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BODY SIZE AND GROWTH IN THE RED-EARED SLIDER (*TRACHEMYS SCRIPTA ELEGANS*) AT THE NORTHERN EDGE OF ITS RANGE: DOES BERGMANN'S RULE APPLY?

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Abstract.—**Although initially applied to endotherms, Bergmann's Rule (body size correlated with latitude) has also been demonstrated for a number of ectothermic taxa, including turtles. We examined body size and growth in the Pond Slider (*Trachemys scripta*) at the northern edge of its range in Indiana. We then compiled body size data from across the range of the species to test for latitudinal trends. Adult females in Indiana were larger than males, and their growth rates began diverging by at least their fourth year. Mean and maximum body size were positively correlated with latitude in female Red-eared Sliders (*T. s. elegans*), but not in males or in Yellow-bellied Sliders (*T. s. scripta*), for which the available data were limited. More data are needed to understand geographic patterns in growth, age and size at maturity, and adult male size in this otherwise well-studied species.**

Key Words.—Bergmann's Rule; Indiana; latitudinal variation; size dimorphism; von Bertalanffy growth model

INTRODUCTION

Bergmann's Rule (Bergmann 1847; Meiri 2011) hypothesizes an adaptive negative relationship between environmental temperature (usually expressed as latitude) and body size in endotherms (Mayr 1956) as a mechanism for heat conservation. Based on surface area to volume ratios, larger bodies, with proportionally less surface area than smaller bodies, result in decreased heat loss by conduction and convection in endotherms at colder, higher latitudes (Bergmann 1847). The rule has also been applied to a number of ectothermic taxa. For example, a latitudinal increase in body size has been demonstrated in several North American and European turtles (Ashton and Feldman 2003; Greaves and Litzgus 2009; Angielczyk et al. 2015; Werner et al. 2015; Joos et al. 2017).

Several adaptive explanations for this pattern in turtles have been proposed (reviewed in Iverson and Smith 1993 and Ashton and Feldman 2003). Similar to endotherms, larger turtles at high latitudes may gain an advantage because of their higher thermal inertia, even though they cannot heat or cool rapidly (Lindsey 1966; Stevenson 1985). Larger bodies may also confer an advantage to turtles in the storage of metabolites (catabolic and anabolic) during the longer winters at high latitudes (Murphy 1985). Large bodies in turtles at high latitudes also might be a response to decreased competition from other turtle species, due to decreased species density at higher latitudes (Moll 1973). In addition, larger body size at high latitudes permits larger clutch sizes, presumably offsetting the short active season, which in turn limits annual clutch frequency (Iverson and Smith 1993; Litzgus and Mousseau 2006). Finally, larger turtles presumably dig deeper nests that are more likely to reach below the frost line, which might result in decreased freezing-mortality of hatchings overwintering in the nest (Iverson and Smith 1993).

If selection does indeed drive larger body size in turtles at higher latitudes, the question remains whether this is accomplished via faster juvenile growth or longer time to maturity, or some combination of these. Several studies have reported that maturity is delayed in turtle populations at higher latitudes (e.g., Tinkle 1961, for Common Musk Turtles, *Sternotherus odoratus*; Galbraith et al. 1989, for Snapping Turtles, *Chelydra serpentina*; St. Clair et al. 1994, for Painted Turtles, *Chrysemys picta*; and Germano and Reidle 2015 for Western Pond Turtles, *Actinemys marmorata*), but only one study (St. Clair et al. 1994) has attempted to compare juvenile growth rates for a turtle species across latitude. That study reported faster juvenile growth in northern populations of *C. picta* (Michigan and Canada) than in a southern population (Louisiana), despite the shorter northern growing season. Unfortunately, that study may be compromised by recent molecular studies suggesting that the southern population is a separate species, *C. dorsalis* (review in Turtle Taxonomy Working Group [TTWG] 2017). Latitudinal patterns of juvenile growth in turtles are thus sorely in need of study.

