

Microclimates and Energetics of Free-Living Box Turtles, *Terrapene carolina*, in South Carolina

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ABSTRACT

We measured microclimate, field metabolic rates (FMRs), water flux, and activity patterns of telemetered box turtles (*Terrapene carolina*) in South Carolina from September 1987 to October 1988. Turtles were inactive for most of the winter and were active only sporadically during the rest of the year. Using the doubly labeled water method, we found that water flux averaged 8.8, 18.9, and 26.4 mL kg⁻¹ d⁻¹ in winter, spring, and summer/fall, respectively. FMR for the same periods averaged 0.028, 0.065, and 0.124 mL CO₂ g⁻¹ h⁻¹. Differences in FMR among seasons were significant but not between sexes. Using operative temperatures, we predicted standard and maximum metabolic rates of turtles. In winter, FMR was elevated above standard metabolic rates and close to maximum metabolic rates, whereas in spring and summer/fall, FMR fell midway between standard and maximum metabolic rates. We used a model to predict metabolic rates, geographical distribution, and potential reproductive output of box turtles across latitudes in eastern North America. Low FMR and low annual reproductive output may allow box turtles to survive and flourish in unpredictable resource environments by minimizing costs and risks, thereby maintaining greater lifetime reproductive success.

Introduction

Reptiles are often constrained by available energy, thermal limitations on digestive processes, or time constraints on foraging (Congdon 1989; Nagy 1989). Ectotherms place a greater percentage of their annual energy intake into production than do endotherms and maintain greater total biomass in many environments (Burton and Likens 1975; Pough 1980). Ectotherms may also benefit from behaviorally lowering their metabolic rates by selecting cooler temperatures within their environment (Nagy 1975). Important benefits from increased activity and higher body temperature may include increased feeding, more rapid food processing, and enhanced reproductive success (Merker and Nagy 1984). Hence, the manner in which a reptile controls its body temperature and consequent energy expenditure is of importance to its survival and reproductive success (Nagy 1982, 1989).

Despite members of the genus *Terrapene* being important components of many terrestrial ecosystems (Stuart and Miller 1987; Williams and Parker 1987), little is known about their metabolic costs in their natural environment or their contribution to the dynamics of energy flow. The objective of this study was to determine the microclimate, field metabolic rate (FMR), water influx rate (WIR), and movement patterns of a wild population of box turtles in South Carolina. We tested the hypotheses that activity of box turtles would be limited by available microclimates, that males would move farther and have higher FMRs than females, and that individuals would have lower FMRs in winter than in other seasons. We constructed a model to predict the daily, seasonal, and annual metabolic expenditures of box turtles for different latitudes spanning North America. The model allowed us to explore potential climatic limitations on the energetics of box turtles and to predict their geographical distribution.

Material and Methods

Natural History of Box Turtles

Box turtles (*Terrapene carolina*) are long-lived omnivorous reptiles whose habitat ranges from the Yucatán Peninsula to southern Maine. Throughout this range, they inhabit forested areas at densities of 10.1 to 34.6 turtles ha⁻¹ (Stickel 1950; Dolbeer 1969; Schwartz and Schwartz 1974; Pritchard 1979). As a result of sperm storage, females have the capacity to lay viable eggs (1–6 yr⁻¹) for years after a single mating (Ewing 1933; Strang 1983; Penick 1992). Box turtles are a major contributor to seed

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dispersal in forested areas and may help keep agricultural pests in check (Braun and Brooks 1987).

Study Site

We studied box turtles along Upper Tinker Creek (33°22'N, 80°37'W) on the Savannah River Plant in Aiken county, near Aiken, South Carolina. The study area was on the eastern flood plain and west-facing hillside of a bottomland hardwood forest. Tinker Creek provided a continuous supply of water through this relatively undisturbed habitat. The flood plain included areas of dense forest vegetation, open, sunlit clearings, and areas of standing water. There was an abrupt change in the habitat at the edge of the flood plain. A distinct line of heavy flood plain vegetation bordered a hillside covered with hardwoods, pines, and a sparse understory. The hillside contained many sunlit areas in winter and some patches of sunlight in spring and fall. A more complete description of the vegetation of these areas can be found in Penick (1992).

