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This research examined the onset, duration, and termination of hibernation in Desert Tortoises (*Gopherus agassizii*) over several years at multiple sites in the northeastern part of their geographic range, and recorded the temperatures experienced by tortoises during winter hibernation. The timing of hibernation by Desert Tortoises differed among sites and years. Environmental cues acting over the short-term did not appear to influence the timing of the hibernation period. Different individual tortoises entered hibernation over as many as 44 days in the fall and emerged from hibernation over as many as 49 days in the spring. This range of variation in the timing of hibernation indicates a weak influence at best of exogenous cues hypothesized to trigger and terminate hibernation. There do appear to be regional trends in hibernation behavior as hibernation tended to begin earlier and continue longer at sites that were higher in elevation and generally cooler. The emergence date was generally more similar among study sites than the date of onset. While the climate and the subsequent timing of hibernation differed among sites, the average temperatures experienced by tortoises while hibernating differed by only about five degrees from the coldest site to the warmest site.

DESERT Tortoises (*Gopherus agassizii*) are distributed in desert and subtropical regions of the southwestern United States and northern Mexico (Germano et al., 1994). The northern extent of this distribution is a temperate zone where some environmental temperatures in winter can be inhospitable or even lethal to Desert Tortoises. Tortoises avoid cold temperatures in the winter by using underground cover sites (hibernacula), which generally consist of burrows (excavated in soil) or dens (natural rocky caves; Burge, 1977; Bulova, 1994). Hibernacula generally have higher temperatures than the open environment during the winter and provide substantial buffering from the daily temperature fluctuations present in the environment. Thus, hibernacula provide tortoises with protection from potentially lethal temperatures in winter.

Research on the timing and temperature of reptile hibernation has focused on snakes (Viitanen, 1967; Sexton and Hunt, 1980; Blouin-Demers et al., 2000), lizards (Garrick, 1972; Etheridge et al., 1983; Wone and Beauchamp, 2003), and turtles (Grobman, 1990; Litzgus et al., 1999; Plummer, 2004), but few studies have focused on tortoises (Vaughan, 1984; Bailey et al., 1995; Rautenstrauch et al., 1998). Understanding the timing of hibernation of Desert Tortoises could have important management implications for this sensitive species (Rautenstrauch et al., 1998).

In the northeastern extent of their range, tortoises may hibernate for up to six continuous months (Woodbury and Hardy, 1948; Bury et al.,

1994). Little is known about the mechanisms cuing the onset and termination of hibernation behavior or the amount of variation that should be expected to occur within the timing of this behavior. Potential cues for hibernation onset include reduced day length/photoperiod, cooler environmental temperatures, reduced forage availability, and timing of precipitation events (Gregory, 1982). Hibernation is thought to be advantageous by facilitating a reduction of metabolism during a time of the year with few resources. Tortoises, like other ectotherms, may be able to conserve energy by hibernating, as there is a concomitant reduction of metabolism with decreased body temperatures (Bennett and Dawson, 1976; Gregory, 1982). Tortoises may further reduce their metabolism by inverse acclimation or other mechanisms of metabolic depression (Gregory, 1982). This could allow tortoises to conserve energy during seasons with essentially no food resources. Alternatively, hibernation may be induced by endogenous cues. There is relatively little literature on endogenous mechanisms cuing hibernation, but observations of behavior such as declining appetite and shelter-seeking behavior under differential exposure to external cues suggest that the hibernation of some reptiles may be influenced by endogenous rhythms (Gregory, 1982). Although intriguing, this hypothesis is beyond the scope of the work we describe here.

In this study we examine correlations between the onset, duration, and termination of hibernation in Desert Tortoises in relation to potential exogenous cues over several years at multiple

sites in the northeastern portion of their range. We report the temperatures experienced by Desert Tortoises and their associated behavior during winter hibernation.

