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LIFE HISTORY OF SPINY SOFTSHELL TURTLES (*APALONE SPINIFERA*) IN WESTERN NEBRASKA, USA, WITH A COMPARISON ACROSS ITS RANGE

***JOHN B. IVERSON*[1,4], *RUTH E. CARTER*[2], *AND MATTHEW LACHIUSA*[3]**

[1]*Deptartment of Biology, Earlham College, 801 National Road West, Richmond, Indiana 47374, USA*
[2]*137 East Lockwood Avenue, St. Louis, Missouri 62119, USA*
[3]*10603 East Speedway Boulevard, Tucson, Arizona 85748, USA*
[4]*Corresponding author, email: johni@earlham.edu*

***Abstract*.—We studied Spiny Softshell Turtles (*Apalone spinifera*; 55 total, 118 captures) in and adjacent to Blue Creek in Garden County, Nebraska, USA, from 1999 to 2018. The smallest gravid female was 31 cm maximum carapace length. A von Bertalanffy growth model based on female recaptures suggested reproductive maturity by 12 y of age. Longevity likely exceeds 40 y. Females produced one or (usually) two clutches each year (early to mid-June and late June to early July). Mean clutch size was 29.9 (range 16–42) and tended to increase with female size. Mean egg size averaged 25.4 × 24.4 mm and 8.9 g and increased with female size. There was no evidence of a trade-off between egg size and clutch size, nor of pelvic constraint on egg size. Relative clutch mass (clutch mass/gravid body mass) averaged 5.7% and relative egg mass (mean clutch egg mass/gravid body mass) averaged 0.18%, with the latter declining with female body size. Across populations of *A. spinifera*, body size and clutch size increased with latitude, but egg size decreased. Reproductive output in this population is more hypoallometric than in most other turtles and the similar increases in both clutch size and egg size with body size suggest a bet-hedging rather than an optimal egg-size strategy. Reproductive output of *A. spinifera* was most similar to that of the Florida Softshell Turtle (*A. ferox*), as well as that of the sister genus *Rafetus*; however, the Smooth Softshell Turtle (*A. mutica*) invested significantly more in relative clutch mass and egg mass than the other species.**

Key Words.—Apalone; reproductive output; sandhills; von Bertalanffy

INTRODUCTION

North American softshell turtles (genus *Apalone*) comprise a clade of three species (Thomson et al. 2021), with broad and often overlapping distributions (Turtle Taxonomy Working Group 2025). Each has been the subject of a number of natural history studies (review in Ernst and Lovich 2009), although these studies have been decidedly biased geographically. Because of the difficulty in capturing softshell turtles (especially repeatedly and over years) compared to hard-shelled North American species, however, many aspects of their reproductive ecology remain understudied.

During our turtle research in the western Sandhills of Nebraska, USA, in the 1990s, we discovered a population of Spiny Softshell Turtles (*Apalone spinifera)* beyond the known range of the species at that time (e.g., Conant 1975) along the middle and upper Blue Creek basin north of Oshkosh, Nebraska. Given the lack of reproductive data for *A. spinifera* at that time from the entire Kansas to Montana region, we carried out nearly annual sampling of the population from 1999 to 2018, with a focus on reproductive output.

MATERIALS AND METHODS

Our primary study site was on a private ranch 16.9 km north north-east of Oshkosh, Garden Co., Nebraska, USA. The site lies near the southwestern margin of the Nebraska Sandhills (Bleed and Flowerday 1989). After finding two females dead on a road crossing Blue Creek in 1989 and observing others basking along the creek in subsequent years, in 1998 we began periodically walking along Blue Creek searching for nest sites on sand banks and hand-capturing occasional adults in the shallow water. That year the owner of the ranch along the creek told us about Rattlesnake Pond (Supplemental Information Fig. S1; 41°32’35”N 102°16’06”W; about 1,200 m elevation), a 0.71-ha pond created by excavating and damming the head springs of a lateral, meandering, seepage tributary of Blue Creek in the early 1900s. Most of the pond was about 1 m deep, but some areas adjacent to the dam reached 3 m in depth (Supplemental Information Fig. S2). The pond was also inhabited by stable and large populations of Painted Turtles (***Chrysemys picta;*** 55 kg/ha; Iverson et al. 2006) and Snapping Turtles (*Chelydra serpentina*; 242 kg/ha; Iverson et al. 2000).

River Otters (*Lontra canadensis*) were reintroduced into Nebraska between 1986 and 1991 and quickly repopulated the state (Bieber et al. 2018). One first appeared in Rattlesnake Pond in 2007, simultaneously with many injuries to captured softshell turtles, and a decline in captures (see also Ligon and Reasor 2007). After 2007 otters were not seen again but were likely present.

Beginning in 1999 our work focused on Rattlesnake Pond, but with sporadic pedestrian surveys along Blue Creek. During various periods between late May to early July in 1999–2007, 2009–2010, 2014, and 2017 (depending on our field schedule at nearby Crescent Lake National Wildlife Refuge), we deployed six fyke nets with 18-m leads between a pair of 90-cm diameter hoop traps (mesh 2.5 cm) baited with large pieces of fresh Carp (*Cyprinus carpio*) salvaged from nearby lakes or streams (frozen until use). Funnel traps always reached at least 30 cm above the water to prevent drowning. We replaced bait and checked traps mid-day nearly every day, weather permitting.

In the area near Rattlesnake Pond, Blue Creek is a clear, fast-flowing, meandering, first-order stream, averaging 1 m deep and varying in width from 4 to 10 m. Average annual stream flow for Blue Creek downstream at Llewellen (just east of Oshkosh) from 1930 to 1985 ranged from 1.61–2.75 m^3/s (53–97 ft^3/s) with a mean about 2.41–2.55 m^3/s (85–90 ft^3/s; Bleed and Flowerday 1989). The flow rate precluded our use of traps in the stream itself.

For each captured turtle, we measured maximum carapace length (CL) and maximum plastron length in mm (PL) with tree calipers and body mass (BM) in grams with spring scales. We determined the sex of turtles of all sizes by their sexual dichromatism (Supplemental Information Fig. S3). The ocelli on the carapace of males (even hatchings) have distinct circular rings, whereas those of females have diffuse edges (Graham 1991; Graham and Cobb 1998). In addition, the overall carapace pattern of adult females becomes diffusely marked with a lichen-like pattern, and the cloaca lies farther posterior on the tail in males than in females (Ernst and Lovich 2009).

Early in the study, we individually marked turtles by drilling one or two holes into the rear margin of the cartilaginous shell in a unique clock-like pattern (see Doody and Tamplin 1992). The openings completely healed over within a year, but left distinct visible scars used to identify individuals (Fig. S4). Although the scars remained discernible for at least 19 y, we do not recommend this method given the trauma to the turtle. When the technology emerged, we later replaced the latter method with the insertion of passive integrated transponders (PIT tags; Trovan™; Electronic Identification Devices, Ltd., Santa Barbara, California, USA). under the carapace dorsal to the tail (Gibbons and Andrews 2004).

We radiographed females (Portable Min-Xray™, Northbrook, Illinois, USA) during 11 summers to obtain maximum X-ray egg diameters (ED), clutch sizes (CS), and pelvic aperture widths (PW). We injected 19 gravid females (eight individuals across years) with oxytocin between 1989 and 2009 (Ewert and Legler 1978) to obtain eggs for raw measurements; however, females usually only released partial clutches by this method and hence we suspended the practice after 2009. We also dug eggs from natural nests located serendipitously and we measured all eggs for maximum diameter (EL), diameter at right angles to EL (EW), and weighed all eggs to the nearest 0.01 g (EM). The raw measurements of those eggs are available in Iverson et al. (2024), along with extensive raw data for eggs of the other two species of *Apalone*. Estimates of reproductive output included relative egg mass (REM; mean egg mass in a clutch /gravid female body mass [BM] × 100) and relative clutch mass (RCM; clutch mass/gravid female body mass × 100). We generated Least Squares Linear Regressions of log-transformed CS, EM, and CM on log-transformed CL to explore allometry in those reproductive traits (King 2000; Iverson et al. 2019). To examine a possible trade-off between CS and EM, we used partial correlation analysis to remove the effect of body size (CL).

In 2004 and 2005, we brought 22 eggs (parts of four clutches) obtained by hormone injection back to Indiana and incubated them at 25°–30° C. We measured carapace and plastron lengths (to 1 mm), body mass (to 1 g), and determined the sex of each hatchling (see above). We also injected them with a PIT tag under the rear of the carapace. We mailed each hatchling using overnight delivery to the owner of the study site, who immediately released them into Rattlesnake Pond.