Micrometeorological Measurements

We established a weather station on the study site and collected micrometeorological data at 15-min intervals with a Campbell Scientific data logger. Temperatures were measured with 24-gauge copper-constantan thermocouples at three sites along a 100-m transect that traversed the flood plain and hillside. The three sites represented bottomland, ecotone between flood plain and upland forest, and upland oak-hickory forest. We measured air temperature (T_a) at 1.2 m and at 3 cm to represent air temperature at turtle-shell height (T_{a-sh}), the temperature of the leaf litter, and the temperature of the substrate in box turtle forms (depressions in the substrate dug by turtles; Stickel 1950). We also measured operative temperatures of freeze-dried turtles on the substrate surface when these models were in forms (see "Operative Environmental Temperature"). In addition, we measured wind speed at 25 cm with a cup anemometer, solar radiation with an Epply pyranometer, and total radiation with a Swissteco net radiometer at the ecotone site. Rainfall and relative humidity were measured at the Savannah River Laboratory, located 6 km away.

Operative Environmental Temperature

Operative environmental temperature (T_e), an integrated index of the microclimate that an animal experiences, sums the effects of radiation, wind, and T_a on an animals' body temperature (T_b ; Bakken 1992). In order to evaluate T_e of turtles, we constructed models by eviscerating and freeze-drying dead box turtles and inserting thermocouples through the plastron into the center of the body cavity. The seams of the T_e models were sealed with weatherproof silicon and the body was coated with flat varnish. These models provided close estimates of cloacal

temperatures of live turtles in a variety of environmental conditions (Penick 1992). Because our models were constructed of actual turtles, our estimates of T_e should be better than those obtained from copper models.

Time-Activity Budgets

We equipped study animals with a three-stage radio transmitter (164 MHz) that weighed <8% of the turtle's mass. Sealed with a combination of HumiSeal, beeswax, and finger cots, transmitters were affixed to the carapace with cable ties and dental acrylic. We located turtles daily and evaluated the straight-line distance that they moved. Because box turtles remained inactive in their forms sometimes for days, we also used the number of days active per week as an index of their activity (Strass et al. 1982). Typically, a strong relationship exists between total distance moved and linear displacement distance for box turtles (Strass et al. 1982).

Metabolic Rates

FMR was estimated as CO_2 production determined using the doubly labeled water method (Nagy 1983; Speakman 1997). We measured FMR of four adult females and five adult males during winter (December 1987–February 1988) and during late spring (March–May 1988). Because of transmitter failures, we only measured FMR for three turtles late summer to early fall (August–September 1988). A detailed description of our methods using doubly labeled water can be found in Penick (1992); we outline our procedures below.

After capturing the turtles, we transported them to the laboratory, weighed them, fitted them with a transmitter (Custom Electronics, Urbana, Ill.), injected them with a mixture of tritium and ^{18}O (98%, 3 mL kg^{-1}), bled them after an appropriate equilibration period (see below), and released them at the point of capture. Isotope equilibration was determined from laboratory trials at 10°, 22°, and 35°C using tritiated water to label the turtle's body water. From equilibration times at these temperatures, we computed a regression equation that enabled us to estimate equilibration time from T_a . A number of validation studies have been done on reptiles that indicate that the accuracy of the doubly labeled water technique is about 8% (Speakman and Racey 1988; Speakman 1997).

We derived standard metabolic rates (SMRs) and maximum metabolic rates (MMRs) for box turtles in the field by assuming that $T_e = T_b$ and by using equations obtained in the laboratory (Gatten 1974):

$$\log SMR = -9.7024 + 1.1661(T_b) - 0.065(T_b)^2 + 0.0016(T_b)^3 - 0.000013(T_b)^4, \quad (1)$$

where T_b is body temperature. MMR was given by

$$\log \text{MMR} = -4.6077 + 0.403(T_b) - 0.0132(T_b)^2 + 0.00015(T_b)^3. \quad (2)$$

Turtle T_b was measured frequently in the field by inserting a thermocouple 3 cm into the cloaca, and T_b was also estimated from T_e models. Predictions from equations were converted to CO_2 production using a respiratory quotient (RQ) of 0.94 during the active season (Ultsch and Anderson 1987) and using a RQ of 0.75 during winter assuming fat catabolism (Schmidt-Nielsen 1983).

