CHELONIAN CONSERVATION AND BIOLOGY
International Journal of Turtle and Tortoise Research

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HUGH R. QUINN[1,2,*], HOLLY QUINN[1,2], AND ALESSANDRA HIGA[1]

[1]*Department of Math and Science, Oglala Lakota College, Kyle, South Dakota 57752 USA [DoubleHQ@aol.com; ahiga@olc.edu];*
[2]*8200 Red Deer Road, Rapid City, South Dakota 57702 USA*
**Corresponding author*

Chelonian Conservation and Biology, 2014, 13(1): 65–71
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Hugh R. Quinn[1,2,*], Holly Quinn[1,2], and Alessandra Higa[1]

[1]*Department of Math and Science, Oglala Lakota College, Kyle, South Dakota 57752 USA [DoubleHQ@aol.com; ahiga@olc.edu];*
[2]*8200 Red Deer Road, Rapid City, South Dakota 57702 USA*
**Corresponding author*

Abstract. – Copulation in South Dakota ornate box turtles (*Terrapene ornata*) was observed from April through September, with oviposition of 2–5 ($\bar{x}$ = 4.3) eggs in June. Growth was rapid during the first few years of life but slowed thereafter, with adult females attaining significantly larger ($p < 0.001$) carapace ($\bar{x}$ = 117.8 mm) and plastron ($\bar{x}$ = 123.9 mm) lengths (CL and PL, respectively) than did adult males ($\bar{x}$ CL = 114.5 mm, $\bar{x}$ PL = 118.1 mm). Both sexes can mature by age nine, with our smallest adult female (CL = 112.1 mm, PL = 115.5 mm) larger than our smallest adult male (CL = 107.9 mm, PL = 110.4 mm).

Key Words. – Reptilia; Testudines; Emydidae; *Terrapene ornata*; ornate box turtle; reproduction; growth; South Dakota

Ornate box turtles (*Terrapene ornata*) are found throughout much of the North American Great Plains from northern Mexico to South Dakota and Wisconsin (Ernst and Lovich 2009). In South Dakota, near the northernmost extent of their range, ornate box turtles occur in the south-central portion of the state (Ballinger et al. 2000; Backlund 2004; Kiesow 2006). Considered a Species of Greatest Conservation Need within the state (South Dakota Department of Game, Fish and Parks [GF&P] 2006), ornate box turtles were known from only 19 specimens as of 2010, prior to the onset of this study (South Dakota GF&P Natural Heritage Database).

Information regarding various aspects of reproduction or growth (or both) of this species has been reported for turtles from Colorado, Illinois, Indiana, Kansas, New Mexico, Oklahoma, and Wisconsin (Brumwell 1940; Marr 1944; Legler 1960; Minton 1972; Blair 1976; Bull 1980; Vogt 1981; Caldwell and Collins 1981; Metcalf and Metcalf 1985; Packard et al. 1985; Temple 1987; Packard and Packard 1988; Doroff and Keith 1990; Collins 1993; Nieuwolt-Dacanay 1997; St. Clair 1998; Converse 1999; Hammerson 1999; Converse et al. 2002; Bowen et al. 2004). However, no life history information has been reported for ornate box turtles from South Dakota. Geographic variation in reproduction and growth has been reported in this species. For example, 2 clutches per year are common in Kansas (Legler 1960), but in Wisconsin and New Mexico not all females reproduce annually (Vogt 1981; Doroff and Keith 1990; Nieuwolt-Dacanay 1997); clutch sizes are smaller in New Mexico than in Kansas or Wisconsin (Legler 1960; Doroff and Keith 1990; Nieuwolt-Dacanay 1997); and males and females mature at an earlier age in Texas than in Kansas (Legler 1960; Blair 1976). Therefore, in designing conservation programs for ornate box turtles, life history traits of populations specific to geographic areas where such programs are to be implemented need to be utilized. It is the purpose of this study to provide such information on South Dakota populations by reporting observations on reproduction and growth.

