

Activity and Thermal Ecology of the Box Turtle, *Terrapene ornata*, at its Southwestern Range Limit in Arizona

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ABSTRACT. – Activity and thermal ecology of *Terrapene ornata luteola* were studied in southeastern Arizona, near the extreme southwestern range limit for *T. ornata*, using a combination of radiotransmitters and temperature data loggers attached to individual turtles. Surface activity was greatly affected by rainfall and operative temperatures both seasonally and daily. Most of the annual activity occurred in a 90-d period from July through September coincident with monsoon rains. On a daily basis, turtles exhibited two periods of surface activity, a 3 hr period in early morning and a 1.5 hr period in late afternoon. Precipitation enhanced both daily and seasonal activity. Burrows of the kangaroo rat, *Dipodomys spectabilis*, provided the most important subterranean refuge. The observed patterns of daily activity, field body temperatures, and laboratory preferred body temperatures in Arizona were similar to those of most other populations of *T. ornata* that have been studied across the species' range, with the exception of extreme northern populations in Wisconsin and Nebraska. Compared to populations of *T. ornata* in the central portions of the species' range, there is no clear evidence of adjustments in either behavioral microhabitat use, thermoregulatory set point temperatures, or field body temperatures at the species' southwestern range limits. Broad thermal tolerances and an ability to behaviorally adjust both daily and seasonal activity times opportunistically may permit the existence of *T. ornata luteola* at its southwestern range margin in Arizona where hydric and thermal factors might be expected to constrain a primarily prairie-adapted species.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Terrapene ornata luteola*; turtle; activity; thermoregulation; body temperature; operative temperature; terrestrial; range limits; geographic variation; Arizona; USA

Reptiles commonly respond to variation in environmental heat loads by relying on behavioral modifications such as changing microhabitats or times of activity (e.g., Hertz and Huey, 1981; Christian et al., 1983). However, when heat load variation is extreme, behavioral changes may not provide essential thermal requirements or be too costly in terms of the time and energy expended in the behavior (Huey and Slatkin, 1976). In such cases, microhabitat or activity adjustments may be enhanced by altering thermoregulatory set point temperatures. For example, in Wisconsin the wide-ranging box turtle *Terrapene ornata* responds to lower heat loads by modifying its behavior and lowering its set point temperatures compared to *T. ornata* from Kansas (Ellner and Karasov, 1993).

Terrapene ornata is a prairie species ranging from southern Wisconsin to Louisiana west to southeast Wyoming and southeast Arizona and extending south into south Texas, northern Sonora, and northern Chihuahua (Conant and Collins, 1991). Four decades ago, Legler (1960) suggested that the most favorable environments and densest populations occurred in the central portions of the species' range in Kansas, Nebraska, Oklahoma, and northern Texas. The general ecology of *T. ornata* has been investigated to various degrees in Wisconsin (Doroff and Keith, 1990), Kansas (Legler, 1960; Metcalf and Metcalf, 1970), central Texas (Blair, 1976), and New Mexico (Norris and Zweifel,

1950; Nieuwolt, 1993, 1996; Nieuwolt-Dacanay, 1997). Relatively little research has targeted populations near the southwestern limits of the species' range; the westernmost limit being an intergrade population (*T. o. ornata* x *T. o. luteola*) in central New Mexico (Norris and Zweifel, 1950; Nieuwolt, 1993, 1996; Nieuwolt-Dacanay, 1997). Apparently, no field data exist for populations of the desert box turtle, *T. o. luteola*, at its southwestern range limit.

Legler (1960) hypothesized that populations of the desert box turtle, *T. o. luteola*, probably were physiologically adapted for living in rigorous arid environments where activity was sometimes possible for only a few weeks in the year. Available field data on thermal ecology and/or diel activity are sparse for southwestern populations (Rose, 1980; Rose et al., 1988), and no field study conducted in New Mexico or western Texas has directly addressed thermal ecology. Available information suggests that activity periods in central New Mexico are limited compared to more northern and eastern populations and, as might be expected in a thermally extreme environment, much of the day is thought to be spent inactive in a thermal refuge, such as in an underground burrow or under surface vegetation (Degenhardt et al., 1996; Nieuwolt, 1996). Apparently, nocturnal activity does not normally occur anywhere in the species' range.

In this paper, I test Legler's (1960) hypothesis by examining activity and thermal ecology of a population of

the desert box turtle, *T. o. luteola*, at its extreme southwestern range limit in the desert grasslands of southeastern Arizona. I also compare my results from Arizona with published data from more northern populations of *T. o. ornata* in Kansas and Wisconsin where activity and thermal ecology of the species are best understood (Legler, 1960; Ellner and Karasov, 1996; Curtin 1995, 1997, 1998).