Results

Microclimate

Mean solar radiation peaked during winter and spring around 1400 hours (Fig. 1A). The pattern for total radiation mimicked solar radiation with means varying diurnally between 307 and 404 W m^{-2} during winter and between 350 and 434 W m^{-2} during spring (Fig. 1B; Penick 1992). Average wind speed in winter ranged from 0.34 to 5.14 m s^{-1} , with peaks in the afternoon and low values in the early morning, whereas in spring, average wind speed varied from 0.31 to 3.75 m s^{-1} (Fig. 1C).

During winter, mean temperatures were higher on the flood plain than on the hillside (Fig. 2A, 2B). At both sites during spring, mean temperatures showed trends similar to those during winter but were less variable, ranging from 8.4° to 23.2°C on the hill and from 8.6° to 22.9°C on the flood plain (Fig. 2C, 2D). Substrate temperatures on the hillside for winter and spring were similar to temperatures of litter, T_{a-sh} , and T_a . However, variation in substrate temperature was lower than other hillside temperatures. Mean temperatures on the hillside ranged from 2° to 15°C with maximums occurring at around 1600 hours during winter, but they varied from 8° to 25°C in spring.

Substrate temperatures on the flood plain were distinct from other temperatures (Fig. 2B, 2D). Although T_{a-sh} tracked T_a , the former was higher during midafternoon. Litter temperatures were more moderate than other temperatures.

Operative temperature varied diurnally ranging from a minimum of -3.2°C to a maximum of 28.9°C for winter and from -2° to 34.2°C in spring (Fig. 2E, 2F). Mean T_e peaked around 1400 hours at 19.6°C in winter and 25.7°C in spring. The seasonal change in T_e between winter and spring was >5°C (Penick 1992). We found a relationship between T_e and T_a :

$$T_e = 2.53 + 0.567(T_a) + 0.0102(T_a)^2. \quad (3)$$

Mean T_a showed less daily variation during summer than during winter. Mean relative humidity varied greatly but never fell below 35% and was usually above 50% (Penick 1992). Rainfall ranged from 0 to 0.62 cm d^{-1} (Penick 1992).

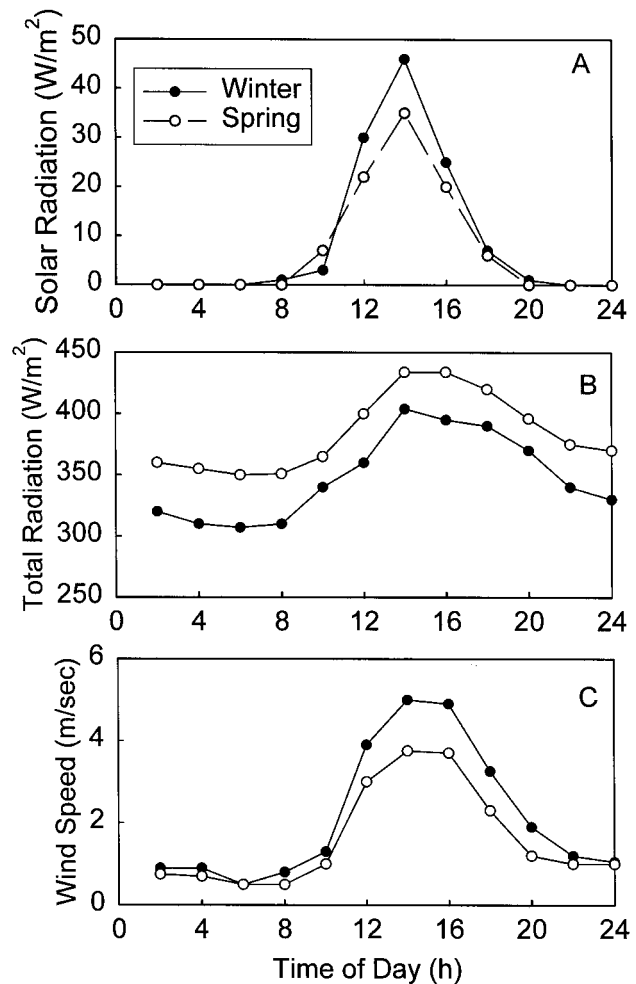


Figure 1. Microclimate of Tinker Creek ecotone site in 1987 and 1988. A, Mean solar radiation (W m^{-2}) averaged over 2-h periods during winter and spring. B, Mean total radiation during winter and spring. C, Mean wind speed during winter and spring.

