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Seasonal Inactivity of the Desert Box Turtle, *Terrapene ornata luteola*, at the Species' Southwestern Range Limit in Arizona

MICHAEL V. PLUMMER

Department of Biology, Harding University, Searcy, Arkansas 72149, USA; E-mail: plummer@harding.edu

ABSTRACT.—At its southwestern range limit in southeastern Arizona, the Desert Box Turtle *Terrapene ornata luteola*, takes refuge in subterranean mammal burrows, primarily those of the Kangaroo Rat *Dipodomys spectabilis*, from November through June. I inferred temporal and physiological characteristics of turtles in burrows from temperatures collected with miniature data loggers buried in the soil and attached to turtles from August 2001 through June 2003. In the fall, entrance into hibernation varied among individual turtles and between years from 18 October to 6 December. Mean daily body temperatures at the beginning of hibernation were about 14–18°C. From December through February, body temperatures averaged about 9°C and were slightly less than and highly correlated with the 30-cm soil temperature. By April, body temperatures of turtles approached levels exhibited by surface-active turtles (minimum approximately 18°C for moving turtles) but turtles did not emerge from burrows until the summer monsoons began about three months later. Thus, the five-month hibernation period of *T. o. luteola* was contiguous with a three-month estivation period for a total annual period of subterranean refuge of about eight months. Except for extending into warm months, the annual inactive period of *T. o. luteola* in southeastern Arizona was not remarkably different from that in other parts of the species' range.

In arid southeastern Arizona, populations of *Terrapene ornata*, primarily a prairie-adapted form (Legler, 1960; Dodd, 2001), are at the species' southwestern range limit and may be active for only a few weeks out of the year. In seasonally cold or dry environments, reptiles commonly spend a substantial portion of the year awaiting favorable weather in hibernation or estivation (Gregory, 1982). Furthermore, in areas such as southeastern Arizona, contiguous periods of cold and hot dry seasons may produce an extended period of weather conditions unfavorable for surface activity.

With low annual reproductive output and the lowest field metabolic rates reported for any reptile, *Terrapene* have the potential to be highly successful in unpredictable resource environments (Penick et al., 2002). Legler (1960) hypothesized that extreme southwestern populations of *T. ornata*, formally recognized as *Terrapene ornata luteola*, were likely to be physiologically adapted for living in rigorous arid environments. However, activity and thermal biology of *T. o. luteola* during the activity season in southeastern Arizona did not differ substantially from that in more central prairie portions of the species' range (Plummer, 2003). In this paper, I show that certain temporal and thermal aspects of hibernation of *T. o. luteola* in southeastern Arizona are also not exceptional; however, hibernation is followed by an estivation period that results in a major portion of the annual cycle being spent inactive in underground refugia.

MATERIALS AND METHODS

The study area was located in semiarid grassland habitat in the Sulphur Springs Valley, 44 km southeast of Willcox, Cochise County, Arizona, at 1400 m elevation. The Valley is a southwestern extension of plains grassland that is heavily influenced by both Sonoran and Chihuahuan Desert flora (Rosen et al., 1996). The study area is active ranchland periodically grazed by cattle. Most of the annual surface activity of *T. ornata* occurs during a distinct 8–12-week summer monsoon period normally beginning in early July. When not active on the surface, turtles usually take refuge in various subterranean retreats (Plummer, 2003). Burrows of the bannertail kangaroo rat (*Dipodomys spectabilis*), a keystone species in southwestern desert grasslands (Brown and Heske, 1990; Hawkins and Nicoletto, 1992), provided the primary subterranean retreat for *T. ornata* on the study area throughout the year. Burrows of other mammals (e.g., *Taxidea*, *Sylvilagus*, *Thomomys*, *Spermophilis*) also provided underground retreats.