METHODS

The study area was located in semi-arid grassland habitat in the Sulphur Springs Valley, 44 km SE of Willcox, Cochise County, Arizona, at 1400 m elevation. The Valley constitutes the major portion of the core distributional area for *T. ornata* in Arizona, where it is considered a sensitive species (Rosen et al., 1996). The Valley, approximately 25–40 km wide and 190 km long, is a southwestern extension of plains grassland heavily influenced by both Sonoran and Chihuahuan desert grasslands (Rosen et al., 1996). On the study area, vegetation consisted mainly of grasses and shrubs. Common grasses included love grass (*Eragrostis*), red three-awn (*Aristida*), tabosa (*Pleuraphis*), gramma (*Bouteloua*), vine mesquite (*Panicum*), and sacaton (*Sporobolus*). Common shrubs included mesquite (*Prosopis*), burro weed (*Isocoma*), catclaw (*Acacia*), and Russian thistle (*Salsola*). Other common plants include morman tea (*Ephedra*), yucca (*Yucca*), and prickly pear (*Opuntia*). The area is active ranchland and is periodically grazed by cattle. The climate is characterized by a distinct 8–12 week summer monsoon beginning in early July when most (ca. 70%) of the annual precipitation occurs. Vegetation density differed markedly on the study area in 1998 and 1999. Specifically, in 1999 grassy vegetation was higher and much more lush and green due to greater precipitation in July and August.

Numerous mounds constructed by the bannertail kangaroo rat (*Dipodomys spectabilis*), a keystone species in southwestern desert grasslands (Brown and Heske, 1990; Hawkins and Nicoletto, 1992), were a conspicuous landscape feature. Burrows of *D. spectabilis* provided the primary subterranean retreat for *T. ornata* on the study area. Burrows of other mammals (e.g., *Taxidea*, *Sylvilagus*, *Thomomys*, *Spermophilus*) also provided underground retreats. The burrow-constructing desert tortoise (*Gopherus agassizii*) occurred in nearby lower elevation deserts to the west but not in the study area.

Surface-active turtles were collected by repeatedly driving a 6.7 km road through the study area in early morning and late afternoon during their activity season in the summer monsoon period (July–August). Captured turtles were measured (carapace length in mm, weight in g), sexed, and given a unique mark by filing notches in the marginal scutes.

I constructed radiotransmitter/data logger devices consisting of a circuit board from a second-generation external probe HOBO-Temp data logger and an AVM Model SM1 164 MHz radiotransmitter. The two units were potted together in epoxy and shaped with a smoothly contoured

surface. Transmitter devices measured approximately 52L x 34W x 16H mm and weighed 30–35 g, approximately 7–9% of the body weight of the turtles, well within the 10% recommended maximum for reptiles in general (Anonymous, 1987). Furthermore, turtles of the genus *Terrapene*, including *T. ornata*, are known to have an unusually high tolerance for extrinsic mass loading (Marvin and Lutterschmidt, 1997; Wren et al., 1998). Transmitters were attached to the posterior edge of the carapace with a short piece of stainless steel wire so that they could freely pivot about the attachment point. The thermister probe was inserted into the body cavity through a small hole drilled in the most posterior vertebral scute and positioned so the probe was fixed adjacent to the cloaca. The probe was fixed to the exterior surface of the carapace with hot glue. After attaching transmitters, I observed each released turtle for 10–15 min to assess gross behavior. The only obvious transmitter-directed behavior I observed was one turtle that rubbed the posterior part of its carapace against the base of a shrub for several minutes in an apparent effort to remove the transmitter. Turtles with transmitters were observed to mate (both sexes), turn around in burrows, and eat, soak, swim, and walk normally. I did not encounter a transmitter entangled in vegetation during the course of the study.

Transmitters were programmed to record core body temperatures (T_b) every 10 min. Because I wanted to compare my results with those of other workers on *T. ornata* who have reported T_b as cloacal temperature, I compared 49 T_b values from 11 turtles obtained from loggers with concurrent temperatures obtained from thermister probes inserted 1 cm into the cloaca. Average differences between these temperatures at equilibrium were $< 0.5^\circ\text{C}$ at temperatures $22\text{--}30^\circ\text{C}$ and up to 1°C in those rare instances when temperatures exceeded 35°C (relatively cooler cloacal temperatures perhaps because of cloacal evaporative cooling). Short-lived temperature differences in individuals of up to 2°C occurred in rapidly heating basking turtles.

Early in the field season of 1998, I located each of 11 transmitter-equipped turtles five times each day throughout the daylight hours. After it became apparent that normal activity was limited to early morning and late afternoon, I continued to locate each turtle five times each day, but restricted my location efforts to about once every 0.75 to 1.5 hr, mostly during the two activity periods. At each location, I recorded the turtle's microhabitat (on open ground, under shrubs, in short grass, in tall grass, in burrows) and behavior (walking, basking, resting, mating, eating, drinking, soaking). Each turtle was tracked for 20 days from 7 July – 3 August at which time the transmitters were removed and the data downloaded.

In 1999, I attempted to determine exact times of emergence from and retreat to burrows for individual turtles by more frequently monitoring fewer turtles within a smaller area. Each of five transmitter-equipped turtles was located every few minutes during critical periods over 10 days from 20 July – 12 August at which time the transmitters were removed and the data downloaded.