Movement

Daily distances that turtles moved, as well as the percentage of days that they were active, varied among individuals (Penick 1992). Turtles remained inactive for long periods and then moved from a few meters to hundreds of meters in 1 d. In general, turtles did not move from November to March (Julian day 340 to 85) but became more active thereafter. Box turtles moved an average of 0.37 m d^{-1} in winter, 6.0 m d^{-1} in spring, and 9.0 m d^{-1} in fall. We found a significant difference in daily straight-line distance moved among seasons and between sexes; males moved 4.5, 7.7, and 20.7 m d^{-1} , and females moved 2.6, 3.9, and 4.8 m d^{-1} in winter, spring, and fall, respectively (Fig.

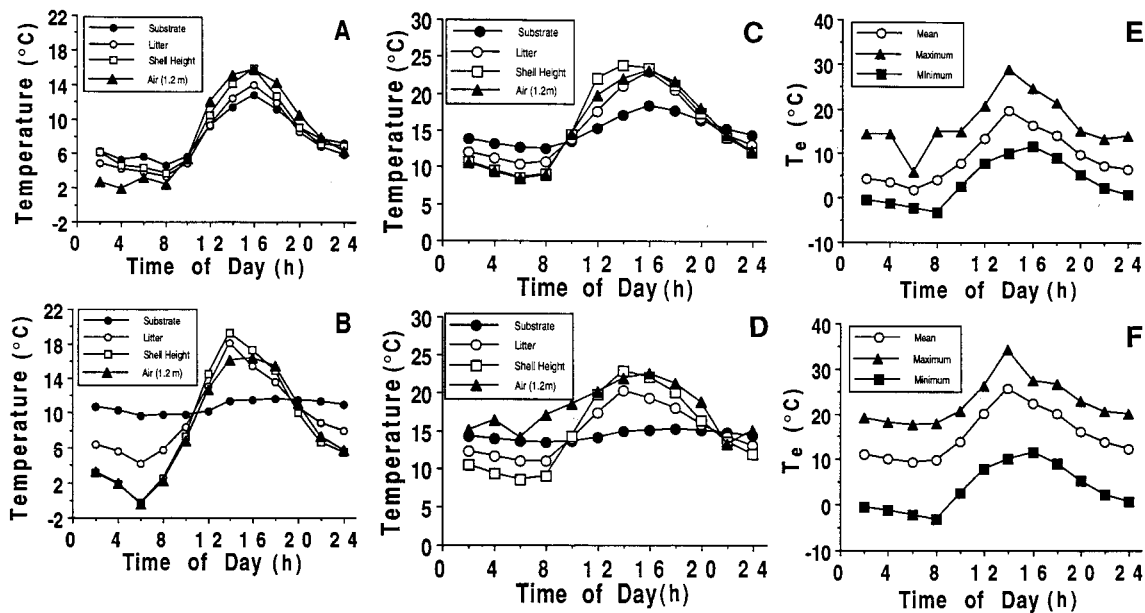


Figure 2. Temperatures of substrate, litter, T_a at 3 cm (turtle shell height), and T_a at 1.2 m in relation to the time of day on (A) the hill study site in winter, (B) the flood plain study site in winter, (C) the hill study site in spring, and (D) the flood plain study site in spring. E, Operative temperatures averaged over 2-h periods for models in the ecotone site in winter. F, Operative temperatures averaged over 2-h periods for models in the ecotone site in spring.

3; two-way ANOVA: $F_{\text{sex}} = 5.2$, $P < 0.03$; $F_{\text{season}} = 5.73$, $P < 0.01$). The interaction term for season and sex was insignificant.

Water Flux and Metabolic Rate

Seasonal water flux rates of box turtles ranged from $8.8 \pm 5.0 \text{ mL kg}^{-1} \text{ d}^{-1}$ in winter ($n = 9$) to $18.9 \pm 6.0 \text{ mL kg}^{-1} \text{ d}^{-1}$ in spring ($n = 9$) to $26.4 \pm 4.5 \text{ mL kg}^{-1} \text{ d}^{-1}$ in summer/fall ($n = 3$). Overall, turtle mass averaged 383 and 426 g for males and females, respectively (Penick 1992). Although water influx differed significantly among turtles during winter, spring, and summer/fall, we did not find a significant difference between sexes (two-way ANOVA: $F_{\text{season}} = 6.2$, $P < 0.02$; $F_{\text{sex}} = 4.2$, $P > 0.05$; $F_{\text{season} \times \text{sex}} = 0.64$, $P > 0.3$).

