
GROWTH AND MATURITY OF SPINY SOFTSHELL TURTLES (*APALONE SPINIFERA*) IN A SMALL URBAN STREAM

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Abstract.—We studied the natural somatic growth of *Apalone spinifera* using mark-recapture in a population inhabiting a small urban stream for 16 y. Growth was rapid and variable in hatchlings and young juveniles, but as body size increased, growth slowed, more rapidly in males than in females. Growth in the largest turtles was slow or immeasurable. Von Bertalanffy growth models indicated that males typically matured in their 4th or 5th year and females in their 12th or 13th year. The general growth pattern of *A. spinifera* was similar to that reported for many sexually dimorphic freshwater turtles, including *A. mutica*, the sister species of *A. spinifera*. Individual growth rate in turtles has important implications for science-based conservation efforts because of its effect on maturation, reproductive output, survivorship, and population recruitment.

Key Words.—body size, determinate growth; mark-recapture; Trionychidae, von Bertalanffy

INTRODUCTION

Individual growth rates affect adult body size, which in turn influences individual survivorship, reproductive output, and, therefore, lifetime fitness (Stearns 1992). The growth rate of many freshwater turtles is characterized by rapid juvenile growth that declines at maturity and is slow to non-existent as an asymptotic body size is attained in older adults (Andrews 1982; Wilbur and Morin 1988; Shine and Iverson 1995; Congdon et al. 2013). Variation in individual growth rate can result in dramatic differences in age and size at maturity, maximum body size, and survivorship (Berry and Shine 1980; Wilbur and Morin 1988; Shine and Iverson 1995; Lindeman 1999). Sources of variability in the growth rate of turtles include environmental factors such as temperature, primary productivity, and latitude (Kennett 1996; Litzgus and Brooks 1998; Germano and Bury 2009; Congdon et al. 2013) and genetic factors such as species, populations, and sex (Berry and Shine 1980; Dunham and Gibbons 1990; Congdon et al. 2003; 2013).

For the approximately 30 species in the turtle family Trionychidae, growth studies are limited (Webb 1962; Shine and Iverson 1995). Some short-term growth rate data for mostly hatchling and juvenile softshells are available from commercial (Mitsukuri 1905) and laboratory research sources (Du and Ji 2003; Lee et al. 2007; Van Dyke et al. 2011), but systematic growth data from mark-recapture field studies are, with one exception, lacking. The only trionychid species for which growth has been intensively studied in the field is *Apalone mutica* (Plummer 1977a).

Apalone spinifera is the most common and broadly distributed trionychid species in North America (Webb 1962; Ernst and Lovich 2009). It occurs in a wide variety of habitats (Webb 1962; Ernst and Lovich 2009), including urban streams and ponds where populations may persist despite the often harmful effects of urbanization (Walsh et al. 2005; Plummer and Mills 2008). It is unknown whether growth rates and size and age at maturity differ in the various habitats inhabited by *A. spinifera*. Our objective in this paper is to describe somatic growth of *A. spinifera* in a small urban stream population that was studied by mark-recapture for 16 y. Because our study stream was small, channelized, and frequently scoured by urban runoff after heavy rains, we questioned whether growth rates and body sizes might be reduced if resources were limited compared to more stable and productive habitats (Gibbons 1967; Gibbons et al. 1981; Germano and Bury 2009).

MATERIALS AND METHODS

Study area.—Gin Creek is a small (6 km length), partially spring-fed first-order urban stream in the Little Red River drainage in White County, Arkansas, USA (35°15'N, 91°43'W). Because Gin Creek is spring-fed 3.5 km upstream from its mouth, the lower 3.5 km flows throughout the year; whereas, the upper 2.5 km of the creek has minimal or no flow during the summer. Like many urban streams, Gin Creek displays visible evidences of the Urban Stream Syndrome (Walsh et al. 2005) including high levels of scouring, low channel complexity, and low retention of organic matter. Radio telemetry studies have established that *Apalone spinifera* is primarily limited to the central 2.5 km of Gin Creek

(Plummer et al. 1997). Within this central portion, creek width averages about 3–6 m and has alternating shallow riffles and deeper pools up to 1.2 m deep. The primary substrate is highly dissected hard bare clay. Frequent scouring of the creek bed results in unconsolidated sediments being limited to pools, shallow slower waters of inside bends, and small backwater areas created by snags. The entire length of Gin Creek is included in the city of Searcy (population approximately 22,000) and provides the major drainage for a large portion of the city (Muncy 1976). The mouth of Gin Creek opens into the lower reaches of Deener Creek, which then empties into the Little Red River 3 km downstream.