Early in the study I identified five primary microhabitats that appeared to be important to turtle ecology: (1) open bare soil, (2) low grass (ca. 10–20 cm, no canopy), (3) high grass (ca. 20–50 cm, partial canopy), (4) under shrubs (mostly *Prosopis*), and (5) mammal burrows (mostly those of *D. spectabilis*). In each of these microhabitats I measured operative temperatures (T_e) every 10 min throughout the period of turtle tracking each year. Operative temperatures were obtained from turtle models consisting of a silicone-sealed *Terrapene* shell (with intact scutes) containing a HOBO-Temp logger.

To plot home range movements, I flagged the outermost locations of turtles and measured distances between them. Home ranges of turtles were roughly elliptical in shape and I estimated home range size by calculating the area of an ellipse using range of turtle locations as the major and minor elliptical axes. To determine the depth and position of inactive turtles in burrows, I dug out 11 turtles, each of which had been inactive in its burrow for at least two consecutive days.

To determine preferred body temperatures, I collected 11 adult *T. o. luteola* from nearby offsite localities and transported them to my laboratory. I closely followed procedures of previous workers (e.g., Ellner and Karasov, 1993; Curtin, 1995) to facilitate comparisons with their data. Turtles were placed in a 45 x 180 cm photothermal gradient having a sand substrate and relatively constant temperatures ranging from ca. 14°C at one end to ca. 50°C at the other. A miniature thermister probe was inserted 1 cm into the turtle's cloaca and temperatures were measured every 10 min with a HOBO-Temp data logger. Turtles were placed into the gradient and allowed to range freely under a 12:12 hr photoperiod regime. Approximately 60 temperature measurements were collected for each turtle during the period 1000–1500 hrs.

RESULTS

There was considerable variation in the daily operative temperatures among microhabitats on the study area (Fig. 1). The most abundant microhabitat, bare soil, was both the hottest (day) and coolest (night) surface microhabitat over 24 hr, whereas under shrubs was the coolest surface microhabitat during the day. Deep subterranean burrow temperatures were greatly moderated with < 2°C daily variation at 35 cm, an ecologically relevant depth as 11 turtles dug from their burrows averaged 35.5 ± 12.1 cm (range 10–50 cm)

Table 1. Pooled body temperatures from 11 *Terrapene ornata luteola* recorded during various behaviors in 1998. "Dug-in" refers to turtles that partially buried themselves in the loose dirt (resulting from gopher activity) at the base of shrubs. The upper portion of the carapace was usually exposed in such turtles.

	Mean	SD	CV	Min-Max	n	% of obs.
Basking	26.4	4.55	17.2	16.2–36.0	102	8.6
Resting	28.5	4.01	14.1	17.4–34.1	164	13.9
Moving	29.6	3.88	13.1	18.8–36.5	118	10.0
Dug-in	28.8	3.71	12.9	21.2–35.7	56	4.7
In burrow	26.9	2.39	8.9	20.3–34.4	744	62.8

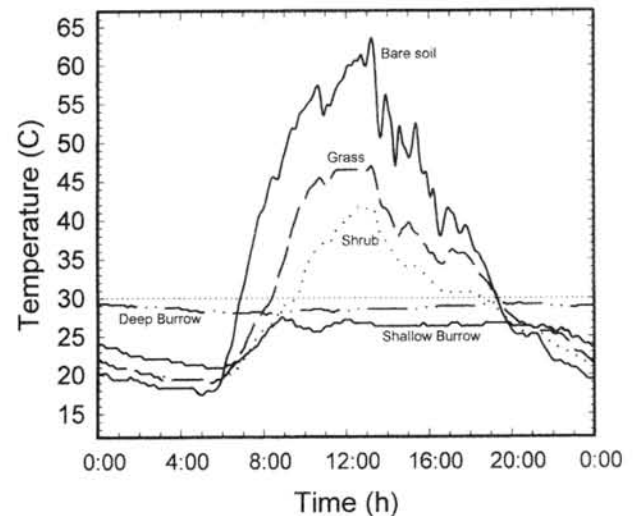


Figure 1. Operative temperatures by time on a typical sunny day in five different microhabitats in a desert grassland in southeastern Arizona. The dotted line is a 30°C reference line. Deep burrow temperatures were taken in *Dipodomys* burrows at ca. 35 cm depth and shallow burrow temperatures at ca. 10–15 cm.

beneath the surface. Operative temperatures on bare soil often exceeded 30°C by 0700 hrs and did not fall below that level until 1930 hrs. Similar operative temperatures were observed under shrubs from about 0930 to 1830 hrs.

Body temperatures during various behaviors in 1998 are shown in Table 1. During the activity season turtles were most frequently (> 60%) inactive in burrows where they maintained relatively low and constant body temperatures. Eating, drinking, soaking, and mating constituted < 5% of observations. The number of observations of the most frequently observed surface behavior, standing rest, may have been biased by the turtles' unusually quick response to cease movement in my presence, even at a considerable distance.

