

## ESTIMATES OF SOMATIC GROWTH RATES OF COMMON SNAPPING TURTLES (*CHELYDRA SERPENTINA*) IN TEXAS, USA

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**Abstract.**—Knowledge of somatic growth rates is important for acquiring information on life-history traits and population demography. Estimating growth rates for long-lived organisms, such as turtles, is challenging because it requires long sampling times for adequate growth rate estimation. Within the same species, growth can vary among populations due to variation in latitude, environmental conditions, diet, competition, genetics, and timing of sexual maturity. Here, we studied the somatic growth rates of male and female Common Snapping Turtles (*Chelydra serpentina*) from Spring Lake, Hays County, Texas, USA. We applied the Wang's modified von Bertalanffy Model to mark-recapture data of individuals with unknown age collected from 1995 to 2021. We found the growth trajectories to follow the patterns observed in other freshwater turtle species: juveniles exhibited a rapid growth rate and the growth slowed as individuals approached the assumed size of sexual maturity. Estimated growth coefficients were higher for females ( $k = 0.40$ ) than males ( $k = 0.22$ ). Female growth slowed significantly after the age of 12 or at a straight-line carapace length (SCL) of 275 mm. Male growth slowed at the age of 20 or at SCL of 312 mm. Although growth rates of *C. serpentina* have been widely studied, previous research focused mainly on northern populations. We estimated growth rates in a region where turtles are active year round, which aids in understanding the life-history traits of *C. serpentina* in the southern portion of their distribution.

**Key Words.**—Chelydridae; female maturity; male maturity; Testudines; von Bertalanffy growth model

### INTRODUCTION

The importance of estimating somatic growth rates during population studies cannot be overstated. Understanding age at maturity and growth patterns among age and sex classes within a population can elucidate life-history traits and population demography. In long-lived organisms, such as turtles, however, long-term studies with adequate sampling time frames (years) are required, which limits the number of researchers and sites available to conduct such studies.

Researchers can estimate growth rates and size at age in various ways such as counting growth rings of scutes or bone rings in long bones (Hammer 1969; Christiansen and Burken 1979). While these methods are excellent indicators in determining age during early growth, the lines become obscured through time and inter-line distances become closer, especially when turtles reach adulthood (Galbraith and Brooks 1987, 1989; Germano and Bury 1998; Armstrong and Brooks 2014). Counting individual growth rings, therefore, can sometime lead to an underestimation of growth and size at sexual maturity, which can lead to inaccuracy of survivorship estimates (Galbraith and Brooks 1987,

1989; Brooks et al. 1997; but see Bury and Germano 1998; Germano and Bury 1998). Often, studies keep track of changes in a morphometric characteristic such as carapace length, or mass, between two points in time (Gibbons 1968; Aresco et al. 2006). Such morphometric data can be used in growth models to estimate the age of turtles (e.g., Plummer and Mills 2015; Sung et al. 2015; Harden et al. 2021). Of greatest interest is determining when females attain sexual maturity, which can aid in projecting population growth (Feng et al. 2019; Turner Tomaszewicz et al. 2022). In many turtles, however, sexual maturity is related to size rather than age (Ernst and Lovich 2009), and because growth rates can vary geographically, it is important to study growth rate patterns at a population level (Marchand et al. 2018).

In turtles, somatic growth is related to reproductive patterns and survivorship. Juveniles exhibit a high growth rate, allowing them to quickly attain a large size that reduces their vulnerability to predation (Congdon et al. 2013). Once this size refuge (Paine 1976) is reached, growth rates decrease as more energy is allocated to reproduction (Rowe 1997). Moreover, male and female turtles can have divergent growth trajectories that are tied to differing reproductive strategies (Agha

et al. 2018). Although this growth pattern is common among turtle species (Congdon et al. 2018), growth rates vary between populations because of variation in diet, temperature, population density, competition, assimilation rates, and genetics (Gibbons 1968; Brown et al. 1994; Mayeaux et al. 1996; Harden et al. 2021). Growth rates and size at maturity differ across latitudinal gradients because of differences in environmental conditions and productivity periods (Brown et al. 1994; Iverson et al. 1997; Marchand et al. 2018). Populations at lower latitudes in warmer climates tend to be active throughout the year and exhibit higher growth rates due to longer growing seasons (Congdon et al. 2013). Recent research also indicates that there is considerable variability in growth among individuals within turtle populations (Armstrong et al. 2018; Harden et al. 2021). This individual variation can affect overall reproductive success and, consequently, population viability (Armstrong et al. 2018).