Capture and measurement of turtles.—We captured *A. spinifera* in Gin Creek from 1994 to 2010. Most captures (89%) were made by hand, while the remainder was made using wire mesh funnel traps. When first captured, each turtle received a unique mark by clipping the edge of the carapace as described in Plummer (2008). Upon capture and recapture, we recorded identity, sex, and plastron length (PL) to the nearest mm using a metal ruler. We defined hatchlings as individuals captured in the fall that had prominent umbilical scars and individuals captured in the spring that were within the size range (24–32 mm plastron length; PL) of the fall individuals exhibiting umbilical scars. Due to the early loss of the juvenile carapacial pattern in females (Graham 1991; pers. obs.), sex could be assigned on most individuals when PL > 40 mm. Males retained the juvenile pattern longer and began the characteristic elongation and thickening of the tail as subadults (PL > 70 mm). For turtles first captured as hatchlings or juveniles, we back-recorded the hatchling/juvenile status as male or female if the turtle was later recaptured at a size where sex could be determined. We X-rayed 12 females > 140 mm PL 22 times from May through early June and found that the smallest females containing shelled oviducal eggs measured 180–190 mm PL. Thus, we used a PL of 180 mm as the estimated minimum size at maturity for females, which is comparable to the size at maturity for females from nearby Tennessee (Robinson and Murphy 1978) and throughout the range of the species (Webb 1962). For an estimate of the size at maturity for males, we used a minimum PL of 80 mm as determined by Robinson and Murphy (1978) and Webb (1962). We calculated the sexual size dimorphism index (SDI) as mean adult PL of the larger sex / mean adult PL of the smaller sex (Gibbons and Lovich 1990).

Empirical estimation of asymptotic body size in turtles has been variously determined, e.g., maximum size (Martins and Souza 2008) and mean upper 10% (Germano and Bury 2009). These methods were unsuitable for the Gin Creek population because the largest individual was likely a transient and its inclusion

would greatly overestimate asymptotic PL (see Discussion) and the upper 10% of adults yielded an unacceptably small sample size for the small population of < 35 adult females (Plummer and Mills 2008). Therefore, we used the mean PL of the 10 largest resident adult males and 10 largest resident adult females as the asymptotic body size for each sex (Frazier et al. 1990; Lindeman 1997). We established residency by radiotracking individuals (Plummer et al. 1997) and/or recapturing individuals over the course of several years.

Individual incremental growth.—Unlike hard-shelled turtles, softshells do not have scutes from which growth rings can be used to determine the age of individuals. Thus, determining the age of softshells is limited to mark-recapture studies that provide data on growth increments of individual turtles. If the body size at a known age can be determined, the incremental data can be fitted to a growth model that predicts age at a given body size within a given population. We fitted our incremental data to the von Bertalanffy growth model, the most commonly used model to effectively describe growth in freshwater and marine turtles (e.g., Andrews 1982; Shine and Iverson 1995; Lindeman 1997; Fordham et al. 2007). The von Bertalanffy model predicts a steady decline in growth rate with age.

We required a minimum of 120 growth days between captures to minimize errors when measuring small increments of growth. We defined a growth day as one of the 196 days between 1 April and 15 October within the normal activity season of *A. spinifera* in Gin Creek (Plummer et al. 1997). Only one growth increment for each turtle was represented in the data set to avoid pseudoreplication in the statistical analyses (Hurlbert 1984). The recapture data were systematically chosen to provide growth increments for all size classes, which is necessary for an accurate estimate of the overall growth rate (Andrews 1982). We used non-linear regression to fit incremental growth data to a von Bertalanffy growth model, $PL_t = PL_\infty (1 - be^{-rt})$, where PL_t is the plastron length, PL_∞ is the asymptotic plastron length, PL_0 is the hatchling plastron length, b is a parameter related to hatchling plastron length ($\sim 1 - PL_0/PL_\infty$), e is the base of natural logarithms, r is the growth rate, and t is the time since hatching. On the von Bertalanffy growth plots, we superimposed body sizes of recaptured turtles that at first capture were judged to be in their first (≤ 45 mm PL) or second (45–60 mm PL) year, depending on the month of capture, against their known age (1 or 2 y plus the time since first capture). We plotted only one body size per year for turtles recaptured multiple times in the same year.