The Pond Slider, *Trachemys scripta*, is one of the best-studied wide-ranging turtle species in North America (e.g., Gibbons 1990; Lovich and Ennen 2013). Previously, the species was described to exhibit a pattern of largest body sizes at northern temperate and at southern tropical latitudes in Mesoamerica, with smaller body sizes at mid-latitudes (Tucker et al. 1999; Ashton and Feldman 2003). However, the taxonomy of this turtle has changed radically since those earlier studies and the distribution of *T. scripta* is now restricted to the USA and extreme northeastern Mexico (Powell et al. 2016; TTWG 2017). Hence, this reevaluation of geographic variation in its body size is merited.

We conducted a mark-recapture study from 1979 to 2016 of *T. scripta* at Dewart Lake in northern Indiana (Smith et al. 2006), near the northern limit of the range of *T. scripta* (Powell et al. 2016; TTWG 2017). To clarify geographic variation in body size in this turtle, we undertook an analysis of growth and body size of Sliders at our Indiana study site and compared our data with previously published data from across the range of the species. If larger body size confers an advantage at colder latitudes as asserted by Bergmann's Rule, then we predicted that adult Sliders from Dewart Lake would be larger and, based on St. Clair et al (1994), that their growth rates would be faster than those of more southern populations.

Materials and Methods

We studied Red-eared Sliders (*Trachemys scripta elegans*) in the marsh at the southeast end of Station Bay (area = 4.5 ha) in the southeast corner of Dewart Lake (Wade and Gifford 1965) near Syracuse, Kosciosko County, Indiana, USA (see Iverson 1988; Smith and Iverson 2002, 2004; Smith et al. 2006, 2016). We sampled turtles nearly annually (usually in late July to early August for 2–5 d) using a variety of trapping and capture methods. Station Bay surveys prior to 1992 used aquatic wire funnel traps (n = 5–15) baited with canned sardines or fresh fish (see Iverson 1979 for design). Beginning in 1992, we surveyed the site with three to twelve 2.5 cm mesh fyke nets deployed with 15 m leads between a pair of 90 cm hoop diameter funnel traps. Fyke nets quickly trapped fish, which served as bait, so no supplementary bait was necessary. Traps were checked every 2–3 h from first light to 1–2 h post-sunset. No turtles entered the traps during the night (Smith and Iverson 2004). To avoid recapture within each sampling period, we held all turtles in large tubs with water during each sampling period, and then released them at the conclusion of trapping. We individually marked all captured sliders with notches in the marginal scutes (Cagle 1939).

Although our study population lies slightly beyond the northern edge of the range of *Trachemys scripta* as generally reported (Ernst and Lovich 2009; TTWG 2017; Powell et al. 2016), this species was first reported there by Wade and Gifford in 1965. In addition, unpublished records from the Earlham College Biological Station reported *T. s. elegans* from the lake in the mid-1950s. Although never common (Smith et al. 2006), we believe that the population is indigenous, although supplementation by releases of pet-store turtles in the mid- to late 20th Century is possible.

We measured the maximum carapace length (CL) and plastron length (PL) of the turtles (± 1 mm) with dial calipers in a plane parallel to the plastron (following Cagle 1946; see also Iverson 1977) and weighed each turtle (± 1 g) with spring scales (PESOLA Präzisionswaagen, Chaltenbodenstrasse 4A, 8834 Schindellegi, Switzerland). When possible, we determined the sex of turtles based on external dimorphic characters (elongate foreclaws, elongate tails; Ernst and Lovich 2009). When clearly visible, we counted abdominal scute growth rings to estimate age in juvenile turtles. Because winters are severe at Dewart Lake, and because turtles there exhibit rapid growth (see below), resident sliders display well-defined and distinctive growth rings as juveniles (see also Cagle 1946), and the validity of their use in this population was confirmed by counts made on recaptures in subsequent years. Realizing the controversy concerning the use of growth rings for determining age of turtles (Brooks et al. 1997; Germano and Bury 1998, among others), we used recaptures of turtles for which age was originally determined using rings as juveniles < eight winters, insuring the accuracy of the time interval used over the growth measure. For our growth calculations, we assumed that the growing season was 6 mo long (Glidewell 1984), lasting from 15 April to 15 October (see also Cagle 1946). Hence, a turtle with three growth rings captured on 15 July was considered to be 3.5 winters old (equivalent to 2.5 seasons of growth).

