

## GROWTH, ALLOMETRY AND SEXUAL DIMORPHISM IN THE FLORIDA BOX TURTLE, *TERRAPENE CAROLINA BAURI*

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Male Florida box turtles, *Terrapene carolina bauri*, grow proportionally longer relative to their height and width, than do females, resulting in a longer, flatter carapace, whereas females develop shorter, higher, and slightly narrower carapaces, possibly as an adaptation to accommodate hard-shelled eggs before oviposition. The subspecies has a typical growth pattern for a North American emydine turtle. Growth is rapid in juveniles, but starts to slow once maturity is reached at an age of 12-13 years. Growth rates approach an asymptote at about age 17 years in males and 16 years in females; very little growth occurs after age 20 years. Florida *T. c. bauri* grows at a slower annual rate than does *T. c. carolina* from Maryland despite having a longer annual activity and growth period. The data presented here may be considered to represent the average growth pattern for *T. c. bauri* in Florida. The cervical scute and all vertebral scutes have a greater width:length ratio in juveniles, but this ratio declines as the scutes lengthen with elongation of the carapace; however, the rate of increase in length varies among the scutes.

### INTRODUCTION

Reports of growth and morphometry in eastern box turtles, *Terrapene carolina*, have been confined to the two northern subspecies, *T. c. carolina* (Ditmars, in Pope, 1939; Rosenberger, in Pope, 1939; Ewing, 1939; Nichols, 1939; Allard, 1948; Carr, 1952; Brisbin, 1972; Yahner, 1974; Dodge, Dimond & Wunder, 1978; and Stickel & Bunck, 1989) and *T. c. triunguis* (Leuck & Carpenter, 1981). No growth data have been published for box turtles of peninsular Florida, the most southern portion of the species' range in the United States, and an area where the turtles may be circumannually active (Dodd, Franz, & Smith, 1994). We examined a series of the Florida box turtles (*T. c. bauri*) in the collections of the United States National Museum of Natural History, Smithsonian Institution (USNM) and George Mason University (GMU) to investigate growth, allometry and sexual dimorphism across the geographic range of this subspecies.

Growth rates in turtle populations may vary both spatially (Gibbons, 1967; Christy, Farlow, Bourque & Gibbons, 1974; Ernst & McDonald, 1989; Mushinsky, Wilson & McCoy 1994) and temporally (Ernst, 1971; Tucker, Mahler & Theilung, 1995). The specimens of *T. c. bauri* examined in this study were from several localities over its range, and were collected over an extended period of time. Although any single specimen was probably not representative of its local population, the data are not specific to one population at one time, but instead apply to a large set of times and places within the range. Thus, these data present a picture of the general growth pattern for *T. c. bauri* across its

range. Data from specific localities may not be representative of the growth regime of the entire subspecies. If the localities are from west Florida, particularly along the central and north central coasts, data may show intergradation in the characters of carapace length and shape with the much larger subspecies *T. c. major* whose range lies to the north (Milstead, 1969; Conant, 1975; Ernst, Lovich & Barbour, 1994). A major purpose of this paper is to present a generalized growth profile for the subspecies that can be used for comparison with data from studies performed at specific localities.

Our results are also compared with those of the two northern subspecies, *T. c. carolina* and *T. c. triunguis*, previously reported in the literature. These two subspecies usually stop feeding and become inactive during the colder portions of the year (Ernst *et al.*, 1994), making their growth strategies interesting contrasts with that of the almost continuously active *T. c. bauri* (Dodd *et al.*, 1994).