In 1999, this acute behavioral change was verified when extended long-distance observations of individual surface-active turtles through binoculars indicated that non-basking turtles most often were moving and that standing rest was usually limited to regularly spaced, but brief (< 3 sec) periods of apparent surveillance behavior when foraging.

Precipitation greatly affected levels of surface activity. Activity of turtles during the summer monsoon was most noticeable immediately after rainfall in thermally favorable

Table 2. Activity, home range size, number of burrows used, and weight change of *Terrapene ornata luteola* in a relatively dry summer (1998: 61 mm; 9 precipitation events) and in a relatively wet summer (1999: 116 mm; 15 precipitation events). Precipitation was measured on the study area from June to the end of the study periods in 1998 (3 Aug) and 1999 (12 Aug). Weight change and days active were measured over 20 days in 1998 and 10 days in 1999. Data on no. of burrows used were not obtained in 1998. Statistics indicate mean \pm SE (no. of turtles). Prob. indicates the results of two-tailed Mann-Whitney tests.

	1998 (dry)	1999 (wet)	Prob.
Days active (%)	61.4 \pm 8.08 (n=11)	97.8 \pm 1.47 (n=9)	<0.01
Home range (ha)	1.1 \pm 0.20 (n=9)	1.7 \pm 0.19 (n=7)	<0.05
No. burrows	—	3.0 \pm 1.22 (n=9)	—
Weight change (%)	-4.4 \pm 1.78 (n=11)	6.2 \pm 1.67 (n=9)	<0.01

Table 3. Mean body, operative, and mean maximum body temperatures (in °C) at which *Terrapene ornata luteola* (1) retreated to their burrows to end their 2.5 hr morning activity period and (2) emerged from their burrows to begin their 1.5 hr afternoon activity period. Body temperature data are the mean of means ± 1 SD for 8 turtles.

	Morning retreat	Afternoon emergence
Body temp.	33.8 \pm 0.42	30.0 \pm 0.43
Operative temp.	37.6 \pm 0.37	36.1 \pm 0.57
Mean max. T_b	35.1 \pm 0.12	36.2 \pm 0.17

periods. Frequency of daily activity was $> 60\%$ greater in 1999, a wet year, compared to 1998, a dry year (Table 2). Furthermore, compared to 1998, in 1999 turtles maintained body mass and moved within 50% larger home ranges (Table 2).

Terrapene ornata is a widely-foraging omnivore and most movements on the surface appeared to be associated with foraging. As noted by other workers (Legler, 1960; Ellner and Karasov, 1993; Claussen et al., 1997), paths of movement appeared to be greatly affected by vegetation cover as most movements were made on bare soil in sparsely vegetated areas. After foraging, turtles usually returned to the burrow from which they began their morning and afternoon foraging episodes (= home burrow). Occasionally turtles used additional burrows, on average using three burrows (range 2–5; Table 2) per individual during the 10-d observation period in 1999. On cloudy or overcast mornings, foraging turtles occasionally were located at considerable distances from their home burrows when cloud cover suddenly cleared, resulting in rapidly increasing operative and body temperatures, a problem also encountered by giant tortoises on Aldabra (Swingland and Frazier, 1979). These turtles

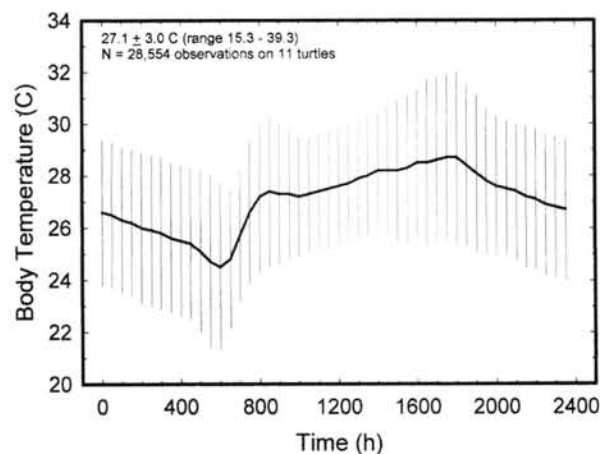


Figure 2. Mean body temperatures (\pm SD) by time in *Terrapene ornata luteola* in southeastern Arizona. The overall mean of $27.1 \pm 3.0^\circ\text{C}$ was determined from 28,554 observations on 11 turtles.

quickly moved back toward their home burrows and often explored other burrows encountered on the return trip. On two occasions, turtles became agitated and sought refuge in alternative burrows. Numerous *Dipodomys* burrows explored were too small in diameter for these two turtles to enter but both eventually found suitable alternative burrows. Data downloaded from these two turtles showed that the agitated searching behavior occurred at body temperatures near the maximum voluntarily tolerated levels (mean max. T_b , $35\text{--}36^\circ\text{C}$; Table 3). These observations suggest that exploratory behavior resulting from seeking refuge from high body temperatures may be a source of burrow switching.