MATERIALS AND METHODS

Study sites.—We studied hibernation in Desert Tortoises at four sites in the northeastern Mojave Desert. The sites were located in the Mojave Desert scrub biome (Turner, 1982). The City Creek Site was located in Washington County north of St. George, Utah (37°9′00″N, 113°35′24″W), and ranged in elevation from 975 m to 1067 m, with highly variable topography: flat areas, dry washes up to 2 m deep, dunes, rocky cliffs and steep hills. The predominant substrate was red Navajo sandstone interspersed with ancient lava flows, sand dunes, and cryptobiotic soils (Esque, 1994). The Littlefield Site was located in Mohave County north of Littlefield, Arizona (36°55′48″N, 113°54′36″W), and ranged in elevation from 576 m to 622 m. The topography was generally flat (2–5% slope), with numerous dry washes up to 3 m deep (Esque, 1994). The substrate was shallow sandy/gravelly loam up to 0.6 m deep with an underlying calcium carbonate (caliche) hardpan layer. The Lake Mead site was located in Clark County, Nevada (36°29′24″N, 114°21′00″W). The site was at the northern end (Overton arm) of the Lake Mead National Recreation Area, near Overton, Nevada. The site elevation ranged from lake level (approximately 325 m) to 597 m and consisted of the top and steep cliff sides of a mesa bordered on three sides by water. The soil consisted of coarse alluvium consolidated by calcium carbonate, interspersed with patches of windblown sand. The Bird Spring Valley site was also in Clark County, Nevada (BSV 35°58′12″N, 115°20′24″W). The valley was an extensive bajada ranging from 900 m to 1300 m in elevation and was of relatively even terrain with shallow arroyos lined by occasional caliche caves. The substrate was sandy/gravelly loam up to 0.75 m deep with an underlying hardpan layer composed of caliche. Mountainous peaks bordered Bird Spring Valley to both the east and west.

Tortoise body temperatures.—We used miniature data loggers (Stowaway #STEB16, Onset Computer Corporation, Pocasset, MA) to record body temperatures during hibernation of wild Desert Tortoises at the City Creek and Littlefield sites. Data loggers were 26.5 g and came encased in a plastic rectangular housing (4.6 × 4.8 × 1.5 cm). They were calibrated in water baths at temperatures over a range of 0 to 45 C before and after use in the field. Data loggers were programmed to record temperatures once per hour. For protection from the environment, they were wrapped in a layer of paper and covered with a layer of duct tape followed by a coating of epoxy (which served as weather-proofing). Each data logger was attached with 5-minute epoxy gel to a location on the anterior half of the carapace to avoid potential interference during copulation. Data loggers were placed on animals prior to the expected onset of hibernation and were removed within several weeks after emergence from hibernation. Temperatures recorded by the data loggers at these two sites were the temperatures measured inside the plastic casing of the data loggers, not body temperatures of the tortoises. Nevertheless, the data from the loggers could be used to discern the timing of hibernation (see below), and temperatures of the loggers were likely similar to body temperatures while the animals were in hibernacula (Gregory, 1982).

Body temperatures of tortoises at the Lake Mead and Bird Spring Valley sites were measured using StowAway™ TidbiT™ temperature data loggers (Onset Computer Corporation, Pocasset, MA), customized by Onset from their standard design (TBICU108; −20 C to +70 C). These were 25 mm in diameter, 14 mm thick, and weighed approximately 15 g. They had a weather-resistant thermistor at the end of a 150-mm wire, which was affixed using fast-setting glue and silicone between the tail and the carapace of the tortoise (Nussear et al., 2002). This location has been shown to approximate cloacal temperatures of Desert Tortoises (Nussear et al., 2002).

Timing of hibernation.—We recorded data on hibernating tortoises over the course of four winters from 1995 to 1998 at the City Creek and Littlefield sites, and for one winter (1998–1999) at the Lake Mead and Bird Spring Valley sites. At City Creek we studied nine animals during the winter of 1995, ten animals in the winter of 1996 and 1997, and six animals in the winter of 1998. At Littlefield we studied four animals in the winter of 1995, six animals in the winter of 1996, 11 animals in the winter of 1997, and five animals in the winter of 1998. During the winter of 1998 we added tortoises at the Bird Spring Valley and Lake Mead sites to the study. We studied seven animals at Bird Spring Valley and nine animals at Lake Mead.

Onset, duration, and termination of hibernation were interpreted from graphs of hourly body temperatures by locating the date when the amplitude of the daily fluctuations became noticeably reduced or increased. The accuracy of this interpretation was verified by weekly

observations of the tortoises in the field. Patterns of temperatures of the data loggers at the City Creek and Littlefield study sites were clearly different when the tortoises were in and out of burrows. We defined onset of hibernation as the Julian date after which a tortoise did not emerge from its hibernaculum for at least 14 days. Likewise, the termination of hibernation was defined as the Julian date when a tortoise emerged from the hibernaculum, without re- turning for at least 14 days. The "14-day" criterion allowed for a consistent quantification of the onset and termination dates for animals that had false onsets or brief emergences during hibernation. These criteria are similar to those used by Bailey et al. (1995). Some data loggers became overloaded with data and stopped re- cording temperatures before the tortoise emerged from hibernation. This was due to logistical constraints encountered when chang- ing the recording intervals of the dataloggers from active season intervals (15 min) to winter intervals (60 min). Thus, for some individuals, duration and termination of hibernation could not be calculated, although hibernation start dates were recorded.