### MATERIALS AND METHODS

One hundred and one *Terrapene c. bauri* (83-166 mm CL) were examined. Each adult turtle was sexed using the characters noted in Ernst, *et al.* (1994); small individuals not showing sexually dimorphic characters were listed as juveniles. All turtles were aged, when possible, by counting growth annuli on the second pleural scute by the method of Sexton (1959) (see also Zug, 1991). The same person counted the annuli on all specimens. Growth annuli are formed in most hard-shelled North American turtles during periods of winter

hibernation, but may also be formed during extended periods of fasting during which the turtle may be active. While *T. c. bauri* does not normally hibernate, temperatures in Florida may drop low enough to cause it to fast for a few weeks in winter, at which time an annulus is formed (Ernst, *pers. obs.*). The accuracy of growth annuli in aging turtles may vary; in Florida *Gopherus polyphemus* (Mushinsky *et al.*, 1994) and in Pennsylvania *Clemmys guttata* and *C. muhlenbergii* annuli have been shown to be accurate estimators of age (Ernst, 1975, 1977). However, Galbraith & Brooks (1987) questioned their use in aging Canadian *Chelydra serpentina*. Subannuli may be formed in more northern populations that undergo variable weather conditions from late spring to early autumn, and these make it more difficult to determine the age of a turtle, particularly if one is not accustomed to such phenomena. Subannuli are shallower and less wide than annuli, and the two can be distinguished with practice (see discussion in Zug, 1991). However, the temperature over the range of *T. c. bauri* in Florida does not become low enough to cause the turtles to stop feeding and form annuli except in winter.

The use of annuli to estimate age is not without potential problems. Within our sample, and mostly among females with at least 20 discernible annuli, some annuli would begin to coalesce at the seams making it difficult to accurately estimate age. Therefore, individuals with annuli that were coalescing but had 20 discernible annuli were categorized in several ways: (1) they were eliminated from the sample; (2) they were put in the 20 year old category; and (3) they were randomly assigned an age between 20 and 35 years. It is believed that *T. carolina* greater than 20 years of age closely approach a growth asymptote and therefore may represent the size at which this asymptote is approached (Stickel & Bunck, 1989). Because more females were characterized by the condition described above, eliminating these individuals from the growth analysis would disproportionately influence the estimation of the female growth asymptote. Analysis of the three data sets described above allows for a discussion of this potentially problematic phenomenon. Maturity was determined by the attainment of the sexually related morphological characters described in Ernst *et al.* (1994).

Measurements recorded from each individual included: maximum parasagittal carapace length (CL), maximum carapace width (CW), carapace height (CH) at the level of the seam separating the second and third vertebral scutes, maximum plastron length (PL), and the widths and lengths of all vertebral scutes (VW1, VL1, VW2, VL2, etc.) and of the cervical scute (CVW, CVL). All measurements were made with dial calipers straight-line to the nearest 0.1 mm.

Growth in turtles has been described by both indeterminate (Stickel & Bunck, 1989; Germano, 1992) and determinate models (Frazer & Ehrhart, 1985; Bjorndal & Bolten, 1988; Lovich, Ernst & McBreen, 1990). Linear models, which assume indeterminate growth, are

best suited to describe growth when relatively brief segments of an organism's total growth are analysed separately. Classification of linear growth analyses into periods of rapid growth and periods of slow to no growth recognizes that growth is not uniform throughout the life of an organism. If the temporal unit is small enough, the predictive value of a linear equation is preserved. However, studies using linear models to describe growth over a large age interval risk misinterpreting growth, especially at the extremities of the fitted line. Where samples are represented by both a wide distribution of body sizes of known ages and by many mature adults, nonlinear models that assume determinant growth may be most appropriate and have the greatest predictive power (Brisbin, 1990).

Because the nature of our data collection methods did not permit longitudinal measurements of growth increments in known individuals, growth was described using an integrated Richards model (Richards, 1959), as modified by Brisbin, White & Bush (1986):

$$L_t = [A^{(1-m)} - (A^{(1-m)} - L_0^{(1-m)}) \exp(-2/T_r(m+1))]^{1/(1-m)} \quad (1)$$

where  $L_t$  is the carapace length at time  $t$ ,  $L_0$  is the estimated carapace length at hatching,  $A$  is the asymptotic length,  $m$  is the Richards shape parameter, and  $T$  is the number of years required to closely approach the asymptote of carapace length. Therefore, in our analysis of growth,  $L_t$  represents the carapace length of the preserved specimen at the age estimated by counting the number of visible annuli. For the estimated carapace length at hatchling, (i.e.  $L_0$ ) the average hatchling carapace length of 32 mm was extrapolated from Iverson (1977).