The Common Snapping Turtle (*Chelydra serpentina*; hereafter, Snapping Turtle) is a good model organism to study differences in population life-history traits across a large habitat scale because the species is common and has a wide latitudinal geographical range. Their range extends from southeastern Newfoundland west to Saskatchewan in Canada, south to the Gulf Coast of the U.S., covering the entire Mississippi River drainage to the Rocky Mountains (Ernst and Lovich 2009). The habitat encompasses numerous kinds of lotic and lentic waterbodies. Snapping Turtles are found in polluted waterways (Gibbons 1968), spring-fed rivers (Johnston et al. 2012; Munscher et al. 2020), and constant temperature springs (Rose and Small 2014). Life-history traits such as clutch and egg size, growth, and size and age at sexual maturity in Snapping Turtles have been studied in many populations; however, far more attention has been directed toward northern populations, such as those in Ontario, Canada (Galbraith et al. 1989; Brown et al. 1994; Armstrong and Brooks 2014), Iowa (Christiansen and Burken 1979), Michigan (Congdon et al. 1994), Nebraska (Iverson et al. 1997), and North Dakota (Dekker 2015) in the U.S.

Among the studied populations, growth rates were higher during the juvenile stages (e.g., Christiansen and Burken 1979; Galbraith et al. 1989); however, growth rates varied by latitude as well as between sexes. Populations in the higher latitudes generally exhibited slower growth and reached a larger asymptotic size at an older age, while populations in the lower latitudes exhibited higher growth rates and reached a smaller asymptotic size at a younger age (Galbraith et al. 1989; Iverson et al. 1997). For example, asymptotic size for male and female Snapping Turtles was higher in North Dakota (447 and 347 mm carapace length, respectively; Dekker 2015) than in Pennsylvania (375 and 276 mm

carapace length, respectively; Hughes and Meshaka 2020) and North Carolina (351 and 279 mm carapace length, respectively; Hanscom et al. 2020). In addition, female Snapping Turtles in North Carolina had higher growth rate estimates ( $k = 0.21$ ; Hanscom et al. 2020) than populations in Pennsylvania ( $k = 0.11$ ; Hughes and Meshaka 2020) and North Dakota ( $k = 0.083$ ; Dekker 2015). Although research on Snapping Turtles in Texas exists (e.g., Riedle et al. 2015; Munscher et al. 2020), there are no reports on the somatic growth rate of this species.

Our objective was to develop somatic growth curves of Snapping Turtles inhabiting Spring Lake, Hays County, Texas, USA, using mark-recapture data. Snapping Turtles in Spring Lake represent one of the southern-most populations in North America monitored over many years. This provides a unique opportunity to study their growth rates and enhance our understanding of Snapping Turtle ecology in the southern part of its range. Furthermore, information presented in this study provides a base line for future analyses of Snapping Turtle life-history traits and population demography.

#### MATERIALS AND METHODS

**Study site.**—Approximately 200 springs, collectively called San Marcos Springs, emerge from the Edwards Aquifer to form the headwaters of the San Marcos River in Hays County, Texas, USA. San Marcos Springs release the second largest spring flow in Texas with an average flow rate of 4.8 m<sup>3</sup>/s. In 1849, the 600 m spring run was dammed to form Spring Lake and a lentic slough (Coley 2016) where we conducted our study (Fig. 1). Combined surface area of the lake and slough is approximately 12 ha. Water temperature ( $22^{\circ} \pm 2^{\circ}$  [standard error] C) in the lake is stable throughout the year (Groger et al. 1997). The slough is the terminal portion of Sink Creek, formed in the Sink Creek Basin by backwater from the dam where water temperatures can vary with season. The Sink Creek watershed is large, but there is no sustained surface water flow in proximity to Spring Lake (i.e., the slough) except during heavy rains and occasional flood events. Therefore, our study area consisted of two habitats: a lotic spring system (i.e., Spring Lake) and a lentic slough (Fig. 1). Because of high flow rates from the springs, there is little bottom sediment in the lake, but the slough has a deep layer of mud, organic debris, logs, and emergent and aquatic vegetation.