We defined "average hibernation tempera- ture" as the mean temperature of all measure- ments while an animal was hibernating. The "mid-hibernation temperature" was defined as the average temperature during the week of the winter solstice (i.e., week 51), and the "minimum temperature" as the lowest temperature experi- enced by the animal at any time during the hibernation period.

We compared Julian dates of onset and termination, duration of hibernation, and the mean, minimum, and mid-hibernation tempera- tures using ANOVA with site and year as factors. Repeated measurements of animals were ac- counted for by using a nested, split-plot design with tortoises nested within site treated as a random effect in order to allow for indepen- dent contrast analyses of the interaction term. Multiple comparisons to discern differences within significant effects were conducted using Tukey's-HSD.

Thermal buffering categories.—Cover sites were classified by the degree of thermal buffering that they provided as interpreted by the daily and biweekly patterns in body temperature. The greatest buffering was represented by a pattern in which the body temperature was nearly constant, with a difference of less than 1 C between the daily maximum and daily minimum temperatures for each tortoise. In addition, the average of the differences of absolute minimum and maximum temperatures for all successive 14- day periods throughout the hibernation period was <1.5 C. Less buffering resulted in body temperatures that still retained differences of daily maximum and minimum temperatures of less than 1 C. However, the body temperatures were influenced by local weather patterns when examined over longer time periods. In this category the average of the differences in the absolute maximum and absolute minimum tem- peratures for successive 14-day periods was greater than 1.5 C. The least buffering resulted in body temperatures that fluctuated greatly on a daily basis where the difference between the maximum and minimum daily temperature was more than 1 C. Analyses of the degree of thermal buffering of hibernacula were conducted for Littlefield and City Creek for the four years studied and among all four sites for the winter of 1998–1999 using Fisher's exact tests for contin- gency tables.

Meteorological data.—Climate data for the study sites were obtained from (1) City Creek: St. George, Utah, weather station 4 km south of the City Creek site, (2) Littlefield: Littlefield 1 NE station 10 km north of the Littlefield site, (3) Lake Mead: Overton station 1 km northwest of the site, and (4) Bird Spring Valley: Red Rock Canyon weather station 4 km northeast of the site (National Oceanic and Atmospheric Admin- istration, 1998). Soil temperatures during the winter of 1998 at Bird Spring Valley were measured at a central location at the site using a CR-10 weather station (Campbell Scientific, Logan, UT) and type K thermocouples (Omega Engineering, Stamford, CT) at the surface and buried 70 cm below the surface, just above the caliche layer. Air temperature data for all four years were not available for the Littlefield site. We conducted regression analyses of the average air temperatures for the months of October and March on the average onset and termination dates of hibernation for each site to examine correlates of regional climate and hibernation patterns.

