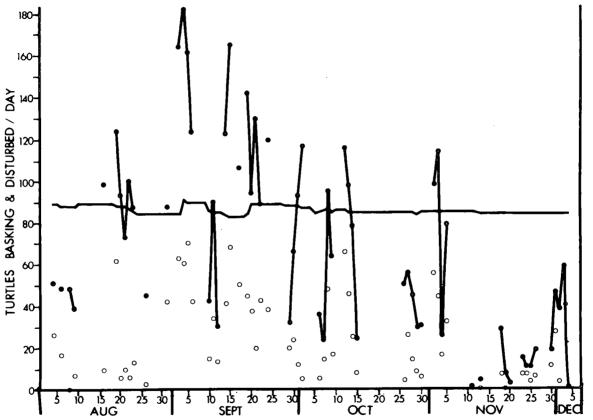


FIGURE 13.—Record of number of turtles basking (solid circles) and departing due to disturbance per day (open circles). Lines connect the number of basking turtles for consecutive days of observation. The horizontal line across the graph is the estimated total number of Chrysemys scripta scripta, Chrysemys floridana peninsularis, and Chrysemys nelsoni in the pond.

basking frequency per day (Fig. 14), and on an individual level by the basking records of specific individuals (Fig. 15).

The total number of turtles basking per day for the four-month observational period is shown in Figure 13. September was the peak basking month, although over 100 turtles emerged as late as November 3. A similar graph extending over a twelve-month period is bimodal, with basking peaks in the spring and fall, a lower number of baskers during the summer, and the least during the winter. Low basking numbers occurred during the October 26-30, November 13-26, and December 4 cold periods, on overcast and rainy days, and during the high water temperatures of August. Minor deviations in the line estimating the pond population in Figure 13 are due to trapping and additions of turtles and the assumed escapes of marked C. s. scripta. The large number of turtles scared off the basking sites (29.9 percent of the total basking departures) is undoubtedly positively correlated with the number of baskers per day as well as with basking frequency. If the sky remained clear and the turtle was not scared into the water late in the afternoon, it commonly emerged again after a time. I have taken care to avoid using the basking frequency data collected on days when many disturbances interrupted turtles that may have basked only once under normal circumstances.

How the mean percentage of the total marked C. s. scripta population basking per day and the mean basking frequency (mean number of appearances per day for those C. s. scripta basking at least once a day) are related to different weather conditions and to each other is illustrated in Figure 14. The weather conditions are as follows:

- 1) clear and warm (mean air and water temperatures above 20°C);
- partly cloudy (total plywood site sun time reduced more than 200 minutes by cloud cover) and warm;
- 3) overcast and warm;
- 4) clear and cool or cold (mean air or water temperature equal to or below 20°C);
- 5) partly cloudy and cool or cold; and
- 6) overcast and cool or cold

(5 and 6 will be used in two subsequent figures). The mean percentage of the total *C. s. scripta* population basking per day and the mean basking frequency were greater on warm-clear and partly cloudy days than on warm-overcast and cold-clear days (i.e. an increase in percentage of the population basking and in the number of times individuals emerged when the temperatures were warm and the skies clear). At such times, it was common for turtles to bask two or three times a day, and occasionally four and five. The percent of the total marked *scripta* population basking per day was usually considerably below the maximum observed value of 92. It is clear that basking is not an absolute daily requirement for *C. s. scripta*, because even during the most favorable weather not all individuals will emerge.

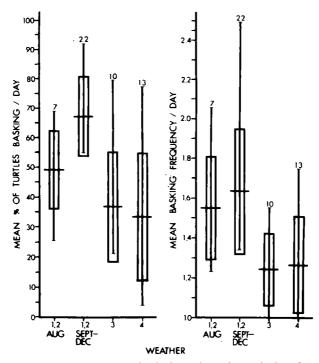
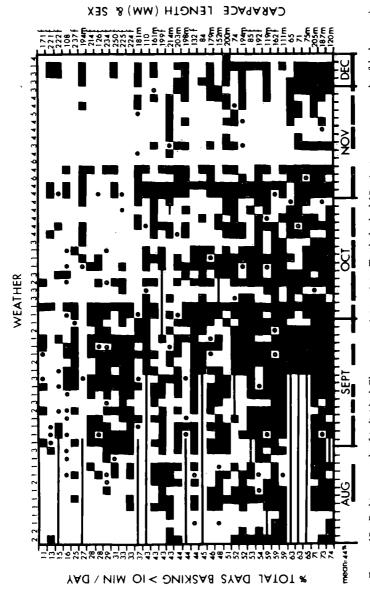


FIGURE 14.—Mean percent of total turtles that bask per day and mean basking frequency in different weather conditions. A total of 26 marked Chrysemys scripta scripta were used. Mean (horizontal line), range (vertical line), and one standard deviation from either side of the mean (open rectangle). Number of days of data used in the calculations is at the top of the range. Weather: 1) clear and warm, 2) partly cloudy and warm, 3) overcast and warm, 4) clear and cool or cold.

The basking records of 37 C. scripta over a 61-day period can be seen in Figure 15. Variability is evident, with one individual emerging on only 11% and another on 74% ($\overline{X}=44\%$) of the 61 days. A high percentage of the individuals were not seen on the sites for long periods of time, although some undoubtedly basked on days I was not in the blind (50.4% of the total days). Females tended to appear less frequently than males, especially when water temperature fell. One may also note the wariness of the 108 mm turtle, which emerged for brief periods on 11 of the 21 total days it appeared.