Turtles were collected as they came to drink at a 0.2-ha cattle tank during their early morning and late afternoon summer activity periods (Plummer, 2003). Captured turtles were measured (carapace length in millimeters, mass in grams), sexed, and given a unique mark by filing notches in the marginal scutes. I attached a radiotransmitter (AVM Model SM1; 16 × 50 mm, 16 g; size N alkaline cell) to the posterior edge of the carapace with a short piece of stainless steel wire so that it could freely pivot about the attachment point. I also firmly attached a miniature iButton® temperature data logger (Dallas Semiconductor Corp.; 6 × 16.5 mm, 3 g) to the left posterio-lateral portion of the carapace with stainless-steel wire such that the sensor measured the immediate surface temperature of the carapace (T_b). The combined mass of the transmitter and data logger was approximately 20 g, $< 5\%$ of turtle body mass. Once in the ground, T_bs of hibernating reptiles should track ground temperatures (Gregory, 1982); therefore, iButton temperatures should be representative of core body temperatures. Turtles were monitored from July 2001 to August 2003. Data were downloaded from the loggers and transmitters refurbished on 21–25 July in 2002 and 1–3 August in 2003. To obtain soil temperatures, I buried iButton loggers at depths of 1 cm, 30 cm, and 60 cm on level ground about 100 m from the tank near known *D. spectabilis* burrow hibernacula of several turtles. The summer home range of each turtle encompassed the tank (unpubl. data). All loggers recorded temperatures every four hours beginning at 0000 h. Based on known T_bs of turtles in burrows during their summer activity period (minimum 20°C, range < 2°C; Plummer, 2003), I defined entrance into hibernation for an individual turtle as a consecutive 5-day period in the fall in which the daily T_b mean was < 20°C and range was < 2°C. Because this procedure might not detect turtles just beginning their hibernation in shallow burrow mouths, it should produce conservative (i.e., err toward a later date) estimates of the date of entrance into hibernation.

Data were analyzed with SYSTAT 10.2 (SYSTAT Software, Inc., Richmond, CA, 2002). Correlates of T_b were examined with Pearson correlation analysis with Bonferroni probabilities. Body temperatures of individual turtles between years were compared with a Wilcoxon signed rank test. Unless otherwise stated, means are given ± 1 SE.

Results

Mean date of entrance into hibernation in 2001–2002 for seven turtles (four males, three females) was 28 November (SD = 8 days) and in 2002–2003 for eight turtles (two males, six females) was 1 November (SD = 11 days; Fig. 1). The beginning of hibernation was more abrupt and defined in 2002–2003 than in 2001–2002 (Fig. 1). Hibernation in late October of 2001–2002 was apparently delayed when inactive turtles responded to a period of unusually warm weather and 5.6 mm of precipitation on 8 November. The range of T_bs increased to approximately 8°C on 8 November and persisted above 2°C until 20 November (Fig. 1). Mean daily T_b of individual turtles beginning hibernation was 14.5°C in 2001–2002 and 17.5°C in 2002–2003 (Fig. 2). There were no obvious differences between males and females in either date or T_b at entrance into hibernation. Differences in date of entrance into hibernation for individual turtles between years ranged from 0–15 days and mean daily T_b ranged from 1.3–4.5°C at beginning of hibernation.

During the central three months of the winter (December through February) when T_bs and soil temperatures were low and relatively invariable, T_bs of turtles averaged 8.8 ± 0.06°C (range 4.0–15.0) in 2001–2002 and 9.2 ± 0.08°C (range 3.0–16.0) in 2002–2003. During this period, T_bs of four of five turtles differed significantly between the two winters (Table 1). Body temperatures were 0.8–1.2 degrees less than concurrent 30 cm soil temperatures and closely tracked them ($r^2 = 0.91$ in 2001–2002 and 0.86 in 2002–2003). Mean minimum T_bs experienced by individual turtles during this period over both years averaged 5.0 ± 1.5°C (range 3.0–9.0°C; $N = 15$).

From September through February, lower level soil temperatures exceeded upper level temperatures. In late February and March, the soil temperature profile reversed with the upper soil levels becoming warmer than the lower (Fig. 2).

Low (< 2°C) range in T_bs in 2001–2002 indicated that turtles apparently remained at midwinter burrow depths through June. The pattern differed substantially in 2002–2003 with periods of variable T_bs in early March, mid-April through mid-May, and mid-June (Fig. 1). The early March increase in T_b range (Fig. 1) followed 17.8 mm of precipitation on 26–27 February and 8.1 mm on 17–19 March. By April, body temperatures of turtles reached the levels at which turtles became dormant the previous fall (approximately 13–16°C; Fig. 2). Mean T_bs of turtles, still in burrows, reached approximately 20°C by May and 25°C by June (Fig. 2). Turtles were still 1–2 months, on average, away from being surface-active after monsoon rains normally begin in early July.