Body size data from first capture to last recapture were used to model somatic growth in a von Bertalanffy growth analysis (Frazer et al. 1990; Dunham and Gibbons 1990; Lindeman 1997), with one modification. Because hatchling sliders in our population overwinter in their nest (Baker et al. 2010, 2013) and we captured a single recently emerged hatchling with a fresh umbilicus and no shell growth on 25 May 1985 (27.65 mm CL; 25.6 mm PL), we assumed no post-developmental growth before the start of the first winter. Therefore, we assumed that a turtle captured on 15 July 2002 with two growth rings (e.g., during the second activity season of that turtle) grew from 27.65 mm CL (after emergence in spring of 2000) to its size of capture following 1.5 y of growth (following Jones 2017). We augmented our recapture data with 30 such individuals with two growth rings (i.e., in their second season of growth). We included recapture data from juveniles for which we could not determine sex in both the male and female analyses.

Table 1. Mean adult body size (carapace length, CL, or plastron length, PL, in mm) in Red-eared Sliders (*Trachemys scripta elegans*) across its range. Data are arranged by decreasing latitude (in parenthesis below location). Some studies only reported CL or PL data (not both); the missing variable was estimated (marked by an asterisk) based on the ratio of PL to CL reported in this study (male PL/CL = 0.916; female = 0.942). Means are followed by sample size and appear above the range in parentheses. Missouri populations were studied in warm and cold-water habitats. Question marks indicate unreported data.

Location	Male CL	Female CL	Male PL	Female PL	Source
Indiana (41.5)	174.5; 108 (108–248)	227.6; 98 (170–277)	160.9; 108 (103–223)	214.0; 98 (161–261)	This paper
Illinois (39.0)	—	221.9*; 25 (199–239)	—	209; 25 (187–225)	Tucker 1997
Illinois (39.0)	—	226.7*; 162 (177–255)	—	213.5; 162 (167–240)	Tucker and Moll 1997
Illinois (39.0)	—	227.1*; 789 (177–274)	—	213.9; 789 (167–258)	Tucker et al. 1998
Illinois (Stump Lake; 39.0)	—	225.5*; 990 (177–267)	—	212.4; 990 (167–251)	Tucker et al. 1999
Illinois (Swan Lake; 39.0)	—	227.3*; 677 (178–268)	—	214.1; 677 (168–252)	Tucker 1999
Illinois (39.0)	—	218; 11 (189–240)	—	207; 11 (178–230)	Tucker et al. 2001
Illinois (39.0)	—	210.7*; 392 (177–255)	—	198.5; 392 (167–240)	Tucker 2001
Southern Illinois (38.0)	179.3; 4 (156–196)	205.9; 9 (166–243)	170.5; 4 (151–188)	191.2; 9 (161–224)	Cahn 1937
Southwest Illinois (38.0)	—	224.1*; 16 (196–248)	—	211.1; 16 (185–234)	Thornhill 1982
Southwest Illinois (38.0)	—	214.9*; 21 (184–254)	—	202.4; 21 (173–239)	Thornhill 1982
Southern Illinois (37.5)	135.4; ? (?–186)	189.1; ? (?–260)	124.0*; ? (?–170)	178.1*; ? (?–245)	Cagle 1946
Southern Illinois (37.5)	—	215.0*; 67 (168–234)	—	202.5; 67 (158–220)	Cagle 1950
Missouri (cold; 36.5)	180.9; 48* (112–257)	224.4*; 48 (189–263)	163.2; 105 (102–225)	207.0; 48 (178–240)	Thomas 1993
Missouri (warm; 36.5)	183.9; 99* (113–235)	222.3*; 39 (185–261)	166.8; 99 (102–210)	204.3; 39 (174–240)	Thomas 1993
Northeast Oklahoma (35.5)	—	188.2; 35 —	—	171.5; 35 —	Hays and McBee 2010
Arkansas (34.5)	—	219.4; 18 (200–240)	—	203.6; 18 (181–226)	Iverson, unpublished
Southern Oklahoma (34.0)	—	207*; 6 (191–216)	—	195; 6 (180–203)	Webb 1961
Mississippi 1977 (33.5)	142.5*; 117 (98–203)	206.5*; 64 (177–239)	130.5; 117 (90–186)	194.5; 64 (167–225)	Parker 1984
Mississippi 1982 (33.5)	157.5*; 80 (102–199)	205*; 31 (170–237)	144.3; 80 (93–182)	193.2; 31 (160–223)	Parker 1984
Louisiana (30.0)	—	202.8*; 59 (159–234)	—	191.0; 59 (150–220)	Cagle 1950

