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Abstract. – Gathering natural history information on a species is a necessary first step in understanding its ecology, which can lead to hypothesis generation and the data necessary for its conservation. I studied desert box turtles (*Terrapene ornata luteola*) at the Sevilleta National Wildlife Refuge in central New Mexico at the northern periphery of this subspecies in the Chihuahuan Desert. I recorded locations and marked all box turtles found in the northeastern part of the refuge over 23 yrs during trips to the site in 1986–1989, 1998, and 2008. I found that desert box turtles at the site sometimes were active in May and early June, but were most active in late June or early July into early October, with greatest activity in July and August. Numbers of box turtles on roads were significantly correlated with air temperature but not precipitation. Daily activity was bimodal during peak activity months. Growth was fairly rapid until about 10 yrs of age and then leveled off dramatically. The largest adults were about 125–130 mm carapace length (CL), and females were significantly longer than males in 2 of 3 survey periods. By 2008, I found a number of adults that were 30–40 yrs old, and several might have been older than 40 yrs. The mean number of eggs in a clutch varied from 2.67 to 3.55, there was no indication of multiple clutches being produced, and variation in egg number was only weakly explained by the CL of the female. Despite low reproductive rates, the population on the Sevilleta has persisted and likely will do well into the future in this protected reserve.

Key Words. – Reptilia; Testudines; age structure; box turtles; longevity; size structure; thermobiology

A necessary first step in understanding the ecology of a species is understanding basic life-history parameters. Once known, these can lead to hypothesis generation and the data necessary for its conservation (Bury 2006). How a species uses its environment in the short and long term can be important to understanding how habitat affects its growth, reproduction, and survival. Also, the timing of activity can show what environmental factors are important for daily activity. Box turtles (*Terrapene* spp.) in North America are increasingly becoming a conservation concern because of habitat loss and because of harvesting for the pet trade (Gibbons et al. 2000; Dodd 2001; Redder et al. 2006).

The nominate ornate box turtle (*Terrapene ornata*) ranges across much of the plains of central North America west to the foothills of the Rocky Mountains, and south to northern Mexico and south Texas (Dodd 2001; Ernst and Lovich 2009). There are 2 subspecies. The subspecies ornate box turtle (*Terrapene ornata ornata*) occurs in the central part of North America in the Great Plains extending from Wisconsin and Indiana in the northeast and North Dakota in the northwest, down through Texas (Dodd 2001). The desert box turtle (*Terrapene ornata luteola*) occurs in the Southwest, including much of New Mexico, the Big Bend region of Texas, southeastern Arizona, and adjacent northern Mexico (Degenhardt et al. 1996; Dodd 2001). It lives in desert grasslands/shrublands and may face a drier, more severe environment compared with other box turtles in North America. The ornate box turtle is a medium-sized turtle that reaches 154 mm carapace length (CL) (Collins 1993), but most adults are 120–130 mm CL (Degenhardt et al. 1996). The species is long-lived, perhaps living up to 50 yrs in nature (Legler 1960). Because of the seasonal droughts, it is possible that growth and reproductive patterns of desert box turtles differ from species found in central North America.

I gathered data on the ecology and life history of a population of desert box turtles on the Sevilleta National Wildlife Refuge, New Mexico, at the northern edge of the Chihuahua Desert during 3 time periods from 1986 to 2008. Activity and reproduction of this same population were reported on by Nieuwolt (1996) and Nieuwolt-Dacanay (1997), but she followed the population from 1990 to 1992, and this study extends the study by comparing daily activity and reproduction of the population across a 23-yr time frame, before and after her study. I also recorded air temperatures and humidity during part of the study to determine if daily activity correlated with these environmental factors. Further, I gathered data on population structure, longevity, and growth. I used this long-term data set to determine if the ecology and life history of box turtles at this site varied across a substantial portion of the lifespan of individuals of this species.

METHODS

Study Site. — I studied desert box turtles at the Sevilleta National Wildlife Refuge and Long-Term

Ecological Research (LTER) site, which is located approximately 85 km south of Albuquerque, New Mexico. The refuge is in the Rio Grande Valley at the northern extent of the Chihuahuan Desert. I worked in the northeastern part of the refuge just south of the refuge boundary at Black Butte. Most of the site where I found box turtles was grassland (*Oryzopsis hymenoides*, *Sporobolus giganteus*, *Sporobolus flexuosus*, *Bouteloua eriopoda*, *Bouteloua gracilis*) with scattered yucca (*Yucca baccata* and *Yucca glauca*). The southern end of the site graded into a creosote (*Larrea tridentata*) scrubland. The elevation of the study area varied from 1565 m at the north end at the junction of the east–west and north–south dirt roads (lat 34°24′18″N, long 106°40′42″W) to 1625 m at the south end on the north–south dirt road (lat 34°19′55″N, long 106°42′07″W) and 1668 m on the east end of east–west road (lat 34°21′11″N, long 106°37′29″W). These were the roads I drove to find box turtles. At Bernardo, New Mexico (elevation 1438 m), about 14 km to the west of the study site, the average annual high temperature in July is 34.7°C and the average annual minimum in January is −8.0°C (World Climate 2010). Mean annual precipitation at Bernardo is 201.4 mm, with 64.2% (129.2 mm) of precipitation falling from July to October (World Climate 2010) with the onset of monsoonal storms. April through June, however, is particularly dry with only 14.4% (29.0 mm) of annual precipitation falling, at a time when temperatures are suitable for turtle activity.