An estimated 35 percent of the $C.\ s.\ scripta$ present in the pond had a carapace length of 100 mm or less. The estimate was obtained from the basking frequency of the 11 small marked $C.\ s.\ scripta$ (since the total numbers of appearances per day of marked and unmarked small $C.\ s.\ scripta$ [A_m and A_u] were known, as well as the number of small marked turtles in the pond [$N_m = 11$], the number of small unmarked turtles [N_u] could be estimated from the equation: $N_u = (N_m A_u)/A_m$). Before 0900 and after 1400, 53-57%



less than 10 minutes per day (solid circle), not present in the pond (horizontal line). Consecutive days of observation are indicated Figure 15.—Basking records of individual Chrysemys scripta scripta. Turtle basked 10 minutes or more per day (black square), by horizontal bars on the abscissa. Weather: 1) clear and warm, 2) partly cloudy and warm, 3) overcast and warm, 4) clear and cool or cold, 6) partly cloudy and cool or cold, 6) overcast and cool or cold.

of the basking C. s. scripta were smaller than 100 mm, 18-22% more than expected (Fig. 16). This may have resulted from physical competition for space on the basking site, because small turtles could not make room by pushing aside larger turtles. Another possible explanation has to do with body temperature rise during basking, which is slower in early morning and mid-to-late afternoon than at midday (when environmental radiations are maximal); this presumably is a more important factor with regard to smaller than larger turtles and may somewhat restrict small turtle basking to the cooler portions of the day. A third possibility is that small turtles start activity earlier in the morning due to spending the night floating at the surface, whereas larger turtles stay on the bottom. Thus, if the start of daily activity is correlated with a specific light intensity in the pond water, small turtles would become active and start basking sooner than large turtles.

For specimens of C. s. scripta weighing over 500 g, there seems to be little correlation between basking frequency and body size, as can be seen from the following data (taken on 15 warm clear days in September): 51-499 g, 1.65

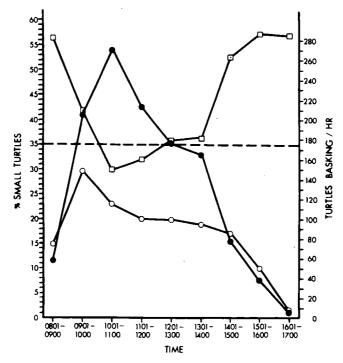


FIGURE 16.—Relation of turtle size to time of basking in *Chrysemys scripta scripta*. Small turtles (carapace length less than or equal to 10 cm) basking per hour (open circles), larger turtles basking per hour (solid circles), percent of baskers which are small turtles (open squares), expected percent of baskers which are small turtles (dashed horizontal line). Data collected on 16 warm clear days in September and October.

mean basking appearances per day, 500-999 g, 1.36, 1000-1499 g, 1.36, and 2000-2651 g, 1.38. C. s. scripta smaller than 500 g may either be forced to leave a basking site more frequently than larger turtles due to high body temperature, or they may more often be physically forced off a site by larger individuals. The latter was occasionally observed.

As seen in Figure 15, nine C. s. scripta that were trapped at two other duckweed covered ponds near Gainesville were added to the pond during the observational period. An additional six turtles, part of the original pond population, were trapped a second time. These 15 turtles were kept in a dry room from 3 to 11 days (mean of 7.3 days). They were released, usually on warm clear mornings (13 of 15 releases) prior to the appearance of the first basking turtle. A high percentage (13 or 87%) basked the same day. On the average, the new releases basked longer and at a higher frequency than the rest of the C. s. scripta population both on the day of release and on the second day observations were made (For 9 of the 15 releases, there was a variable break in continuous daily observations between the first and second days) (Fig. 17). Subsequent declines in basking frequency and duration on the second and third days were not due to unfavorable weather. Turtles defecated repeatedly

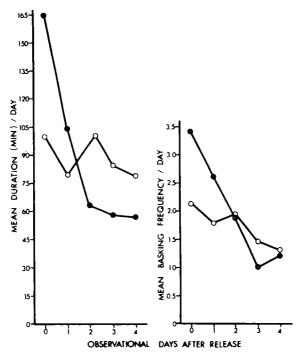


FIGURE 17.—Mean basking duration and frequency of newly released Chrysemys scripta scripta (N = 15). Newly released turtles (solid circles), rest of population (open circles). Turtles were released on five different days, most of which were warm and clear.

while in captivity and were thus probably released with relatively empty guts. Perhaps, the turtles basked more intensively in response to duckweed eaten the day of release.

Daily and Monthly Variation in Basking Number, Duration, and Frequency

Daily basking started at about the same time in August and September (Fig. 18). The first individual usually emerged on the western plywood site just before or soon after the site was in full sunlight. Overcast skies delayed the time of first emergence. During October and November, basking activity started at later times during the day and was not correlated so closely with the illumination of the western site. The delay in basking activity was probably due to decreasing environmental temperatures and photoperiod. Except for August days, which usually had two maxima, a single peak in basking activity occurred daily, as determined from the maximum number of turtles basking simultaneously. This maximum number usually occurred during midmorning from August to October, but like the time of first emergence, became more variable and occurred at later times in October and November. The maximum number of basking turtles observed at any one time during the period of study was 51 (an estimated 55% of the total population), this occurring on 3 November. The late date is correlated with the fact that basking durations averaged longer later in the year.

Two variables (the mean number of basking turtles and the mean basking duration per appearance) along a common daily time axis for the four months of the study are compared in Figure 19. The graphs will be discussed separately and then compared. Three types of basking number curves are shown in the upper graph. The typical August curve for a clear day was bimodal, with a midday decline in basking number due to high surface water temperature and insolation. During the early morning and early afternoon, the rate of emergence was greater than the rate of departure, resulting in an overall increase in the number of turtles. The reverse was true as midday and evening approached. The basking number curves for warm, clear days in September through early November were asymmetrical and unimodal, with a midmorning peak and generally decreasing numbers of individuals during the rest of the day. The third type of basking number curve was unimodal and symmetrical, occurring on warm, partially or completely overcast days and on clear, cool to cold days in November. The number of baskers declined after 1400 in all cases. If basking has a thermoregulatory function, the declines would be expected based on declining environmental temperatures and insolation. Also, most of the turtles that will emerge have already done so by midafternoon. In the lower graph, the increase in basking duration from August to November can be seen. Basking durations for each month are rela-

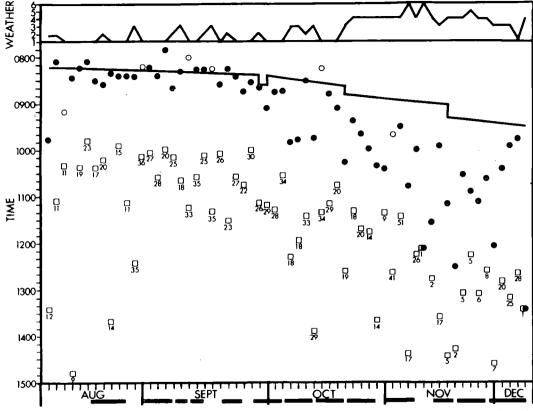


FIGURE 18.—Time of first basking emergence (solid circles), time of first basking emergence prior to arrival of the observer at the pond (open circles; time given is observer arrival at the pond, not time of turtle emergence), time of maximum number of turtles basking at once (open squares; maximum number of turtles basking at once given under each open square), approximate time the first western basking site was sunlit (varying horizontal line), consecutive days of observation (horizontal bars on the abscissa). Weather: 1) clear and warm, 2) partly cloudy and warm, 3) overcast and warm, 4) clear and cool or cold, 5) partly cloudy and cool or cold, 6) overcast and cool or cold.