We did not record midline lengths of abdominal scute growth rings and use those measures to construct juvenile growth, even though Sergeev (1937) demonstrated its use (see also Cagle 1946). This method requires accurate counts and measures of growth rings and assumes that the ratio of abdominal midline seam length to plastron length remains constant throughout life. The latter was untested in our population, and hence, not used. Because we could not determine size at maturity in our study population, we followed Cagle (1944, 1948) in considering all females > 170 mm CL (about 160 mm PL) and males > 100 mm CL (about 90 mm PL) as adults.

Table 2. Plastron length (in mm) by age for populations of juvenile Red-eared Sliders (*Trachemys scripta elegans*) across latitude. Age is corrected across studies to numbers of seasons of growth post-emergence; methods follow Sergeev (Sergeev; 1937) or von Bertalanffy (von Bert; Dunham and Gibbons 1990). For sex, M = males and F = Females.

			Estimated Age (years)									
Location			1	2	3	4	5	6	7	8	9	
(Latitude)	Sex	Method	Plastron Length (mm)									Source
Indiana	M	von Bert	60.3	87.8	109.4	126.4	139.7	150.3	158.5	165.1	170.2	This paper
(41.5)	F	von Bert	62.1	92	116.7	137.1	154	167.9	179.5	189	196.9	This paper
Illinois-lake (39.0)	mix	Sergeev	49.1	70.4	103.4	130.2	152.1	167.8	186.4	199.5	206	Tucker 1999; Tucker and Moll 1997
Illinois-ditch (37.5)	mix	Sergeev	47	55.2	65.2	–	–	–	–	–	–	Cagle 1946
Missouri-warm (36.5)	mix	Sergeev	53.2	69	83.5	–	–	–	–	–	–	Cagle 1946
Missouri-cold	mix	Sergeev	46.8	63.9	81	98.1	–	–	–	–	–	Thomas 1993
(36.5)	mix	Sergeev	37.6	47	56.4	63.8	–	–	–	–	–	Thomas 1993
Oklahoma	M	Sergeev	54	71	89	–	–	–	–	–	–	Webb 1961
(34.0)	F	Sergeev	62	91	114	145	–	–	–	–	–	Webb 1961
Texas	M	von Bert	43	56	68	78	88	98	107	115	122	Glidewell 1984
(33.0)	F	von Bert	62	89	112	131	147	161	172	182	190	Glidewell 1984

To test the applicability of Bergmann's Rule to sliders, body size data (CL and/or PL) were extracted from the published literature. *Trachemys scripta* includes three subspecies (Powell et al. 2016; TTWG 2017): the Yellow-bellied Slider, *T. s. scripta*, along the Atlantic seaboard; the Red-eared Slider, *T. s. elegans*, found primarily in the Mississippi River basin; and the Cumberland Slider, *T. s. troosti*, restricted to a small region in the Cumberland and Tennessee River Valleys. To minimize longitude and intraspecific taxonomy as potential confounding factors in understanding latitudinal body size patterns, we performed our analyses separately for *T. s. scripta* (spanning 8° latitude in the eastern USA) and *T. s. elegans* (13° in the central USA). We estimated latitude of each study site to the nearest 0.5° north latitude based on the original paper or Google Earth. We evaluated latitudinal trends in carapace and plastron length with least squares linear regression analysis and mean body size measurements by sex within our study population were compared with a Student's *t*-test ($\alpha = 0.05$). Means are followed by ± 1 SD. We performed all analyses using Statview software.