We calculated a von Bertalanffy growth model from our female recapture data using SVL only at first and last capture (Fabens 1965) and anchored using the mean size of hatchlings. We used One-way ANOVAs for multiple mean comparisons, Student's t-tests for two sample comparisons, and Least Squares Linear Regressions to test for linear relationships. For all analyses, we used the STATVIEW™ statistical package (Abacus Concepts, Berkeley, California, USA) with alpha = 0.05. We present all means with

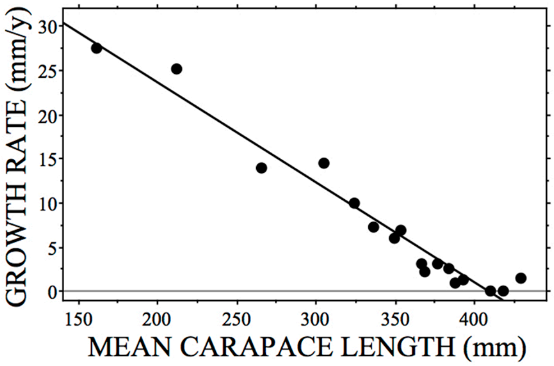

Figure 1. Growth rate (change in carapace length in mm/y between first and last capture) versus mean of carapace lengths at first and last capture for 17 female Spiny Softshell Turtles (*Apalone spinifera*) from Rattlesnake Pond in western Nebraska, USA. The regression line describing the relationship is GR = -0.113MNCL + 46.251; $F_{1,15} = 324.28$, $P < 0.001$, $r^2 = 0.96$).

± 1 standard deviation.

Results

Gravid females captured in late May to mid-June left Rattlesnake Pond, moved overland to Blue Creek, and then traveled up or downstream in search of appropriate nesting sites (unpubl. data). We do not know if softshell turtles overwinter in Rattlesnake Pond. Although spring-fed, dissolved oxygen levels in the pond during winter may not be high enough to allow softshells to overwinter there (e.g., see Reese et al. 2003); the turtles were always present in late May (unpubl. data), presumably taking advantage of higher water temperatures and the abundant food there (crayfish, small fish, and a dense bullfrog tadpole population; unpubl. data).

We captured 55 softshell turtles 118 times, with 16 (29%) recaptured over the course of the study. Two females were captured in 11 y and only one male was recaptured, in 3 y. Our data set was too small to estimate annual survival, but it is noteworthy that every nest we found (n > 50) was depredated before or after we located it. Suspected local predators included Coyotes (*Canis latrans*), Northern Raccoons (*Procyon lotor*), and American Badgers (*Taxidea taxus*).

***Body size and growth*.**—Adult females (91 capture records over 35 y of 43 individuals) averaged 382 ± 29 mm CL (range of values, 314–444 mm CL), 278 ± 20 mm PL (range of values, 221–323 mm PL), and 5,013 ± 1,128 g BM (range of values, 2,350–7,300 g BM). Female plastron length averaged 0.726 ± 0.016 (range of values, 0.688–0.771) that of carapace length. Males presumed to be adults based on elongated tails (15 captures over 11 y of eight individuals) averaged 160 ± 26 mm CL (range of values, 112–194), 114 ± 18 mm PL (range of values, 82–139), and 420 ± 169 g BM (range of values, 139–665). Male plastron length averaged 0.713 ± 0.004 (range of values, 0.680–0.733) that of carapace length.

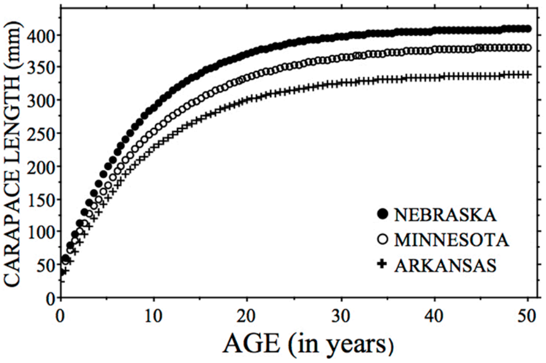

Figure 2. Von Bertalanffy growth models of carapace length (in mm) for female Spiny Softshell Turtles (*Apalone spinifera)*. Locations include Rattlesnake Pond in western Nebraska, USA (this study; see text), the Mississippi River in Minnesota, USA, with a model calculated from data in Table III in Breckenridge 1955: $CL = 383.4(1–0.897e^{-0.097t}$; n = 25), and Gin Creek in Arkansas, USA (transformed from plastron length equation in Plummer and Mills 2015 to carapace length based on the PL/CL ratio 0.726; see text).

Body mass for our entire sample was related to CL by the equation $BM = 0.000161CL^{2.898}$ ($F_{1,163} = 100{,}034$, $P < 0.001$, $r^2 = 0.99$) based on 165 measurements for 87 turtles, including all recaptures and laboratory hatchlings. Hatchlings from parts of four clutches (n = 22) averaged 38.9 mm CL, 28.7 mm PL, and 6.41 g, and did not differ by sex (Table 1). Final recaptures of 17 females (initially 99 mm to 418 mm CL) after 1–19 y (mean 9.1 ± 7.4 y) allowed the construction of a von Bertalanffy growth model (Figs. 1–2): $CL = 409.30(1–0.90496e^{-0.113t}$; $F_{1,15} = 324.28$, $P < 0.001$, $r^2 = 0.96$; where t = age in years, and 409 mm CL is asymptotic size. Three males were recaptured six times, including two tagged hatchlings, and despite the small sample size, provided a preliminary growth curve for males (Fig. 3). These meager male growth data suggest maturity in 4–5 y in western Nebraska, assuming body size maturity at 80–100 mm PL (Webb 1962).

***Maturity and longevity*.**—Our smallest gravid females were 314 mm CL (226 mm PL; 2,818 g) and 329 mm CL (243 mm PL; 3,150 g). We captured two juvenile females, which were 259 and 264 mm CL, and 182 and 192 mm PL, respectively, in mid-June

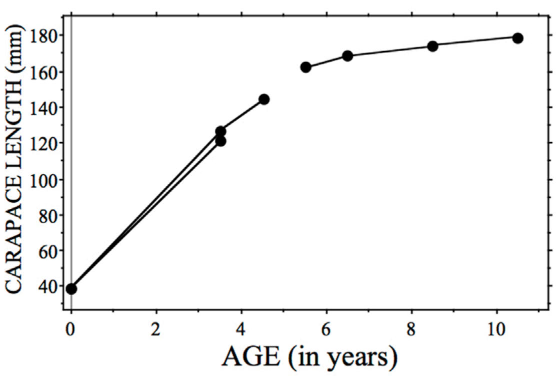

Figure 3. Growth of three male Spiny Softshell Turtles (*Apalone spinifera*) in western Nebraska, USA. Data include two recaptured hatchlings (one recaptured twice) and another male captured four times. Age at first capture of the latter male was estimated from the growth rates of the recaptured hatchlings.

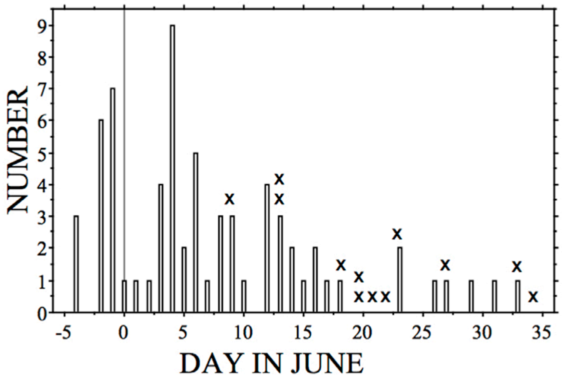

Figure 4. Capture dates of 67 gravid Spiny Softshell Turtles (*Apalone spinifera*) in western Nebraska, USA (bars). Dates of 12 observed nest constructions are indicated with Xs. Note that monitoring was not continuous during each season.

(estimated ages 8.5 y), as well as a 290 mm CL (195 mm PL) female on 30 June with no eggs visible on X-ray. We cannot be certain if the latter female was mature (i.e., it may have nested earlier in the month). Based on our growth curve, 290 and 314 mm CL were reached at estimated ages of 10.0 and 12.0 y, respectively, which are the sizes and ages between which we assume reproductive maturity is reached in this population. We were unable to determine size at maturity in males.

Three females captured in 1999 provided estimates of longevity for females in this population. The first (364 mm CL in 1999) was estimated to be 18.5 y by the growth curve above and was last captured in 2014 (403 mm CL), when she was possibly 33.5 y old (von Bertalanffy age estimate based on size = 36 y). The second (379 mm CL in 1999) was estimated to be 22.2 y old by that growth curve and was last captured in 2017 (396 mm CL) at a possible age of 40.2 y. The last (410 mm CL in 1999) exceeded the asymptotic size (409 mm) at first capture but was estimated by the curve to be at least 30 y old (estimated size 397 mm CL at age 30 y), and was last captured in 2017 (410 mm CL) at a possible age of 48 y. These data suggest that some females in Nebraska may live beyond 40 y.