We used SYSTAT 12 (SYSTAT Software, Inc., San Jose, California, USA) for statistical analyses. We used parametric tests when the assumptions of normality and equality of variances were met. We used non-linear

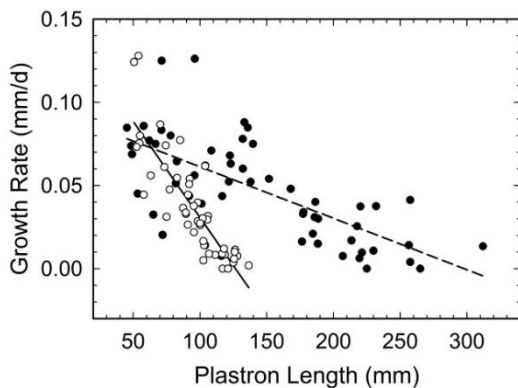


FIGURE 1. The relationship of growth rate per day (GR) and plastron length (PL; mean of first and last captures) for male and female *Apalone spinifera* from Gin Creek. The regression equation for males (open circles, solid line) is $GR = 0.145 - 0.0011 PL$, $r^2 = 0.74$. The regression equation for females (closed circles, dashed line) is $GR = 0.103 - 0.0004 PL$, $r^2 = 0.53$.

regression to regress daily growth rates on body sizes. We used analysis of covariance to compare the slopes of the male and female growth rate regressions, and Mann-Whitney tests to compare mean adult male and female PLs and asymptotic male and female body size. We used Growth II (Pisces-Conservation Ltd, Lymington, Hants, UK) to fit incremental growth data to a von Bertalanffy model. Alpha was set at 0.05 for all tests. Descriptive statistics are reported as mean \pm SE.

RESULTS

We captured 349 individual *A. spinifera* 750 times (range 1–13 recaptures), with 151 (43.3%) *A. spinifera* captured multiple times. We captured 66 males 229 times (71.9% recaptured), 148 females 329 times (45.3% recaptured), and 135 hatchlings and juveniles 192 times (26.9% recaptured). From these captures, we calculated growth increments of 47 males and 47 females.

Hatchlings averaged 30.4 ± 0.79 mm PL ($n = 10$; range 24–32) at initial capture and grew at a rate of 0.115 ± 0.010 mm/d ($n = 4$) up to 60 mm PL. Growth per day thereafter was a declining function of body size in both sexes (Fig. 1). Male growth decreased significantly more rapidly than female growth (test for homogeneity of slopes; $F_{1,92} = 20.29$, $P < 0.001$; Fig. 1).

The differential decline in growth between the sexes resulted in a substantial divergence of male and female body sizes with age (Fig. 2A). Adult males (105 ± 2.1 mm PL) were significantly smaller than adult females (224 ± 5.7 mm PL; $U_{61,25} = 0.0$; $P < 0.001$; SDI = 2.13). The von Bertalanffy model for males (Fig. 2B), $PL = 127(1 - 0.846 e^{-0.233t})$, predicts a mean asymptotic size of 127 mm, which compares favorably with that measured empirically from the 10 largest males in the population

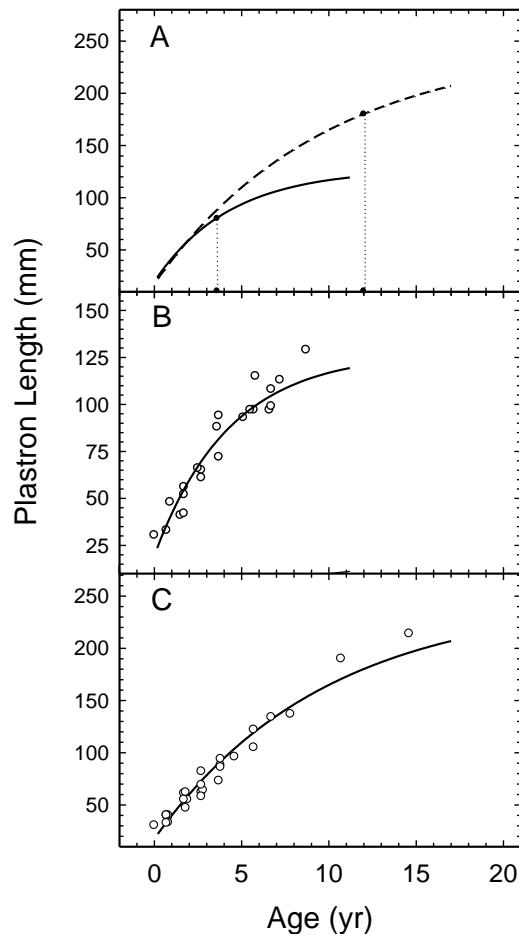


FIGURE 2. A.) Male (solid line) and female (dashed line) von Bertalanffy growth curves for *Apalone spinifera* from Gin Creek. The vertical dotted lines indicate estimated ages at maturity based on the plastron length of males (80 mm) and females (180 mm). B.) von Bertalanffy growth curve for males ($PL = 127.3(1 - 0.846 e^{-0.233t})$) superimposed with points representing 22 annual captures of eight male turtles. C.) von Bertalanffy growth curve for females ($PL = 246.8(1 - 0.929 e^{-0.103t})$) superimposed with points representing 28 annual captures of nine female turtles. The two points beyond 10 years of age represent successive captures of an individual that apparently was fast growing at some point in its life.