Results

Over our 37-y study period, we captured 108 males (20 recaptured a total of 27 times), 98 females (28 recaptured a total of 52 times), and 76 juveniles (four recaptured a total of six times) from Dewart Lake. Mean interval between first and last captures for all 20 males was 4.0 ± 3.9 y (range, 1–14 y) and for all 28 recaptured females it was 4.6 ± 3.4 y (range, 1–14 y). For the combined four recaptured juveniles and 30 estimates from second year turtles, the mean interval was 1.4 ± 0.2 y (range, 1–2 y).

Adult females at our site were significantly larger than adult males (Table 1; for CL, 227.6 ± 31.2 vs. 174.5 ± 38.3, $t = 11.5$, df = 204, $P < 0.001$; for PL, 214.0 ± 28.2 vs. 160.9 ± 32.6, $t = 13.3$, df = 206, $P < 0.001$). Plots of body size by estimated age based on recaptures of juvenile turtles of known age suggested that female body size diverged from that of males as early as the fourth year of life at between 100–150 mm CL (Fig. 1); the same pattern of divergence between 100–150 mm CL was evident from our growth rate data (Fig. 2). Von Bertalanffy growth models based on recaptures of 20 males, 28 females, 4 juveniles, and estimated recaptures (from hatchling size) of another 30 second-year juveniles also indicated the divergence in size of males and females by the fourth growing season (Fig. 3; Table 2).

Mean and maximum female carapace and plastron lengths in *T. s. elegans* varied positively with latitude (Fig. 4; for mean CL, $r = 0.54$, $t = 2.76$, df = 19, $P = 0.013$; for maximum CL, $r = 0.64$, $t = 3.52$, df = 18, $P = 0.002$; for mean PL, $r = 0.54$, $t = 2.82$, df = 19, $P = 0.011$; and for maximum PL, $r = 0.67$, $t = 3.84$, df = 18, $P = 0.001$). Males exhibited no latitudinal relationships with body size ($P > 0.29$ for all regressions), but data were available for only eight populations. Similar analyses of body size across populations of *T. s. scripta* (Table 3) revealed no significant relationship between body size and latitude for mean or maximum CL or PL or for either sex ($P > 0.25$ for all regressions; Table 3).

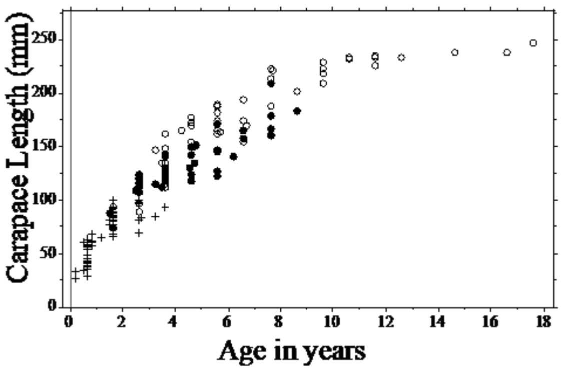

Figure 1. Carapace length by age for all known age captures for Red-eared Sliders (*Trachemys scripta elegans*) at Dewart Lake, Indiana, USA. Data include recaptures of turtles first captured and aged by growth rings as juveniles (< eight rings). Age is plotted in seasons of growth after emergence from the nest (see Methods). Solid dots are males; open dots are females; crosses are unsexed turtles. Some turtles are plotted more than once (if recaptured).

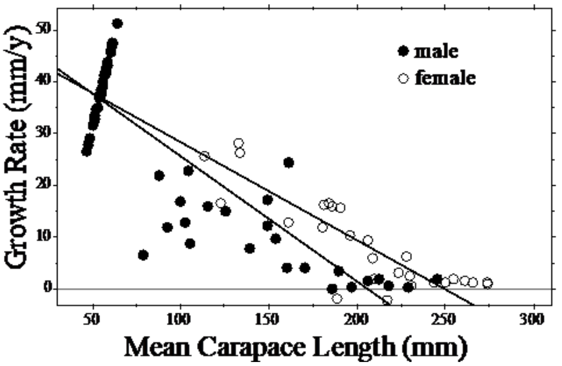

Figure 2. Relationships of carapacial growth rate (mm/y) to mean carapace length (mm) at first and last capture for Red-eared Sliders (*Trachemys scripta elegans*) in Dewart Lake, Indiana, USA. Solid dots for carapace lengths < 75 mm are unsexed juveniles included in both regression calculations. Some solid dots represent male and female turtles with identical data.