**Capture methods.**—We captured snapping turtles between 1995 and 2021 throughout all months of the year using various methods that included traps (hoop nets and basking traps), dip netting, hand capture (after floods), volunteer divers, and during nesting

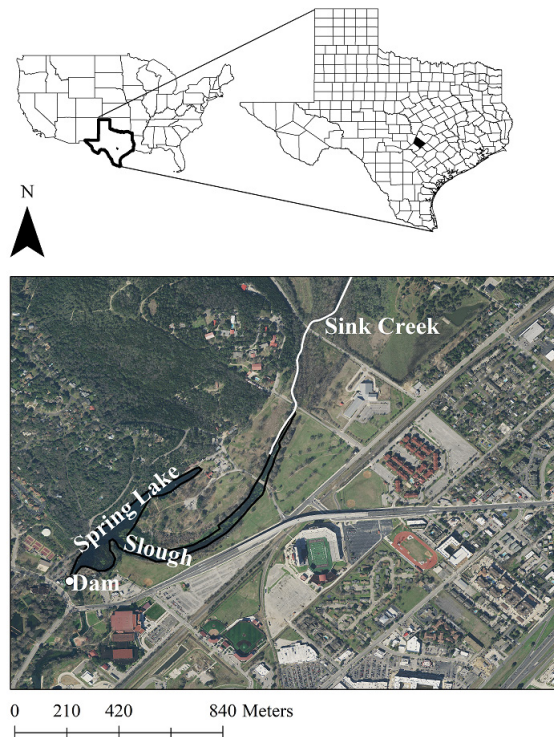


FIGURE 1. Map of the USA (top left) and Texas highlighting Hays County (top right) where Spring Lake (bottom) is located. Spring Lake and the slough were surveyed annually for the Common Snapping Turtle (*Chelydra serpentina*) from 1995 to 2021.

seasons. Because four species were under investigation simultaneously, the methods we used for captures were inconsistent through time and we did not survey every month for all 27 y. Dip netting occurred from an 8.8 m (29 ft)-long barge and along a boardwalk. We set six to eight traps (Memphis Net & Twine Co., Memphis, Tennessee, USA) along the edges of both sides of the slough and along the edges of Spring Lake where accessible. Traps had a single throat and were composed of three metal rings, 78.7 cm in diameter, with nylon mesh (2.5 cm). We modified the throat of each trap to produce an opening that was wider than the original and more slit-like to accommodate entry and retention of larger turtles. We baited traps with chicken, fish, and various meats hung in a  $12.7 \times 13.9 \times 5$  cm metal mesh frame to thwart easy access to bait. Initially, we set traps systematically (see Rose and Small 2014), but those efforts were interrupted over the years due to different environmental restoration projects.

We measured straight-line carapace length (SCL) using Mantax tree calipers (Forestry Suppliers, Jackson, Mississippi, USA) to the nearest 1 mm. We inserted a Passive Integrated Transponder (PIT) tag (American Veterinary Identification Devices, Norco, California, USA) subcutaneously at the lateral base of the tail of each turtle. In addition, we etched the capture number of

each turtle into the first mid-dorsal scute using a Dremel tool (Robert Bosch Tool Corporation, Mount Prospect, Illinois, USA). We determined sex of turtles following the protocol established by Mosimann and Bider (1960) or by observing the presence of an extruded penis while a turtle was handled. Based on decades of experience of the second author and following the literature (Steyermark et al. 2008; Keevil et al. 2017), we were able to determine sex with confidence for turtles with  $SCL > 200$  mm. Because it is difficult to determine sex and sexual maturity with certainty for smaller turtles, we placed all turtles  $< 200$  mm SCL that were not recaptured when SCL was  $> 200$  mm in the category Sex Undetermined (SUD;  $n = 3$ ). Following processing, we released turtles at or near their site of capture.