(131 ± 1.3 mm). The von Bertalanffy model for females (Fig. 2C), $PL = 247(1 - 0.929 e^{-0.103t})$, predicts a mean asymptotic size of 247 mm, which is identical with that measured empirically from the 10 largest females in the population (247 ± 4.1 mm). The 10 largest recaptured males grew significantly more slowly (0.010 ± 0.0027 mm/d) than the 10 largest recaptured females (0.027 ± 0.0074 mm/d; $U_{10,10} = 13.5$, $P = 0.002$). In some cases, large individuals of each sex ceased growing. Two males (121 and 135 mm PL) failed to grow over intervals of 1.2 and 3.7 y respectively, and two females (216 and 265 mm PL) failed to grow over intervals of

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Table 1. Comparison of hatchling size and growth to 60 mm PL, mean and maximum adult body size, sexual size dimorphism index, and size and age at maturity for *Apalone spinifera* (Gin Creek, Arkansas, USA) and *A. mutica* (Kansas River; data from Plummer 1977a).

Species	Mean hatchling PL (mm)	Juvenile growth (mm/d)	Mean adult PL (mm)	Max PL (mm)	SDI	PL at maturity (mm)	Age at Maturity (y)
<i>Apalone spinifera</i>	30.4	0.115			2.1		
males			105	135	-	80	4–6
females			224	265	-	180	12–14
<i>Apalone mutica</i>	24.5	0.097			1.6		
males			98	123	-	80	4
females			154	186	-	140	9

5.0 and 5.9 y, respectively. The von Bertalanffy models indicate the body size at sexual maturity for males (80–90 mm PL) is on average reached during their 4th or 5th year (Fig. 2A) and body size at sexual maturity for females (180–190 mm PL) is on average reached during their 12th or 13th year (Fig. 2A).

DISCUSSION

North American trionychid (*Apalone*) females grow larger than males and mature at a greater body size and presumably age (Webb 1962; Berry and Shine 1980; Gibbons and Lovich 1990; Pritchard 2001) but these attributes have rarely been quantified from recaptures of individuals in a natural *Apalone* population. The pattern of individual growth exhibited by *A. spinifera* in Gin Creek is consistent with these attributes and more broadly with the pattern of growth and maturity commonly observed in fully aquatic non-trionychid freshwater turtles that show female mate choice (Berry and Shine 1980). The pattern has been particularly well-studied in various emydid species (e.g., *Actinemys marmorata*, Germano and Bury 2009; *Chrysemys picta*, Gibbons 1967; *Graptemys* spp., Berry and Shine 1980; *Trachemys scripta*, Dunham and Gibbons 1990).

Judging from the close correspondence of known-aged turtles and predicted age-size curves and the similarity in measured and predicted asymptotic body sizes, our growth analyses seem biologically reasonable for the study population. The von Bertalanffy models permitted us to estimate age at maturity for *A. spinifera* in Gin Creek. Assuming *A. spinifera* mates primarily in the spring as in *A. mutica* (Plummer 1977b), males generally begin maturing in their 4th or 5th year and first breed in the spring of their 5th or 6th year; whereas, female *A. spinifera* generally begin maturing in their 12th or 13th year and first breed in spring of their 13th or 14th year. Given variability in time of hatching, hatchling size, individual growth rates, and size at maturity of *A. spinifera*, there likely is substantial variation in the age at maturity (Gibbons et al. 1981), as characterizes the closely related *A. mutica*, whose growth rates are also known to exhibit seasonal and annual variability (Plummer 1977a).

The von Bertalanffy growth models are less useful to estimate age of older individuals because small differences in plastron length for large turtles can result in considerable errors in estimating age. Age estimation errors can also result from various environmental and genetic factors (Andrews 1982; Dunham and Gibbons 1990; Kennett 1996; Germano and Bury 2009), and various forms of physical measurement error such as compensating for damage to the soft margin of the plastron. Furthermore, although reptilian growth has traditionally been considered to be indeterminate (Andrews 1982; Congdon et al. 2013), long-term mark-recapture studies have shown that a sizable proportion of adults of several freshwater turtle species exhibit determinate growth, i.e., they cease growing (Congdon et al. 2013). Although it is not apparent in our growth models, our recapture data show that at least some large individual *A. spinifera* cease to grow, as was also reported for *A. mutica* (Plummer 1977a). Thus, older individual *A. spinifera* exhibiting determinate growth are not necessarily larger (Congdon et al. 2013).