METHODS

Study Area. — Our approximately 310-ha study site was located in northern Shannon County, South Dakota. Two macrohabitat types were identified within the area, which we termed uplands and lowlands (described in the literature as Sands and Clayey, respectively) (US Department of Agriculture–Natural Resources Conservation Service [USDA-NRCS] 2001, 2008), separated by transition zones. Upland habitat was characterized by deep sandy soils, and representative vegetation included sand sagebrush (*Artemisia filifolia*), western ragweed (*Ambrosia psilostachya*), prairie sand reed (*Calamovilfa longifolia*), annual wild buckwheat (*Eriogonum annuum*), and hairy grama (*Bouteloua hirsuta*). Lowland habitat was characterized by clay soils, and representative vegetation included wooly verbena (*Verbena stricta*), western ragweed (*Ambrosia psilostachya*), western wheat grass (*Agropyron smithii*), Japanese brome (*Bromus japonicus*), slimflower scurfpea (*Psoralea tenuiflora*), and blue grama (*Bouteloua gracilis*).

Locating Turtles. — Ornate box turtles were located by walking in habitat during their active season, from the end of April through mid-October 2010 and 2011, and also during the first 2 wk of June in both years by using turtle-sniffing dogs (which have been successfully used to locate ornate box turtles as well as other terrestrial turtle species; Converse 1999; Converse et al. 2002; Cablk and Heaton 2006). A few turtles were captured as they crossed roads or were brought to us by individuals in response to ''Wanted'' posters placed in key areas such as stores, schools, and a park visitor center near our study site. These posters were also distributed to individuals encountered in the field and elsewhere.

Reproduction. — Ornate box turtles were assumed to be juveniles if they were smaller than approximately 110

mm carapace length (CL) and had no obvious secondary sex characteristics (Legler 1960; Converse 1999). Males demonstrate secondary sex characteristics at maturity (red eyes and red or orange coloration on the forelimbs), but females do not (Legler 1960). However, Legler (1960) determined by dissection that Kansas ornate box turtle females matured at approximately 110 mm CL, so this was the measure we adopted to indicate female maturity in our population. Turtles were also marked by shell notching using a system adapted from Cagle (1939).

On 7 June 2010, 13 ornate box turtles were X-rayed to detect oviducal eggs following the method described by Gibbons and Greene (1979). Egg-laying dates of a subsample of those X-rayed were determined by weighing 3 gravid females in the field daily to detect weight loss approximately equivalent to 10 g/egg (Legler 1960). To track these females, they were fitted with 3.6-g model R1680 transmitters and were located using an R410 receiver and collapsible three-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN). Each turtle was also fitted with a temperature data logger (Thermochron iButtons, model #DS1922L-F5, Embedded Data Systems, Lawrenceburg, KY) as part of a broader ecological study involving 25 ornate box turtles in 2010 and 24 in 2011 (all equipped with transmitters and temperature data loggers; results to be presented elsewhere). Transmitters and data loggers were glued to carapaces using 5-min epoxy, with transmitters positioned on the third and fourth right pleural scutes and data loggers positioned on the same scutes on the left side. Both devices were smoothly contoured with plumber's epoxy putty for ease of turtle movement, and the putty was rubbed with dirt for camouflage. Transmitters, data loggers, glue, and putty did not exceed 6% of turtle body mass.

Growth. — Standard methods were used for measuring CL, plastron length (PL), interabdominal seam length, abdominal lamina growth ring length (scute growth zones), and body mass for each ornate box turtle captured (e.g., Legler 1960). When plastrons were not in a flat plain due to closure of the shell, PL was measured as the sum of the anterior and posterior lobes, which are divided by the hinge. An estimate of age was made by counting growth rings (Legler 1960; Zug 1991; Germano and Bury 1998); however, the plastrons of many turtles were too worn to accurately detect such rings. If some, but not all, growth rings could be counted the age was indicated as being greater than the number of rings observed. Several authors have questioned the reliability of using growth annuli to estimate turtle age (Cox et al. 1991; Kennett 1996; Brooks et al. 1997). Germano and Bury (1998) reviewed these and other studies and concluded that, with few exceptions, counting scute annuli is a reliable method of estimating ages of chelonians (1 annulus corresponds to 1 yr) and can be used to determine the age of individuals, often to or near the age of maturity. Furthermore, the validity of scute rings being deposited annually has been shown for many turtle species including ornate box turtles (Legler 1960; Schwartz et al. 1984). We therefore concluded that counting scute annuli to estimate age of ornate box turtles in our study population was a reliable method for those turtles that did not have too much shell wear.