***Nesting season and frequency*.**—Across years, we captured 67 gravid females between 27 May and 3 July and recorded 12 nests deposited (and immediately depredated) from 9 June to 4 July (Fig. 4). Although trap captures and nest sightings were not random, these data suggest the possibility that two clutches can be produced each year by many females. This possibility was confirmed by a female in 2000 captured when gravid (33 eggs) on 30 May and again on 23 June (26 different eggs), and another captured the same year when gravid on 1 June (CS uncertain; X-ray unclear) and again on 23 June (28 eggs). In addition, two females killed on the road by vehicles while nesting (13 June 1989 and 18 June 1992) were dissected and found to have

Table 1. Comparisons of mean (± 1 standard deviation) carapace length (CL), plastron length (PL), and body mass (BM) for 22 hatchling Spiny Softshell Turtles (*Apalone spinifera*) from western Nebraska, USA, by sex. Range of values in parentheses. Statistical comparisons of males to females are by one-tailed *t*-tests (predicting females to be larger).

Trait	All (n = 22)	Males (n = 12)	Females (n = 10)	*t*-value	*P*-value
CL	38.90 ± 2.11	39.13 ± 1.40	38.63 ± 2.79	-0.55	0.29
	(33.5–42.0)	(37.3–41.3)	(33.5–42.0)		
PL	28.67 ± 1.57	28.55 ± 1.30	28.82 ± 1.91	0.39	0.35
	(25.5–30.9)	(27.0–30.9)	(25.5–30.8)		
BM	6.41 ± 0.33	6.32 ± 0.20	6.51 ± 0.43	1.37	0.09
	(5.68–6.99)	(5.98–6.59)	(5.68–6.99)		
PL/CL	0.74 ± 0.03	0.73 ± 0.03	0.75 ± 0.03	1.31	0.10
	(0.66–0.81)	(0.66–0.76)	(0.70–0.81)		

Figure 5. Nest site of Spiny Softshell Turtle (*Apalone spinifera*) in western Nebraska, USA, which was abandoned mid-nesting when the female was accidentally disturbed. Note the diagnostic pair of lateral aprons of excavated soil, often evident long after nesting. Female was faced toward Blue Creek (top of image), into which she bolted upon our approach. (Photographed by John Iverson).

shelled clutches of 33 eggs each and also enlarged ovarian follicles numbering 30 (16–21 mm diameter) and 22 (18–19 mm), respectively, suggesting second clutches. Finally, a female that drowned in a trap on 30 May 1999 also had 38 shelled oviducal eggs as well as 18 enlarged follicles (16–19 mm) and six others (12–15 mm). None of these three dissected females had enough smaller follicles to suggest the production of a third clutch.

Based on our telemetry, it appears that several females may have produced only a single clutch in the year of telemetry, even though they were known to produce two clutches in other years, possibly due to transmitter attachment. Of the two most frequently captured turtles, one was captured in each of the 11 y during which we radiographed and was gravid in at least 10 of those years. In 2007 she was captured but not found with eggs; however, that year she exhibited serious shell lacerations that we attributed to otters and she may not have reproduced as a result. She recovered and was found gravid during two subsequent sampling years. The second female was captured during 10 of the 11 y during which we radiographed and was found gravid in each year. Based on the two most frequently captured turtles, females rarely skip reproduction in a given year.

***Nesting sites, construction, and size*.**—We never observed nesting or depredated softshell turtle nests in the uplands anywhere within 200 m of Ratttlesnake Pond; however, we identified dozens of nesting crawls, depredated nests, and a few undisturbed nests in sand banks along Blue Creek, most within 10 m of the stream. Our telemetry work in 2000–2001 demonstrated that females were most abundant in Rattlesnake Pond by late May. The pond water was much warmer than that in the stream at that time (unpubl. data), which may have facilitated more rapid follicle maturation, ovulation, and shelling of oviducal eggs (Ewert 1979, 1985).

Table 2. Comparison of clutch size between first and second clutches for five individual female Spiny Softshell Turtles (*Apalone spinifera*) in western Nebraska, USA. Females in 1989 and 1992 found killed on nests on sandy, unpaved roads; dissected 1999 female drowned in trap. Second clutch size in dissected females estimated from counts of enlarged ovarian follicles. The means (± 1 standard deviation) of first and second clutch sizes differed significantly ($t = 17.0$, df = 4, $P < 0.001$).

First date	Clutch size	Second date	Clutch size	Basis
13 June 1989	30	–	29	Dissection
18 June 1992	33	–	22	Dissection
6 June 1999	32	27 June 1999	28	X-rays
30 May 1999	38	–	24	Dissection
30 May 2000	33	23 June 2000	26	X-rays
Means	33.2 ± 3.0		25.8 ± 2.9	

We observed parts of nest construction numerous times, but because females were so wary, we never observed a complete sequence. Nevertheless, construction was very stereotypical. Once a female chose a site (always in open sandy, unvegetated ground away from any cover), she began excavating the nest with her rear feet. As she pulled out soil alternately with each foot, she forcefully flung the soil to the side opposite the foot. Hence, as construction proceeded, she produced a wide apron of spoil up to 2 m from either side of the nest site (Fig. 5). These aprons were often evident up to several days following nest completion.

Six undisturbed nests that we excavated were Florence flask-shaped, although the nest chamber itself was narrower side-to-side than from anterior to posterior because the female excavated more soil forward in the bowl, under her body. Nest neck diameter averaged 54 mm (40–63 mm), length of neck averaged 78 mm (76–80), distance from soil surface to top of eggs averaged 97 mm (69–122), maximum nest depth averaged 168 mm (154–183), nest chamber width averaged 110 mm (98–118), and nest chamber length averaged 130 mm (119–141). No consistent directional orientation of nests was evident.

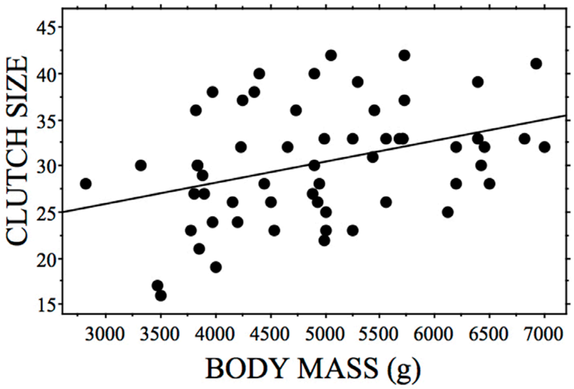

Figure 6. Relationship between body mass (BM) and clutch size (CS) for 59 clutches of Spiny Softshells (*Apalone spinifera*) from western Nebraska ($F_{1,57} = 9.03$, $P < 0.004$, $r^2 = 0.14$).

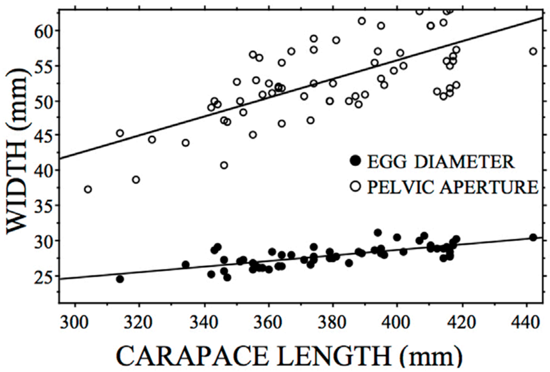

Figure 7. Relationship of x-ray egg diameter (mean per clutch) and X-ray pelvic aperture width to carapace length (in mm) for Spiny Softshell Turtles (*Apalone spinifera*) in western Nebraska, USA, demonstrating a lack of pelvic constraint. For egg diameter, $F_{1,54} = 63.81$, $P < 0.001$, $r^2 = 0.55$, n = 56; for pelvic aperture, $F_{1,66} = 61.27$, $P < 0.001$, $r^2 = 0.48$, n = 68.

***Clutch size*.**—Clutch size averaged 29.9 ± 6.5 (range of values, 16–42; n = 64) and was significantly related to body mass (Fig. 6; $F_{1,57} = 9.03$, P < 0.004, $r^2 = 0.14$), but not with CL ($F_{1,57} = 3.24$, $P = 0.077$, $r^2 = 0.05$). Clutch size of 56 clutches laid early in the year (20 June or before) did not differ significantly from that of eight late clutches ($t = 0.61$; df = 62, $P = 0.273$). Actual and estimated clutch sizes for first and second clutches were available for five females (Table 2) and suggested that the later clutch was typically smaller than the first within individuals. The slope of the log-log regression of CS on CL (logCS = 0.766logCL–0.504; $F_{1,57} = 4.15$, $P = 0.046$, $r^2 = 0.07$) suggests that CS varies hypoallometrically with body size.