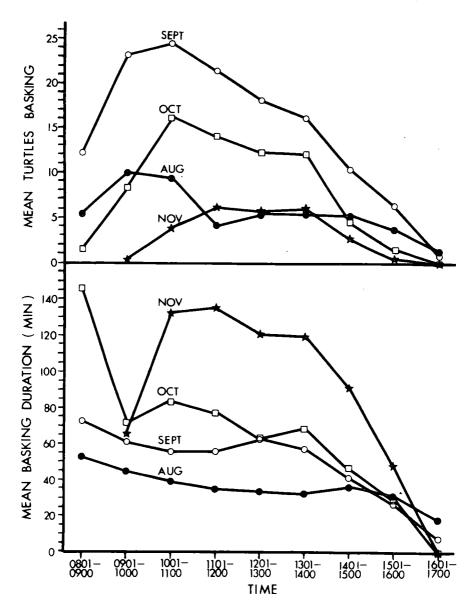


FIGURE 19.—Monthly rhythms of basking number and duration. Values are means for the following days: 8 clear days in August, 10 clear days in September, 10 clear days in October, and 14 clear or overcast days in November.

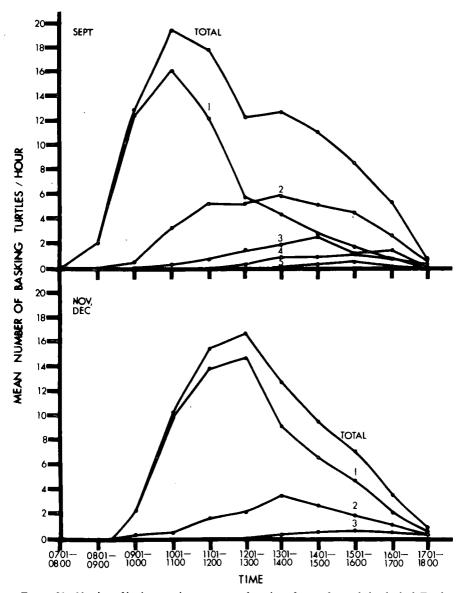


FIGURE 20.—Number of baskers per hour in terms of number of times the turtle has basked. Total turtles basking per hour (total curve), turtles basking per hour for the first time (curve 1), turtles basking per hour for the second time (curve 2), turtles basking per hour for the third time (curve 3), etc. Data were collected on five warm clear days in September and five clear warm or cool days in November and December. Only Chrysemys scripta scripta are included.

tively constant from 1000 until 1400. Late afternoon declines resulted from the paucity of turtles remaining on the basking sites after the sun had set. The high October 0800-0900 duration mean was due to a few large turtles that stayed nearly all day on a western basking site. These large turtles emerged early in the morning, attained high body temperatures, and spent the afternoon on the site in the shade. A comparison of the two graphs shows that the number of basking turtles was high in September, although basking durations were relatively low, whereas the reverse was true in November. In August both basking numbers and duration were low, and in October values were intermediate.

In Figure 20, the basking number curves for five clear days in September and five clear days in November were broken down according to the number of basking appearances per day. During the September period, 46% of the total number of turtles emerging basked once a day, 34% twice, 13% three times, 5% four times, and 2% five times. In November, mean basking frequency was lower, with 75% of the baskers basking once a day, 21% twice, and 4% three times. It was found that most turtles either emerged during the morning or not at all, those appearing in the afternoon being, with few exceptions, repeaters from earlier in the day. During November, however, no such preponderance of early morning emergences was noted, a high percentage of individuals basking during the afternoon having come out for the first time.

THE BASKING ACT

The basking act may be divided into four stages, based on changes in turtle body orientation, head and limb posturing, and movement on the basking site. The present description is based on an adult male and female $C.\ s.\ scripta$ situated on a horizontal site out of water on a clear warm day, with no disturbances and no other turtles close enough to restrict the subject's movement. Numbers in parentheses correspond to numbers in Table 1.

Arrival at the Basking Site.—The prospective basker usually was first seen less than a foot from the basking site, but on occasion individuals were observed as much as 30 feet away. After a period of stationary floating, the turtle swam to the site with its head above water. Some turtles disappeared below the duckweed, reappearing momentarily at another ramp or farther along the log. This occurred most commonly when the first site approached was occupied by a larger turtle. Turtles often surfaced their front legs, paddling laterally while simultaneously surfacing the head. The leg movement temporarily cleared duckweed from the water surface, resulting in the turtle's eyes being fairly free of the plant. It seems clear that C. s. scripta was locating the basking site visually, by surface and, likely, subsurface exploration. The turtles commonly returned day after day to the same basking site.

TABLE 1.—SUMMARY OF BASKING MOVEMENTS AND POSITIONS.