Mean hourly body temperatures calculated from 28,554 data points pooled from 11 individual turtles are shown in

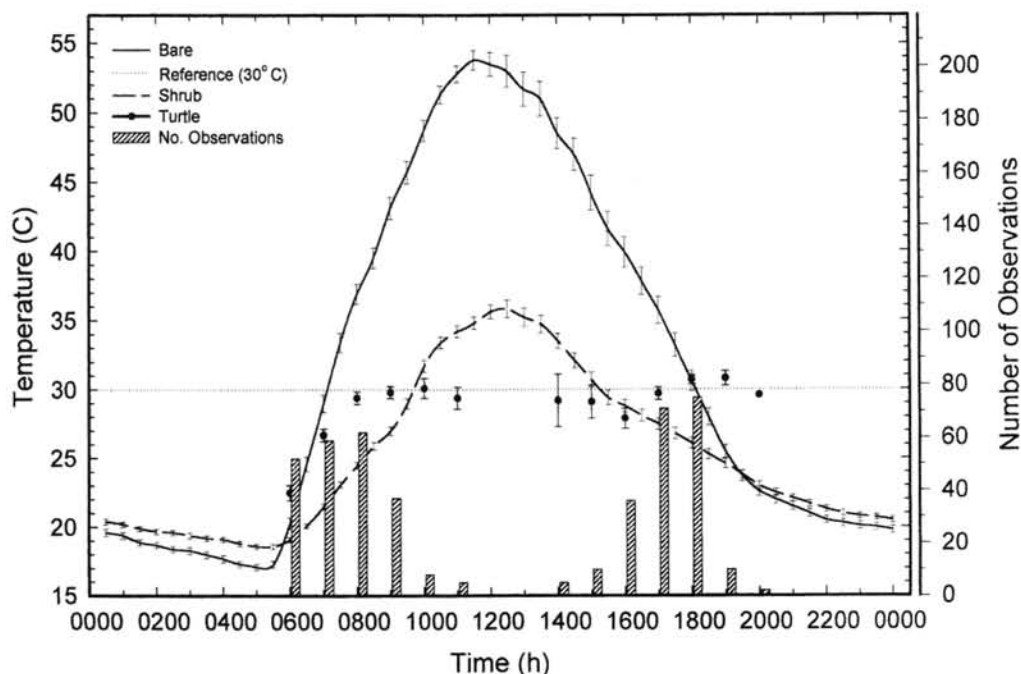


Figure 3. Mean operative temperatures (\pm SD) of the hottest and coolest surface microhabitats (bare soil and shrub), frequency of surface activity, and mean body temperatures (\pm SD) of *Terrapene ornata luteola* by time in a desert grassland habitat in southeastern Arizona.

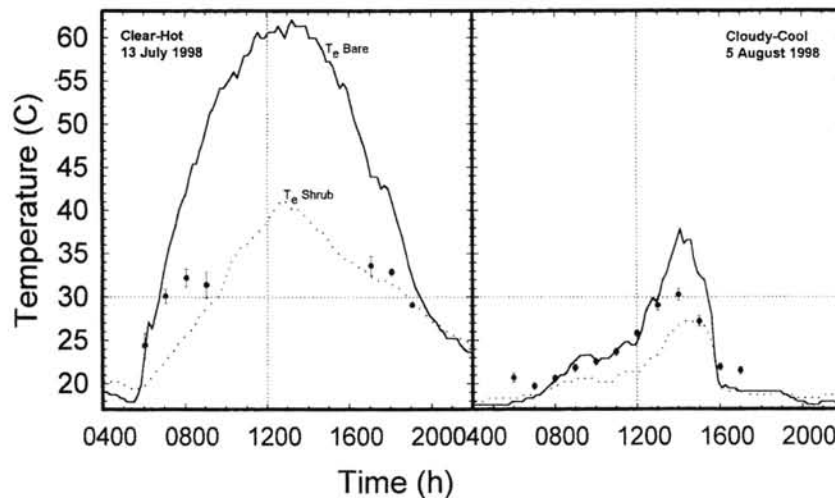


Figure 4. Operative temperatures of the hottest and coolest surface microhabitats (bare soil and shrub) and mean body temperatures (\pm SD) of *Terrapene ornata luteola* by time on a clear, hot day and on a cloudy, cool day in a desert grassland habitat in southeastern Arizona. Dotted lines represent 30°C and 1200 hrs reference lines.

Fig. 2. Individual data points ranged from 15.3 to 39.3°C. The lowest mean T_b (ca. 24°C) was observed at 0600 hrs just before sunrise, and the highest mean (ca. 29°C) at 1800 hrs just before sunset. The period of most rapid change in T_b was just after sunrise between 0600 and 0830 hrs when turtles were most frequently observed to bask. Mean T_b for the remainder of the daylight hours gradually increased to the daily high and then decreased throughout the night to the daily low. Mean maximum and minimum daily body temperatures (mean max. = 31.1°C, SD = 1.54; mean min. = 23.5°C, SD = 2.30) were variable among 11 individual turtles.