Field Methods. — I searched for box turtles from April to October 1986–1989 (34 surveys), 1998 (28 surveys), and 2008 (46 surveys). To locate box turtles, I drove roads at about 25 km/hr either alone or with assistants. I drove 8.6 km of the east–west road and 9.0 km of the north–south road every time I went to the Sevilleta but I occasionally drove completely around this part of the refuge to check for box turtles. From 1986 to 1989, I searched roads from June to October either in the morning or in the evening but not at both periods during a trip. In 1998 and 2008, I drove roads both in the morning and the evening each day I was on the site. In 1998, I surveyed for turtles in July, and in 2008, I made survey trips in April, May, July, and August. When a turtle was found, I noted the time, its location relative to the junction of dirt roads at Black Butte based on odometer readings (to 0.1 mile; converted to kilometers). In 1998 and 2008, I recorded air temperature (at 1.3 m aboveground) at the point of box turtle capture. In 2008, I also recorded temperature and relative humidity (TMH-300 Thermo-hygrometer, Pen Type, EAI Education, Oakland, NJ) at the beginning and end of surveys.

For each captured turtle, I recorded mass, straight-line CL along the midline, sex, and age. I individually marked turtles by notching marginal scutes with a file (Cagle 1939). I estimated the age of an individual using scute annuli from the carapace and plastron (Legler 1960). Countable scute annuli only form for a few years past sexual maturity in all turtle species that have been studied (Germano and Bury 1998), and some biologists have incorrectly tried to determine ages of turtles beyond this limit (Wilson et al. 2003). Some box turtles at my site, therefore, could only be classified as older than 14 yrs because scute rings were worn and edges of scutes were beveled; these animals were no longer depositing discernible rings. In 1998 and 2008, I was able to determine exact ages of some turtles > 14 yrs because I had estimated ages based on annuli in an earlier survey period. Even though the technique cannot be used to determine the age of all adult turtles, it still allows comparisons of age structure of a large segment of individuals among populations and for determining growth rates. I defined the difference between adults and juveniles as 100 mm CL, the size at which most males developed secondary sexual characteristics such as red eyes (in most); longer, thicker tails; thicker, turned-in first toe on hind foot; and a greenish dorsal head color compared with females (Legler 1960; Degenhardt et al. 1996; Dodd 2001). In 1988, 1998, and 2008, I took X-ray photographs of all females to determine if they were gravid and to count the number of eggs they were carrying.

Activity Analysis. — I did not find any box turtles during surveys in April and I found only 2 turtles in May. Therefore, I excluded these months from analyses that compared the mean number of box turtles I found per month of survey. The data were nonnormal, so I tested for differences in the mean number of box turtles found per survey by month using the Kruskal-Wallis test followed by Mann-Whitney tests of ranks of paired months. The data for number of box turtles active in the morning and evening were normally distributed and I tested for differences in means using a 2-way analysis of variance (ANOVA) with sex and time (morning, evening) as main effects and with an interactive term of sex and time. Similarly, I tested differences in mean air temperature when turtles were active using a 2-way ANOVA with sex (male, female, unsexed juveniles) and time (morning, evening) as main effects and with an interactive term of sex and time. I compared the distribution of times when turtles were seen in the morning (time after sunrise) and separately in the evenings (time before sunset) across 3 census times (1986–1988, 1998, 2008) using the Komolgorov-Smirnov test. Because virtually all box turtles in 1998 and 2008 were found in July and August, I only used data from July and August for 1986–1988 to compare with 1998 and 2008 data. I used correlation analysis to compare the number of box turtles that I found active in daily surveys in July and August 2008 with the mean temperature and relative humidity taken at the beginning and end of a survey. Moreover, I used correlation analysis to compare the mean number of box turtles I found per month for all the months I surveyed for all years with the amount of precipitation for that month. I also correlated the mean number of box turtles I found per month to the combined amount of rainfall for that month and the preceding month and to the maximum and minimum temperatures for that month.

Size and Population Structure Analysis. — I used a 2-way ANOVA to test for differences in mean CL of adults among survey periods and between sexes, with survey period times sex the interactive term. To minimize the effect of age structure on size estimates (Case 1976), I also determined the upper decile CL (UDCL) of adult turtles and I tested for differences in UDCL among survey periods and between sexes also using a 2-way ANOVA. I tested for differences from a 1:1 sex ratio by survey period using χ^2 analysis with a Yates correction for continuity. I also compared both the size (CL) and age structure of turtles found during survey periods using the Kolmogorov-Smirnov test. For all tests, $\alpha = 0.05$.

Growth Analysis. — I constructed growth curves by fitting age and CL data to the Richards growth model (Richards 1959). The Richards growth model can estimate 4 parameters using CL and age data: asymptotic size (A), the shape of the growth curve (M), the growth constant (K), and the point at which curve inflection begins (I). The model uses the following general formula:

$$\mathrm{CL} = \mathrm{A}\left\{1 + [\mathrm{M} - 1]e^{[-\mathrm{K}(\mathrm{Age}-\mathrm{I})]}\right\}^{[1/(1-\mathrm{M})]}$$

to solve for CL at various ages. I used continuous age estimates (Lindeman 1997) based on a yearly period of 1 May to 30 September that could support growth. Precision of the estimate of the growth period is not critical, but estimating age to a decimal fraction of a year improves curve fit (Lindeman 1997). I made comparisons of growth rates among surveys using the statistic G, which represents the time required to grow from 10% to 90% of asymptotic size and is an indicator of the duration of primary growth (Bradley et al. 1984). It is defined in the following way:

$$\mathrm{G} = \ln\left[\left(1 - 0.10^{1-\mathrm{M}}\right)/\left(1 - 0.90^{1-\mathrm{M}}\right)\right]/\mathrm{K}$$

The raw parameters K and M are closely linked in determining growth curves and neither is useful for comparing growth between populations (Bradley et al. 1984). The best overall growth measure is G because it is less affected by instability of the nonlinear fit than either K or M, and it produces values on an easily interpreted scale (Bradley et al. 1984), in this case, years. I also compared growth rates among survey periods and sex using calculated carapace lengths (CCL) derived from the growth equations using 3-yr intervals from ages 3 to 12 yrs. I used ANOVA ($\alpha = 0.05$) on mean and 95% confidence interval values of CCL among years at each year interval to test for differences of growth rates among survey periods and sex.