Time of Occurrence Movement HEAD Characteristic of Stage I and early 1. Extension II, occurs less often in other stages. Especially common during a disturbance. 2. Rotation Characteristic of I, occurs less often in other stages. I-III, most commonly in II and III. 3. Bobbing 4. Protracted Eye Closure Characteristic of later III. Characteristic of later III, commonly Extension and Retraction occurs in IV. 6. Eye Watering Characteristic of later III. I-IV, least in I, most often in III. 7. Eye Blinking 8. "Smelling" the Substrate Occasionally in any stage, least commonly in II. Bending Toward a Disturbance I-IV 10. Yawning Occasionally in any stage. 11. Pumping of the Occurs in all stages, with highest Hyoid Apparatus frequency in Stage III. FRONT LEGS 12. Walking Position Characteristic of I, observed less often in other stages. Occurs before and after a walk, before departure, and when disturbed. Intermittently in II and III, sometimes 13. Extension in IV. 14. Rotation and Partial Intermittently in stages when legs Retraction are extended. Characteristic of III, occurs less 15. Kicking often in IV, infrequently in I and II. 16. Retraction Characteristic of III, sometimes occurs in IV. 17. Head Rubbing Occurs in all stages, most commonly in III. REAR LEGS 18. Walking Position Same as for front legs. Intermittently in II, III, sometimes in IV. 19. Extension (Not Touching Substrate) 20. Digit Spreading Characteristic of II, occurs sometimes in IV. Same as for front legs. 21. Kicking 22. Extension (Relaxed on Intermittently in II, III, sometimes IV. Substrate) 23. Rotation and Partial Same as for front legs. Retraction 24. Retraction Same as for front legs. TAIL 25. Relaxation and Retraction Alternates in all stages. More commonly retracted in III and IV. Characteristic of IB, III. Rotation (Sun Orientation) 27. Rotation Occasionally in IV.

TABLE 1 (CONTINUED)

28. Walking

29. Departure

Fairly common in III, especially among smaller turtles, less common in IV, sometimes occurs in IB. Characteristic of the end of III, IV, and during disturbance, but occurred voluntarily at any time.

STAGE IA: Partial Emercence from the Water.—The turtle approached the site, usually at an unoccupied spot, grasped the site with its front legs, and pulled itself partially out of the water. Large individuals sometimes experienced considerable difficulty in climbing out. For example, a large C. f. peninsularis female (4,743 g) and two large C. nelsoni females (3,054 and 4,838 g) sometimes struggled two to three minutes, trying all three ramps of a plywood site, before pulling themselves onto the horizontal surface. One or two strokes with a front leg (17) removed any duckweed clinging to an eye. The head was fully extended (1), with the eye level above the level of the site. Small turtles commonly did not climb the ramp far enough to see the surroundings directly ahead. Turtles repeatedly rotated their heads in all directions, moving in small increments with a pause between each movement (2). The maximum rotation was only occasionally greater than a 90° angle with the long axis of the body. Rotation and maximum head extension continued throughout Stage I.

Stage IA usually lasted less than 10 minutes. Turtles with carapace length longer than 20 cm commonly bypassed this stage, crawling immediately to a horizontal position.

STAGE ÎB: STABILIZATION OF POSITION.—After crawling completely out of the water, the turtle rested with its legs either placed on the substrate (12, 18), dangling down toward or into the water, or in a nearly retracted position. The turtle either paused a few minutes or oriented itself immediately with respect to the sun. If the turtle's initial position happened to be the most advantageous one with regard to location of the sun, the animal made no further rotational movement. Otherwise, it moved so that the orientation angle (Fraenkel and Gunn 1961:107) was approximately 180°, with the turtle's head directly away from the position of the sun (26). If the sun was near its zenith in a summer declination (i. e. almost directly overhead), orientation was random. Having achieved the desired position, the turtle either extended its rear legs (thus entering Stage II) or remained for a time with its legs resting on the substrate.

It is clear from the extension and rotation of the turtle's head and the position of the legs on the substrate that Stage I represents a period of high awareness, during which the surroundings are scanned for possible danger and the turtle can depart with maximum efficiency. Turtles were most likely to depart during this stage, either due to cloud cover, wariness, or disturbance.

Stage I behavior occurred more consistently than behavior of later stages, and was repeated under all light and temperature regimes. The only exception was body orientation, which was random on heavily overcast days.

STAGE II: EXTENSION OF THE REAR LEGS.—The rear legs were either extended simultaneously or one at a time (19). They were held above, and approximately parallel to, the substrate and long axis of the body. The webbed digits were spread apart to a variable degree (20) and partly pronated, with the medial side held higher off the substrate than the lateral side. Occasionally, the rear legs were rotated slightly, or partially retracted and extended again (23). Subsequently, tension in the interdigital skin was reduced and the legs rested on the substrate (22).

The front legs were curled back along the bridges of the carapace or extended parallel to the long axis of the body (13), with the medial edges of the legs resting on the plastron. However, the legs were also occasionally in intermediate position.

The head was extended less than in Stage I, but still was held above a horizontal position. Head rotation decreased and eye blinking (7) became more common. The turtle occasionally bobbed its head during Stages II and III (3). The head was quickly moved vertically, diagonally, or in a circular path, the motion lasting less than a second. Bobbing possibly is a response to drying of the head skin or some other irritation. Turtles often bobbed when insects flew about their heads.

STAGE III: PERIODS OF QUIESCENCE ALTERNATING WITH PERIODS OF INCREASING ACTIVITY.—This was usually the longest stage, although Stage IV was sometimes longer. Stage III consisted of periods of relative quiescence, alternating with shorter periods of activity. As body temperature continued to increase, the periods of quiescence shortened and activity increased.

During early periods of quiescence, the head was horizontal and partly retracted. The front legs were usually curled back along the bridges of the carapace or resting on the substrate in a walking position. The rear legs were usually partly to completely extended and relaxed on the substrate. During later periods of quiescence, the turtle retracted its head, limbs, and tail into the shell (5, 16, 24, 25). On occasion, the head was quickly and fully extended, as in Stage I. After a short period of rotation, the turtle retracted its head again. The elevation of the head may be adaptive, since with its head completely retracted a turtle is vulnerable to attack. If a turtle is alone on a basking site and has its head retracted, one may sometimes approach closely enough to pick the turtle up. However, since C. s. scripta usually basks in groups, at least one turtle will usually have its head out. The vibrations caused by departing turtles is usually a sufficient stimulus to cause any Stage III baskers to raise their heads.

During periods of activity, turtles kicked their legs, rotated their bodies, walked about the basking site, and rubbed their heads with a front leg. A back-

leg kick (15, 21) started with the leg extended and relaxed on the substrate or retracted into the shell. The leg was moved quickly anterolaterally, bent at the knee, sometimes so far forward that the webbing extended over the dorsal surface of the marginals. The leg was then smoothly extended posteriorly. One fore or rear leg was kicked at a time, up to 25 kicks in quick succession, followed commonly by kicking of one or more other legs. The time between kicking bouts decreased and the number of kicks per leg increased as the stage progressed.