***Egg size*.**—Maximum egg length (EL) of 407 eggs averaged 25.45 ± 1.31 mm (range of values, 22.5–30.0), egg width (EW, perpendicular to EL) of 312 eggs averaged 24.43 ± 1.32 mm (range of values, 21.0–27.65), and egg mass (EM) of 407 eggs averaged 8.89 ± 1.31 g (range of values, 5.93–12.93). EL was related to EM by the equation EM = 0.960EL–15.545 ($F_{1,405} = 5{,}000$, $P < 0.001$, $r^2 = 0.92$). Averaged across individual clutches, mean EL was 25.8 ± 1.3 (22.8–28.3; n = 26), mean EW was 24.8 ± 1.2 (23.0–27.0; n = 17), and mean EM was 9.14 ± 1.30 (7.21–12.05; n = 26). One female in 2006 produced a single, spherical, yolk-less egg (20.9 EL; 4.91 g EM) among a clutch of 27 normal eggs.

Mean EL across clutches was significantly related to both CL ($F_{1,19} = 16.49$, $P < 0.001$, $r^2 = 0.47$) and BM ($F_{1,19} = 17.33$, $P = 0.005$, $r^2 = 0.48$), as was mean EW ($F_{1,10} = 19.66$, $P = 0.001$, $r^2 = 0.66$; and $F_{1,10} = 19.85$, $P = 0.001$, $r^2 = 0.67$; respectively). Mean clutch maximum egg diameter (ED) from radiographs was also significantly related to CL ($F_{1,54} = 63.81$, $P < 0.001$, $r^2 = 0.55$; Fig. 7), although mean ED over time in the four females with the most data showed no clear pattern of increase (Fig. 8). Radiographs were available for two females for both their first and second clutches within the same year. Mean ED increased very slightly in the first female (27.72 to 27.89 mm) but decreased in the second female (29.19 to 28.88 m). Whether egg size varies across clutch number could not be detected.

Mean EM ($F_{1,19} = 17.32$, $P < 0.001$, $r^2 = 0.48$) across clutches was also significantly related to CL ($F_{1,19} = 17.32$, $P < 0.001$, $r^2 = 0.48$; Fig. 9) and BM ($F_{1,19} = 23.28$, $P < 0.001$, $r^2 = 0.55$). For all available mean clutch egg masses, those from 20 June or before (9.35 ± 1.22; n = 21) averaged significantly larger than those after that date (8.28 ± 1.22; n = 5; $t = 1.78$; df = 24; $P = 0.044$). Egg elongation (EL/EW) averaged 1.04 ± 0.02 (range of values, 1.00–1.12; n = 312), but EL/EW by clutch was not significantly related to CL ($F_{1,10} = 0.02$, $P = 0.880$) or BM ($F_{1,10} = 0.01$, $P = 0.922$). Pelvic aperture width (PW) from radiographs significantly increased with CL ($F_{1,66} = 61.27$, $P < 0.001$, $r^2 = 0.48$; Fig. 7). In addition, PW averaged about twice mean egg diameter from the same radiographs (Fig. 7), clearly demonstrating a lack of pelvic constraint on egg size.

Relative egg mass (REM; mean clutch egg mass/gravid body mass) averaged 0.18 ± 0.02% (range of values, 0.15–0.23; n = 21) and was significantly negatively related to CL ($F_{1,19} = 9.78$, $P = 0.006$, $r^2 = 0.34$) and BM ($F_{1,19} = 13.97$, $P = 0.001$, $r^2 = 0.42$). The log-log relationship of CL to EM (logEM = 1.508logCL–2.934) was significant ($F_{1,19} = 18.89$, $P < 0.001$, $r^2 = 0.50$) and the slope of the line suggests that CS varies hypoallometrically with body size. CS

Table 3. Adult female carapace length (CL in mm) in Spiny Softshell Turtles (*Apalone spinifera*) from across its range, in order of declining latitude. Literature values with n ≤ 3 and/or including juveniles are not included. Some CL values were estimated (*) from published plastral lengths (PL) based on the PL/CL ratio in the present study (0.726). CL value for Montana reported as curved CL. Question marks for low range values indicate the inclusion of juveniles by the authors.

State	Latitude	Mean CL	Range	n	Source
Montana	47.7	329	—	43	Tornabene 2014
Minnesota/Wisconsin	45.5		?–412	207	DonnerWright et al. 1999; Donner and Brown 2022
Minnesota	45	368	326–398	6	Schneider et al. 2019
Minnesota	45	317	279–394	40	Breckenridge 1955 (Table II; assumes maturity at 279 mm)
Vermont/NY	45	345	300–397	9	Galois et al. 2002
Vermont	44.6	—	?–365.3	17	Graham and Graham 1997
South Dakota	42.9	—	?–405	17	Bandas 2003; Bandas and Higgins 2006
South Dakota	42.9	354	294–415	4	Timken 1968 (estimated from Fig. 20)
Nebraska	41.5	382	314–444	91	This paper
Pennsylvania	—	362	—	—	Hulse et al. 2001
Indiana	41.5	355	283–433	45	Iverson unpublished
Indiana	41.1	309	279–330	5	Evermann and Clark 1920
Illinois/Missouri	37.5	—	?–442	37	Barko and Briggler 2006
Missouri	36.5	404	—	15	Nickerson et al. 2019
Tennessee	35.9	293*	—	25	Robinson 1974 (Fig. 7); Robinson and Murphy 1978
Arkansas	35.2	315*	262–427	25	Plummer and Mills 2008
New Mexico	—	—	?–367	51	Degenhardt et al. 1996
Texas	—	337	280–426	40	Brown et al. 2020 (assuming maturity at 280 mm)
Coahuila	26.9	252	232–294	9	Legler and Vogt 2013
Texas	26.2	307	248–364	37	Grosmaire 1977

and EM were not significantly related ($F_{1,21}$ = 1.57, P = 0.233), nor were the residuals of their regressions with CL ($F_{1,16}$ = 0.02, P = 0.879). Hence, there is no evidence of tradeoff between these two variables.

Clutch mass.—Clutch mass averaged 267.2 ± 60.1 g (range of values, 166.6–397.7; n = 23) and was not significantly related to CL ($F_{1,16}$ = 0.96, P = 0.342) but was significantly related to BM ($F_{1,16}$ = 5.32, P = 0.035, r^2 = 0.25). The log-log regression of CM on CL was not significant ($F_{1,16}$ = 0.82, P = 0.379) suggesting extreme hypoallometry in CM relative to body size. RCM (clutch mass/gravid body mass) averaged 5.7 ± 1.0% (range of values, 4.3–7.6%; n = 18) and was significantly negatively related to CL ($F_{1,16}$ = 7.02, P = 0.018, r^2 = 0.31), but not BM ($F_{1,16}$ = 1.99, P = 0.177).

***Range-wide life-history variation*.—**Adult female *Apalone spinifera* in western Nebraska are on average larger than for all other studied populations but one (Table 3). Females in northern populations (Missouri northward, between 36° and 48° N) average larger than those in more southern populations (between 26° and 36° N; Table 3) with means of means = 355 mm CL versus 301 mm CL (t = 3.22*;* df = 12; P = 0.004)*,* although the relationship between CL and latitude was not significant ($F_{1,10}$ = 4.61, P = 0.057). Growth data for *A. spinifera* show that Nebraska females grow faster and reach a greater asymptotic size than those from Minnesota, USA, and both exceed those from Arkansas, USA (Fig. 2). Despite the differences in these trajectories, however, all three studies indicate approximately the same age at maturity (12–13 y), although at different sizes. Size at maturity in female *A. spinifera* seems to be highly variable across populations of *A. spinifera* (Table 4), but these data suggest reproductive maturity between 250 mm and 300 mm CL across most of the range of the species (Table 5).

Nesting in *Apalone spinifera a*cross its range has been recorded from 11 May to 28 July (Table 6), although most records fall during the second half of June. Females in Nebraska generally produce two

Table 4. Estimates of carapace length (in mm) and age (in years) at maturity for female Spiny Softshell Turtles (*Apalone spinifera*), arranged in approximate order of declining latitude. Asterisks (*) indicate values estimated from the PL/CL ratio 0.726 (see text). For Louisiana and Texas, latitude values are approximate. Question marks indicate lack of locality data in original publication. *Pallida* refers to data reported for that subspecies only, without specific locality data.