Reproduction. — I compared the mean number of eggs per clutch among 1988, 1998, and 2008 using ANOVA, and I used the Student-Newman-Kuels test if means differed significantly. To determine if precipitation was related to reproductive output, I correlated average clutch size to yearly precipitation using my clutch data and those of Nieuwolt-Dacanay (1997). I defined yearly rainfall as the amount falling from October of the previous year until September of the year of interest. I correlated average clutch size to both the current and previous year's precipitation levels. I also used linear regression to determine if there was a relationship between CL of females and the number of eggs they produced in a clutch.

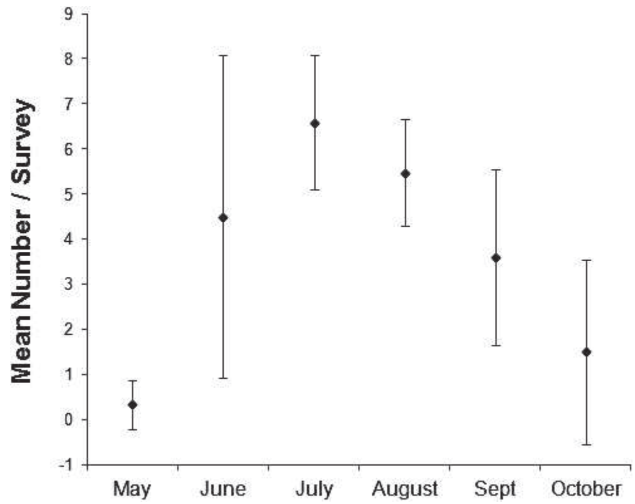

Figure 1. Mean number of desert box turtles (*Terrapene ornata luteola*) found during road surveys in 1986–1989, 1998, and 2008 at the Sevilleta National Wildlife Refuge site, Socorro County, New Mexico. Error bars are the 95% confidence intervals.

RESULTS

I found 125 individual box turtles (51 males, 65 females, 9 juveniles) in 34 trips to the Sevilleta from 1986 to 1988. In 1988, I found 84 box turtles (30 males, 48 females, 6 juveniles) in 28 surveys and in 2008, 94 individuals (41 males, 43 females, 10 juveniles) in 46 surveys. Sex ratios of males to females was 0.78:1 in 1986–1988, 0.63:1 in 1998, and 0.95:1 in 2008, but none of these ratios differed significantly from 1:1 ($\chi^2 = 0.012$–3.71, $p = 0.054$–0.913).

Activity. — Excluding April, when I did not find box turtles in 9 surveys, the mean number of box turtles I found per survey by month varied from 0.33 in May ($n = 6$) to 6.58 in July ($n = 53$), and decreased each month thereafter to 1.5 turtles in October ($n = 4$; Fig. 1). Excluding April and May, there was a significant difference in the mean number of box turtles found per month ($H = 18.37$, df = 4, $p = 0.001$), with the mean number found in October significantly lower than for July and August ($n = 17$; $W = 217.5$–1622.0, $p = 0.007$–0.008). I found a few box turtles on roads at sunrise with a peak of morning activity 2–3 hrs after sunrise continuing until about 5 hrs after the sun came up (Fig. 2). In the afternoon, I found box turtles on roads 3 hrs before sunset with a peak of evening activity 1.0–0.5 hrs before sunset and with a cessation of movement on roads as the sun set (Fig. 2).

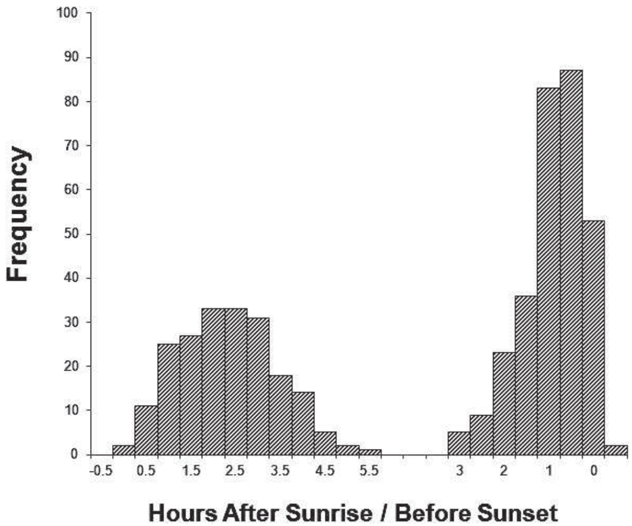

Figure 2. Histogram of time after sunrise (left) and before sunset (right) when desert box turtles (*Terrapene ornata luteola*) were found during road surveys in 1986–1989, 1998, and 2008 at the Sevilleta National Wildlife Refuge site, Socorro County, New Mexico.