The turtle occasionally rotated its body before or after kicking, usually from 90 to 360°. A change of orientation angle from 180 to 90° resulted in partial shading of two legs and half the carapace, provided the sun was not directly overhead. Thus, the movement possibly could decrease heat intake. Most turtles rotated at least once after the Stage I orientation, with some rotating four or five times during Stage III. The probability of rotation increased with time.

Walking for short distances (28) increased (especially among small individuals) as density of turtles on the site increased. This usually resulted from physical displacement by larger individuals although occasionally a turtle moved voluntarily for distances up to a foot, returning to a Stage III posture after stopping. Voluntary walking was more common late in the stage.

The turtle commonly rubbed its head with its front legs (17) during Stage III. Rubbing was a response to irritation caused by watering eyes, clinging duckweed, insects flying near the head, and drying of the skin. Eye watering (6) started approximately halfway through the stage, with a corresponding increase in eye blinking. The eyes were closed (4) for longer periods, especially during head retraction.

Yawning (10) occurred occasionally during any of the basking stages. It consisted of a maximum lowering and then closure of the lower jaw, lasting two to three seconds.

Pumping of the hyoid apparatus (11) commonly occurred throughout the basking appearance, with greater frequency at higher body temperature. Gaping, common in Panamanian C. scripta (Moll and Legler 1971), was not observed at the Gainesville pond.

At the end of Stage III, the turtle returned to the water (29). Turtles often departed earlier, before the CTM was approached. Departure was usually preceded by a period of activity, rather than a quiescent period of head and limb retraction. Some turtles simply rotated toward the water and pushed off. Others remained balanced on the log or ramp edge, raised the plastron off the substrate as though preparing to depart, but sitting down again on the substrate. The turtle extended its head toward the water or into the water several times before finally pushing off. Turtles usually took the shortest route to the water.

STAGE IV: SITTING IN THE SHADE AFTER BASKING IN THE SUN.-When a

basking site was shaded in the afternoon or when the sky became overcast, turtles usually did not return immediately to the water, but rather sat in the shade for a time. The duration of Stage IV was dependent on at least five factors: (1) previous length of time in the sun (Fig. 12); (2) size of the turtle (Fig. 12); (3) time of day the sky became overcast or the site shaded (turtles departed sooner from sites shaded in the late afternoon than in midafternoon); (4) air temperature; and (5) solar energy flux.

If a turtle was previously in Stage I, departure usually occurred after a short time. If previously in Stage II, the rear legs remained extended and the digits spread for a few minutes, then relaxed more of the time. If previously in Stage III, activity soon decreased, the eyes stopped watering, and the turtle kicked its legs less often. Retraction of the head and limbs was common after the first few minutes in the shade, whether the turtle was previously in Stage II or III. The head was occasionally extended and rotated, then retracted again.

"Smelling" the substrate (8) was observed occasionally in all stages, but was most common in Stage IB when the turtle first emerged, Stage III, and late Stage IV. "Smelling" consisted of a slow dirolent movement of the head, with the nostrils approaching the substrate.

A few minutes before departure in Stage IV, the legs were returned to the walking position. Activity sometimes became more common, including short walks, kicking, and rotation of the body (27). Departure movements were the same as for Stage III.

C. s. scripta displayed little aggressive behavior while basking. Turtles usually remained near the periphery of the plywood sites, the new arrivals emerging at unoccupied spots. As density increased, more turtles emerged where others were basking. If the resident basker was smaller, the emerging turtle soon nudged the resident, which moved inward away from the water. If the emerging turtle was smaller than the resident, it (the former) either ceased its efforts entirely or swam to an open place farther along the site. A strict correlation with size was evident, regardless of species. For example, the largest C. s. scripta, a 2,651 g female, was nudged aside by the two female C. nelsoni (3,054 and 4,838 g) and the large female C. f. peninsularis (4,743 g). The size of the turtle was also important during body rotation. Smaller turtles were pushed off the site by larger ones in 88 percent of the 43 cases observed; the reverse occurred only 12 percent of the time. On rare occasions a resident individual would snap at an intruder, thus causing the intruder to move quickly out of the way. Bury and Wolheim (1973) have reported aggressive behavior during basking in Clemmys marmorata, but at a much higher frequency (145 aggressive acts in 37 hours of observation) than in Chrysemys scripta.

During only four of 4,441 basking appearances was a turtle found to be balancing itself on the carapace of another. Each time this involved small C. s. scripta (less than 10 cm carapace length) balancing on larger individuals of the same species.

Turtles basking on submerged sites did not perform some of the Table I movements. Eye watering, protracted eye closure, leg kicking, and Stage III orientation, all characteristic of high body temperature, were not observed. However, head extension and rotation, "smelling the substrate," bending the head toward a disturbance, yawning, head rubbing (duckweed removal), front and rear leg extension, rear leg digit spreading, and Stage IB orientation all were seen. Leg extension was observed only in turtles sitting fairly high in the water. Moll and Legler (1971) saw C. scripta in Panama fully extend their legs while floating in surface water. In the present study, however, the duckweed coat made observation of the legs impossible, unless the turtle was partly out of the water. Stage IB orientation also occurred in stationary floating turtles, but not when feeding on surface duckweed nor when moving across the pond. Although one may assume that Stage IB orientation increases heat intake, it is interesting to note that orientation occurred in turtles in water, in which the temperature was little different from the animal's body temperature. This suggests that Stage IB orientation is a sun compass reaction, whereas the Stage III orientation is a response to both the position of the sun and the turtle's increasing body temperature.

The orderly sequence of basking movements also did not occur on completely overcast days. Stage I remained the same, except that IB body orientation was random. Stage II leg extension and digit spreading occurred much less often. Extension and spreading were more frequent during lightly overcast than heavily overcast periods. Activity characteristic of the higher body temperature of Stage III was also less frequent. Eye watering did not occur.