**Statistical analyses.**—To obtain growth estimates for *C. serpentina*, we applied the Wang's modified von Bertalanffy model for mark-recapture data of individuals with unknown age while accounting for individual variation in growth (Wang 1998):

$$\Delta L = [L_{\infty} + \beta(L_m - \bar{L}_m) - L_m](1 - e^{-k\Delta t})$$

where  $\Delta L$  represents the change in length between initial marking and recapture,  $L_{\infty}$  is the asymptotic length,  $L_m$  is the size at initial marking,  $\bar{L}_m$  is the mean size at initial marking,  $\beta$  is the parameter related to individual variation in growth,  $k$  is the Brody growth coefficient, and  $\Delta t$  is time in fractions of years between the exact capture and recapture dates. The parameters  $L_{\infty}$ ,  $k$ , and  $\beta$  were estimated using the Maximum Likelihood Approach of a normal log-likelihood function. We constructed models separately for males and females. We placed all individuals that were categorized as SUD upon the first capture but were large enough to determine sex upon recapture into their respective sex category. We included the three SUD individuals that we did not recapture at a large enough size to determine sex with certainty in both male and female analyses. Although not ideal, this approach was used previously in turtle research with limited data and under the assumption that juveniles of both sexes initially grow at similar rates (Martins and Souza 2008; Marchand et al. 2018). Moreover, Hughes and Meshaka (2020) found that male and female Snapping Turtles had nearly indistinguishable growth rates for approximately the first 12 y of life while Armstrong and Brooks (2013) showed that males and females grow similarly until they reach 240 mm SCL.

We included individuals with larger measurements taken at the initial capture than measurements taken upon recapture in the analyses. These slight differences (i.e.,  $1.39 \pm$  [standard deviation] 1.33 mm) were likely a result of measurement errors and should not influence

the results of our analyses. Although decreases in body size have been observed in turtles that experience nutrient deficiency (Avery et al. 1993), reductions in turtle body size were not apparent in our study and we were not able to test whether the decrease in size was related to body condition.

We predicted length-at-age based on the estimated parameters (i.e.,  $L_\infty$  and  $k$ ) using the von Bertalanffy growth model (von Bertalanffy 1938):

$$L = L_\infty - (L_\infty - L_0)e^{-kt}$$

where  $L$  is length,  $L_\infty$  is the asymptotic length,  $L_0$  is length at birth,  $k$  is the Brody growth coefficient, and  $t$  is age in years. For length at hatching, we averaged the SCLs of all Snapping Turtles that were hatched at Spring Lake ( $L_0 = 30.8$  mm;  $n = 8$ ). We estimated the 95% confidence intervals (CI) of the predicted length-at-age using a bootstrap method. Based on the estimated growth curves, we determined at what age males and females substantially slowed or plateaued their growth. We used R (version 4.2.0; R Core Team 2020) for all analyses.