RESULTS

City Creek and Littlefield.—There was no overall difference for the average date of hibernation onset between tortoises at City Creek and Littlefield ($F_{1,32} = 3.26$; $P = 0.08$; Fig. 1). There were differences in the onset date among years. The average date of onset in the fall of 1995 (3 Nov. ± 1 SD = 12 d) was approximately nine days later than the average date of onset in the fall of 1996 (25 Oct. ± 1 SD = 8 d; Tukey's HSD
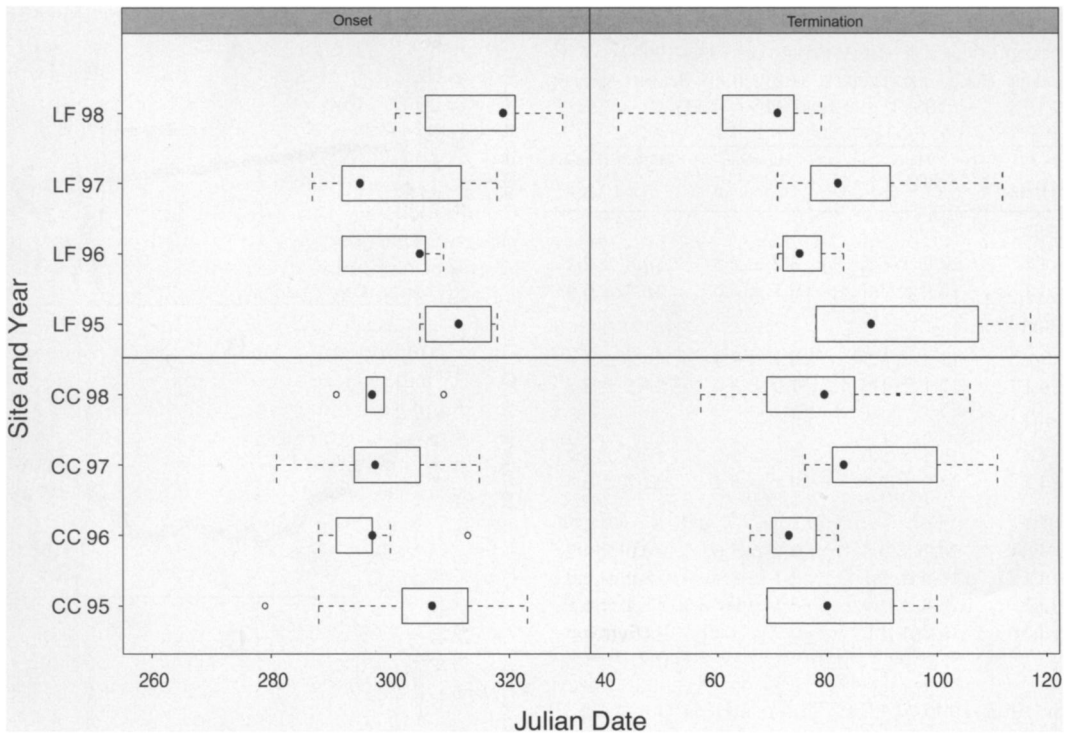
Fig. 1. Onset, duration, and termination of hibernation at the City Creek and Littlefield sites for the four winters from 1995 through 1998. The four winters at Littlefield are in the top half of the figure; City Creek is given in the bottom half. Years are sorted from bottom to top in each panel and listed as the year in which each hibernation period began. The distance between the onset and termination dates is the duration of hibernation. The median onset and termination dates for each site are shown as filled circles. The box surrounding the filled circle depicts the 25th and 75th quartile. The range of values for each measure is given by the dotted lines ("whiskers") outside of each box, and possible outliers are given by the open circles outside the box.

$Q = 2.72$; $P < 0.05$). The onset dates for all other years were statistically indistinguishable from one another. There were no site-by-year interactions for onset date ($F_{3,29} = 0.65$; $P = 0.59$).

Tortoises at the City Creek and Littlefield sites spent a similar number of days in hibernation, ranging from 106 to 182 days ($F_{1,23} = 2.22$; $P = 0.15$; Fig. 1). The duration of hibernation varied among years coincident with a twenty-one day difference in duration of hibernation in the winters of 1997–1998 and 1998–1999 (154 ± 1 SD = 21 vs. 133 ± 1 SD = 21 days, respectively; Tukey's HSD $Q = 2.73$; $P < 0.05$). The durations of hibernation for all other years were statistically indistinguishable from one another. There was a significant year-by-site interaction due to animals at Littlefield during the 1998–1999 season having a shorter duration (134 ± 1 SD = 40 days) than the City Creek or Littlefield animals in the 1997–1998 season (154 ± 1 SD = 17 and 155 ± 1 SD = 25 days respectively; Tukey's HSD $Q = 3.27$; $P < 0.05$; Fig. 1).

The ending date for hibernation in the spring did not differ between the two sites and ranged between 11 February to 27 April ($F_{1,23} = 0.07$; $P = 0.79$; Fig. 1). There were significant differences in the termination date among years. In particular, the termination of hibernation (averaged for both sites) was earlier in the spring of 1996–1997 (15 March ± 1 SD = 5 d), and in the spring of 1998–1999 (14 March ± 1 SD = 17 d) than in the spring of 1995–1996 (25 March ± 1 SD = 15 d) or 1997–1998 (1 April ± 1 SD = 19 d; Tukey's HSD $Q = 2.72$; $P < 0.05$). There was a marginally non-significant site-by-year interaction for termination date ($F_{3,29} = 2.76$; $P = 0.06$).