The lengths of growth rings on the abdominal lamina were used to estimate the approximate lengths of the plastron at the time each was formed. This process is based on a formula derived by Legler (1960) and can estimate PL at ages estimated from plastral annuli. The formula is $AB/PL = AB^n/X$, where AB is the current abdominal length, PL the current plastron length, AB^n the length of the growth ring at age n winters, and X is the plastron length at the time the growth ring AB^n was formed.

Data were examined for homogeneous variances using Levene's test. We used Student t-tests to compare mean estimated plastron sizes between sexes for each age class as well as to compare CL and PL between sexes of adults encountered in the field. Statistical inferences were made at $\alpha = 0.05$ for all comparisons unless otherwise stated in the text. We performed statistical analyses with SPSS Statistics for Windows (IBM Corp 2011).

RESULTS

Turtles Located. — A total of 170 living and 9 dead individual ornate box turtles were found during the course of the 2-yr study. While most of these specimens (87%) were found at our study area, a few (13%) were located in scattered locations in Shannon, Jackson, Pennington, and Todd counties. Of the live turtles, 67 were males, 69 were females, and 34 were juveniles (0.97:1:0.49). Sex could not be determined on the dead turtles as they either were juveniles, were too mutilated, or were represented by only bone fragments.

Reproduction. — Copulation was observed on 6 occasions, once in each month from April through September, and all were seen during morning hours except 1 in early afternoon (Table 1). One male was observed copulating twice, with separate females on each occasion. All other individuals were observed copulating only once. Minimum and maximum CLs of males observed copulating were 111.4 and 120.6 mm and those of females 114.4 and 125.3 mm. Minimum and maximum PLs of males were 110.7 and 126.5 mm and those of females 116.8 and 129.1 mm. Two females, 1 observed copulating on 26 July 2010 and 1 on 9 August 2010, had been X-rayed earlier in the year (June) and contained oviducal eggs. With one exception, the plastrons of all animals observed copulating were too smooth to accurately count complete sets of growth rings (complete sets are those in which all growth rings formed on a plastral scute can be counted, and incomplete sets are those with some rings distinct and others too worn to accurately count), but 1 male had more than 8 and 1 female more than 12. The exception was a male with 15 growth rings.

Eleven adult females were X-rayed on 7 June 2010 and 7 contained eggs (64%) (Tables 2 and 3). Additionally,

Table 1. Observed copulations of South Dakota ornate box turtles (*Terrapene ornata*) during 2010–2011. Dashes in the age columns indicate that the plastron was too worn to count growth rings. Dashes in the carapace and plastron length columns indicate no such measures were made.

Date	Time (hrs)	Male age (yrs)	Female age (yrs)	Male carapace length (mm)	Female carapace length (mm)	Male plastron length (mm)	Female plastron length (mm)
20 Sep 2010	0820	—	—	—	115.7	—	122.5
26 Jul 2010	0730	—	—	—	114.4	—	121.7
9 Aug 2010	0850	> 8	—	120.6	122.2	123.3	129.1
28 Apr 2011	1100	—	> 12	111.4	125.3	110.7	127.4
3 May 2011	1315	15	—	111.7	116.5	115.3	119.6
20 Jun 2011	0919	—	—	119.0	115.3	126.5	116.8