Average FMRs were lowest in winter ($0.028 \pm 0.01 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ [$\pm 1 \text{ SD}$; $n = 9$]), intermediate in spring ($0.065 \pm 0.02 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ [$n = 9$]), and highest in summer/fall ($0.124 \pm 0.02 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ [$n = 3$]). FMR differed significantly among seasons but not between sexes (two-way ANOVA: $F_{\text{season}} = 21.0$, $P < 0.001$; $F_{\text{sex}} = 1.0$, $P > 0.3$; $F_{\text{season} \times \text{sex}} = 1.1$, $P > 0.3$). We found a significant effect of T_e on FMR ($F = 31.7$, $P < 0.001$, $r^2 = 0.63$):

$$\text{FMR} = -0.0444 + 0.0079(T_e). \quad (4)$$

For box turtles, we computed SMR as 0.004, 0.01, and 0.017 $\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ and MMR as 0.034, 0.154, and 0.205 $\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ for winter, spring, and summer/fall turtles, respectively, using equations (1) and (2).

Discussion

Microclimate influenced the activity of box turtles. Average solar radiation was higher below the canopy during winter than during spring because of a lack of leaves on deciduous trees. Box turtles elevated their T_b by basking during sunny days in winter. In contrast, total radiation was higher during spring than winter. By digging their forms under layers of vegetation in winter, box turtles sheltered themselves from the radiant cooling that occurred before dawn on clear winter nights. During spring and fall, turtles were less selective in the location of their forms during winter. Stickel (1950) noted that box turtles placed their forms under cover of brush, debris, and vines. Reagan (1974) reported that locations of turtle forms were related to temperature, moisture, and cover aspects of the habitat. Our data indicate that turtles locate their forms in sites where total radiation is potentially high.

Following a similar pattern during winter and spring on both hillside and flood plain, temperatures reached a maximum around 1400 hours and a minimum near dawn. T_a 's on the

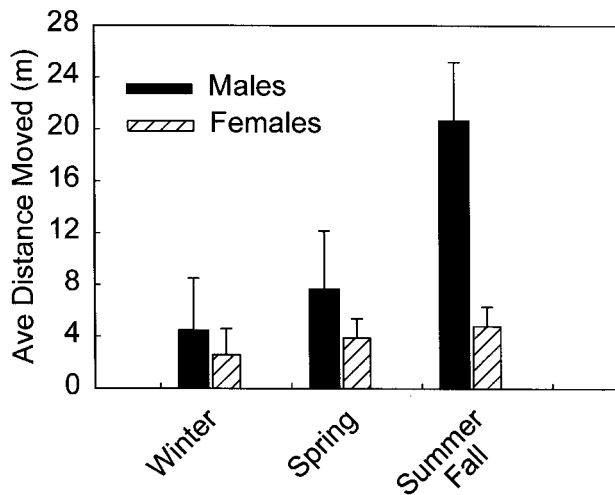


Figure 3. Average daily straight-line movement distances (m d^{-1}) of box turtles on the Tinker Creek study site for male ($n = 5$) and female ($n = 4$) box turtles in winter, spring, and summer/fall of 1987–1988. Error bars represent SEs.

flood plain often dropped below freezing at about 0600 hours during winter but remained higher on the hillside. At this time, most box turtles avoided low T_a 's by moving onto the hillside near the top into sites that also provided open areas for basking on sunny days. By placing their forms in leaf litter under vegetation, turtles also avoided radiant cooling at night. A few box turtles stayed on the flood plain and burrowed deep into the substrate where temperatures remained stable and elevated relative to T_a .

The microclimatic factors affecting box turtles on the Tinker Creek site were integrated into T_e , a metric that showed a smaller range in winter than spring. Maximum T_e in winter was achieved in sunny locations on the hillside. Minimum T_e in winter was similar to low temperatures recorded for the flood plain.

Turtles were sedentary for long periods, a pattern consistent with their low FMR (Reagan 1974; Congdon et al. 1989). Turtles moved infrequently in winter but occasionally basked near their forms. During the remainder of the year, turtles moved sporadically and often spent days in food-rich areas or in standing water. In spring, summer, and fall, turtles utilized diverse sites and were often found under fruiting bushes, among mushroom patches, basking in the sun, or in standing water. Turtle movement appeared to be a function of relative humidity and precipitation (Penick 1992). Reagan (1974) found that box turtles in Arkansas changed their location from open fields to forest depending on moisture and temperature conditions.