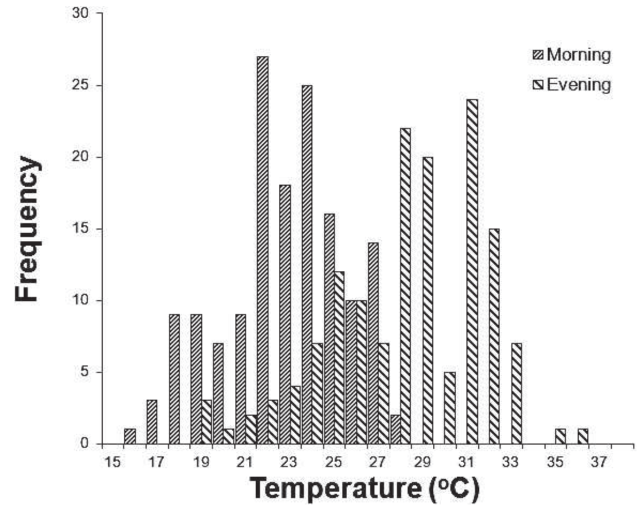

Figure 3. Histogram of air temperatures when desert box turtles (*Terrapene ornata luteola*) were found during morning and evening road surveys in 1998 and 2008 at the Sevilleta National Wildlife Refuge site, Socorro County, New Mexico.

There was no significant difference ($F_{1,182} = 1.82$, $p = 0.179$) between the mean number of box turtles found per survey in the morning (4.83) compared with the evening (5.86), nor was there a significant interactive term ($F_{1,182} = 2.19$, $p = 0.141$). However, the mean number of females found per survey (2.91) was significantly higher ($F_{1,182} = 3.95$, $p = 0.048$) than the mean number of males (2.22) irrespective of time of day. The distribution of times when box turtles were found in the morning did not differ between 1986–1988 and 1998 ($D = 0.278$, $p = 0.088$) nor between 1998 and 2008 ($D = 0.181$, $p = 0.163$); however, it did differ significantly between 1986–1988 and 2008 ($D = 0.387$, $p = 0.008$) with the distribution of times more spread out in 2008. In the late afternoon and evenings, the distribution of times when turtles were found did not differ significantly between 1998 and 2008 ($D = 0.152$, $p = 0.326$), but distributions differ significantly between 1986–1988 and 1998 ($D = 0.237$, $p = 0.010$) and 2008 ($D = 0.331$, $p < 0.001$), with more turtles found earlier in the evening in 1998 and 2008 than in the 1980s.

In the morning, I found box turtles active when air temperatures were 16.4°–28.3°C and in the late afternoon into evening at 18.9°–35.6°C (Fig. 3). The peak of activity in the morning occurred when air temperatures were from 22°C to 24°C, and in the evening, from 28°C to 31°C (Fig. 3). Mean air temperatures when I found box turtles were significantly lower in the morning ($\bar{X} = 22.9$°C) than in the evening ($\bar{X} = 28.1$°C; $F_{1,290} = 79.99$, $p < 0.001$), but air temperatures when I found males, females, or juveniles did not differ significantly ($F_{2,182} = 1.80$, $p = 0.167$) nor was there an interactive effect ($F_{2,182} = 0.15$, $p = 0.859$).

The mean number of turtles I found on roads daily in July and August 2008 were not correlated with relative humidity or air temperatures (Table 1). The mean number of box turtles I found in a month was not correlated with either rainfall in that month or the combined amount of rainfall in that month and the preceding month (Table 1). The mean number of box turtles I found in a month was correlated with the mean maximum temperature for the month and mean minimum monthly temperature (Table 1). In all cases, the number of box turtles I found on the roads increased with increasing monthly temperatures.

Size and Population Structure. — In all time periods, the population structure was highly skewed to adult turtles and turtles for which I could not determine age (Fig. 4). There were no significant differences in the size structures among the 3 survey periods (1986–1989, 1998, 2008;

Table 1. Pearson correlations of environmental variables monthly (across 23-yr study) and daily (July–August 2008) with the number of desert box turtles (*Terrapene ornata luteola*) found on roads (means for monthly variables) at the Sevilleta National Wildlife Refuge, New Mexico, from 1986 to 2008. Precip + PrecMonth is monthly precipitation plus the preceding month's precipitation. The letters M and E refer to correlations of daily activity for the number of turtles found only in the morning (M) or in the evening (E). Asterisks indicate significant correlations ($p \leq 0.05$).

Factor	*r*	*p*
Monthly		
Precipitation	0.267	0.300
Precip + PrecMonth	0.147	0.575
Maximum temperature	0.713	0.001*
Minimum temperature	0.498	0.042*
Daily		
Relative humidity	−0.138	0.511
Temperature	0.207	0.321
Relative humidity-M	0.346	0.271
Temperature-M	0.308	0.330
Relative humidity-E	−0.392	0.185
Temperature-E	0.316	0.293