Stage III usually lasted longer than Stage II, which in turn was longer than Stage I. Stage IV was of variable length, ranging from shorter than Stage I to longer than Stage III. In general, the mean duration of Stages I-III increased and Stage IV decreased as air temperature and the sun's energy flux decreased. Large turtles still reached the end of Stage III when air temperature was below 15°C, if the turtle emerged early enough during the day. On cold days, the movements of Stage I were slower, due to the turtle's low body temperature. Also, retraction of the legs and tail occurred earlier in Stage IV.

Turtles with carapace length less than 15 cm voluntarily walked farther and more frequently than larger turtles. During Stage II, small turtles held their legs off the substrate more often and spread their rear leg digits more consistently than larger turtles. C. s. scripta from near hatchlings to old adults were seen basking. The smallest C. s. scripta caught while basking had a carapace length of 3.9 cm, slightly less than a centimeter longer than would be found in a hatchling (Carr 1952:246). Brattstrom (1965) reported that C.

picta hatchlings were not seen basking. He suggested that hatchlings reach sufficiently high body temperatures by floating in the warm surface water.

Chrysemys f. peninsularis and C. scripta basking movements were similar, except for leg extension. C. f. peninsularis held its legs off the substrate more of the time and spread its rear leg digits more extensively during Stage II than C. scripta, on both clear and overcast days.

TEMPERATURE-TELEMETRY

Illustrated in Figure 21 are three days of basking by the C. s. scripta female with the implanted interpleural temperature probe. Included are data on interpleural, air, and water temperatures (water temperature is a mean of surface and 5 cm depth measurements); time the turtle was in the sun, shade, and water; and the basking stage. The turtle's core temperature on emergence was about 1°C below water temperature, because water temperature was measured at the surface, whereas the turtle had been in the colder bottom water prior to emergence. By basking, the turtle raised its body temperature as much as 10°C above water temperature on all three days. On October 22, which was partly cloudy, air and body temperatures were about the same. But with longer periods in direct sunlight on 20 and 23 October, body temperature was also considerably above air temperature during basking. On 22 October, when the turtle was temporarily shaded, core temperature continued to increase for a time. The lag time of continued core temperature increase was probably due to the large temperature difference between the surface of the carapace and the core. On 23 October core temperature showed an almost immediate leveling off or decline with shading (1200-1300), due to the smaller temperature difference between the core and the carapace surface. As Mackay (1964) suggests, the "driving force" that changes the rate of heat movement between shell surface and core is the difference in temperature between the two; the greater the difference, the greater the rate of heat flow. The bone of the shell may not be so good an insulator as first appears, since the bone is well supplied with blood vessels (Spray and May 1972). There is little doubt, however, that the scutes are insulative (Rose 1969). On 20 October the turtle moved short distances from shade to sun seven times, as the shadow of a building advanced over her carapace (partial shade in the figure). Movement from shaded to sunlit parts of the basking sites was never observed at the experimental pond. Note that the rates of heating on 20 and 23 October are greater than the rates of cooling in the afternoon shade. The main reason for the rapid rise in body temperature is, of course, the high heat input from solar radiation. However, differences in basking behavior of Stage II vs. Stage IV may also be important; i.e. extension of the head and legs and sun orientation in Stage II vs. retraction of the head and legs in Stage IV. Also.

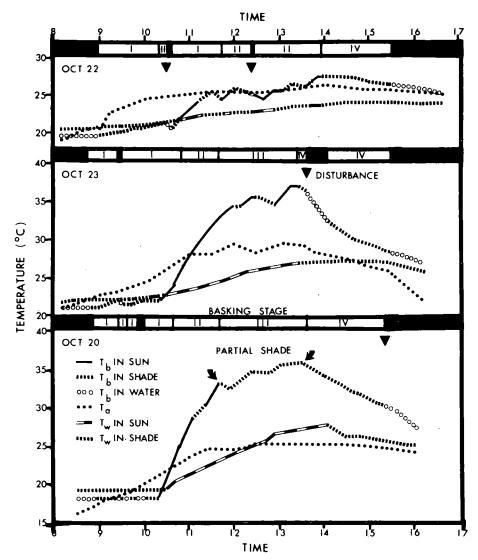


FIGURE 21.—Summary of three days of temperature-telemetry data. T_b is interpleural body temperature, T_a is air temperature, and T_w is water temperature.

blood supply to the carapace may be greater during heating than during cooling (Spray and May 1972).

Body temperature ranges can tentatively be assigned to C. s. scripta basking stages, based on field data, temperature-telemetry data, and information from the literature. Body temperature at the start of Stage I varies with am-

bient water temperature. C. s. scripta basks atmospherically within a water temperature range of 7°C to an unknown maximum, somewhere above 28.5°C mean water temperature (Fig. 7). The body temperature at the start of Stage II is probably quite variable, from just above 7°C to 31-33°C, the body temperature at the start of Stage III. Stage III ends near the CTM, which is approximately 41°C in C. s. scripta (Hutchison, Vinegar, and Kosh 1966). Note that on October 22 (Fig. 21), when body temperature did not reach 31°C, Stage III basking movements were not observed. The body temperature at the start of Stage IV is highly variable, from just above 7°C to near 41°C. The turtle cools in the shade to near the ambient air temperature (Fig. 21) before returning to the water. The body-air temperature difference at departure is probably greater when the air temperature is low.

DISCUSSION

The question may be asked whether a turtle's elevated body temperature during basking is an unavoidable consequence of sitting in the sun (Pritchard and Greenhood 1968) or a desirable result, achieved through active behavioral and physiological control. Boyer (1965), Moll and Legler (1971), and Spray and May (1972) suggest that turtle basking is primarily thermoregulatory. I also have concluded that basking in *Chrysemys scripta scripta* and *Chrysemys floridana peninsularis*, which results in a body temperature that is higher than either the ambient air or water temperature for significant periods of time, is thermoregulatory.