Discussion

Reptiles normally hibernate at temperatures between 1 and 15°C (Gregory, 1982). The T_bs of hibernating *T. o. luteola* in subterranean burrows of *D. spectabilis* were within this range and suggest hibernation at soil depths between 1 cm and 30 cm. Minimum T_bs experienced in the burrows were well above lethal temperatures for the naturally freeze-tolerant *Terrapene* (Costanzo et al., 1995; Dodd, 2001). Hibernacula of *T. o. luteola* do not appear to differ substantially from the normal daily summer burrow refugia selected at this locality (average 35 cm depth); daily summer variation in burrow temperatures at this depth was less than 2°C as it was in the winter (Plummer, 2003; Fig. 1). In more northern populations (e.g., Kansas, Wisconsin, Nebraska), *T. ornata* hibernates at greater depths (Legler, 1960; Doroff and Keith, 1990; Converse et al., 2002).

As in many temperate zone reptiles, the immediate stimulus to enter hibernation for *T. o. luteola* is likely a combination of temperature and photoperiod (Gregory, 1982). Separate factors may be responsible for arousal of reptiles from hibernation and actual emergence from the hibernaculum (Gregory, 1982). For *T. ornata*, suggested factors likely important for arousal include warming and reversal of the soil temperature profile (Gregory, 1982; Grobman, 1990) and for emergence, precipitation, and ground moisture (Fitch, 1956; Metcalf and Metcalf, 1970; Grobman, 1990). In southeastern Arizona, the primary stimulus to end subterranean dormancy for *T. o. luteola* appears to be precipitation as turtles in burrows may attain T_b levels for activity many weeks before they actually emerge to become surface-active at the start of the summer monsoon (Plummer, 2003). Thus, the annual cycle of *T. o. luteola* at its arid southwestern range margin includes a five-month hibernation period followed by a three-month estivation period (sensu Gregory, 1982) for a total annual dormancy of about eight months.

Many reptiles are known to be active within their hibernacula (Gregory, 1982), including *Terrapene carolina* and *T. ornata* (Grobman, 1990). Unlike *T. carolina*, unseasonably warm midwinter weather normally does not stimulate winter surface activity in *T. ornata* (Legler, 1960). However, when air temperature is warm, winter rainfall may stimulate surface activity in both *T. carolina* and *T. o. luteola* (Dolbeer, 1971; M. Tuegel, unpubl. data). Hibernation behavior and response to precipitation seem to be a phylogenetically conservative trait in *Terrapene*, being similar in both the *carolina* and *ornata* sister groups (Minx, 1996; Dodd, 2001). Although thermal, moisture, and arthropod resources are predictable and favorable in *D. spectabilis* burrows (Kay and Whitford, 1978; Hawkins and Nicoletto, 1992), it is unknown whether *T. o. luteola* are subterraneanly active during estivation.

Overwintering strategies and hibernation behavior of many reptilian species are known to vary geographically (Gregory, 1982). In most areas, *T. ornata* dig their own hibernation burrows (Dodd, 2001). For *T. o. luteola*