There were no differences found in the average hibernation body temperature between City Creek and Littlefield ($F_{1,23} = 1.52$; $P = 0.23$; Table 1), but there were differences among years ($F_{3,30} = 6.86$; $P = 0.0012$). The average hibernation body temperature of tortoises during the winter of 1996–1997 (12 C) was approximately two degrees cooler than either 1997–1998 (14 C)

TABLE 1. TORTOISE BODY TEMPERATURES DURING HIBERNATION FOR THE WINTERS OF 1995–1999 AT CITY CREEK (CC), LITTLEFIELD (LF), BIRD SPRING VALLEY (BSV), AND LAKE MEAD (LM).

Year/site	Mean temperature (°C) ± 1 SD	Minimum temperature (°C) ± 1 SD	Mid-hibernation average (°C) ± 1 SD
1995			
CC	12.2 ± 1.1	8.2 ± 2.3	10.3 ± 2.4
LF	16.0 ± 3.8	9.7 ± 6.0	16.3 ± 6.4
1996			
CC	11.4 ± 1.5	6.5 ± 2.4	10.2 ± 1.4
LF	12.1 ± 1.5	7.9 ± 3.4	11.3 ± 2.2
1997			
CC	13.4 ± 2.0	9.3 ± 2.2	10.7 ± 3.2
LF	14.9 ± 4.4	10.1 ± 5.4	12.7 ± 6.3
1998			
BSV	14.7 ± 3.3	9.4 ± 4.6	10.0 ± 3.5
CC	11.9 ± 3.1	8.1 ± 3.4	8.9 ± 3.9
LF	12.8 ± 4.9	8.3 ± 6.6	11.4 ± 6.1
LM	15.2 ± 1.9	9.9 ± 4.29	12.7 ± 2.5

or 1995–1996 (14.2 C; Tukey's HSD $Q = 2.72$; $P < 0.05$). There were no significant site-by-year interactions ($F_{3,30} = 1.33$; $P = 0.29$). The mid-hibernation temperature did not differ between the two sites ($F_{1,23} = 1.89$; $P = 0.18$). There were differences among years in that the animals' temperatures during the 51st week of 1998 (9.88 C) were significantly cooler than during the same week in 1995 (13.13 C). The average minimum temperature experienced did not significantly differ for either site ($F_{1,23} = 0.17$; $P = 0.68$) or year ($F_{3,30} = 2.79$; $P = 0.058$).

We categorized the degree to which tortoises were insulated from environmental variation in temperature into three distinct patterns (Fig. 2). The numbers of animals that used hibernacula with these patterns differed among sites during three of the four winters of our study (Table 2). In those three years, tortoises at City Creek were mostly found in hibernacula with medium buffering (Fig. 2B), whereas tortoises at Littlefield occupied either no hibernacula in that category (1995) or had a more even distribution among categories (1997, 1998).

Four-site comparisons.—All four study sites were monitored in the winter of 1998–1999, allowing comparison of regional differences in tortoise hibernation characteristics. There were significant differences in the beginning of hibernation among sites ($F_{3,21} = 10.10$; $P = 0.003$; Fig. 3). Tortoises at Bird Spring Valley (onset date = 15 Oct. ± 1 SD = 15 d) entered hibernation earlier
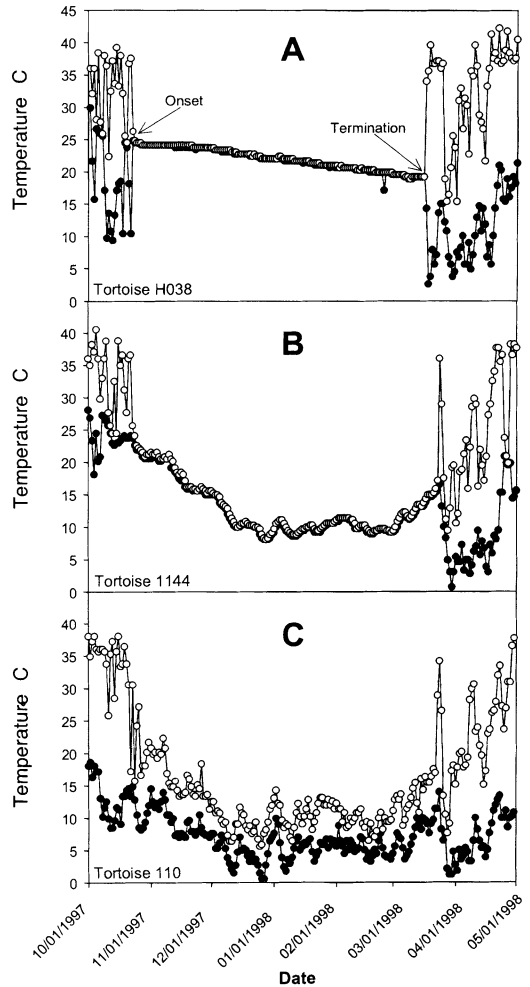