State	Latitude	CL in mm	PL in mm	Age	Source
Minnesota	45	279?	203*	12	Breckenridge 1955 (Fig. 4)
S. Dakota	42.9	290	211*	—	Dixon 2009
Nebraska	41.5	314	226	12	This study
Pennsylvania	39.5–42	225	163*	—	Hulse et al. 2001
Missouri	36.5–40.5	248–275*	180–200	—	Johnson 2000
Tennessee	35.9	248–275*	180–200	—	Robinson and Murphy 1978
Arkansas	35.2	248-262*	180–190	12–13	Plummer and Mills 2015
New Mexico	32–36.5	248–275*	180–200	—	Degenhardt et al. 1996
??	—	248–275*	180–200	8–9	Webb 1962:575
pallida	30–34.5	273*	198	—	Webb 1962:561
Louisiana	ca. 31.5	296*	215	—	Webb 1962:561
Texas	ca. 29.5	223*	162	7	Webb 1962:562, 571, 575
Texas	ca. 29.5	269*	195	—	Webb 1962:561

clutches per year, as reported to be typical across the range by Webb (1962). Mean CS in *A. spinifera* in western Nebraska was the highest of any other population with a sample size > 1 (30; Table 5). Clutch size increased with body size in western Nebraska, as it does for other populations with reasonable sample sizes (e.g., Webb 1962, n = 18). Across populations of *A. spinifera,* clutch size also increases significantly with carapace length ($F_{1,9}$ = 21.61, P < 0.001, r^2 = 0.71; Table 5), although the data include several populations with very small sample sizes. Mean CS for samples > 2 was not significantly related to latitude ($F_{1,9}$ = 4.23, P = 0.070); however, the high mean CS at our Nebraska site was an outlier, and after excluding that value, the relationship was significant ($F_{1,8}$ = 7.32, P = 0.027, r^2 = 0.48). Although female *A. spinifera* (Doody 1995, 2023) and Smooth Softshell Turtles (*A. mutica*; Fitch and Plummer 1975) have been reported to split clutches among nests, we found no evidence of such behavior in Nebraska; however, we focused primarily on radiographs rather than nests in our study.

Although egg size increased with body size in Nebraska, this relationship has not been studied in other populations. Across populations, both mean EL and mean EM decreased significantly with mean CL (EL: $F_{1,6}$ = 14.16, P = 0.009, r^2 = 0.70; and EM: $F_{1,6}$ = 11.06, P = 0.016, r^2 = 0.65). In addition, mean EL and EM for populations with > 2 females decreased significantly with latitude across the species range

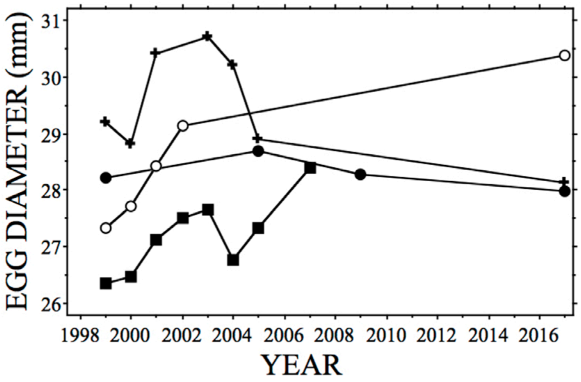

Figure 8. Change in mean X-ray egg diameter (ED) over time for four female Spiny Softshell Turtles (*Apalone spinifera*) from western Nebraska, USA, with the most records. Carapace lengths in 1999 were (from bottom curve to top) 364, 414, 379, and 410 mm, respectively.

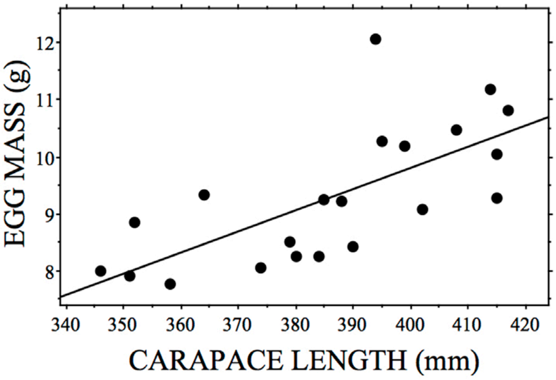

Figure 9. Relationship between carapace length (CL) and mean egg mass (EM) for 21 clutches of Spiny Softshell Turtles (*Apalone spinifera*) from western Nebraska, USA. The regression line describing the relationship is EM = 0.037CL–4.94 ($F_{1,19}$ = 17.32, P < 0.001, r^2 = 0.48).

Table 5. Geographic variation in carapace length (CL), clutch size (CS), and egg size (EL, length; EM, egg mass) in Spiny Softshell Turtles (*Apalone spinifera*). Asterisks indicate values estimated from the EL-EM equation in Iverson et al. (2024; EM = 1.0358EL–14.434; n = 655). Data are listed in order of declining latitude.

State		CL	Mean CS	CS range	n	Mean EL	n	Mean EM	n	Source
Quebec	47.2	—	19.4	11–31	75	25.30	621	10.10	32	Lazure et al. 2019
Minnesota	45.1	368	24.67	12–30	6	—	—	—	—	Breckenridge 1944
Minnesota	45.1	—	17	—	1		—	—	—	Breckenridge 1960
Vermont	44.6	—	16.2	13–21	14	25.50	73	9.38	74	Graham and Graham 1997
Wisconsin	—	—	—	15–38	—	26.00	—	9.50*	—	Vogt 1981
Iowa	42.8	—	20.8	11–42	15	26.56	249	10.25	249	Tamplin 2010
Iowa	42.8	—	28	—	2	26.16	28	10.08	28	Feltz and Tamplin 2007
Michigan	42.1	—	21	—	1	27.00	21	10.53*	21	Conant 1951
Pennsylvania	42.1	379	29.5	24–34	2	—	—	—	—	Lindeman pers. comm.
Iowa	41.5	—	24.3	20–32	3	—	—	—	—	LeClere 2013
Nebraska	41.5	382	29.89	16-42	64	25.45	403	8.89	407	This paper
Nebraska	—	—	25	—	1	24.60	25	8.05*	25	Gehlbach and Collette 1959
Indiana	—	—	19.17	9–32	6	—	—	—	—	Eigenmann 1896
Indiana	41.2	—	18	9–24	—	—	—	—	—	Newman 1906
Indiana	41.2	309	15.33	10–21	3	25.40	2	8.88*	2	Evermann and Clark 1920
Indiana	—	—	—	?–32	—	—	—	—	—	Minton 1972
Colorado	40.7	—	39	—	1	27.76*	39	11.32	39	Miller et al. 1989
Ohio	40.2	—	15	—	1	—	—	—	—	Davis and Krusling 2021
Ohio	39.3	—	21.5	11–32	2	—	—	—	—	Davis and Krusling 2021
Illinois	39.1	402	31	—	1	24.10	31	7.92	31	Tucker and Warner 1998
Illinois	—	—	18.08	9–25	12	28.30	217	11.88*	217	Cahn 1937
Indiana	38.9	344	24	—	1	27.10	24	10.84	24	Iverson unpublished
Virginia	36.6	250	13	—	2	27.00	26	10.53*	26	Mitchell 1994
Tennessee	35.9	293	14.0	9–19	5	26.80	—	10.33*	—	Robinson 1974; Robinson and Murphy 1978
North Carolina	35.5	410	22	—	1	23.00	22	6.39*	22	Palmer and Braswell 1995
Oklahoma	—	—	32	—	1	—	—	—	—	Force 1930
Arkansas	34.8	315	24	—	1	—	—	—	—	Iverson unpublished
Alabama	—	—	—	3–25	—	—	—	—	—	Mount 1975
Louisiana	32.6	—	15	14–16	3	29.13	55	13.10	55	Blanco-Pérez and Carr unpubl.
Louisiana	30.5	—	11.7	—	68	—	—	—	—	Doody 1995
Florida	30.4	—	—	20–24	3	29.34*	41	12.96	41	Ewert 1979: Table 9; Moler 2006
Latitude < 36.5°	—	283	9.62	3–17	17	—	—	—	—	Webb 1962; Table 9
Coahuila	26.9	252	7	—	1	29.70	7	14.2	7	Legler and Vogt 2013

(EL: $F_{1,6} = 28.41$, $P = 0.002$, $r^2 = 0.83$; EM: $F_{1,6} = 12.06$, $P = 0.013$, $r^2 = 0.67$).

Relative egg mass (REM) across five populations of *A. spinifera* was highly variable (0.14–0.69%), averaged 0.37% (Table 7) and varied inversely with female CL ($F_{1,3} = 459.7$, $P < 0.001$, $r^2 = 0.99$). Hence, populations with larger mean body sizes tended to invest less in each egg than those with smaller body

Table 6. Nesting dates and dates of capture of gravid female Spiny Softshell Turtles (*Apalone spinifera*), arranged in approximate order of declining latitude.