C. s. scripta and C. f. peninsularis basked less frequently on shaded basking sites and during cloudy and rainy weather. Basking in these situations did not produce an appreciable body-environmental temperature difference. If basking were thermoregulatory, basking frequency should decrease under these "unfavorable" conditions. One may ask why C. s. scripta basking frequency should also decrease at low temperatures and cease below a water temperature of 7°C, even though basking results in an elevated body temperature. Goodman (1971) found that the brown water snake, Natrix taxispilota, did not emerge from the water, no matter how high the air temperature, if the water temperature was below 10°C. He suggested that emergence at low water temperature would be futile, since activity and thus food capture are minimal. Adult C. s. scripta and C. f. peninsularis were often seen feeding on duckweed, using a seining movement similar to the South American turtle, Podocnemis unifilis (Belkin and Gans 1968), but neither of these species ate duckweed at low water temperatures. It may be hypothesized that basking would serve no purpose at low water temperature, assuming that basking is primarily a means of digesting food. On the other hand, atmospheric basking at high water temperatures would be unnecessary, since body temperature can be kept in an optimum range by aquatic basking.

By basking up to five times a day during warm weather, C. s. scripta increased the time its body temperature was above environmental temperature. Turtles returning to the water at the end of Stage III often reemerged quickly, before body temperature had fallen to near the water temperature. Basking behavior during the second to fifth appearance was often different from the first appearance, Stage I being abbreviated and Stage II being abbreviated or absent. This presumably resulted from the fact that the turtle's body temperature was already elevated upon emergence from the water.

There was an inverse correlation between basking duration and frequency. At warm environmental temperatures and relatively high solar energy flux, basking frequency was high and durations short. As environmental temperatures and solar energy flux decreased, basking frequency decreased but duration increased. Thus, the body-environmental temperature difference was maintained over a wide range of environmental temperatures for a longer time each day than if basking frequency and duration were constant.

C. s. scripta and C. f. peninsularis usually did not emerge at a shaded site, but sometimes sat in the shade for long periods after basking in the sun (Stage IV). In the first case, body temperature is not far above ambient air temperature, but in the second case, body temperature may be at least 10°C above ambient air temperature, especially if the turtle is in Stage III when the site is shaded. Return to the water would result in a fairly rapid loss of the heat gained by basking. By remaining in air, the elevated body temperature is maintained for a longer time. In smaller turtles and low air temperature, the rate of heat loss during Stage IV is more rapid. Return to the water, therefore, is also more rapid.

Some of the movements of the basking act appear to be thermoregulatory. Extending the legs and spreading the rear digits, common in emydids during basking, has been suggested as a means of drying the skin (Boyer 1965) and for synthesis of vitamin D from skin sterols under the influence of solar ultraviolet light (Pritchard and Greenhood 1968). Another possibility is that the sequence of limb and head movements in C. s. scripta and C. f. peninsularis are a means by which the animals can more rapidly approach and maintain an optimum basking temperature range. Extension of the head and limbs, and digit spreading of the rear legs during Stage II may increase body temperature rise, due to the greater vascularity and heat conductivity of the head and limbs than the carapace.

The mean water temperature above which atmospheric basking begins to decrease (28.5°C), the mean water temperature of maximum aquatic basking (31.5°C), and the body temperature at the start of Stage III (31-33°C) are about the same. This may mean that the high body temperatures of Stage III are above the optimum temperature range. Stage III body orientation, leg kicking, and retraction of the limbs and head under the carapace may be means of slowing down body temperature rise. Leg kicking increases as Stage

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III progresses. Kicking, alternating with retraction of the limbs under the carapace, may decrease the rate of body temperature rise by increasing radiation heat loss, assuming that kicking increases blood flow to the extremities. In Chrysemys floridana, blood flow to the extremities is known to increase with heating (Weathers and White 1971). Heart rate also increases with increasing body temperature (Akers and Damm 1963) and with voluntary activity in Chelodina longicollis and Emydura macquari (Webb and Johnson 1972). Retraction of the head, limbs, and tail into the shell later in Stage III may decrease temperature rise by reducing exposed surface area. The same behavior in Stage IV may reduce heat loss, increasing the time a body-environmental temperature difference is maintained.

Chrysemys scripta scripta and Chrysemys floridana peninsularis appear to have some physiological control of body temperature rise during basking. Control appears to be exerted primarily through changes in blood flow to the periphery of the body with changes in body temperature. Spray and May (1972) found that Chrysemys scripta becomes heated more rapidly than it cools in both air and water, and they stated that the turtle may actively control conductance by altering blood flow. Spray (1972) found that shifts in body weight during heating and cooling occur in opposite directions in Chrysemys picta and Terrapene ornata. He interpreted this to be a shift in blood volume, which in C. picta moved toward the periphery during heating and away from the periphery during cooling, and in the reverse direction in T. ornata. In Chrysemys floridana the half time of 133xe clearance from the carapace and subcutaneous area of the hindleg during cooling was significantly greater than during heating, indicating that blood flow to these areas was greater during heating than during cooling (Weathers and White 1971). Stitt, Semple, and Sigsworth (1971) found a plasma sequestration (blood flow cut off from a region of the body) in Graptemys geographica during cooling from 20 to 5°C. The sites of plasma sequestration were the skin, shell, kidney, gut, and muscle, whereas blood flow to the liver and lungs were maintained during cooling (Stitt and Semple 1971). Rewarming resulted in recirculation of sequestered plasma. Although the above studies were performed on restrained turtles in the laboratory, basking turtles in the field may also change blood flow patterns during heating and cooling.

The anterior hypothalamus is the center of thermosensitivity in the turtle. Localized hypothalmal heating in *Chrysemys scripta* resulted in a significant rise in arterial blood pressure and cooling resulted in a decrease (Rodbard, Samson, and Ferguson 1950, Heath, Gasdorf, and Northcutt 1968). The apparent contradiction of vasodilation of blood vessels in the carapace and limbs during heating and increased blood pressure during hypothalmal heating are perhaps resolved by hypothesizing concomitant visceral vasoconstriction (Heath *et al.* 1968). Surgical removal of the sensory nerve supply to the carapace of *Chrysemys picta* resulted in equivalent heating and cooling rates, in-

stead of the faster heating rate found in controls (Spray and May 1972). Perhaps, the change in temperature of peripheral receptors, as well as heating of the hypothalamus, is important in blood shift control.