Fig. 2. Three examples of tortoise body temperatures prior to, during, and following hibernation. Data are presented as the daily minimum (filled circles) and maximum (unfilled circles) temperatures (C). Panel A is an example of a high buffering in the body temperature pattern. Panel B demonstrates a medium level of temperature buffering during hibernation. Panel C is an example of a low temperature buffering.

than tortoises at either Lake Mead (10 Nov. ± 1 SD = 7 d) or Littlefield (11 Nov. ± 1 SD = 11 d). The onset date for tortoises at City Creek (25 Oct. ± 1 SD = 6 d) did not differ significantly from the onset dates at the other sites.

There were also significant differences in the duration of hibernation among sites ($F_{3,15} = 5.96$; $P < 0.007$; Fig. 3). The animals at Lake Mead (114 ± 1 SD = 18 days) and Littlefield (115 ± 1 SD = 14 days) hibernated for significantly fewer days than animals at City Creek (146 ± 1 SD = 13 days). Hibernation duration at Bird

TABLE 2. THE NUMBER OF ANIMALS IN EACH TEMPER-
ATURE BUFFERING CATEGORY FOR THE HIBERNACULA
SELECTED BY ANIMALS AT CITY CREEK (CC) AND LITTLE-
FIELD (LF) SITES FOR THE FOUR WINTERS (1995–1998).

Year/site	High (n)	Medium (n)	Low (n)	P
1995				
CC	0	7	2	0.01
LF	2	0	2	
1996				
CC	0	8	2	1.0
LF	0	5	1	
1997				
CC	0	10	0	0.035
LF	3	6	2	
1998				
CC	0	6	0	0.044
LF	0	4	5	

TABLE 3. THE NUMBER OF ANIMALS IN EACH TEMPER-
ATURE BUFFERING CATEGORY FOR THE HIBERNACULA
SELECTED BY ANIMALS AT CITY CREEK (CC), LITTLEFIELD
(LF), BIRD SPRING VALLEY (BSV), AND LAKE MEAD (LM)
FOR THE WINTER OF 1998–1999.

Site	High	Medium	Low
CC	0	6	0
BSV	0	4	3
LF	0	4	5
LM	0	4	5

April 1999. There were no differences among sites in the average hibernation temperatures ($F_{3,23} = 1.61$; $P = 0.21$), minimum temperatures ($F_{3,23} = 0.87$; $P = 0.76$), or mid hibernation temperatures ($F_{3,21} = 1.23$; $P = 0.32$).

Fifty-eight percent of the hibernacula provided medium buffering from thermal environments, while 42% had low buffering, and none provided high levels of buffering. The distribution of animals in each of these patterns did not differ among the four sites for this year ($P = 0.12$; Table 3). Animals at the sites were relatively evenly distributed between medium and low buffering patterns, with the exception of tor-

Spring Valley (131 ± 1 SD = 7.7 days) did not differ significantly from the other sites. The four study sites did not differ in termination date for hibernation ($F_{3,17} = 1.40$; $P = 0.28$; Fig. 3). The termination dates ranged from 11 February to 16
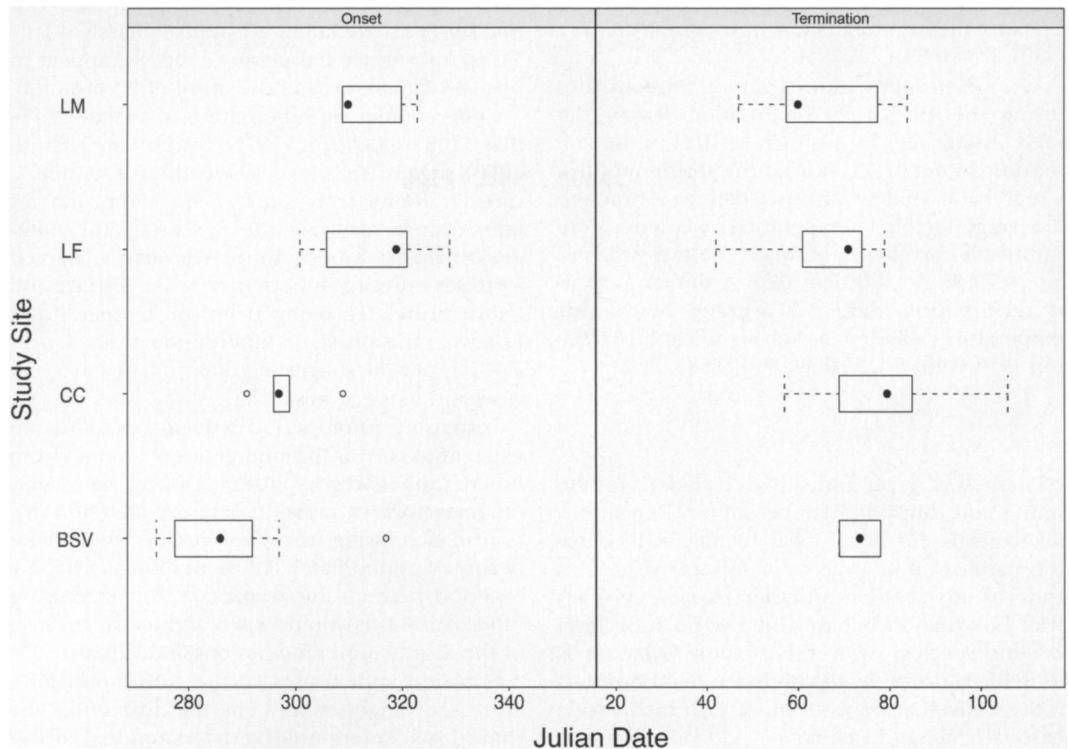