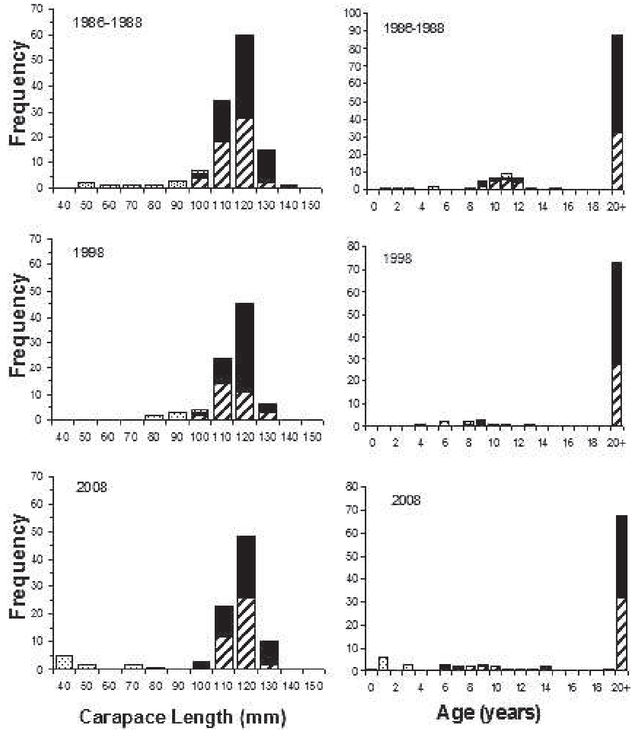

Figure 4. Frequency distribution of carapace lengths (left) and ages (right) of desert box turtles (*Terrapene ornata luteola*) at the Sevilleta National Wildlife Refuge, Socorro County, New Mexico, site over 3 survey periods. Black bars are females, striped bars are males, and gray bars are turtles for which sex could not be determined.

$D = 0.182–0.364$, all $p = 0.374–0.985$) nor did age structures differ significantly ($D = 0.200–0.267$, all $p = 0.589–0.890$). Only 6.0%–10.6% of box turtles I found in any survey period were < 100 mm CL (juveniles), although the percentage of turtles for which I could determine age (< 15 yrs) varied from 13.1% to 28.0%.

The mean CL of male box turtles varied from 115.0 to 116.2 mm in the 3 survey periods and mean CL of females varied from 117.9 to 119.2 mm (Table 2). The largest CL recorded for males was 128 mm, and 136 mm for females. Mean CL of box turtles differed significantly by sex ($F_{1,272} = 14.31$, $p < 0.001$) but not by survey period ($F_{2,272} = 0.29$, $p = 0.750$), or the interaction of survey period and sex ($F_{2,272} = 0.84$, $p = 0.431$). Mean CL of males was significantly smaller than female CL in 1986–1988 ($F_{1,114} = 10.44$, $p = 0.002$) and 1998 ($F_{1,76} = 4.39$, $p = 0.039$), but not in 2008 ($F_{1,82} = 1.99$, $p = 0.162$). Mean UDCL of box turtles ranged from 124.5 mm (males) to 131.6 mm (females) and differed significantly by sex ($F_{1,22} = 24.19$, $p < 0.001$) and the interaction of survey period and sex ($F_{2,22} = 7.10$, $p = 0.004$), but not by survey period ($F_{2,22} = 2.19$, $p = 0.136$). Mean UDCL of males was significantly smaller than female CL (Table 1) in 1986–1988 ($F_{1,10} = 27.57$, $p < 0.001$) and 2008 ($F_{1,6} = 19.11$, $p = 0.005$), but not in 1998 ($F_{1,82} = 0.05$, $p = 0.836$).

Table 2. Mean carapace lengths (CL) and upper decile CL (UDCL), standard error (SE), and sample size (*n*) of adult male (M) and female (F) *Terrapene ornata luteola* from 3 time periods at the Sevilleta National Wildlife Refuge in New Mexico. Sexual size dimorphism was calculated using the sexual dimorphism index (SDI) and, by definition, if male and female mean CLs are not significantly different, SDI = 1.00 (Gibbons and Lovich 1990). There were no significant differences ($p > 0.05$) for CL or UDCL among years. Significant differences ($p < 0.05$) between sexes within years are designated with an asterisk.

Time period	CL (mm)	SE	*n*	SDI	UDCL (mm)	SE	*n*	SDI
1986–1988								
All	117.3	7.26	116		130.0	2.52	12	
M	115.0*	6.66	51	1.04	124.8*	1.72	5	1.05
F	119.2*	7.17	65		131.6*	2.19	7	
1998								
All	116.8	6.10	78		126.1	1.83	8	
M	115.0*	6.67	30	1.03	126.3	1.25	3	1.00
F	117.9*	5.42	48		126.0	2.10	5	
2008								
All	117.1	6.04	84		128.5	2.19	8	
M	116.2	4.62	41	1.00	124.5*	1.29	4	1.04
F	118.0	7.08	43		130.0*	2.16	4	

Growth. — Model fit of size to age using the Richards growth model was high, particularly for 1998 and 2008 curves with r^2 of 0.980 and 0.982, respectively (Table 3). Growth rate was rapid under 10 yrs of age and leveled off precipitously in 1998 and 2008 (Fig. 5). The duration of primary growth (G) in 1986–1988 (14.4 yrs) was ca. 30% longer than the duration in 1998 (11.1 yrs) and ca. 78% longer than turtles in 2008 (8.1 yrs; Table 3). However, based on the estimated CLs for ages 3, 6, 9, and 12 yrs, there were no significant differences in growth across time periods (Table 4). Because growth did not differ significantly across survey periods, I combined years and compared male growth with that of females (Fig. 5). For both sexes $r^2 > 0.91$, and the duration of primary growth (G) was similar at ca. 11 yrs. The estimated CLs for ages 3, 6, 9, and 12 yrs between males and females were not significantly different (Table 4). Neither period of survey or sex gave significantly different growth models, so I combined all data to produce 1 growth curve for box turtles on the Sevilleta (Fig. 6). The duration of primary growth was 10.1 yrs (Table 3). Further, the 95% confidence interval about the regression line is fairly narrow (Fig. 6), indicating this curve captures the growth of box turtles at this site well. Using this overall growth model, box turtles reached 100 mm CL in 6.9 yrs and 115 mm CL in 18.3 yrs (Fig. 6).