2 juveniles of unknown sex were X-rayed and neither contained eggs. Both juveniles were 8 yrs old and had CLs of 104.6 and 105.9 mm and PLs of 110.5 and 106.3 mm. For the adult females clutch sizes ranged from 2 to 5, with an average of 4.3 (Table 2). The 3 females, which were weighed daily to detect egg deposition, laid their eggs during the night of 15–16 June, presumably in upland habitat because the closest lowland habitat was approximately 0.5 km from the site, and the female pre– and post–weight-loss locations were all within a few meters of each other. No nests were found in spite of intensive search efforts. Based on weight loss of females, average egg mass was estimated at 12.0 g. Clutches averaged 13.6% of female mass (Table 2). With 2 exceptions, the plastrons of all females X-rayed with eggs were too smooth to count complete sets of growth rings accurately. The 2 exceptions had 9 and 14 growth rings. Three females had more than 12 growth rings, one had more than 13, and no growth rings could be counted on the remaining animal as the plastron was too worn. Minimum and maximum CLs for females with eggs were 113.2 and 125.3 mm. The smallest clutch size ($n = 2$) was from the smallest female.

The 4 X-rayed females that contained no eggs ranged in CL from 112.1 to 124.3 mm (Table 3). One of these females had 9 growth rings and 1 had more than 19 (with additional rings that could not be reliably counted), and 2 had plastrons too worn to count rings.

Growth. — Complete sets of growth rings were visible enough to count on 28 (16%) ornate box turtles, with ages ranging from 1 to 15 yrs. While 15 was the maximum number of growth rings we counted in the above sample (ornate box turtles with complete sets of growth rings), we estimated that many turtles older and younger than 15 yrs had growth rings too worn to count. For example, 1 turtle had 19 growth rings but also had additional rings that could not be reliably counted. The first growth ring is formed during the first winter, which begins a month or so after hatching, and turtles may or may not grow during this period (Legler 1960). Based on growth ring size data, mean PL at their first winter was 31.7 mm (Table 4). Although males were estimated to be larger than females each year until age 8 yrs, none of these differences were significant ($p > 0.05$). At this age, female size surpassed that of males until age 11. However, beyond age 9, sample sizes were too small to make reliable growth assessments. Samples were small because plastrons became worn in older animals, making age estimation difficult.

Based on growth ring measurement data, the annual percent increase in PL was greatest in young animals and gradually decreased as animals aged (Table 4). Animals continued to grow through age 9, and may have continued to do so at later ages but, as noted above, samples were too small to make reliable growth assessments for older turtles.

For all adults measured in the field, females were significantly larger than males in both CL and PL ($t_{124} = 3.31$, $p = 0.001$, and $t_{107.7} = 5.87$, $p < 0.001$, respectively) (Table 5).

Of known-age turtles, the youngest males exhibiting secondary sex characteristics were 9 yrs old and had a mean CL and PL of 110.8 and 111.7 mm, respectively (Table 6). Of these, the smallest individual had a CL and PL of 107.9 and 110.4 mm, respectively. The youngest adult females had a mean CL and PL of 112.6 and

Table 2. Clutch sizes of 7 South Dakota female ornate box turtles (*Terrapene ornata*) as visualized on X-ray 7 June 2010. Estimated clutch mass represents changes in weight of females before and after egg laying. Percentage of female weight loss from laying eggs was calculated as [(female pre–egg-laying weight − female post–egg-laying weight)/(pre–egg-laying weight)] × 100. Dashes in the age column indicate that the plastron was too worn to count growth rings. Dashes in the remaining columns indicate no data are available.

Age (yrs)	Carapace length (mm)	Plastron length (mm)	No. of eggs	Estimated clutch mass (g)	Estimated mean egg mass (g)	Female % weight loss
> 12	116.4	121.5	5	65	13	13.8
> 12	125.3	127.4	4	60	12	11.8
> 12	—	—	5	55	11	15.3
9	113.2	117.9	2	—	—	—
—	122.1	129.1	5	—	—	—
> 13	119.3	123.2	5	—	—	—
14	114.4	121.7	4	—	—	—

Table 3. Female South Dakota ornate box turtles (*Terrapene ornata*) found not to contain eggs upon X-ray 7 June 2010. Dashes in the age column indicate that the plastron was too worn to count growth rings.

Age (yrs)	Carapace length (mm)	Plastron length (mm)
> 19	118.4	121.5
9	112.1	115.1
—	124.3	130.4
—	116.7	125.0

116.7 mm, respectively, and were 9 yrs old. The smaller of these 2 females had a CL and PL of 112.1 and 115.5 mm, respectively.