Most surface activity occurred in two distinct periods, a morning period between 0600 and 0900 hrs and an afternoon period between 1600 and 1800 hrs (Fig. 3). After a

morning heating period, mean T_b hovered around 30°C, exceeding it only in late afternoon. On average, surface activity occurred primarily when shrub temperatures, the coolest surface microhabitat, did not greatly exceed 30°C. All of the relatively few instances of activity between 0900 and 1600 hrs involved turtles that had recently emerged from burrows and were only briefly active on the surface. Cloudy and overcast days provided lower operative temperatures and opportunities for increased levels of activity throughout the day (Fig. 4). Choice of microhabitat greatly affected body temperatures of both active and inactive turtles (Fig. 5).

In each of three behavioral categories, the mean field body temperatures of *T. o. luteola* were similar to those of *T. ornata* from Kansas, but higher than those of *T. ornata* from

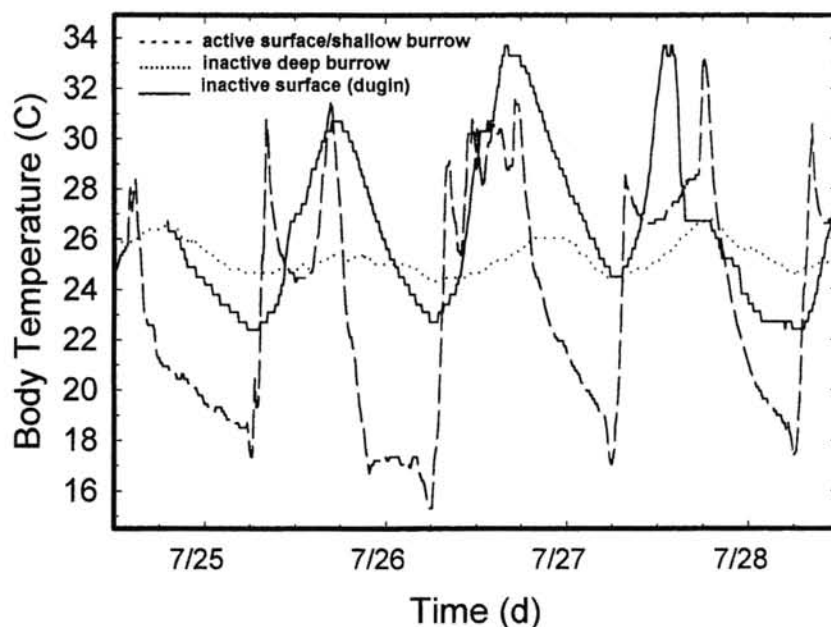


Figure 5. Body temperature variation by time in three individual *Terrapene ornata luteola* in different microhabitats in a desert grassland habitat in southeastern Arizona.

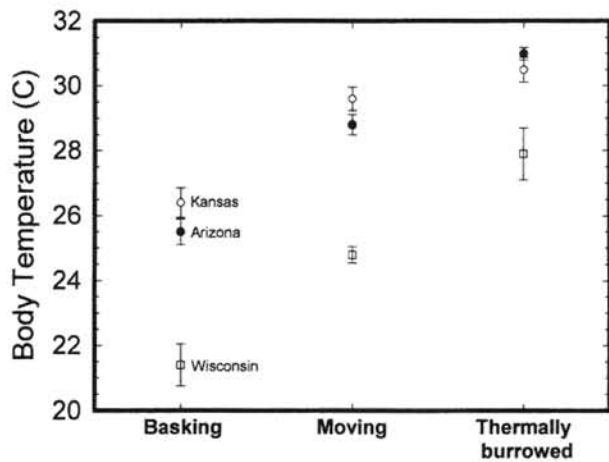


Figure 6. Field body temperatures (mean \pm SE) of basking, moving, and thermally burrowed *Terrapene ornata luteola* from Arizona (present study), compared with *T. ornata* from Kansas (Legler, 1960) and Wisconsin (Curtin, 1995). Thermally burrowed turtles are those that have burrowed in response to high environmental temperatures.

Wisconsin (Fig. 6). Mean preferred body temperature of *T. o. luteola* in a laboratory thermal gradient was bracketed within the known range of variation of preferred body temperatures of *T. ornata* from other parts of its range (Table 4).

Although I did not visit the study area throughout the year to determine seasonal activity, the restricted activity period of *T. ornata* seems to be common knowledge among local residents and by field observations of particularly knowledgeable observers, mostly local ranchers who have worked on the study area for several decades. One astute observer has kept written records of observations on individually marked turtles that have been supplementarily fed at a ranch house for many years. In addition, from 1997–2000 this observer served as a clearing house for turtle sightings and kept me informed by e-mail of turtles seen outside of the summer monsoon period by local ranchers. Only seven turtles (2 in May, 3 in June, 2 in November) were reported seen during these times, most of which occurred during isolated precipitation events. Virtually all local observers reported that turtles were seen primarily during the summer monsoon which usually begins in early July and ends in September. Turtles may be seen less frequently at other times from May to November, coincident with stochastic rainfall events. Detailed information from year-

round radiotracking of *T. ornata* in the nearby San Pedro Valley shows a similar overall pattern, one which is particularly responsive to stochastic precipitation events (M. Tuegel, pers. comm.). Activity in the San Pedro population is primarily limited to the summer monsoon, but extends into October and may include a secondary activity period in April–May following winter rains. Compared with data from both a Texas population at a similar latitude (Blair, 1976) and a well-studied Kansas population (Legler, 1960), the major activity period in Arizona is shifted to later in the year, July–September (Fig. 7). A caveat here is the Texas and Kansas data may not be directly comparable to those from Arizona because of the different methods of collection.