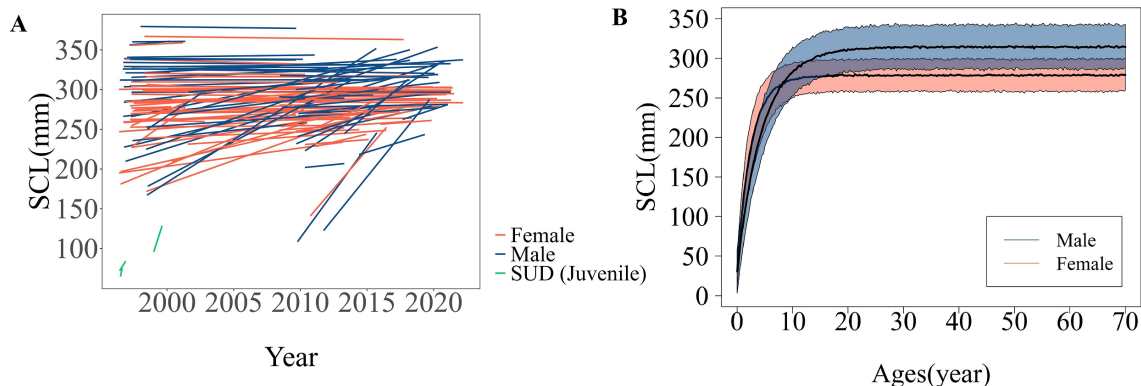
## RESULTS

Between 1995 and 2021, we marked 118 unique Snapping Turtles, which consisted of 60 females ( $L_m = 263.20 \pm$  [standard deviation] 54.32 mm), 55 males ( $L_m = 266.65 \pm 67.47$  mm), and three SUD ( $L_m = 79.84 \pm 16.71$  mm; Fig. 2). The number of recaptures for an individual turtle ranged from one to eight times, with a mode of two and a mean of 3.1. The slough was the primary capture area (84% of all captures). Time between initial marking and recapturing ranged from 0.008 to 19.44 y, with a mean of 4.49 y. Based on the estimated growth curve, female Snapping Turtles had a higher growth rate until they reached approximately 275

mm SCL (12 y of age; Fig. 2), although the difference was not significant. In contrast, males continued to grow, although with a slower rate, until approximately 312 mm SCL (20 y of age; Fig. 2). For both sexes, the rapid rate of growth in the initial years gradually decreased as the carapace length increased. Based on Wang's growth model, estimated asymptotic SCL ( $L_\infty$ ) was 314.5 mm (95% CI = 310.4–318.7 mm) and 278.9 mm (95% CI = 275.7–281.7) for males and females, respectively. Growth coefficients ( $k$ ) were 0.22 (95% CI = 0.18–0.27) for males and 0.40 (95% CI = 0.24–0.58) for females. Individual growth variation estimates ( $\beta$ ) were 0.11 (95% CI = 0.04–0.18) for males and 0.43 (95% CI = 0.35–0.50) for females.

## DISCUSSION

Understanding somatic growth patterns in turtles is an active area of research (Edmonds et al. 2021; Harden et al. 2021; Germano et al. 2022). Because of the longevity and late maturity of freshwater turtles, relatively few studies apply von Bertalanffy growth models to mark-recapture data even for well-studied species such as the Snapping Turtle (Armstrong et al. 2018; Hughes and Meshaka 2020). Moreover, most of the current knowledge of Snapping Turtle life history is based on studies of northern latitude populations in Canada, and U.S. states of Iowa, Nebraska, and Michigan (Iverson et al. 1997; Congdon et al. 2013; Armstrong et al. 2018). Our study contributes to the understanding of the somatic growth rates of the species in a southern population living in an environment where turtles remain active all year. The growth coefficients ( $k$ ) of Snapping Turtles for this southern population are higher than the coefficients reported in North Carolina, North Dakota, and Pennsylvania populations (Dekker 2015; Hanscom et al. 2020; Hughes and Meshaka 2020) and were generally similar to the growth trajectories



**FIGURE 2.** (A) Raw data of size (straight-line carapace length: SCL) at capture for each unique Common Snapping Turtle (*Chelydra serpentina*) at Spring Lake, Hays County, Texas, USA, and (B) predicted length at age based on estimated growth parameters with 95% confidence intervals.

reported in many freshwater turtle species, where rapid growth occurred in juveniles and decreased as the turtles approached sexual maturity (e.g., Spencer 2002; Congdon et al. 2013; Marchand et al. 2018; Hughes and Meshaka 2020). These changes in growth rates among age classes are expected among reptiles based on their life-history traits and survival strategy (Mogollones et al. 2010; Hanscom et al. 2020; Hughes and Meshaka 2020).

Geographic distribution along latitudinal gradients could be a factor in predicting the rate of somatic growth and variation in body size of turtles (Iverson et al. 1997; Marchand et al. 2018). In many turtle species, females of northern populations attain larger size and mature at an older age in comparison to their conspecifics in the southern populations due to severe winters and shorter growing seasons (Galbraith et al. 1989; Brooks et al. 1992; Litzgus and Brooks 1998; Marchand et al. 2018). Snapping Turtles in our study did grow faster and reached a smaller asymptotic size (i.e., had smaller  $L_{\infty}$ ) in comparison to the northern populations. This is likely the result of a milder climate. In northern populations, having larger  $L_{\infty}$  increases the likelihood of survivorship in harsh environmental conditions such as prolonged winter periods (Gibbons et al. 1981; Galbraith et al. 1989; Armstrong et al. 2018). It is important, however, to acknowledge that variation in growth is not only influenced by latitude, but also elevation, water temperature variability, productivity of the habitat, reproductive strategy, genetics, and time to attain sexual maturity (Galbraith et al. 1989; Brown et al. 1994; Iverson et al. 1997).