Discussion

The available data strongly suggest a latitudinal increase in body size in female *T. s. elegans*; however, additional data for males are needed to determine whether they also follow Bergmann's Rule (Ashton 2004). It should be noted that different authors frequently used different methods for measuring carapace and plastron length. For example, some authors measure maximum plastron length as we did (see Methods; Cagle 1946), whereas others measured PL along the midline (Pritchard 1969; Tucker et al. 1999), which can be substantially shorter than maximum length (see Iverson and Lewis 2018). This variation in methods has the potential to affect the statistical significance of our results; however, we believe that the large number of samples for *T. s. elegans* and the small degree of difference in measurements among populations did not affect our conclusions.

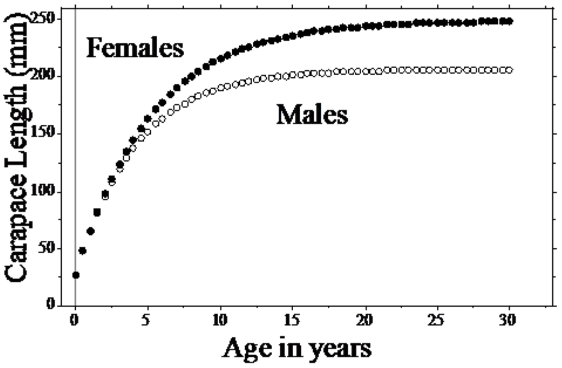

Figure 3. Estimated growth curves for Red-eared Sliders (*Trachemys scripta elegans*) at Dewart Lake, Indiana, USA, based on von Bertalanffy growth model analyses. Juvenile turtles (sex not determined) were included in both male and female analyses. Age is plotted in seasons of growth after emergence from the nest. The von Bertalanffy curve for males and unsexed juveniles was CL (in mm) = $206.4(1-0.866e^{-0.240t})$, and for females and unsexed juveniles it was CL (in mm) = $249.1(1-0.899e^{-0.190t})$.

Numerous studies of juvenile growth in *T. scripta* lumped males and females in their growth analyses (Cagle 1946; Thomas 1993; Tucker et al. 1999). Our data, however, suggest that growth rates in male and female *T. s. elegans* in Indiana diverge by the fourth season of growth if not before. Webb (1961) and Glidewell (1984) reported that females grew faster than males during their first growing season. In contrast, Dunham and Gibbons (1990) claimed that, as juveniles, male and female *T. s. scripta* grow at the same rate. Growth data are needed from additional populations to determine if juvenile growth patterns differ by sex between the two subspecies.

The meager available data on juvenile growth rates in *T. s. elegans* suggest considerable variation among populations, with perhaps a weak latitudinal pattern of increasing growth rate. Any pattern is obscured by the fact that previous authors lumped the sexes in their analyses. In addition, substantial variation is expected given that

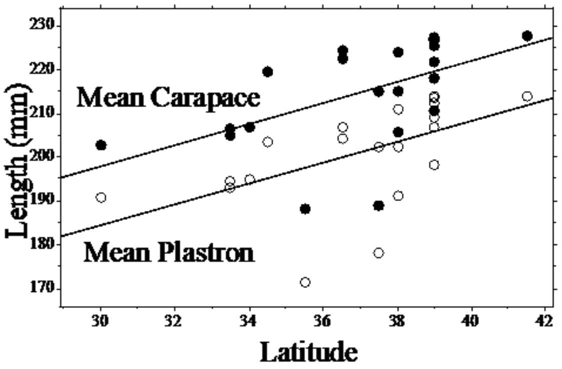

Figure 4. Latitudinal variation in mean carapace (filled circles; $r = 0.54$; $P = 0.013$) and plastron lengths (open circles; $r = 0.54$; $P = 0.011$) for adult females across populations of Red-eared Sliders (*Trachemys scripta elegans*; see Table 1).