Unlike fixed-shape mathematical models that are commonly used to describe growth, the shape parameter  $m$  of the Richards model can be allowed to vary until convergence, or it can be fixed at a specific value. By fixing the shape parameter at a specific value, the Richards model becomes a fixed-shape sigmoidal model. For example, if  $m$  in equation (1) is fixed at 0.667 or 1.0 the Richards model becomes either a Von Bertalanffy or a Gompertz model, respectively (Richards, 1959).

Linear carapace measurements at estimated ages were fitted to equation (1) using a least squares method for nonlinear regression (Proc NLIN; SAS, 1989) with parameters  $A$ ,  $m$ , and  $T$  allowed to vary until convergence. Carapace length data were also fitted to equation (1) with the shape parameter  $m$  fixed at 0.667 to investigate whether the use of the reduced model resulted in a reduction of the residual error mean square (REMS). Four unsexed juveniles were included in the calculations of both the male and female growth curves.

Allometry of linear measurements was analysed by bivariate linear regression using the method of least squares (Proc Reg; SAS, 1989). Carapace length, plastron length, or carapace width were used as independent variables for regression analyses of other body measurements.

TABLE 1. Shell dimensions (in mm) of male and female turtles examined. Dimensions: CL = carapace length; CW = carapace width; CH = carapace height; PL = plastron length; CVL = cervical length; CVW = cervical width; V1L -V5L = vertebrae 1-5 length; V1W - V5W = vertebrae 1-5 width.

D	Females				Males			
	N	Mean	SD	Range	N	Mean	SD	Range
CL	\	126.78	12.53	83-149	38	137.03	15.11	97-166
CW	45	90.31	10.31	59-110	38	92.71	10.33	71-115
CH	44	66.82	6.95	44-78	36	64.56	6.78	44-76
PL	45	121.18	13.11	81-140	37	126.95	13.47	91-157
CVL	39	7.00	1.97	0-10	38	7.87	2.44	0-12
CVW	39	3.21	1.10	0-5	38	3.16	1.33	0-5
V1L	43	26.63	3.06	20-34	37	27.62	3.66	21-35
V1W	43	25.30	3.79	17-34	37	26.14	3.58	21-39
V2L	39	28.62	3.17	18-33	35	30.23	3.73	22-37
V2W	38	33.18	3.51	26-40	35	33.00	3.77	25-41
V3L	37	27.88	3.62	18.2-33.5	34	29.18	4.25	14.1-35.4
V3W	35	36.26	3.53	26.5-41.2	34	37.86	4.40	26.2-46.4
V4L	38	31.07	4.49	19.1-40.6	35	33.63	5.58	20.0-41.9
V4W	38	32.21	3.72	24.6-40.1	35	33.48	5.06	24.2-46.2
V5L	41	22.73	3.51	14-34	36	24.08	2.98	18-31
V5W	41	30.00	4.28	20-37	37	31.35	3.99	23-41

TABLE 2. Estimated parameters for the Richards nonlinear model where  $A$  is the asymptotic length,  $m$  is the Richards shape parameter,  $T$  is the number of years required to closely approach the asymptote of carapace length; and REMS is the residual error mean square. (One asymptotic standard error in parentheses.) Juveniles turtles were used in both male and female models.  $N$  is the number of individuals at least 20 years old which could not be positively aged: <sup>1</sup>eliminated from the sample; <sup>2</sup>assigned to 20 years of age; <sup>3</sup>randomly assigned an age between 20 and 35 years.