At Spring Lake, males grew slower over a longer period and attained larger size in comparison to females, similar to findings of Hughes and Meshaka (2020). Post maturity growth and attainment of a larger size can be beneficial to the sex that exhibits aggressive behavior, such as male Snapping Turtles (Hughes and Meshaka 2020). Keevil et al. (2017) found that male Snapping Turtles mature at smaller sizes than females and their aggression (i.e., male-to-male combat) increases with body size, where smaller males likely avoid competition for mates. While we did not determine size at sexual maturity for males, our study generally corroborates conclusions that it is beneficial for males to continue growing and that likely increases their chances to mate. Through simulations and empirical data testing, Wang (1998) demonstrated that allowing the size asymptote to vary from individual to individual ( $\beta$ ) was an important step in eliminating biases in growth parameter estimates. For our dataset, the estimates of  $\beta$  were substantially different from zero for both males and females; however, it is important to note that  $\beta$  does not directly estimate individual variability, it only takes into account individual variation to obtain reliable growth parameters (Wang 1998).

In female Snapping Turtles, Galbraith et al. (1989) hypothesized that growth patterns could be based on two reproductive strategies: delayed maturation to attain a larger size at maturity (size-matters) or early maturation to gain more reproductive years (age-matters). If a population exhibits the age-matters strategy, then female turtles reach sexual maturity earlier and at a smaller size (Galbraith et al. 1989). Previous research suggested that the growth of female freshwater turtles slowed once they reached sexual maturity and began allocating energy for development of eggs and nesting (Christiansen and Burken 1979; Iverson et al. 1997; Congdon et al. 2013; Hanscom et al. 2020; Hughes and Meshaka 2020). Based on this premise, females at Spring Lake reached maturity at about 275 mm SCL and an estimated age of 12 y. In our study area, however, we only found three nesting females over the years, which had SCL of 251, 258, and 300 mm. This could indicate that females at Spring Lake show greater variation in the timing of sexual maturity than we estimated, but unfortunately, we do not have a more robust dataset on nesting females and no data on ovarian follicle development, which would help elucidate size at maturity. In contrast, the smallest gravid female was 185 mm SCL in Florida, USA (Aresco et al. 2006), and 236 mm SCL in Ontario, Canada (Galbraith et al. 1989). In Iowa, females did not start ovulating until after they reached 229 mm SCL (Christiansen and Burken 1979). It is important to note that smaller size classes were scarce in our dataset. Specifically, we captured only five female and four male turtles at small sizes. While this is not uncommon, whether due to elusive behavior or scarcity of juvenile turtles, this lack of data could influence parameter estimates and the overall growth curve (Harden et al. 2021). We recommend future studies at Spring Lake focus on the assessment of female reproductive status (e.g., ultrasound or radiographic examination) to better understand size at maturity and to increase efforts to capture juvenile turtles to improve the growth models.

Elucidating somatic growth patterns is important for understanding life-history traits and reproductive strategy. Relationships among growth trajectory, size at maturity, and reproductive pattern can be used to predict reproductive success and reproductive outputs such as clutch size and fecundity (Brown et al. 1994; Wilkinson and Gibbons 2005; Congdon et al. 2013). Due to variation in growth trajectories, age, and size at maturity across habitat conditions (Brown et al. 1994; Rowe 1997), conducting research in areas of interest for management is needed to obtain accurate information about a specific population. Future studies should also focus on microhabitat characteristics and productivity at each study site in addition to geographic location. Nonetheless, data obtained from our study could be used for assessing reproductive output and variation in size,

as well as comparing von Bertalanffy growth models of the Snapping Turtle, both within Texas and among other areas with similar environmental conditions.

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