Fig. 3. Onset, duration, and termination of hibernation at the City Creek, Littlefield, Lake Mead, and Bird Spring Valley sites for the winter of 1998–1999. See Fig. 1 for figure explanation.

toises at the City Creek site, at which all animals were categorized as medium.

Meteorological data.—Average air temperatures near the City Creek site indicated differences among years in the temperatures during the fall when tortoises are entering hibernation, and during the spring when animals are terminating hibernation, which were the two periods of specific interest to this study. The two warmest fall periods were during the fall of 1995 and 1997, while the fall months of 1996 and 1998, in contrast, were cooler by about 10 C. Spring temperatures also differed by about 10 C among years during the spring months of March and April when tortoises are typically exiting hibernation. Data for the Littlefield site were available from the spring of 1997 and later. This site had warmer and more consistent temperatures than the City Creek site. A regression analysis of the average date of entry into hibernation at City Creek as a function of the average October air temperatures yielded a non-significant correlation of these two variables ($r = 0.74$; $F_{1,3} = 2.5$; $P = 0.26$). There were not sufficient climate data available to include Littlefield in the analysis. A mixed model analysis of termination date versus average air temperatures in March with Site entered as a random effect to account for repeated measurements was non-significant ($F_{2,6} = 1.5$; $P = 0.33$).

Average air temperatures among the four sites during the 1998–1999 hibernation season differed among sites by as much as 10 C in the fall, but only by about 5 C during the spring months. A regression analysis of onset date as a function of average October temperatures yielded a non-significant correlation between the two variables ($r = 0.70$; $F_{1,3} = 1.9$; $P = 0.3$). A similar analysis of termination date on average March air temperatures yielded a non-significant correlation ($r = 0.46$; $F_{1,3} = 0.54$; $P = 0.54$).

DISCUSSION

There was great individual variation in the timing and duration of hibernation. Exogenous mechanisms did not appear to dictate hibernation patterns at any site or within any year. This leads us to question whether exogenous cues drive hibernation behavior at a population level for this species, or if hibernation behavior is more likely driven by the endogenous conditions of the individuals in association with broad scale seasonal changes in climate.

Among all of our sites and for all years of our study, there was great individual variation in the onset date of hibernation. The onset of hiberna-

tion was only weakly correlated with interannual temperature variation, with cooler temperatures associated with earlier onset of hibernation. Onset dates for both the City Creek and Littlefield sites combined were earlier in 1996 than in 1995, which corresponded with an average air temperature in the fall that was 10 C cooler at City Creek, but no significant correlation between onset of hibernation and average October temperatures for 1995–1998 at City Creek was observed. When all four sites were compared within a single year, tortoises appeared to enter hibernation earlier at the sites with cooler fall temperatures, which is consistent with earlier observations (Woodbury and Hardy, 1948; Rautenstrauch et al., 1998). However, this tendency was not statistically significant.