Table 3. Adult body size (carapace length, CL, or plastron length, PL, in mm) in Yellow-Bellied Sliders (*Trachemys scripta scripta*) across its range. Data are arranged by decreasing latitude. Some studies only reported CL or PL data (not both); the missing variable was estimated (and marked by an asterisk) based on the ratio of PL to CL calculated from data in Mitchell and Pague (1991; male PL/CL = 0.906; female = 0.936). Mean is followed by sample size and appears above the range in parentheses.

Location (Latitude)	Male CL	Female CL	Male PL	Female PL	Source
Virginia (36.5)	158.4; 20 (102–215)	248.2; 21 (232–272)	143.5; 20 (94–189)	232.2; 21 —	Mitchell and Pague 1990, 1991
North Carolina (ca. 35.5)	—	224.1; 12 (198–249)	—	208.6*; 12 (185–233)	Palmer and Braswell 1995
South Carolina (all populations)	—	224.4*; 61 (160–296)	—	210; 61 (150–277)	Congdon and Gibbons 1983
South Carolina (Kiawah; 33.5)	220.8*; 19	273.5*; 17	200; 19	256; 17	Gibbons and Lovich 1990
South Carolina (Capers; 33.5)	206.4*; 14	269.2*; 45	187; 14	252; 45	Gibbons and Lovich 1990
South Carolina (Kearse; 33.5)	—	206.2*; 15	—	193; 15	Congdon and Gibbons 1983
South Carolina (Lodge; 33)	—	223.0*; 10	—	208.7; 10	Congdon and Gibbons 1983
South Carolina (Ellenton; 33)	153.4*; 570	198.7*; 353	139; 570	186; 353	Gibbons and Lovich 1990
South Carolina (Par; 33)	174.4*; 760	250.0*; 354	158; 760	234; 354	Gibbons and Lovich 1990
South Carolina (Risher; 33)	156.7*; 63	203.0*; 58	142; 63	190; 58	Gibbons and Lovich 1990
South Carolina (Lost; 33)	161.1*; 653	208.3*; 653	146; 653	195; 328	Gibbons and Lovich 1990
South Carolina (Pond B; 33)	150.1*; 185	225.4*; 78	136; 185	211; 78	Gibbons and Lovich 1990
Georgia (31)	—	207.7*; 6	—	194.4; 6	Congdon and Gibbons 1983
Northwest Florida (30.5)	—	217; 25 (189–237)	—	199; 87 (171–225)	Aresco 2004
North Florida (29.5)	—	224.7*; 18 (196–246)	—	210.3; 18 (183–230)	Jackson 1988

growth in turtles has been shown to be affected by aerial and aquatic temperatures (Cagle 1946; Parmenter 1980; Thornhill 1982; Avery et al. 1993; and Thomas 1993; among others), diet and food quality (Gibbons 1967; Ernst and McDonald 1989; Avery et al. 1993), food abundance (Cagle 1946), pond bottom type (Quinn and Christiansen 1972) and even changing wetland water levels (Webb 1961). Although a latitudinal pattern of slower juvenile growth in temperate regions would be expected due to temperatures alone, our preliminary data for *T. s. elegans* and those of St. Clair et al. (1994) for *C. picta* suggest that growth rates may actually increase with latitude in at least those two species. In addition, if sexual maturity is more dependent on size than on age, as is usually assumed (Cagle 1950; Legler 1960; Moll 1979; among others), any latitudinal variation in growth rates should be reflected in variation in age at maturity. Unfortunately, no geographic pattern in age at maturity is evident from the available data for sliders (Table 4). Hence, despite how well studied this species is (e.g., Gibbons 1990; Lovich and Ennen 2013), we still do not understand the geographic patterns of juvenile growth and maturity that contribute to the latitudinal increase in adult body size. The collection of those data is important to understanding the newly emerging, confounding factor of global warming. Furthermore, as suggested by St. Clair et al. (1994), common garden studies of juvenile growth among turtle populations across latitude would be helpful in sourcing the genetic versus environmental bases for the variation in growth and sexual maturity observed to date.