DISCUSSION

Set point and field body temperatures of *T. ornata* differ in extreme northern populations compared to most populations throughout its range (Ellner and Karasov, 1993; Curtin, 1995). Despite being the only known turtle species in which body temperatures vary along a latitudinal gradient, set point temperatures of reptiles most often are highly conserved traits and it should not be surprising that such temperatures of *T. ornata* in Arizona do not differ from those of most other *T. ornata* populations. In addition to body temperatures experienced during normal activity, critical temperatures estimated by the maximum body temperature voluntarily tolerated in the field in Kansas (33–35°C; Legler, 1960) and by the onset of physiological thermoregulation (frothing) in the laboratory by turtles from eastern New Mexico (36°C; Sturbaum and Riedesel, 1974) compare favorably with my estimates of voluntary maximum temperatures in Arizona (35–36°C; Table 3). Critical temperatures such as CTM (critical thermal maximum) are known to vary geographically independently of activity temperatures (Schwarzkopf, 1998), but the CTM for Arizona turtles ($41.0 \pm 0.17^\circ\text{C}$; Plummer et al., in press) is similar to that of Kansas turtles (ca. 40°C , Legler, 1960).

Several behavioral and ecological characteristics of *T. o. luteola* in Arizona, e.g., opportunistic mammal burrow use, open microhabitat preference, restricted annual activity period, bimodal daily activity period, rain-stimulated activity, thermal gradient preference, and field body temperatures, are similar to those of *T. ornata* in other parts of its range and/or to other species of *Terrapene* (e.g., *T. carolina*;

Table 4. Geographic comparison of preferred body temperatures of *Terrapene ornata*. Data are the means of body temperatures ($^\circ\text{C}$) selected in laboratory thermal gradients except for that of Rose et al. (1988) which was determined from turtles in an outdoor enclosure.

Locality	Mean \pm SE	95% of Cases	Source
SW Wisconsin	23.5 \pm 1.3	16.1–30.1	Ellner and Karasov, 1993
SW Wisconsin, NW Nebraska ('93)	22.3 \pm 0.4	20.1–24.5	Curtin, 1995
SW Wisconsin, NW Nebraska ('94)	23.6 \pm 0.3	22.2–25.0	Curtin, 1995
E Kansas	24.9 \pm 0.5	22.1–27.7	Curtin, 1995
E Kansas	29.8 \pm 0.4	27.3–32.3	Gatten, 1974
N Texas, Oklahoma ('93)	25.9 \pm 0.4	23.7–28.1	Curtin, 1995
N Texas, Oklahoma ('94)	26.4 \pm 0.3	25.0–27.8	Curtin, 1995
NW Texas	26.0 \pm 0.7	16.5–33.0	Rose et al., 1988
SE Arizona ('97)	24.6 \pm 0.2	23.3–25.9	Present study