In all North American trionychids (*Apalone* spp.) adult females are larger than adult males (Webb 1962; Meylan 1987) yielding a SDI with a positive value (Gibbons and Lovich 1990). The SDI of Gin Creek *A. spinifera* is comparable to that measured from the 10 largest specimens collected throughout *A. spinifera*'s range (1.94; Webb 1962). In comparison to its sister species *A. mutica*, *A. spinifera* is larger with regard to size of hatchlings, early growth rate, size, and age at maturity, and mean and maximum size of adults (Table 1; Webb 1962; Plummer 1977a).

Because the small channelized streambed of Gin Creek is regularly scoured by urban runoff after heavy rains, we anticipated that growth rates and adult body sizes of the mostly carnivorous (Webb 1962; Ernst and Lovich 2009; Michael Plummer, unpubl. data) *A. spinifera* might be reduced due to a limited availability of appropriate nutrition, especially protein (Gibbons 1967; Parmenter 1980; Avery et al. 1993; Kennett 1996), compared to what has been observed in lakes and larger river systems (Williams et al. 2004). It is known that individual *A. spinifera* grow larger in some areas of the range of the species than in Gin Creek, where the largest

female considered resident in Gin Creek and included in the growth analysis was 265 mm PL. For example, much larger females have been reported from Louisiana (362 mm PL, Halk 1986), Minnesota (329 mm PL, Breckenridge 1957), Arkansas (300 mm PL; Michael Plummer, unpubl. data), and from across the range of the species (310 mm PL, Webb 1962). The largest female captured in Gin Creek (318 mm PL; 8 mm growth over three years) and considered to be a transient in the creek is consistent with the notion that growth of *A. spinifera* was resource limited in Gin Creek. This turtle was 20% (53 mm PL) larger than the largest female considered resident in Gin Creek. She was radiotracked over 40 months from 1999 to 2002 (Plummer and Mills 2008) and spent most of her time 3–4 km downstream from the study area in the Little Red River. In three of the four years she was radiotracked, she spent 11–17 d between 20 May and 6 June in Gin Creek. This behavior contrasted sharply with resident adults in Gin Creek. For example, only four of 1,855 daily movements of 16 radiotracked adults occurred outside of the central 2.5 km portion of the creek (Plummer et al. 1997), thus limiting access to nutritional resources that may have been available further downstream. These growth and behavior characteristics suggest the largest female may have been a transient in the Gin Creek population that normally had access to a larger food base in the Little Red River and is the reason we did not include her in our growth analysis.

The above scenario suggests that growth and body size of individual *A. spinifera* may respond to different nutritional environments as is known to occur in hard-shelled turtles in other families, especially the emydids (e.g., *Chrysemys picta*, Gibbons 1967; *Trachemys scripta*, Dunham and Gibbons 1990; *Actinemys marmorata*, Germano and Bury 2009). Unfortunately, growth data for individual *A. spinifera* in the field are sparse (Breckenridge 1955; Graham and Graham 1997) and a definitive comparison of somatic growth among populations with access to differing resource bases is not possible at this time.

Conservation.—*Apalone spinifera* has an extensive natural range in eastern, central, and western North America and has been successfully introduced in peripheral areas (Ernst and Lovich 2009). In general the species is locally common with little evidence of substantial population declines. It is listed as a species of least concern on the IUCN Red List of Threatened Species (Available at <http://www.iucnredlist.org/details/163451/0> [Accessed 24 April 2015]) and its global status is ranked G5 (secure) by NatureServe (Available at <http://www.natureserve.org/explorer> [Accessed 24 April 2015]). *Apalone spinifera* has broad habitat tolerances and is relatively insensitive to habitat disturbances (Plummer and Mills 2008; Plummer et al. 2008), a trait

that likely contributes to its secure status. Nevertheless, there are some localities at the periphery of the range of the species where it is of conservation concern. For example, *A. spinifera* is ranked S1 (critically imperiled) in Maryland, Vermont, and Quebec; S2 (imperiled) in South Dakota, Virginia, and Ontario; and S3 (vulnerable) in Alabama, Florida, Montana, New York, and North Carolina (NatureServe. 2015. *op. cit.*). The growth and maturity results reported herein should be of value to science-based conservation efforts at these localities, especially with regard to assessing the sex ratio and age structure of populations of concern.

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