Longevity. — I found 11 box turtles in 1998 that I had marked in 1986–1988. Three had estimated ages of 20 yrs (female), 23 yrs (male), and 23 yrs (male) in 1998 based on scute annuli. For the other 8 (2 males, 6 females), I could not determine age accurately in the earlier survey period but I estimated them to be at least 20 yrs old, based on the worn condition of the shell. These turtles were, therefore, at least 30 yrs old in 1998. In 2008, I found 8 turtles first marked in

Table 3. Growth parameters of Richards (1959) growth curves for *Terrapene ornata luteola* from 3 time periods and for males and females (years combined) and all turtles at the Sevilleta National Wildlife Refuge in New Mexico. Parameters describing model fit and growth curves are coefficient of determination (r^2), shape of curve (M), growth constant (K), inflection point of curve (I), and the time (years) required to grow from 10% to 90% of asymptotic carapace length (G).

Site	r^2	M	K	I	G
1986–1988	0.815	−1.01	0.114	−6.11	14.4
1988	0.980	−0.748	0.159	−4.14	11.1
2008	0.982	1.90	0.523	1.64	8.12
Males	0.915	1.07	0.297	0.841	10.6
Females	0.934	0.164	0.209	−1.16	11.1
All turtles	0.915	1.18	0.327	0.979	10.1

1986–1988 and 2 females first marked in 1998. The 2 females from 1998 were 14 and 19 yrs old in 2008. Of the 8 turtles first marked in 1986–1988, 3 had also been found in 1998 and were 30 yrs old (female), 33 yrs old (male), and at least 40 yrs old (female) in 2008. The others were 3 females that were 30, 31, and 33 yrs old, and 2 males that were $>$ 40 yrs old.

Reproduction. — In 1988, I X-rayed females from 28 June to 20 July and found 12 of 27 (44.4%) gravid. In 1998, 18 of 47 females (38.3%) that I X-rayed were gravid starting 8 July (11 of 12 females), but none had eggs from 13 July until I stopped checking on 20 July, including 14 females that I X-rayed twice. In 2008, 10 of 32 females (31.3%) were gravid in July, but only 1 of 17 females (5.9%) had eggs in August; 5 of these females had been X-rayed in July. The gravid female (2 eggs) was found 20 August and had not been seen in July.

The mean number of eggs per clutch for females with eggs in 1988 was 2.75 $\pm$ 0.125 SE (n = 12; range, 2–3); in 1998, 2.67 $\pm$ 0.157 (n = 18; range, 1–4), and in 2008, 3.55 $\pm$ 0.236 (n = 11; range, 2–5). These means differed significantly ($F_{2,38} = 6.495$, $p = 0.004$). The mean number of eggs per clutch in 2008 was significantly greater than that in 1988 ($q = 4.032$, $p < 0.05$) and 1998 ($q = 4.858$, $p < 0.05$) but the mean number in 1988 did not differ significantly from the mean number in 1998 ($q = 0.473$, $p > 0.05$). Combined, I found only 1 female with a clutch size of 1, 9 females with a clutch size of 2, 24 females with 3 eggs, 5 females with 4 eggs, and 1 female with 5 eggs. The average clutch size across 6 yrs was not significantly correlated with that year's precipitation ($r = -0.242$, $t = -0.498$, df = 4, $p = 0.644$) or precipitation in the preceding year ($r = 0.322$, $t = 0.680$, df = 4, $p = 0.534$). There was a significant linear relationship between the number of eggs per clutch and CL of females ($F_{1,37} = 4.499$, $p = 0.041$), although CL only explained 10.8% of the variation in clutch size (Fig. 7).

DISCUSSION

I found that desert box turtles at the northern end of their range sometimes were active in May and early June, but were most active in late June or early July into early October, with greatest activity in July and August. Numbers of box turtles on roads were significantly correlated with air temperature but not precipitation. Daily activity was bimodal during peak activity months. Farther north in the Great Plains, ornate box turtles are most active from late April until June, although turtles can be found into October (Minton 1972; Blair 1976; Vogt 1981; summarized in Redder et al. 2006). The lack of correlation with precipitation is surprising as desert box turtles at this site are not found out much before summer monsoons begin, usually in late June or July (Nieuwolt 1996; *pers. obs.*). Plummer (2003, 2004), who studied desert box turtles in southeastern Arizona, stated that summer monsoons triggered turtle emergence from underground sites. According to Plummer (2004) desert box turtles went into winter torpor from mid-October until the summer monsoon season in late June or early July. This occurred despite the fact that air temperatures were reportedly adequate for box turtle activity by April of each year. Desert box turtles emerge dehydrated from this prolonged inactivity and typically had lost 18%–20% of their body mass (Plummer et al. 2003).