To maintain a positive energy balance, box turtles face trade-offs in resource allocation to various compartments of their energy budget (Congdon 1989), choices that have significant

implications for reproductive output. Box turtles had the lowest FMR of any reptile yet measured including the desert tortoise (Nagy 1982). Values of FMR for box turtles during spring ($0.065 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) were less than half those reported for desert tortoises in spring ($0.15 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) and lower than the average for desert tortoises in summer ($0.08 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$).

Values of FMR reported here are consistent with low metabolic rates from laboratory studies on box turtles. Gatten (1974) found that SMR's of ornate box turtles (*Terrapene ornata*) were lower than those of *Trachemys scripta* and lower than those values reported for other species of turtles. Ultsch and Anderson (1987) reported a SMR of $0.016 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ for *Terrapene carolina* and $0.0125 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ for *Gopherus polyphemus* at 22°C . Painted turtles (*Chrysemys picta*) have SMR's two to three times higher than box turtles (Stockard and Gatten 1983). Tinkle (1969) thought that low metabolic rates may be related to low annual reproductive output and longer lives. Box turtles appear to have a conservative life-history strategy in which they minimize standard metabolic costs and movement.

Two noteworthy findings of this study are the higher FMRs in fall as compared to those in spring and the similarity of energy expenditure between sexes. Our hypothesis that box turtles have a lower metabolic rate in winter was supported by our results. We also predicted that males would move greater distances than females and would have a correspondingly higher FMR. Even though males did move larger distances than females, this increased movement did not translate into a higher FMR for males.

In order to determine the effect of energetic constraints on reproductive output and geographical distribution of box turtles, we constructed an energy-budget model following O'Connor and Spotila (1992). Input parameters of the model were based on FMR and micro- and macroclimate data obtained during this study.

Model inputs of time of day, latitude, and Julian date were used to construct maximum and minimum T_a regression equations derived from 15 yr of data at >150 sites in North America (M. P. O'Connor, unpublished data). From these equations, we predicted patterns of T_a at 2-h intervals. Patterns of T_e , predicted from equation (3), were used to obtain FMRs using equation (4). In addition, we calculated upper and lower limits of metabolic rates using equations (1) and (2). Energy assimilation rates were computed to derive the upper boundaries of the energy budget diagram. Because the only assimilation rates quantified for box turtles were experiments run at 25°C (Russo 1972), we used the relationship of temperature to assimilation rates for *T. scripta* (Avery et al. 1993), an emydid turtle similar to *T. carolina*. We lowered the *Trachemys* processing rate curve to fit the *Terrapene* rate at 25°C to yield a processing rate estimate for box turtles. Because turtles in the field may not eat ad lib. as do those fed in the laboratory, our estimates of assimilation likely represent maximum values.