State	Dates	Source
Montana	14 June-23 July	Tornabene et al. 2018
Quebec	11 June	Daigle et al. 2002
Quebec	2 June-5 July	Lazure et al. 2019
Minnesota	6 June–29 June (46% 8–11 June)	Vose 1964
Minnesota	14 June-6 July	Breckenridge 1944
Minnesota	28 June	Breckenridge 1960
Ontario	26 May-23 July	Gillingwater in Doody et al. 2024
Vermont	14 June	Galois et al. 2002
Vermont	15-June-12 July	Graham and Graham 1997
Wisconsin	early June-mid July	Vogt 1981
Michigan	18 June (gravid)	Conant 1951
South Dakota	29 May-28 June	Dixon 2009 (includes *A. mutica*)
South Dakota	29 May-28 June	Dieter et al. 2014 (includes *A. mutica*)
Nebraska	27 May-3 July (gravid); 9 June-4 July+	This study
Iowa	17 June	Tamplin 2010
Illinois	June	Smith 1961
Illinois	10 June	Tucker and Warner 1998
Illinois	June-11 July	Cahn 1937
Indiana	2nd week June-most of July	Minton 1972, 2001
Indiana	26 June; 9 July (multiple)	Eigenmann 1896
Indiana	14, 17, 27 (2) June (gravid); 25, 26 June, 21 July	Evermann and Clark 1920
Indiana	10 June-mid July (22 June nest)	Newman 1906
Indiana	5 June (gravid)	Iverson unpublished
Colorado	13 June	Miller et al. 1989
New Jersey	1 July	Conant 1961
Missouri	2 July (gravid)	Anderson 1965
Tennessee	"June or July"	Robinson and Murphy 1978
North Carolina	12 July	Palmer and Braswell 1995
Oklahoma	20 May (gravid)	Force 1930
Arkansas	1 May (preovulatory)	Iverson unpublished
Alabama	May-July	Mount 1975
Louisiana	20 May-3 July	Blanco-Pérez and Carr unpubl.
Louisiana	11 May-28 July	Doody et al. 2024
Range-wide	"as early as May… to August"	Ernst and Lovich 2009

sizes. REM did not vary significantly with latitude ($F_{1,3} = 4.45$, $P = 0.126$).

We found no tradeoff between CS and egg size for *A. spinifera* in Nebraska, but no other study of this species has examined this relationship. We also found no trade-off across populations of *A. spinifera* with female samples > 2 (EL: $F_{1,6} = 0.85$, P = 0.393; EM, $F_{1,6} = 1.05$, $P = 0.346$). Relative clutch mass (RCM) averaged 5.70% for Nebraska *A. spinifera* and 5.57% across five populations (Table 7). Although the sample size was small, RCM did not vary significantly with mean population CL ($F_{1,3} = 0.04$, $P = 0.857$) or latitude ($F_{1,3} = 0.49$, $P = 0.533$). Hence, relative clutch mass varied little among populations across the range of the species.

DISCUSSION

Apalone spinifera occurs primarily in flowing water (review in Ernst and Lovich 2009), but does

Table 7. Geographic variation in relative egg mass (REM = mean clutch egg mass/gravid body mass × 100) and relative clutch mass (RCM = clutch mass/gravid body mass × 100) in softshell turtles in the genera *Apalone* and *Rafetus.* The traits CL (carapace length), BM (body mass), CS (clutch size), EL (egg length), EM (egg mass), CM (clutch mass), REM, and RCM were calculated based on other parameters in this table unless reported in original publication. Data for each species are listed in order of declining latitude. Species are Florida Softshell Turtle (*Apalone ferox*), Smooth Softshell Turtle (*A. mutica*), Spiny Softshell Turtle (*A. spinifera*), Euphrates Softshell Turtle (*Rafetus euphraticus*), and Yangtze Giant Softshell Turtle (*R. swinhoei*). Notes are [1]Estimate from PL/CL ratio in Iverson and Moler (1997), [2]Estimated from Fig. 7 in Robinson (1974), [3]Estimate from PL-BM regression in Iverson and Moler (1977), [4]Estimated from CL-BM regression for *A. spinifera* in text, [5]Estimated from Fig. 2 in Robinson and Murphy (1978), [6]Estimated from species-specific EL-EM regressions in Iverson et al. (2024), and [7]Estimated from the EL-EM regression for *A. ferox* in Iverson et al. (2024).

Species	Location	CL (mm)	BM (g)	CS	EL (mm)	EM (g)	CM (g)	RCM	REM	Source
Apalone ferox	Georgia	410.0	6,591[3]	24.00	30.70	15.27[6]	366.54	5.56	0.232	Goode 1983
A. ferox	Louisiana (Introduced)	495.7[1]	11,502[3]	32.33	25.17	8.88[6]	287.23	2.50	0.077	Elsey and Platt 2021
A. ferox	Florida	532[1]	14,159	20.00	25.00	12.00	240.00	1.70	0.085	Goff and Goff 1935
A. ferox	South Florida	405.0	6,650	20.60	28.20	12.20	290.30	3.90	0.189	Iverson and Moler 1997
A. mutica	South Dakota	232.3	1,158[4]	13.00	23.00	6.506[6]	84.58	7.30	0.562	Timken 1968; Table V
A. mutica	Kansas	231.0	1,092	16.33	22.90	6.72	116.93	10.71	0.656	Fitch and Plummer 1975
A. spinifera	Vermont	322.8	2,556	16.20	25.50	9.38	151.96	5.95	0.367	Graham and Graham 1997
A. spinifera	Nebraska	372.5	4,765	31.50	24.70	9.32	293.58	6.16	0.196	Present study
A. spinifera	Illinois	402.0	5,625	31.00	24.10	7.92	245.52	4.36	0.141	Tucker and Warner 1998
A. spinifera	Tennessee	293[2]	2,169[4]	14.00[5]	26.80	10.18[6]	142.52	6.57	0.469	Robinson 1974; Robinson and Murphy 1978
A. spinifera	Mexico	233.0	2,067	7.00	29.70	14.20	99.40	4.81	0.687	Legler and Vogt 2013
Rafetus euphraticus	Iran	471.8	9,607	12.00	28.95	13.25[7]	159.01	1.66	0.138	Yousefi et al. 2018 (CS estimated)
R. swinhoei	Captive	–	35,000	50.00	30.00	14.64[7]	723.20	2.07	0.041	Pritchard 2012 (composite estimates)

occasionally inhabit lentic systems (e.g., Dreslik et al. 2005; Stone et al. 2005). It appears that females at our study site exploit both systems, possibly taking advantage of the warmer, food-rich Rattlesnake Pond while shelling eggs, and then returning to the cold waters of Blue Creek for access to nesting sites and other activities. This behavior required a hazardous overland migration of about 200 m, suggesting that it offers a distinct advantage to the turtles. We speculate that the turtles may have originally located the pond based on their detection of the warm-water effluent from the pond entering Blue Creek (see Supplemental Information Fig. S1), which they may have followed up the seepage. Plummer and Mills (2008) reported a similar exploitation of a pond near a stream in Arkansas

***Body size*.**—Adult female *Apalone spinifera* in western Nebraska are on average larger than all other studied populations but one; however, understanding geographic patterns in body size in this species is complicated because some studies measured curved CL rather than straight-line CL (e.g., Bandas 2003; Bandas and Higgins 2006; Porter et al. 2024), some included juveniles in their calculations of average body size (e.g., Graham and Graham 1997; Ostovar et al. 2021; among many others), some lumped measurements of males and females (e.g., Bandas 2003; Bandas and Higgins 2006), and some lumped data from *A. spinifera* and *A. mutica* (e.g., Dieter et al. 2014). Females in northern populations (Missouri northward) average larger than those in more southern populations, suggesting a latitudinal pattern, even though the relationship between CL and latitude was not significant. Perhaps with a larger sample size, the relationship would be significant, as expected from Bergmann's Rule (Lewis et al. 2018; Yang et al. 2024). Additional geographic sampling is needed to test these preliminary results, and future workers are encouraged to report mean body sizes (especially CL) for mature adults (by sex, and excluding juveniles). In addition, reports in the literature claiming male *A. spinifera* > 300 mm CL (e.g., Degenhardt et al. 1996; Bandas 2003; among others) should be considered highly suspect because the record largest male measured only 275 mm CL (Barko and Briggler 2006).

***Growth*.—**Despite being sexually dichromatic at hatching, we found no sexual dimorphism in size at hatching, as did Graham and Cobb (1998), Lazure et al. (2019), and Porter et al. (2024). It is well established, however, that males grow slower than females and reach maturity sooner and at smaller sizes (review in Ernst and Lovich 2009). Growth data for female *A. spinifera* are available for only three populations, suggesting that Nebraska females grow faster and reach a greater asymptotic size than those from Minnesota, and both exceed those from Arkansas. Although these trajectories differ, all three studies indicate approximately the same age at maturity (12–13 y; see below), although at different sizes.