DISCUSSION

Reproduction. — While we found nearly an equal number of male and female ornate box turtles (0.97 males:1 female), sex ratios in other populations suggest that females predominate, with 0.58 males:1 female in Kansas (Legler 1960), 0.7:1 in Illinois (Bowen et al. 2004), 0.64:1 in Wisconsin (Doroff and Keith 1990), and 0.58:1 (Converse 1999) and 0.51:1 in western Nebraska (Converse et al. 2002). However, recent data from Wisconsin and Arizona suggest that sex ratios are approximately equal in those populations (Hall and Steidl 2003; Redder et al. 2006). Variation in observed sex ratios across the range of this species could be due to variation in differential survival between sexes. Additionally, temperature may play a key role in sex ratio variation, as ornate box turtles demonstrate temperature-dependent sex determination, with females usually resulting from incubation temperatures above 29°C (Bull 1980; Packard et al. 1985; Packard and Packard 1988); however, the pivotal temperature at which equal sexes are produced is unknown. Vogt and Bull (1982) reported that sex ratios in chelonians might vary due to the interacting effects of weather, environmental temperature and humidity, nest site location and depth, and oviposition dates. Also, differences in behavior between sexes may impact detection, but no such differences have been observed in adult ornate box turtles for such behaviors as the extent of seasonal movements (home range size) or the timing and duration of daily movements (except female nocturnal nesting activity) (Legler 1960; Doroff and Keith 1990).

Table 5. Comparison of mean carapace and plastron lengths of adult male and female South Dakota ornate box turtles (*Terrapene ornata*).

	Mean (mm) ± SD (*n*)[a]	
Sex	Carapace	Plastron
Male	114.5 ± 6.1 (59)*	118.1 ± 6.1 (59)*
Female	117.8 ± 5.2 (67)*	123.9 ± 4.6 (67)*

[a] * Significant differences between sexes, $p \leq 0.05$.

Legler (1960) reported that courtship and mating in Kansas are most common in the spring, soon after emergence from hibernation, but occasionally take place in the summer or fall. Brumwell (1940) also noted mating in May from Kansas. Copulation was observed in Wisconsin from 28 May until 6 September (Vogt 1981; Temple 1987; Doroff and Keith 1990), but the earliest and latest matings for the species were observed in Texas on 5 April and 13 October (Blair 1976). We observed mating 6 times, once during every month from 28 April to 20 September (Table 1). Ernst and Lovich (2009) reported that both males and females might copulate several times a season, particularly during the spring, and with more than one partner. We did not observe any individuals mating more than once a year, but we did see a male copulating with 2 different females, one on 26 July 2010 and the other 28 April 2011.

Nesting has been reported from early May to mid-July in Kansas but was most frequent in mid-June (Legler

Table 4. Plastron lengths as calculated for various ages from annual growth rings measured in adult male and female South Dakota ornate box turtles (*Terrapene ornata*). Combined figures are those calculated from males, females, and juveniles collectively. H represents plastron length during the first winter. Percentages represent length increases from previous year. Dashes indicate either current or previous year measures are unavailable.