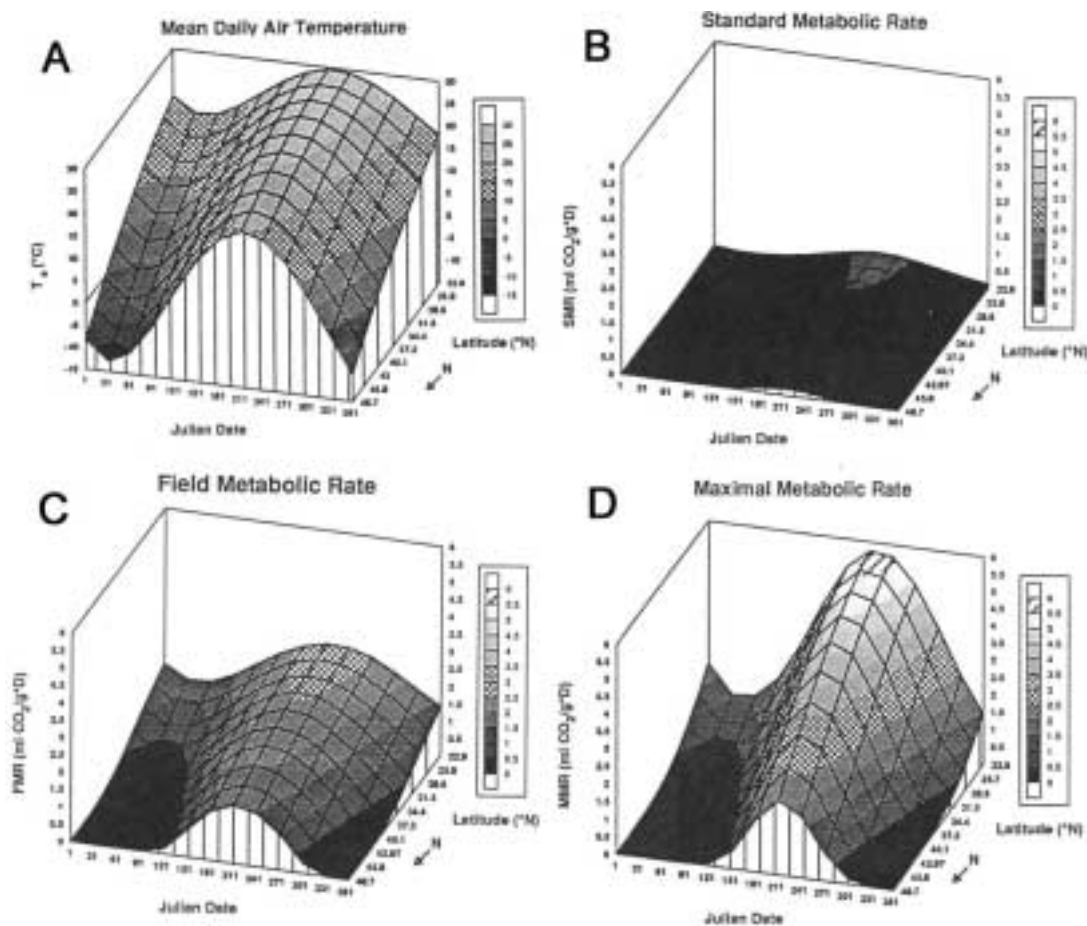


Figure 4. Microclimates and metabolic rates of turtles predicted from a mathematical model. A, Mean daily air temperatures ($^{\circ}\text{C}$) as a function of Julian day and latitude. B, Standard metabolic rate ($\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) as a function of Julian day and latitude. C, Field metabolic rate ($\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) as a function of Julian day and latitude. D, Maximum metabolic rate ($\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) as a function of Julian day and latitude.

Average daily T_a for different latitudes indicate that higher daily T_a 's occurred at lower latitudes and that these latitudes had lower annual fluctuations in T_a (Fig. 4A). According to the model, high temperatures for the year are similar in the North and the South, but the average daily T_a in northern latitudes in winter is -15°C , whereas in the southern latitudes it is 10°C .

Because they are all related to T_a , SMR, FMR, and MMR show the same latitudinal trends (Fig. 4B–4D). Metabolic rates in southern populations are higher for a greater part of the year than in northern populations; these latter populations have lower annual metabolic costs (Congdon 1989; Dunham et al. 1989). However, northern populations likely have lower rates of energy assimilation because box turtle assimilation rates are negligible at T_b 's below 15°C (Russo 1972).

The model predicts that energy assimilation rates are highest in midsummer as would be expected (Fig. 5A). Box turtles at high latitudes have low assimilation rates during cooler parts of the year, but at lower latitudes, they can process energy even

in midwinter. MMR should exceed energy assimilation, but in general, energy assimilation exceeds FMR reflecting the low activity of box turtles and indicating a positive energy balance (Fig. 5B). In southern latitudes, there is potentially more energy available for growth and reproduction of box turtles than in northern latitudes because the difference between energy assimilation and FMR increases as southern latitudes. Above 45°N , FMR approaches the energy assimilation rate, the maximum potential rate of energy acquisition, suggesting that box turtles reach an energetic limit around this latitude. In support of this idea, 45°N is the northern limit of box turtles' historic range in Michigan and in Maine.

Although limitations on box turtles in the southern parts of their range are less clear, it could be that seasonal availability of high-quality food coupled with high FMR imposes restrictions on turtle populations. Despite their ability to process food during the entire year, a result of high T_a 's, turtles may have access to many foods such as berries, insects, and mushrooms