Decreases in air or ground temperature in the fall are the most frequently suggested cue for the onset of hibernation (Gregory, 1982). For example, tortoises were observed to begin hibernation in Kern County, California, when surface temperatures fell below 20 C (Voigt, 1972). We found that daily averages of soil surface temperature at the Bird Spring Valley site fell below 20 C on 27 September 1998, and the first tortoise entered hibernation three days later. However, the last tortoise entered hibernation at the site on 13 November; at that time the temperature of the surface had fallen to approximately 12 C. Thus, soil surface temperature did not appear to be a strong cue driving the onset of hibernation.

Other studies on hibernation in snakes (Viitanen, 1967; Aleksiuk, 1976; Sexton and Hunt, 1980) suggest that reversals in the soil temperature gradient from surface to deep burrow temperature may cue the onset of, and emergence from, hibernation. We also observed tortoises entering hibernation when surface soil temperatures fell below deep soil temperatures; however, the onset of hibernation ranged over a 44-day period, suggesting that this cue has a very weak influence at best.

Increasing photoperiod is hypothesized as an exogenous cue for the emergence of animals from hibernation (Gregory, 1982). During the 35-day range over which individuals terminated hibernation in the spring, the photoperiod would have become approximately 1.5 hours longer. If photoperiod were an important cue for terminating hibernation, we would expect tighter correlation of the termination dates among individuals.

Surface temperatures of the substratum have also been suggested as a cue that influences the timing of emergence. For example, Desert Tortoises in the west Mojave reportedly did not emerge from hibernation until surface temperatures reached 20 C (Voigt, 1972). Moreover,

Terrapene carolina and *T. ornata* in Missouri reportedly emerge from hibernation after five consecutive days of subsurface (10–20 cm) temperatures of 7 C or higher (Grobman, 1990). We did not observe a relationship between subsurface temperatures and the termination of hibernation at our sites.

Differences between air and surface temperatures in the fall and the spring have also been suggested as a cue for animals to begin or end hibernation (Sexton and Hunt, 1980; Gregory, 1982). However, to make such measurements, hibernating Desert Tortoises would be required to approach the surface and "test" the temperature for comparison with deep temperatures, and our results indicate no such behavior. For example, the animals at Littlefield that were in highly buffered hibernacula had no variation in body temperature while hibernating, not even just before they emerged (Fig. 2A). Thus, these animals were not apparently experiencing any external cues and were not sampling the environment, yet they emerged from hibernation at about the same time as other animals. We found that the dates of emergence from hibernation were not statistically correlated with the spring air temperatures at City Creek and Littlefield, with emergence date varying by 35 days at the sites. The average termination date was highly variable and not statistically different among the four study sites during the winter of 1998.

While there were large differences in the air temperatures at the four sites among years, the hibernacula chosen by the tortoises had similar thermal properties, and the average hibernation temperatures were well above outside air temperatures. It should be noted that tortoises chose one of the warmest microclimates in the environment for hibernation, which reduces the likelihood that hibernation is strictly an energy conservation strategy for these animals. Hibernating Desert Tortoises at Rock Valley, Nevada, had a similar duration as found in this study and had low metabolic costs and almost no loss of body mass during hibernation (Nagy and Medica, 1986), which is consistent with other reports for this species (Peterson, 1996; Henen et al., 1998). Tortoises in sites that had colder climates sought shelters that were deeper, and therefore had more stable temperatures as they were more buffered from the environment (Woodbury and Hardy, 1948). Some of the animals at the Littlefield site had body temperatures that had almost no fluctuation, not only on a daily basis, but also over the course of the entire winter.

The temperatures of reptile hibernacula have been previously reported to range between 1 and 15 C (Gregory, 1982). Our data generally fall within this range; however, some individuals chose hibernacula that had temperatures above it. The mean minimum and maximum hibernation temperatures in our study were similar to those observed in the San Pedro Valley, Arizona (Bailey et al., 1995). The female tortoises in Arizona, however, had lower minimum temperatures than did males, while there were no apparent differences in hibernation temperatures between the sexes of our study animals.

Our ability to quantify environmental variability and animal behavior has increased dramatically due to advances in micro-technology. The application of small temperature loggers allowed us to thoroughly examine hibernation behavior and temperatures and to test whether exogenous cues are likely driving hibernation behavior in Desert Tortoises. We found that the timing of hibernation behavior was sufficiently variable that we doubt this behavior is driven predominantly by exogenous cues. Hibernation may prevent tortoises from being exposed to extreme temperatures and potentially lethal ones in the winter, but the onset of hibernation, while variable within a site, was certainly always early enough to avoid this problem at our sites. It may be that endogenous conditions are more important drivers of hibernation than exogenous cues for this species.

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