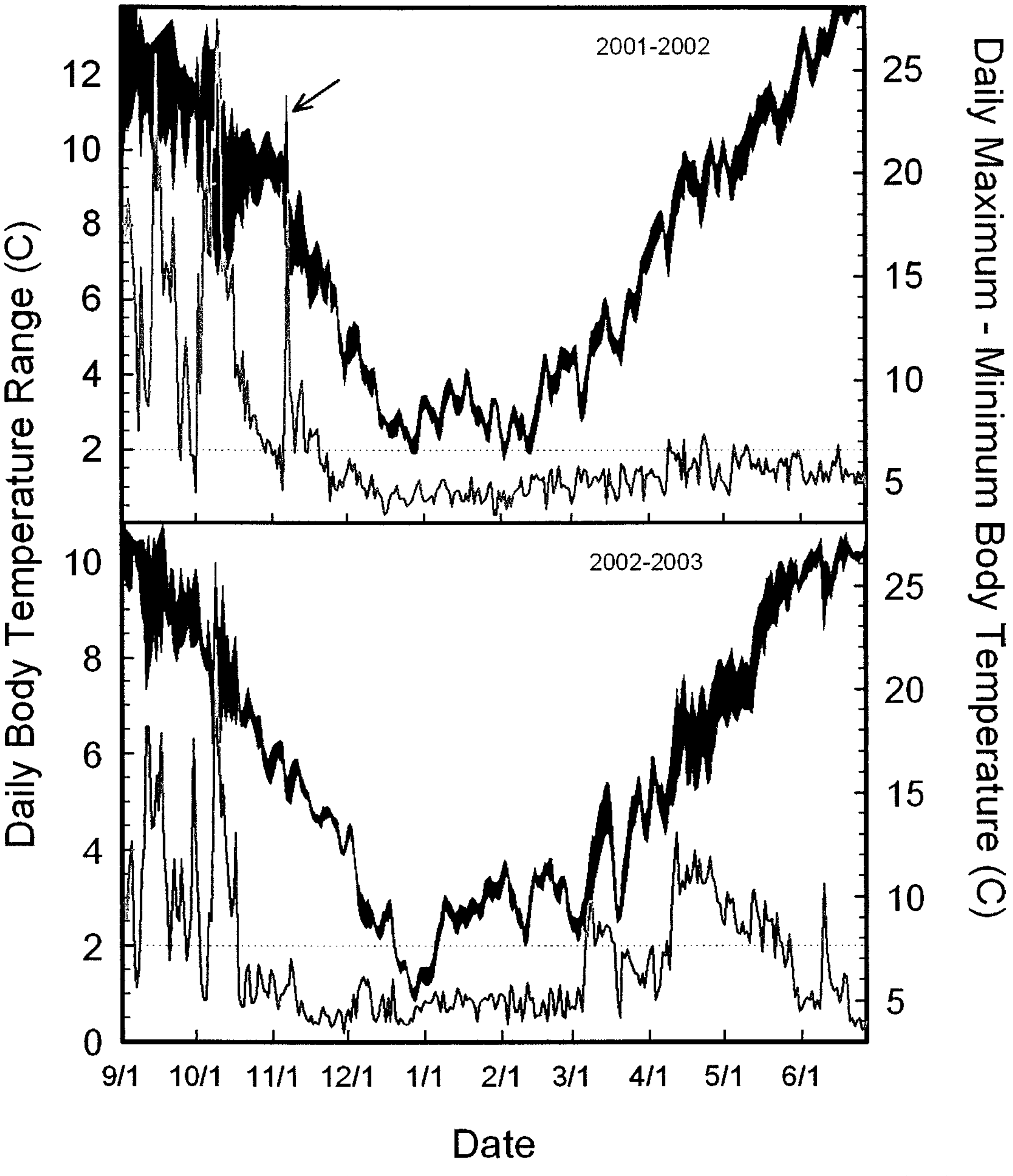

FIG. 1. Mean daily range (gray line) and maximum-minimum (black area) T_bs of *Terrapene ornata luteola* over two years. The dotted line is a 2°C reference line for daily range. Arrow indicates an increase in T_bs coincident with 5.6 mm of precipitation on 8 November 2001.

in southeastern Arizona, using existing mammal burrows as hibernacula may be a function of the high availability of mammal burrows and the compaction of the dry Chihuahuan Desert soil (Dodd, 2001). In New Mexico at a similar elevation and approximately 350–400 km northeast of my study site, Nieuwolt (1996) reported that *T. o. luteola* hibernated in *D. spectabilis* burrows from mid- to late October until May, but surface activity was sporadic until the summer monsoons started in late June.

Legler (1960) hypothesized that *T. o. luteola* was likely to be physiologically adapted for living in rigorous arid environments. However, activity and thermal biology of *T. o. luteola* during the activity season was similar to that in more central prairie portions of the species' range (Plummer, 2003). Similarly, it also appears that temporal and thermal aspects of hibernation of *T. o. luteola* do not differ substantially from populations in the central portions of the range. The major difference is that hibernation is followed by a period of estivation,