No well-sampled, wide-ranging chelonian species for which data on body size across latitude have been analyzed has been shown to contradict Bergmann's Rule. Of the 20 North American turtle species with distributions exceeding 10° of latitude, six have been shown quantitatively to follow Bergmann's Rule: *Chelydra serpentina* (Iverson et al. 1997), Rough-footed

Table 4. Latitudinal variation in age at maturity in Slider Turtles, *Trachemys scripta*. Annotations of cold or warm refer to thermally altered, human-impacted sites.

Population	Age at maturity (years)		
(latitude)	Male	Female	Source
T. s. elegans			
Illinois (39.0)	—	6–7	Tucker 2001; Tucker and Moll 1997
Illinois (38.0)	—	4 (normal) 3 (warm)	Thornhill 1982
Illinois (37.5)	2–5	—	Cagle 1948
Missouri (36.5)	7–8 (cold) 4–5 (normal)	14 (cold) 7–8 (normal)	Thomas 1993
Oklahoma (34.0)	3+	4+	Webb 1961
Texas (34.0)	6	9	Glidewell 1984
T. s. scripta			
Virginia (36.5)	about 5	> 8	Mitchell and Pague 1990
South Carolina (33.0)	4–5 (normal) 3–4 (warm)	9 (normal) 5 (warm)	Gibbons 1970; Gibbons et al. 1981

Mud Turtle, *Kinosternon hirtipes* (Table 1 in Iverson 1985), *Sternotherus odoratus* (Tinkle 1961; Edmonds and Brooks 1996; Iverson and Meshaka 2006), *Chrysemys picta* (Moll 1973; Iverson and Smith 1993; Tesche and Hodges 2015), Spotted Turtle, *Clemmys guttata* (Litzgus and Brooks 1998; Litzgus et al. 2004), Wood Turtle, *Glyptemys insculpta* (Greaves and Litzgus 2009), and *Trachemys scripta* (this study). For an additional five species, the available preliminary data suggest a positive correlation between latitude and body size (Ashton and Feldman 2003): Eastern Mud Turtle, *Kinosternon subrubrum* (Iverson 1979), *Actinemys marmorata* (Bury et al. 2012; Germano and Riedle 2015), Diamond-backed Terrapin, *Malaclemys terrapin* (Seigel 1980; Lovich and Gibbons 1990; Aresco 1996), Western Box Turtle, *Terrapene ornata* (Legler 1960; Blair 1976), and Spiny Softshell, *Apalone spinifera* (Webb 1962; Iverson, unpubl. data). For the remaining nine wide-ranging North American taxa, geographic variation in body size has not yet been evaluated.

Six additional wide-ranging turtle species from other parts of the world that have been studied also follow Bergmann's Rule: Black Spine-neck Swamp Turtle *Acanthochelys spixii* (Bager et al. 2016), European Pond Turtle, *Emys orbicularis* (females only: Joos et al. 2017), Chaco Tortoise, *Chelonoidis chilensis* (Fritz et al. 2012), Leopard Tortoise, *Stigmochelys pardalis* (Fritz et al. 2010), Spur-thighed Tortoise, *Testudo graeca* (Werner et al. 2015), and Hermann's Tortoise, *Testudo hermanni* (Willemsen and Hailey 1999). Taken together these data argue that selective pressures for larger body size in turtles at higher latitudes (and presumably colder temperatures) are nearly universal within wide-ranging turtle species, strengthening the earlier conclusion of Ashton and Feldman (2003). Hence, future investigations of intraspecific variation in body size in turtles should shift from whether they follow Bergmann's Rule, to why they do. In addition, attention needs to be devoted to understanding the interaction between juvenile growth rate and size and age at maturity that produces the latitudinal body size pattern demonstrated for turtles. Further work will be needed to address the discrepancy concerning the application of Bergmann's Rule across (rather than within) turtle species (e.g., Angielczyk et al. 2015 versus Lindeman 2008).

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