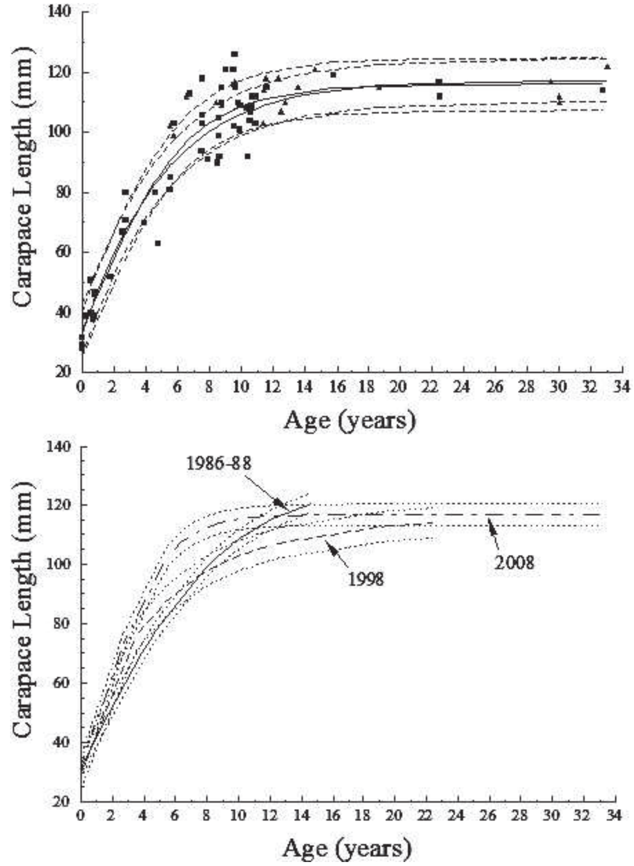

Figure 5. Growth curves (carapace lengths on ages) of desert box turtles (*Terrapene ornata luteola*) at the Sevilleta National Wildlife Refuge, Socorro County, New Mexico, site over 3 survey periods (bottom) and for males and females, irrespective of survey period (top), using the Richards (1959) growth model.

Table 4. Estimated mean carapace lengths (95% confidence intervals) of *Terrapene ornata luteola* based on Richards (1959) growth curves for ages 3, 6, 9, and 12 years from 3 time periods at the Sevilleta National Wildlife Refuge in New Mexico, USA. No carapace lengths by age group across survey periods were significantly different.

	Age (yrs)			
Time period	3	6	9	12
1986–88	74.0 (43.1–104.7)	95.6 (56.6–136.3)	109.8 (64.4–155.3)	118.3 (69.3–167.3)
1998	72.0 (66.8–77.3)	90.4 (83.8–96.9)	100.5 (93.2–107.8)	106.4 (98.6–114.1)
2008	77.6 (75.2–80.0)	105.7 (102.5–109.0)	114.2 (110.6–117.7)	116.1 (112.5–119.7)
F	0.074	0.325	0.207	0.147
P	0.929	0.735	0.818	0.866
Males	69.5 (64.2–74.7)	93.8 (86.7–100.9)	106.3 (98.2–114.3)	111.9 (103.4–120.4)
Females	77.6 (65.6–74.4)	105.7 (85.8–97.3)	114.2 (96.9–109.9)	116.1 (102.9–116.8)
F	0.016	0.181	0.229	0.116
P	0.904	0.692	0.657	0.762

I observed daily activity patterns that were similar to those found by Nieuwolt (1996) and Plummer (2003). Box turtles were active from sunrise through much of the morning and from late afternoon until sunset. Nieuwolt (1996) showed that only a few box turtles with radio transmitters were sporadically active midday. This generally bimodal activity pattern is similar to that of ornate box turtles farther north in the Great Plains (Legler 1960; Converse et al. 2002; Ernst and Lovich 2009). Box turtles in the far north in Wisconsin, however, are active from 0900 to 1800 hrs daily (Ellner and Karasov 1993). Cooler, moister conditions in the far north of the range may account for this difference.

Like other North American box turtles (both *Terrapene carolina* and *T. o. ornata*), the population structure of box turtles on the Sevilleta are skewed to large older turtles. Both Legler (1960) reporting on a population of ornate box turtles in Kansas and Dodd (2001) on a population of Florida box turtles (*Terrapene carolina bauri*) on Egmont Key in Florida had low numbers of turtles < 100 mm CL, although both show higher numbers of juveniles than I found. In part this could be because I found almost all turtles by driving roads, which may have made small turtles harder to detect than large turtles. Both Legler (1960) and Dodd (2001) commented that the number of small turtles they found probably underrepresented the true number of young box turtles on their study sites. I found a much higher percentage of turtles < 15 yrs (28% in 2008) than turtles classified as juveniles based on size. As found for western pond turtles (*Actinemys marmorata*), the age structure of a population often shows that the population is producing recruitment better than what is indicated by size structure (Germano and Bury 2009; Bury et al. 2010).

Turtles in general are known to be long-lived animals (Williams 1957; Gibbons 1987; Wilbur and Morin 1988), which allows for maintenance of a population even with overall low juvenile survivorship (Wilbur and Morin 1988; Congdon and Gibbons 1990). Some desert box turtles on the Sevilleta were 30–33 yrs old and 3 were at least 40 yrs old in 2008. Although there is a report of an eastern box turtle living > 100 yrs in the wild (Graham and Hutchison 1969), verified ages of the oldest eastern box turtles generally are younger than 70 yrs (Stickel 1978; Williams and Parker 1987; Schwartz and Schwartz 1991;

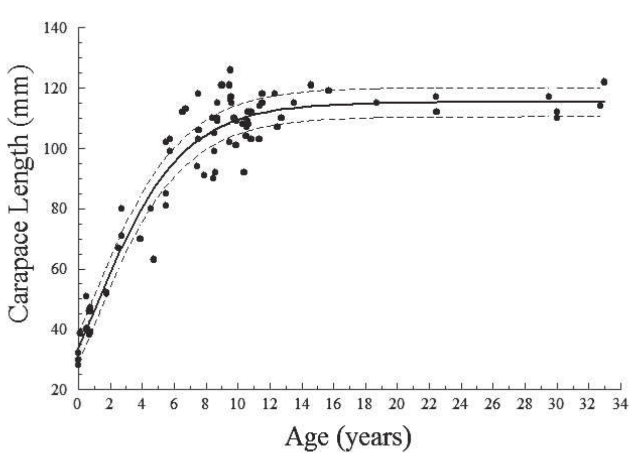

Figure 6. Growth curves (carapace lengths on ages) of desert box turtles (*Terrapene ornata luteola*) at the Sevilleta National Wildlife Refuge, Socorro County, New Mexico, site of all box turtles using the Richards (1959) growth model.