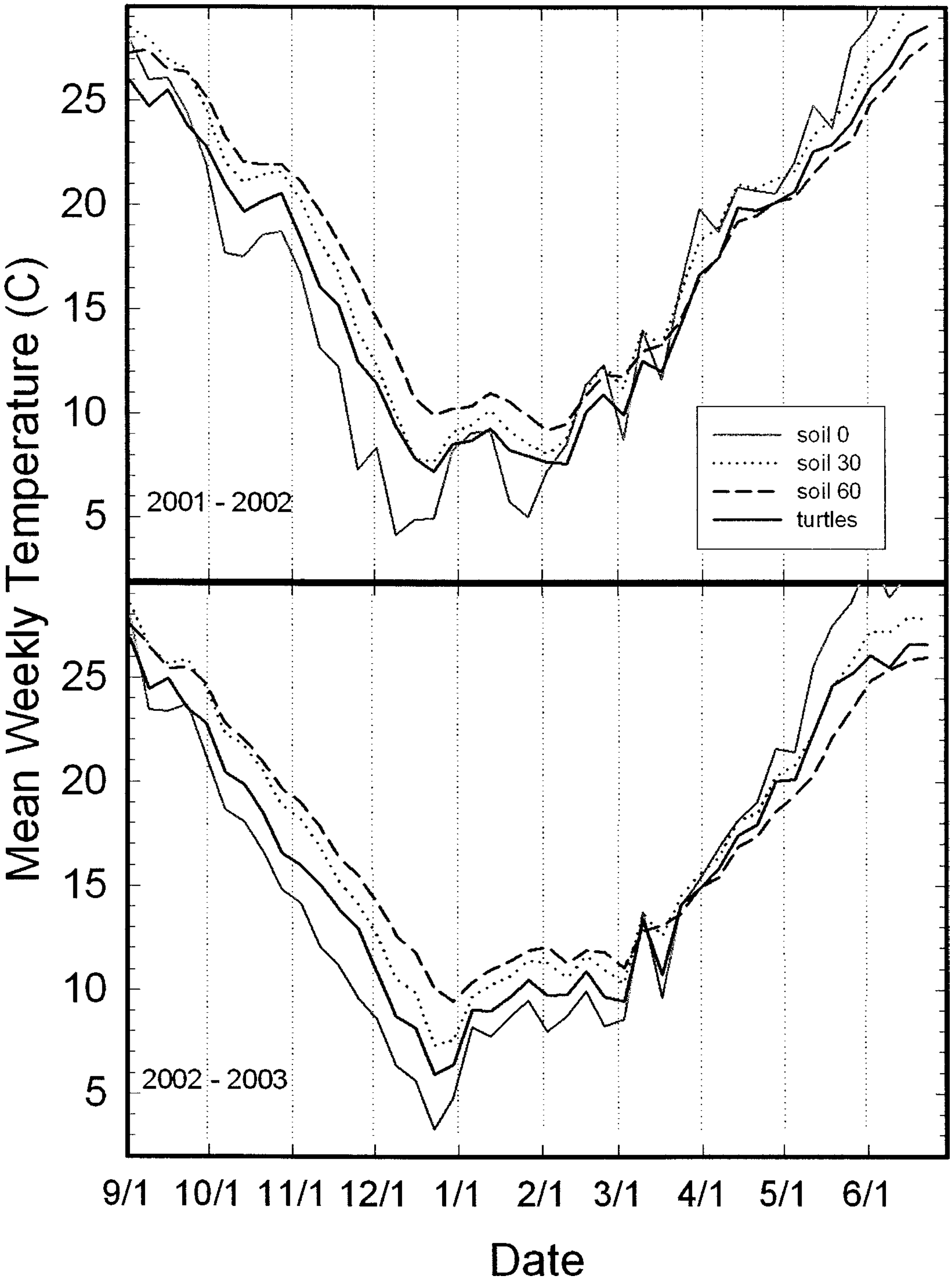

FIG. 2. Mean weekly soil temperatures at three different depths and mean weekly T_bs of *Terrapene ornata luteola* from September through June over two years.

which results in a major portion of the annual cycle being spent inactive in subterranean refugia.

Low reproductive output and field metabolic rates permit *Terrapene* to be generally successful in unpredictable environments (Penick et al., 2002). Variation among activity periods of *T. o. luteola* may influence life-history traits among and within populations. In addition to extending hibernation and estivation in

TABLE 1. Mean (± SE) T_bs of hibernating *Terrapene ornata luteola* during the central three months of the winter (December through February) when T_bs and soil temperatures were low and relatively invariable. Also shown are test statistics from Wilcoxon signed-ranks tests and probability values.

		Temperature (°C)			
ID	Sex	2001–2002	2002–2003	*Z*	*P*
AJN	F	8.3 ± 0.06	8.5 ± 0.09	14.45	<0.001
AJU	F	9.5 ± 0.08	9.9 ± 0.09	1.75	>0.05
ALN	F	11.3 ± 0.05	9.1 ± 0.08	3.08	<0.01
ALU	M	8.1 ± 0.06	8.8 ± 0.07	8.13	<0.001
AMN	M	8.4 ± 0.08	10.1 ± 0.09	−18.90	<0.001

response to drought, females may skip reproduction. For example, of the 44 adult females x-rayed during the 1999–2001 monsoons, none contained shelled eggs (unpubl. data). Combined, the results suggest that the life-history trait values of *T. o. luteola* are plastic and that both time and resource budgets are limiting at its arid southwestern range limit.

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