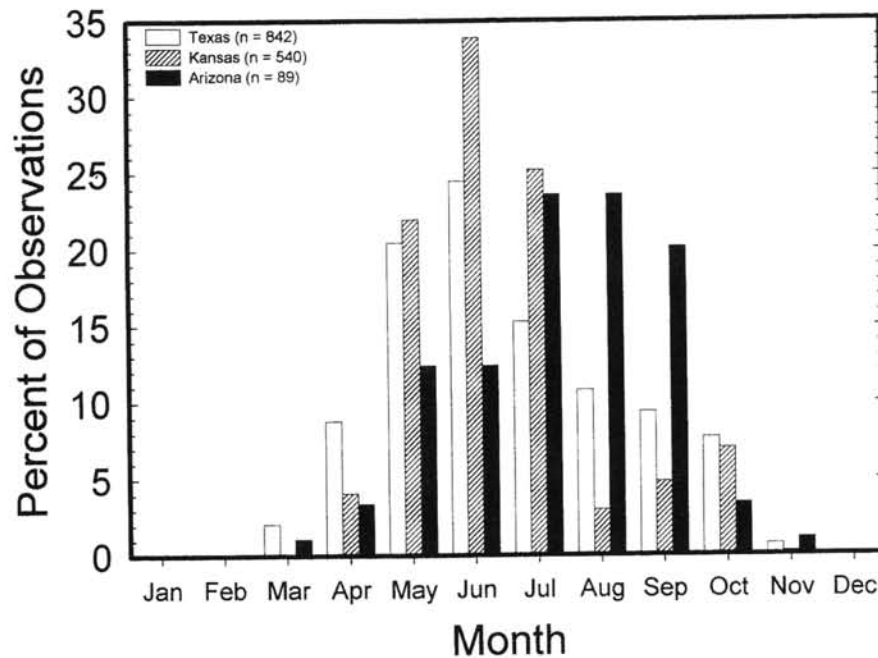


Figure 7. Seasonal activity of *Terrapene ornata* in three different geographic areas. Data from Kansas (Legler, 1960) and Texas (Blair, 1976) represent the number of individuals systematically captured by month by a single investigator in two well-studied discrete populations over several consecutive years. Data from Arizona (present study) also represent the number of individuals collected or observed in the field by month (based on museum or field note records). However, the Arizona data were opportunistically collected by various researchers from different localities over several decades. The normal summer monsoon in southeastern Arizona extends from July through September.

Ernst et al., 1994). Thus, contrary to Legler's (1960) view, at least from a thermal perspective, it appears that *T. ornata* is able to exist at its southwestern range margin because of the species' broad thermal tolerances and a great ability to behaviorally adjust both daily and seasonal activity times on a highly opportunistic basis to avoid hydric and thermal constraints (Grant and Dunham, 1988).

There is no clear evidence of geographical adjustments in either behavioral microhabitat use, physiological thermoregulatory set point temperatures, or field body temperatures. Unlike the physiologically arid-adapted tortoise *Gopherus agassizii* found just west of my study area (Ruby et al., 1994; Zimmerman et al., 1994; Peterson, 1996a,b), *T. o. luteola* does not possess the ability to tolerate elevated body temperatures, reduce evaporative water loss, nor endure large losses of body water (Olson, 1989). Thus, periodic water replenishment and retreat from harsh thermal surface conditions are probably essential. Activity limited primarily to early morning, late afternoon, and at other times on cloudy days provides sufficient thermal resources for survival. Water availability may be more critically limiting than temperature for *T. ornata* at its southwestern range margin.

Historically, most studies of reptilian thermoregulation have concentrated on problems of gaining sufficient heat for normal functioning. However, the opposite problem, i.e., avoiding the acquisition or ridding the body of excess heat, is perhaps more commonly experienced by reptiles on a global scale (Shine and Madsen, 1996). Under such circumstances at a hot range margin, the ability of *T. ornata* to cool off faster than it heats up (Bethea, 1972) and dissipate heat

by evaporative water loss (Sturbaum and Riedesel, 1976) should be advantageous.

Although classified as an environmentally sensitive species in Arizona (Rosen et al., 1996), *T. o. luteola* in the Sulphur Springs Valley is perceived by locals to be common and population density on my study site does, in fact, appear to be high (pers. obs.). This abundance occurs despite the population being close to the turtle's southwestern range limit (ca. 200 km; M. Tuegel, pers. comm.) where abundance of some species is often reduced (Brown, 1984; Brown et al., 1996). Interesting questions regarding the distribution and abundance of *T. o. luteola* in this area include what ultimately limits the species' southwestern distribution and to what extent is the species dependent on the availability of subterranean retreats. Surface activity is primarily limited to the summer monsoon which normally begins in early July and extends through September, a period of about 90 d. During this time, surface activity of turtles averages about 5 h/d. This restricted activity yields an estimated annual time spent on the surface of about 5%. Thus, ca. 95% of the life of an adult *T. o. luteola* is spent inside a burrow. Is this time spent entirely in an inactive state or are there significant other life history events that occur within burrows? I have observed turtles to forage and mate in burrows and to bask at burrow mouths. In contrast to other available microenvironments, burrows are favorable, moderate, without abiotic extremes, and predictable, at least in terms of temperature, moisture, and arthropod availability (Kay and Whitford, 1978; Hawkins and Nicoletto, 1992). Consequently, burrows would seem to be attractive not only as adult retreats from an otherwise extreme surface environment, but per-

haps also as favorable locations for sensitive early life history stages such as eggs, hatchlings, and yearlings (Packard et al., 1985). The four youngest turtles found on the surface over the course of three years were determined from growth rings to all be 2–3 yrs old. Are younger animals not found because they remain in burrows?

Finally, on a conservation note, Rosen et al. (1996) recommended that *T. o. luteola* be retained on the list of sensitive species for Arizona. Because the abundance of the kangaroo rat, *Dipodomys spectabilis*, a keystone species in southwestern desert grasslands, has declined dramatically in some areas over the last 20 years (Brown, pers. comm.; Valone et al., 1995), the effects on burrow symbionts may be of considerable interest. Conversely, if the distribution and abundance of *T. o. luteola* is in fact dependent on the presence of *D. spectabilis* burrows for subterranean retreats, the status of *T. o. luteola* may be in greater jeopardy than currently recognized because of the decline in *Dipodomys*. Further research at other localities at the southwestern range margin is needed to better understand the nature of the relationship between box turtles and kangaroo rat burrows.

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