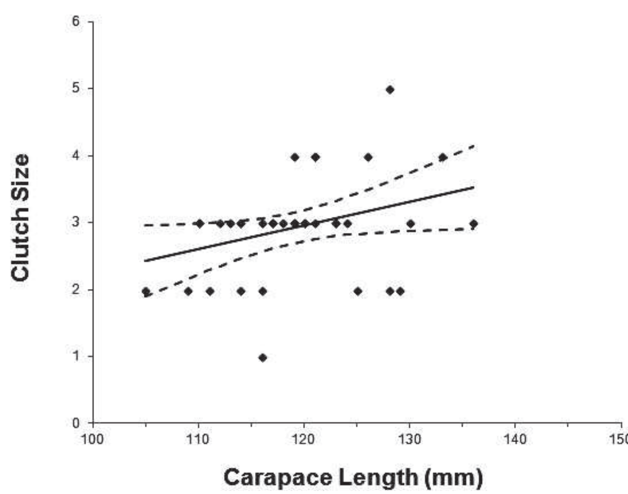

Figure 7. Relationship of the number of eggs in a clutch to female carapace length (mm) for desert box turtles (*Terrapene ornata luteola*) at the Sevilleta National Wildlife Refuge site, Socorro County, New Mexico.

Hall et al. 1999) and those of ornate box turtles are $<$ 40 yrs (Legler 1960; Blair 1976; Metcalf and Metcalf 1985).

I determined age of younger (up to 14 yrs) desert box turtles using scute annuli, which have been shown to be accurate for ornate box turtles in Kansas (Legler 1960). The use of scute annuli has been criticized because it does not always match age in turtles (Dodd 2001; Wilson et al. 2003). However, that largely occurs because some have tried to determine the age of all turtles in a population, when it has been shown that annuli counts only are accurate for a defined period leading up to and slightly past maturity (Legler 1960; Germano 1988, 1992; Germano and Bury 1998). Besides using annuli to determine the age structure of desert box turtles at the Sevilleta, I was able to construct the first precise growth curve for this species. I found fairly rapid growth of juveniles up to 10–12 yrs, at which time desert box turtles have reached $>$ 98% of their asymptotic size. Based on percentage of incremental increase in plastron length, ornate box turtles in Kansas grew at virtually the same rate (Legler 1960). It took 16–18 yrs for eastern box turtles (*T. c. carolina*) in Maryland to approach the largest sizes measured, although these sizes were ca. 145 mm CL (Stickel and Bunck 1989).

I found reproductive rates similar to what has previously been found for desert box turtles at the Sevilleta (Nieuwolt-Dacanay 1997). Average clutch size was not correlated with precipitation amounts, although Nieuwolt-Dacanay (1997) found much higher percentages of females gravid in 1990 and 1992, which had wetter springs than in 1991. For all North American box turtles, mean clutch size for a population is fewer than 5 eggs (Dodd 2001), although a clutch may contain up to 11 eggs (in *T. carolina*; Zieller 1969; Warner 1982). For the ornate box turtle, the mean number of eggs per clutch in Kansas was 4.7 with a range of 2–8 (Legler 1960); in Wisconsin 3.5 eggs, range not given (Doroff and Keith 1990); and in Nebraska, 2.60 eggs, range of 2–4 (Converse et al. 2002). At the Sevilleta, there is little evidence for multiple clutches in a season. Neither Nieuwolt-Dacanay (1997) nor I detected a second clutch in 6 yrs of X-raying. However, I did find a female in 2008 with a clutch of eggs in late August, and in 1992 Nieuwolt-Dacanay (1997) found 3 gravid females in early August. The lack of solid evidence of multiple clutch formation contrasts with studies of other North American box turtles. Legler (1960) found evidence for multiple clutching in ornate box turtles, Brown (1974) found 1–3 clutches per year for the Coahuilan box turtle (*Terrapene coahuila*), Tucker et al. (1978) and Jackson (1991) found evidence for multiple clutches in the Gulf Coast box turtle (*Terrapene carolina major*), and Dodd (1997) found that Florida box turtles laid up to 3 clutches a season. Low average clutch size, low maximum number of eggs per clutch, and the lack of multiple clutches in a year at the Sevilleta may reflect the harsher environmental conditions that desert box turtles encounter compared with the environments of other populations of *Terrapene* that allow for greater reproductive output.

Daily activity of desert box turtles did not change over my 23-yr study. Desert box turtles were more active in the middle of summer than conspecific ornate box turtles farther north, and monthly activity of desert box turtles was correlated with increasing air temperatures. I did not find a correlation between the number of desert box turtles on roads and precipitation, as has been found in other studies, but I think that the first big rain event in summer causes turtles to emerge and become active, even if conditions become relatively dry for a period after that event. Despite a seemingly low rate of annual reproduction, my size and age structures show that the population of desert box turtles on the Sevilleta has been relatively stable for 23 yrs. Even without finding large numbers of small or young turtles, the population structure stayed very similar over the years. Each survey period I caught many new box turtles not found in the previous decade. The study site is part of a larger national wildlife refuge (and is a LTER site) with restricted access and it can be expected that this population of box turtles should persist well into the future because it will not be affected by most impacts associated with human populations.

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