Age (yrs)	Male mean plastron length (mm) ± SD (*n*)	Male % length increase	Female mean plastron length (mm) ± SD (*n*)	Female % length increase	Combined mean plastron length (mm) ± SD (*n*)	Combined % length increase
H	33.9 ± 5.4 (13)	—	29.6 ± 5.0 (9)	—	31.7 ± 5.9 (39)	—
1	43.8 ± 6.0 (13)	29.3	39.2 ± 4.6 (9)	39.2	40.6 ± 6.3 (37)	28.3
2	52.2 ± 6.1 (12)	19.1	49.3 ± 5.1 (8)	25.6	49.8 ± 6.6 (35)	22.4
3	59.9 ± 7.8 (12)	14.8	57.5 ± 2.8 (7)	16.6	57.5 ± 7.8 (32)	15.7
4	67.1 ± 7.2 (12)	12.0	65.2 ± 6.5 (7)	13.4	63.7 ± 8.7 (29)	10.8
5	75.2 ± 8.3 (11)	12.1	71.3 ± 4.4 (7)	9.5	72.2 ± 9.8 (27)	13.2
6	81.7 ± 9.8 (10)	8.8	78.7 ± 4.9 (8)	10.3	78.4 ± 10.6 (26)	8.7
7	89.5 ± 9.5 (10)	9.5	88.8 ± 6.8 (8)	12.8	86.1 ± 10.8 (24)	9.8
8	95.3 ± 8.9 (8)	6.5	97.1 ± 5.7 (8)	9.4	92.8 ± 10.6 (22)	7.8
9	100.8 ± 8.1 (6)	5.7	107.7 ± 6.4 (7)	10.9	101.9 ± 9.8 (17)	9.8
10	99.6 ± 11.5 (2)	−1.2	103.4 (1)	−4.0	99.8 ± 7.2 (4)	−2.0
11	107.3 (1)	7.8	104.7 (1)	1.3	106.0 ± 1.8 (2)	6.2
12	—	—	120.5 (1)	15.0	120.5 (1)	13.6

Table 6. Carapace and plastron lengths of known-age South Dakota ornate box turtles (*Terrapene ornata*). M, F, and J are male, female, and juvenile turtles, respectively.

Age (yrs)	Sex	*n*	Mean carapace length (mm) ± SD	Mean plastron length (mm) ± SD
1	J	2	44.5 ± 3.0	44.5 ± 6.5
2	J	2	62.7 ± 10.8	63.8 ± 8.4
3	J	1	67.2	71.6
4	J	3	67.5 ± 2.2	68.9 ± 3.2
7	J	2	93.2 ± 3.1	98.3 ± 8.1
8	J	2	96.3 ± 11.8	98.7 ± 16.6
9	M	3	110.8 ± 3.1	111.7 ± 2.0
	F	2	112.6 ± 0.8	116.7 ± 1.8
	J	2	103.6 ± 5.6	108/.0 ± 7.8
10	M	2	111.5 ± 3.0	115.8 ± 1.8
	F	1	111.6	113.4
	J	1	103.2	97.3
11	M	1	135.0	130.0
	F	2	116.7 ± 0.9	121.9 ± 1.6
12	F	1	116.2	124.1
15	M	1	111.7	115.3

1960). In Wisconsin, nesting has been reported from May through June (Vogt 1981; Temple 1987; Doroff and Keith 1990). Nieuwolt-Dacanay (1997) found gravid female desert box turtles, *Terrapene ornata luteola*, from May through August in New Mexico. Based on weight loss, 3 females we followed laid eggs during the night of 15–16 June (Table 2). Although we never found the nests, they were assumed to be constructed in upland habitat that consists of deep sandy soils with scattered grasses, forbs, and shrubs. Ernst and Lovich (2009) reported that preferred nesting sites are similar to our South Dakota turtles, with open, well-drained areas that provide soft substrates.

Not all adult females we X-rayed contained eggs. Possible reasons for this observation are that 1) eggs were already laid, 2) eggs were not developed enough to visualize on X-ray but may develop and be laid later in the year, or 3) not all females reproduce every year. Our project was too short in duration to determine frequency of egg laying. In Kansas, all adult females apparently laid eggs each year, with about 33% producing a second clutch in late June or early July (Legler 1960). In contrast, over a 3-yr period in New Mexico, percentages of gravid female *T. o. luteola* ranged from 41.9% and 61.3% for 2 wet years to only 10% during a dry year (Nieuwolt-Dacanay 1997). Additionally, only 58% of females laid eggs in consecutive years. Doroff and Keith (1990) did not observe double-clutching in their Wisconsin population and noted that during a 2-yr period only 57% of the females laid eggs. Of the 11 females we X-rayed on 7 June 2010, 7 (64%) contained eggs (Tables 2 and 3). This is roughly in line with the New Mexico population figures during wet years, as well as those for Wisconsin populations, but is well below the 100% figure cited for Kansas. Variation in these figures could be due to spring rainfall amounts, as proposed by Nieuwolt-Dacanay (1997), with more females nesting in wet years than in dry. Because we only X-rayed females 1 yr, we have no information with which to judge how our population would respond to rainfall variation. Redder et al. (2006) postulated that because sperm storage is possible in this species, the disparity between localities in the number of breeding females and the number of clutches per year per female is likely due to energy intake, thermoregulatory limitations, or both.