***Maturity*.**—Size at maturity in female *A. spinifera* is highly variable across populations of *A. spinifera,* likely due to small samples in most studies. Only three studies were based on large samples (Breckenridge 1955; Plummer and Mills 2015; this study) and estimates of size at maturity varied from about 314–279 mm to about 248–262 mm CL, respectively. These data, along with most other reports, suggest reproductive maturity between 250 mm and 300 mm CL across most of the range of the species. In contrast, Hulse et al. (2001) reported maturity of females in Pennsylvania at 225 mm CL (without stating any basis), and Webb (1962) dissected three gravid females from an unnamed southern population of *A. s. emoryi* at 162 mm PL (about 223 mm CL). Additional fieldwork will be necessary to confirm whether other female *emoryi* mature at such a small size. For the three studies with the largest samples, all suggest female reproductive maturity at about 12–13 y; however, Webb (1962) reported maturity at 7 y for a sample of *A. s. emoryi* from an unnamed population, as well as 8–9 y for another sample with unspecified provenance. Until more long-term mark-recapture data are available for additional populations, particularly in southern populations, these latter estimates must be considered suspect.

Although we were not able to determine size at sexual maturity in males, most previous studies have suggested maturity at 80 to 100 mm PL (about 112–140 CL) at an age of 4–5 y (Webb 1956, 1962; Robinson and Murphy 1978; Ernst and Lovich 2009; Mahoney and Lindeman 2017). Our meager male growth data also suggested maturity in 4–5 y in western Nebraska, assuming those body size data. Trauth and Worley (1997) attempted a skeletochronological study of *A. spinifera* from northeastern Arkansas but unfortunately found little evidence that the number of lines of arrested growth in the femur were related to age, apparently due to extensive bone resorption and remodeling.

***Longevity*.**—Our data suggest that female *Apalone spinifera* in Nebraska may often live beyond 40 y. The previous longevity record for the species was based on an adult captive female that lived 25.2 y (Slavens and Slavens 2000). No longevity data are available for *A. mutica*, but a Florida Softshell Turtle (*A. ferox*; unknown sex) lived for 36.7 y. The only trionychid with a longer known longevity is the African Softshell Turtle (*Trionyx triunguis*); a captive male lived 50.6 y (Slavens and Slavens 2000). Based on the general relationship between age at maturity and longevity in turtles (Iverson 2024), however, estimated longevity for *A. spinifera* would be 71 y. In addition, generation time estimated from the same publication would be 27 y.

***Nest season and frequency*.**—Nesting in *A. spinifera* has been recorded from 11 May to 28 July, although most records fall during the second half of June. Surprisingly, the latest reported nests were at the northern (23 July) and southern (28 July) limits of the range. In contrast, the earliest northern nest date was 26 May, and the earliest southern record was 11 May, suggesting that nesting begins earlier in the south (as would be expected), but can extend nearly as late into the season in the north as in the south.

The production of two clutches per season is found across most of the distribution (Webb 1962): in Quebec, Canada (Lazure et al. 2019); Ontario, Canada (Gillingwater in Doody et al. 2024); Iowa, USA (Tamplin 2010); Nebraska, USA (this study); Tennessee, USA (Robinson and Murphy 1978); and Louisiana, USA (Doody 1995). Tornabene et al. (2018) reported the production of only a single clutch per year in Montana, USA, however, and Timken (1968) suggested that smaller females in South Dakota, USA, might only produce one clutch per season, whereas larger adults produced two. We captured few small adult females in Nebraska, and it is possible that this pattern also occurs at our site. Webb (1962; southern populations) and Mount (1975; Alabama, USA) speculated that three clutches might be possible in some southern locations.

Moll (1979) speculated that four to five clutches might be produced in a year in Illinois, USA, which seems aberrant in light of data published subsequently. Edward Moll (pers. comm.) shared that his claim was based on a 367 mm CL female from Oakland Lake in Coles County that died in a trap on 8 July 1973 (see Fig. 4 in Moll 1979). Upon dissection she held 14 unshelled eggs in the oviducts and 14 corresponding, large, fresh corpora lutea in the ovaries. In addition, she bore 59 old corpora lutea of three or four size groups. Corpora lutea are generally resorbed between reproductive seasons in non-marine turtles (Kuchling 1999), leading to speculation by Moll about the high clutch frequency. It is possible that this clutch was the last of the season (and hence smaller; see above), and represented the third clutch of the season, and that the two previous clutches averaged about 30 eggs each, which would be expected by a female of this size. *Apalone mutica* is also known to produce two clutches per year (Lindeman 2001), and a third clutch is speculated (Webb 1962; Plummer et al. 1997). In contrast, the southern-most congener *Apalone ferox* is hypothesized to produce as many as five or six clutches per year (Iverson and Moler 1997), although field confirmation of that frequency is lacking.

Although we found little evidence that females in Nebraska skip reproduction in some years, Webb (1962) found several females of adult size that appeared to be non-reproductive upon dissection. Iverson and Moler (1997) made the same observation based on a few dissected *A. ferox*. Unfortunately, collecting rigorous data on the frequency of non-reproduction in turtles generally requires destructive sampling (e.g., Bruno et al. 2026) and hence will remain elusive. Radiotelemetry studies with radiography or ultrasound can provide some data on clutch frequency, although the repeated physical disturbance of the turtles with these methods can potentially bias the results (e.g., Bolton 2007; Tornebene et al. 2018).

Nesting sites and construction.—As we found, female *A. spinifera* are known to move considerable riverine distances to find suitable nesting sites at other locations (Plummer et al. 1997; Daigle et al. 2002). Once a general site is selected, most *A. spinifera* nest in open areas within 20 m of the water, although some may nest as much as 175 m away (Doody et al. 2024). Our observations of nest construction and size corroborate the previous descriptions by Gehlbach and Collete (1959), Breckenridge (1960), Vose (1964), Minton (1972, 2001), Harding (1977), and Gillingwater (2004); however, we are the first to report the elongate anterior-posterior shape of the nest chamber.

Clutch size.—Mean CS in western Nebraska was the highest of any other population with a sample size > 1, and maximum CS (42) approached the record for the species of 43 eggs in Ontario, Canada (Gillingwater and Mackenzie in Doody et al. 2024). Clutch size increased with body size in *A. spinifera* in western Nebraska, as it does for other populations with reasonable sample sizes (e.g., Webb 1962). This relationship has also been demonstrated for *A. ferox* (Iverson and Moler 1997) and *A. mutica i*n Arkansas (Plummer et al. 1977), but not for *A. mutica i*n South Dakota (Timken 1968). Across populations of *A. spinifera*, clutch size also increases with carapace length, although the data include several populations with very small sample sizes. This pattern is also typical across turtle species in general (Moll 1979; Wilbur and Morin 1988). Second clutches in Nebraska tended to be smaller than first clutches, a pattern also reported by Lazure et al. (2019) in Quebec.

Latitudinal variation in mean population CS was evident only if our outlying Nebraska sample is excluded. Webb (1962) and Fitch (1985) both suggested that clutch size in *A. spinifera* was higher at high latitudes, although more rigorous geographic sampling is needed. Lindeman (2001, for *A. mutica*) and Lazure et al. (2019, for *A. spinifera*) reported similar positive trends that also were non-significant; however, Rachmansah et al. (2020) demonstrated a significant latitudinal pattern in CS across turtle species, as did Iverson et al. (1993).

Egg size.—Egg size increased with body size in the Nebraska population, as suggested by Newman (1906) in Indiana, USA, although the relationship has not been studied in other populations of *A. spinifera*. In contrast, egg size did not vary with body size in *A. ferox* (Iverson and Moler 1997), and the pattern has not been studied in *A. mutica.* Our meager data suggested that eggs in second clutches of *A. spinifera* did not differ in size from those in first clutches. Similarly, Lazure et al. (2019) reported no change in egg size over the nesting season in Quebec, but did not track individual females. Iverson and Moler (1997) also found no change in egg size by date across the year for *A. ferox*.

Across populations, egg size in *A. spinifera* decreased with body size. Similarly, Moll (1979), Rachmansah et al. (2020), and Jorgewich-Cohen et al. (2022) reported that egg size was generally inversely related to carapace length across turtle species. In addition, egg size across populations of *A. spinifera* decreased with latitude, a pattern that was also reported for *A. mutica* (Webb 1962) and across turtle species (Iverson et al. 1993).