Does basking facilitate more rapid or efficient digestion of a meal? Rates of substrate digestion by the enzymes pepsin, trypsin, erepsin, and amylase increase with temperature in various turtles (Kenyon 1925, Chesley 1934, Wright, Florey, and Sanders 1957). However, no one has investigated the possible correlation of turtle basking and digestive efficiency (the animal's capacity for decreasing caloric content of its food by digestion). Boyer (1965) found no correlation between basking frequency and feeding time in Chrysemys scripta elegans. Moll and Legler (1971) did find a basking-feeding correlation in C. scripta from Panama. In a group of juveniles, basking was most frequent within 48 hours after feeding. After 48 hours the turtles distributed themselves more equally between illuminated and nonilluminated sites. In the present study, basking numbers were high on the first warm clear day after a series of cloudy days. On subsequent clear days, basking numbers decreased. The same phenomenon was reported for C. scripta in Panama (Moll and Legler 1971), and in the present study C. s. scripta returned to the pond after confinement in a dry room. It is not known whether the increased basking is correlated with increased feeding. Gatten (1974) found that C. s. elegans increased its thermal preferendum from 24.6 to 29.1°C in fasting vs. recently fed animals placed in a thermal gradient. The body temperature 29.1°C correlates well with the mean water temperature in the present study above which atmospheric basking decreased (28.5°C).

Clearly, considerable work is still required to explain why some turtles bask atmospherically and others do not. Comparative studies in the following areas would probably clarify the situation considerably: (1) telemetric monitoring of hypothalmal, interpleural, cloacal, and carapace surface temperatures of unrestrained aquatically and atmospherically basking turtles under varying controlled air and water temperatures and heat inputs; (2) determination of digestive efficiency in turtles allowed to bask, aquatically and atmospherically, and those prevented from basking, again under varying controlled air and water temperatures and heat inputs; (3) determination of digestive enzyme temperature optima; and (4) more extensive analysis of diets in aquatically and atmospherically basking turtles.

SUMMARY AND CONCLUSIONS

1) Light intensity has considerable effect on basking behavior in *Chrysemys scripta scripta* and *Chrysemys floridana peninsularis*. Both the number of basking turtles per day and the number of times individual *C. s. scripta* bask per day decrease on overcast days. Turtles respond rapidly to clouds screening the sun on partly cloudy days by decreasing their rate of emergence

from the water. Turtles rarely emerge on shaded basking sites, but commonly remain on shaded sites after basking in the sun. In C. s. scripta, and probably in C. f. peninsularis, the time spent sitting on a shaded site is positively correlated with body temperature, body size, sun basking time, and air temperature.

- 2) Turtles respond to the position of the sun in the sky by orienting their bodies away from the sun early in the basking appearance. Orientation is random on heavily overcast days, and when the sun is near its zenith during August and September. Orientation is away from the sun, even when the sun is near zenith during October and November, as the southward declination of the sun increases. The daily movement of the sun in the sky from east to west results in a shift in basking and surface activity from the west side to the east side of the pond. The turtles may respond directly to the sun's position as well as to the daily cycle of basking site illumination and shading. Turtles are found to be either regional or diffuse baskers, emerging on sites in one region of the pond or showing no preference.
- 3) Atmospheric basking reaches a maximum at a mean water temperature of 28.5°C, but decreases at higher and lower mean water temperatures. Aquatic basking increases with increasing water temperature to the maximum mean water temperature recorded during the experimental period (31.5°C). Chrysemys s. scripta females bask less frequently than males as water temperature decreases, no longer basking when mean water temperature falls below approximately 14°C. C. s. scripta males still bask at a mean water temperature of 10.5°C, though at a much reduced rate, whereas C. f. peninsularis does not bask below 14°C. No C. s. scripta bask below a water temperature of 7°C. Water temperature is probably more important than air temperature in determining whether a turtle does or does not bask.
- 4) Mean basking duration in *Chrysemys s. scripta* increased on clear days from August to December, because of decreased sunshine and generally decreased air and water temperatures. Basking duration and body size are directly related in *C. s. scripta*. The relationship is not precise since many factors besides body size influence basking duration as, for example, time of day of emergence, sun energy flux, air and water temperatures, amount of duckweed on the carapace, variation in turtle wariness, and frequency of disturbances. Many turtles leave the basking sites before the CTM is approached.
- 5) The number of atmospherically basking turtles increased during August, reached a peak in early September, decreased toward October, and subsequently fluctuated between relatively low and high numbers as cold fronts alternated with warming trends. Basking is not a daily requirement in C. s. scripta, even when air and water temperatures and light are most favorable. Basking frequency is, roughly speaking, inversely proportional to basking duration from September to December. Basking frequency and duration are greater for the C. s. scripta released after a period of confinement than

for the undisturbed population. The newly released turtles may bask in order to digest recently eaten duckweed.

- 6) Chrysemys s. scripta less than 10 cm carapace length bask more often per day than larger individuals of the species, comprising a greater percentage of the total baskers before 1000 and after 1400 than expected (based on their estimated percentage of the population) and reach a basking number peak earlier in the day.
- 7) The time of first emergence is correlated with the illumination of the first major basking site during August and September, but this correlation weakens during October to December as basking activity commences progressively later during the day. The maximum number of turtles basking at one time occurs between 1000 and 1100 during August and September, shifting to as late as 1400 as photoperiod and air and water temperatures decrease in October and November.
- 8) Three curves of hourly change in basking numbers are described: (1) the bimodal August curve, with morning and afternoon peaks in basking numbers and a midday decline; (2) the unimodal asymmetrical curve, with a midmorning maximum of basking numbers and a decline in numbers during the rest of the day; and (3) the unimodal symmetrical curve, with a midday maximum in basking number. The importance of individual basking frequency per day in determining the shape of these curves is elucidated.
- 9) The basking act is described for an adult *C. s. scripta* basking on a clear warm day. The act is divided into four stages, based on changes in body orientation, position of the head and limbs, and activity with changing body temperature. Variations in the act correlated with environmental conditions, turtle body size, and species are discussed. Basking stages of *Chrysemys s. scripta* are assigned body temperature ranges based on field data, temperature telemetry, and the literature.
- 10) Many aspects of turtle basking behavior appear to be thermoregulatory: body orientation, leg and head extension and retraction, rear leg digit spreading, and leg kicking during basking; sitting on the basking site in the shade after basking in the sun, but rarely emerging to bask in the shade; inverse correlation of basking duration and frequency with changes in air and water temperatures and sunshine (shown for *C. scripta* only); and sitting on submerged basking sites or floating in warm surface water.

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