Clutch sizes vary across the range of the species from 1 to 8, with mean clutch sizes of 3.5 for Wisconsin (Doroff and Keith 1990), 4.7 for Kansas (Legler 1960), and 2.7 in New Mexico for *T. o. luetola* (Nieuwolt-Dacanay 1997). Our clutch sizes ranged from 2 to 5, with an average of 4.3 (Table 2), which surpasses the averages for Wisconsin and New Mexico but is slightly less than that reported for Kansas. Ernst and Lovich (2009) reported average egg mass for 65 eggs as 10.5 (8.0–14.3) g per egg. Based on weight loss of females pre– and post–egg laying, our eggs were estimated to average 12.0 g (Table 2), which is within the range of the above figures by Ernst and Lovich (2009). In addition to losing weight from egg mass during oviposition, females also lose weight by placing fluids into the nest cavity. Therefore, our estimated egg mass values exceed actual egg mass. Ernst and Lovich (2009) calculated relative clutch mass (clutch mass as a percent of postpartum female mass) from Legler's (1960) data as 12%, which is lower than our overestimate of 13.6%. Therefore, in terms of overall reproductive strategy, when comparing the South Dakota and Kansas populations, South Dakota females appear to be producing fewer clutches (64% of females laying eggs annually vs. 100% annually plus 33% double clutching) and slightly fewer eggs per clutch (4.3 vs. 4.7) than those in Kansas, but are producing similar or perhaps slightly larger relative clutch masses in the process (12% vs. 13.6%).

Incubation period length is temperature-dependent in ornate box turtles (Legler 1960), but average duration in naturally incubated clutches in Wisconsin was 80 (79–84) d (Doroff and Keith 1990). Based on this incubation period, our clutches would have hatched in early September. Legler (1960) reported that young ornate box turtles in Kansas became active and alert as soon as they hatched and remained so until low temperatures induced quiescence. However, Converse et al. (2002) and Costanzo et al. (1995) reported that the young usually hatched and emerged from the nest in August and September, but some dug beneath the nest cavity and overwintered there, emerging the next spring. Caldwell and Collins (1981) reported that hatching in Kansas usually occurs in the fall but may be delayed until spring if nest conditions are dry. It is unknown whether our South Dakota turtles emerged upon hatching in the fall, buried directly beneath their nests upon hatching to spend the winter, hatched in the spring, or did all the above. However, the adult turtles we observed did not enter hibernation until late September to mid-October, which indicated that conditions were appropriate for at least adult activity after the hatching season. This may or may

not have translated to appropriateness of conditions for hatchling activity. If South Dakota hatchlings did not emerge in the fall, they may not have grown prior to formation of their first growth ring. However, if they did emerge, some growth may have occurred. Thus, our data presented in Table 4 may have overestimated the size of hatchlings, as those figures were based on the relative size of the first growth ring.

Legler (1960) found that sexual maturity seemed more closely correlated with size than age. He found that males matured when smaller and younger than females, with 76% of the males maturing at a PL of 100–109 mm and an age of 8–9 yrs. For females, 66% were mature at a PL of 110–119 mm and an age of 10–11 yrs. For Texas populations, Blair (1976) reported that both sexes matured at a CL of nearly 100 mm, with males achieving that length in 7 yrs and females in 8 yrs. In Colorado, Hammerson (1999) reported that females first reproduced when 11 yrs old. Captive males held under seminatural conditions in Oklahoma matured in 5 yrs and at 100 mm (curved CL), and captive females matured in 8 yrs and at 128 mm (curved CL) (St. Clair 1998). Our smallest male exhibiting secondary sex characteristics had a CL and PL of 103.3 and 104.0 mm, respectively, and this same male was also among the youngest to exhibit these characteristics, at age 9 yrs (Table 6). Therefore, it seems that males in our population mature at roughly the same size and age as those in Kansas, at roughly the same size but an older age than those in Texas, and at an older age than the captives from Oklahoma. CL comparisons cannot be made with the Oklahoma ornate box turtles, as they were measured along the curvature of the shell rather than the straight-line measurements as reported by all other investigators.