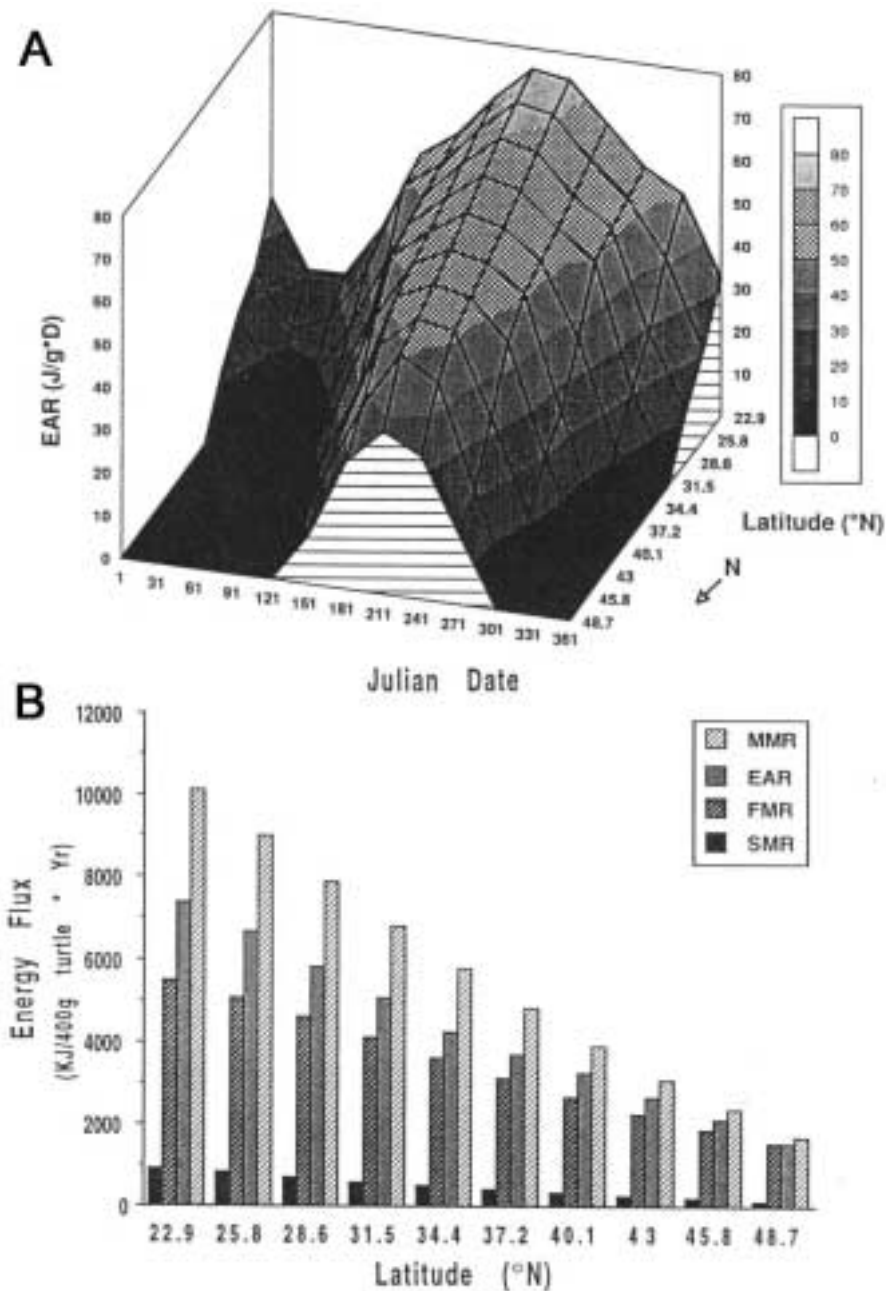


Figure 5. A, Energy assimilation rates (kJ) for box turtles at different latitudes at 30-d intervals throughout the year. B, Annual energy budget (kJ) for a hypothetical 400-g box turtle at different latitudes.

only seasonally. When food is less abundant mid- to late summer and energy costs are elevated by high T_a 's, box turtles may elect to select cool microhabitats to reduce overall metabolic costs. Such an energy minimizing strategy is similar to that employed by the chuckwalla (*Sauromalus obesus*), which retreats to thermal refuges during the hottest parts of the year in the Mojave Desert (Zimmerman and Tracy 1989).

The low metabolic rates of box turtles allow them to rely on resource peaks for their energy, allowing them to “coast” through periods of less productive forage using stored energy. Box turtles live at a slower pace than some other ectotherms and as such have evolved a strategy allowing them to survive in an uncertain resource environment by minimizing costs and risks, thereby maintaining greater longevity

and overall greater lifetime reproductive output than short-lived ectotherms.

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