Relative egg mass (REM) across five populations of *A. spinifera* averaged 0.37%, and varied inversely with female CL, suggesting that populations with larger mean body sizes tend to invest less in each egg than those with smaller body sizes. Because body size in *A. spinifera* tends to increase with latitude, we expected REM also to vary inversely with latitude; however, the latter relationship was not significant, although the sample was very small. Relative egg mass averaged 0.15% for *A. ferox* and 0.61% for *A. mutica,* suggesting that *A. mutica* invests more in each egg than *A. spinifera,* despite having a similar clutch frequency.

The allometric relationships we found with CL suggest that Nebraska softshells might be fundamentally different from other studied turtles. For 46 populations of 25 turtle species, Iverson et al. (2019) found that logCS generally scaled with logCL with a slope between 1.7 and 2.0 (compared to an expected isometric slope of 3.0), that logEM generally scaled with a slope between 1.1 and 1.3 (expected slope 3.0), and logCM generally scaled with a slope between 2.4 and 2.8 (expected slope 3.0). The respective slopes for *A. spinifera* in Nebraska were 0.77, 1.51, and 0.73, suggesting unusually depressed CS and CM allometry, but that egg size exhibited above average allometry (though still hypoallometric).

It should be noted that Iverson et al. (2019) also hypothesized that CL might not be an appropriate surrogate for body volume (i.e., body size), because it may increase ontogenetically at a faster rate than carapace width or height. If so, this could partly explain the general patterns of hypoallometry relative to CL in reproductive output in turtles. This pattern may be especially true for softshell turtles that presumably experience selective pressures for low shells that facilitate aquatic mobility. The logs of CS, EM and CM were each also significantly related to the log of BM, however, with respective slopes of 0.416, 0.558, and 0.601 (each with an expected isometry slope of 1.0). Hence, Nebraska *A. spinifera* are indeed decidedly hypoallometric reproductively.

We found no tradeoff between clutch size and egg size for *A. spinifera* in Nebraska, but this relationship has not been examined in any other study of this species. We also found no trade-off across populations. In addition, no such trade-off also has been reported for *A. ferox* (Iverson and Moler 1997) and *A. mutica* (Fitch and Plummer 1975), suggesting a genus-wide pattern.

Clutch mass.—Relative clutch mass (RCM) averaged 5.70% for Nebraska *A. spinifera* and 5.57% across five populations. Although the sample was small, RCM did not vary with mean population CL or latitude, suggesting minimal variation across the species range. For comparison, RCM for *A. ferox* averaged 3.42% and that for *A. mutica* averaged 9.01%. The small RCM value for *A. ferox* is perhaps compensated for by having an estimated clutch frequency of 5–6 per year. In contrast, *A. mutica* invests much more per clutch than *A. spinifera,* despite having smaller clutch and egg sizes (but larger relative egg sizes). Indeed, RCM for *A. mutica* exceeds that of all other studied trionychids (e.g., Iverson and Moler 1997). Furthermore, preliminary data for the sister genus *Rafetus* (Thomson et al. 2021) suggest that the high output of *A. mutica* is the derived condition for the clade, although the adaptive significance for this divergence is not yet clear.

Conclusions.—Despite having the third largest distribution of all North America non-marine turtles (after *Chelydra serpentina and Chrysemys picta;* Turtle Taxonomy Working Group 2025) the details of the life history of *A. spinifera* are still surprisingly poorly known. Our study provides the most complete set of those data for a single population to date. In Nebraska, females grow relatively slowly, requiring about 12 y to reach maturity. Once mature, they produce one or (usually) two large clutches (mean = 30 eggs) of relatively small eggs each year, with no pelvic aperture constraints. Relative egg mass (0.18%) and relative clutch mass (5.7%) are in line with those estimated for the family (0.30% and 5.2%, respectively; n = 10 species; Iverson and Greene 2022).

Both egg and clutch size increased with body size in Nebraska *A. spinifera* and, surprisingly, the rate of increase of egg mass and clutch size were similar (whether using raw data or log-transformed data), though still decidedly hypoallometric. In addition, no egg size-clutch size tradeoff was evident in that population. Across turtles, egg size generally varies much less within species than does clutch size (review in Iverson and Smith 1993), as expected by optimal egg size theory (OES), but unlike that for *A. spinifera* in Nebraska. A prediction of OES theory is that increases in reproductive output should be directed to increases in CS rather than egg size (Smith and Fretwell 1974; Brockelman 1975; Jorgewich-Cohen et al. 2022), which does not seem to apply to *A. spinifera*. Iverson et al. (2019), however, suggested that the general pattern of hypoallometry in CS, EM, and CM in turtles supports a bet-hedging strategy (Olofsson et al. 2009). Thus, turtles in general (and *A. spinifera* in particular) may have evolved not to maximize their reproductive output in a given clutch, but instead to maximize their long-term reproductive output (Congdon and Tinkle 1982). Why *A. spinifera* in such a productive system as in western Nebraska would seem to take hypoallometry to such an extreme is not yet clear. Perhaps future studies of other populations will shed more light on this conundrum.

The available comparative data for *A. spinifera* suggest that body size and clutch size increase with latitude, while egg size decreases, and relative clutch mass shows no relationship. These patterns have previously been demonstrated across turtle species by Iverson et al. (1993) among others. Those authors discussed the seven most plausible hypotheses that might explain this predominant pattern in turtles, but most are speculative and untestable practically. Perhaps the most viable theory is the summer-length hypothesis (i.e., the developmental window hypothesis; Marshall et al. 2018) that argues that selection at high latitudes should favor eggs that hatch before the end of summer, allowing neonates to accumulate the resources needed to survive their first winter. Support for that theory comes from the fact that incubation times are generally inversely related to egg size in at least temperate turtles (Ewert 1985; Iverson and Ewert 1991), and the eggs of *A. spinifera* decline in size with latitude. In addition, selection for larger clutches with latitude must also be operating in *A. spinifera* (as well as other trionychids) that all produce round eggs, presumably allowing more eggs to be held in limited oviductal space (Iverson and Ewert 1991; Jorgewich-Cohen et al. 2022).

We still have much to learn about the natural history of softshells in North America and even more so in the Old World. Our study made it clear that (1) most of the published literature on the genus *Apalone* is anecdotal (i.e., based on very few animals), (2) much of it has focused only on nests, (3) eggs and turtles are rarely weighed, (4) long-term studies are almost absent (but see work in Arkansas; Plummer and Mills 2015), and (5) no other study has reported a full suite of life-history traits (i.e., including growth rate, maturity, adult body size, reproductive phenology, clutch size and frequency, and egg size) from a single softshell population. In the future, long-term studies are particularly needed, and workers should strive to collect more complete suites of life-history traits for their softshell populations (after Fitch 1949; Cagle 1953).

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John B. Iverson holds a Ph.D. in Biology from the University of Florida, Gainesville, USA, and is Biology Research Professor at Earlham College in Richmond, Indiana, USA. Because of his interests in the natural history, ecology, and evolution of iguanas and turtles, he is currently on the steering committees (and founding member) of the International Union for Conservation of Nature Iguana Specialist Group and Tortoise and Freshwater Turtle Specialist Group. He has been involved with the Turtle Survival Alliance since its inception in 2001 (currently a Board member) and serves on the Board of the Turtle Conservation Fund. He has been active in several herp societies, serving as Editor and President of the Herpetologists League. He has maintained long-term field research sites from 1980–2024 for rock iguanas (*Cyclura*) in the Exumas in the Bahamas and 1981–2026 for turtles at the Crescent Lake National Wildlife Refuge in western Nebraska, USA. (Photographed by Kirsten Hines).

Ruth E. Carter received her B.S. in Biology from Earlham College, Richmond, Indiana, USA, in 2011 and her Graduate Certificate in Geographic Information Science and Technology from the Dornsife's Spatial Sciences Institute at the University of Southern California, Los Angeles, USA, in 2014. She currently works in the animal behavior field observing canine social cues, determining effective nonverbal communication strategies to manage reactivity, and monitoring play behaviors. (Photographed by Kat Street).

Matthew P. Lachiusa holds a B.S. in Biology and M.A.T. in Life Science Education from Earlham College, Richmond, Indiana, USA. In his past field work for the U.S. Forest Service and current field work for environmental consulting companies, he specializes in rare plant and wildlife species surveys. His current research includes a Section 6-funded study investigating the effects of potential management actions to promote the growth and recruitment of Goodding's Onion (*Allium gooddingii*), a rare plant species under consideration for U.S. federal protection by the U.S. Fish and Wildlife Service. Matthew also conducts volunteer fieldwork for federal agencies, which has included discovering new locations for rare plants and tracking Sonoran Desert Tortoise (*Gopherus morafkai*) movements using radio telemetry in Saguaro National Park in Arizona, USA. (Photographed by Mark Lotterhand).