Adult females are defined as individuals > 110 mm CL that do not demonstrate male secondary sex characteristics (Legler 1960; Converse 1999). Our smallest ornate box turtle fulfilling these requirements had a CL and PL of 110.2 and 121.3 mm, respectively. The age of this animal could not be estimated, but she had more than 9 growth rings. Another female had a slightly longer carapace (111.6 mm) but had a shorter plastron (113.4 mm). The youngest known-age turtles fulfilling the above requirements were 9 yrs old (Table 6). The youngest known-age female we X-rayed who contained eggs was also 9 yrs old, and she was the smallest female with eggs (CL = 113.2, PL = 117.9 mm) (Table 2). The smallest female observed copulating was larger (CL = 114.4, PL = 121.7 mm). Age could not be determined on any copulating females, as their shells were too worn, but one was > 12 yrs. Therefore, South Dakota female ornate box turtles can mature by age 9, with a CL and PL of 110.2 and 113.4 mm, respectively. Thus, our female turtles matured at roughly the same size as those in Kansas but at a slightly younger age. They also matured at a younger age than those in Colorado but at an older age and larger size than those in Texas. Oklahoma captive females also matured at an earlier age than our animals.

Growth. — In Indiana, hatchlings ranged in size from 28.8 to 37 mm (Marr 1944, Minton 1972). Our hatchling size as calculated from growth-ring data averaged 31.7 mm (Table 4), which falls within the range cited above. Legler (1960) reported mean increments in plastron growth of 68%, 29%, and 18% for the first 3 yrs of life. From the fourth to the 14th yr the growth rate gradually slowed from 13.3% to about 3%. The growth rates we observed in South Dakota were slower during the first 3 yrs of life, averaging 28.3%, 22.4%, and 15.7% (Table 4). Our growth rates then varied from 8.7% to 9.8% to the age of 9 yrs, beyond which time sample sizes were too small to estimate growth. The growth variation observed from animals ages 4–9 yrs may be due to variations within factors contributing to growth. For example, high precipitation and correspondingly high grasshopper numbers have been associated with rapid growth of hatchlings (Legler 1960). Such factors also may explain the slower growth during the first 3 yrs of life in South Dakota turtles compared with those in Kansas. Because our females mature at roughly the same size as those in Kansas, but at a slightly younger age, it suggests that South Dakota females grow faster after their first 3 yrs of life than do Kansas females. Overall, our females grew more rapidly than did males (Table 4), but our sample sizes were too small to estimate growth beyond age 9, the age of the youngest adults of both sexes we observed in our population. However, St. Clair (1998) found that captive Oklahoma males grew more, when adult, than did females.

ACKNOWLEDGMENTS

Funding for this project was provided by South Dakota Game, Fish and Parks Wildlife Action Plan Competitive Grant; the US Fish and Wildlife Service; the National Science Foundation – Tribal Colleges and Universities Program; and Oglala Lakota College. For assistance in the field, we thank Oglala Lakota College students Rebecca Bingham, Osceola Blue Horse, Wendy Green, Michelle LeBeau, Requaw Pavy, and Sheronne White. We thank the Oglala Sioux Parks and Recreation Authority and the South Dakota Department of Game, Fish and Parks (GF&P) for providing the appropriate permission and permits (GF&P permits no. 11 and 18 for 2010 and 2011, respectively) to conduct this research. Our study site was partially located on private land, and we thank Curtis Temple for granting us access. We thank John B. Iverson, Daniel W. Uresk, and two anonymous reviewers for critically evaluating earlier drafts of this manuscript.

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Received: 1 April 2013

Revised and Accepted: 1 October 2013

Handling Editor: Cristina A. Jones