Model/Sex	N	A	T	m	REMS
Richards:					
Female	23 <sup>1</sup>	127.2 (3.5)	15.9 (1.8)	1.472 (1.065)	66.1
	42 <sup>2</sup>	134.6 (4.2)	16.6 (3.1)	0.618 (0.818)	75.1
	42 <sup>3</sup>	132.5 (2.1)	16.4 (2.8)	0.719 (0.667)	73.5
Male	30 <sup>1</sup>	142.8 (6.1)	17.8 (3.1)	0.989 (1.020)	156.8
	39 <sup>2</sup>	142.8 (4.8)	17.8 (3.0)	0.989 (0.957)	146.9
	39 <sup>3</sup>	141.5 (3.7)	17.6 (2.7)	1.180 (0.956)	148.3
Von Bertalanffy:					
Female	23 <sup>1</sup>	129.9 (7.9)	15.1 (3.5)	0.667 (fixed)	68.7
	42 <sup>2</sup>	134.4 (2.5)	16.7 (1.9)	0.667 (fixed)	73.3
	42 <sup>3</sup>	132.6 (2.4)	16.3 (1.8)	0.667 (fixed)	72.7
Male	30 <sup>1</sup>	144.3 (9.6)	17.1 (3.5)	0.667 (fixed)	157.5
	39 <sup>2</sup>	144.1 (3.9)	17.0 (2.4)	0.667 (fixed)	143.5
	39 <sup>3</sup>	142.7 (2.5)	16.3 (2.5)	0.667 (fixed)	149.9

## RESULTS

Male turtles on average were larger than adult females in linear measurements recorded except for carapace height (CH) and the second vertebral width (V2W) (Table 1). A MANOVA revealed significant variation between sexes for CL, CW, CH, and PL (Wilk's Lambda=0.496,  $F_{4,75}=19.07$ ,  $P<0.0001$ ).

Nineteen females and nine males with at least 20 discernible annuli were excluded from the first analysis of growth because their age could not be accurately assessed. The exclusion of the nine males had little effect on the estimation of the growth parameters (Table 2). However, the exclusion of females from the sample had a dramatic affect on the estimation of the upper growth

asymptote and the shape parameter  $m$ . This result is not surprising considering that the individuals excluded represent the majority of older animals in the female sample. When the shape parameter was fixed at 0.667 the estimate of the female upper growth asymptote was more similar to the estimate given when all of the data were analysed with the complete model. Given that the estimation of model parameters, such as curve shape  $m$ , is often less reliable when a reduced data set is analysed, it may be more appropriate to consider a less parameter-rich model such as the von Bertalanffy model (Lindeman, 1997). Randomizing the age of individuals that were at least 20 years old but could not be positively aged had almost the same effect as classifying these individual as 20 years of age.

TABLE 3. Expected carapace length and percent annual growth based on the growth parameters derived from the complete Richards model.

Age	Female		Male	
	Expected	Percent	Expected	Percent
	CL	Growth	CL	Growth
0	32.00	-	32.00	-
1	44.00	27.27	43.30	26.09
5	85.38	10.33	87.92	11.51
10	114.36	3.57	121.95	3.89
15	126.69	1.31	135.65	1.29
20	131.55	0.49	140.44	0.42
25	133.42	0.18	142.04	0.138
27	133.79	0.12	142.32	0.088

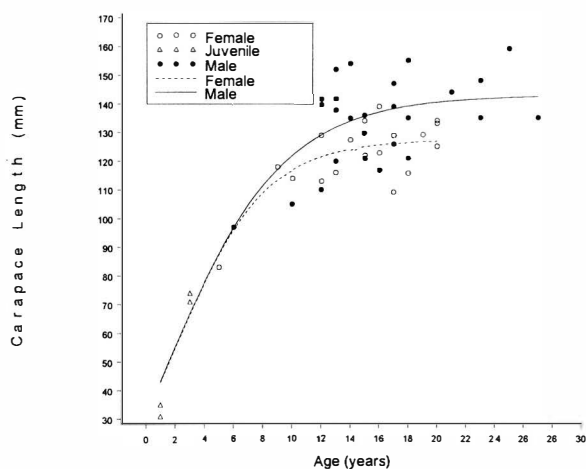


FIG. 1. Richards growth trajectories as a function of age and sex. Four juveniles were included in the calculation of both male and female trajectories.

When all of the data were analysed little difference was observed between the parameters obtained by the complete Richards model and the reduced Richards model (Von Bertalanffy when  $m$  is fixed at 0.667). This was especially true for the female growth trajectory where the shape parameter estimated by the complete model was nearly the same as that of the reduced model (i.e.  $m=0.667$ , Table 2). The male shape parameter more closely resembled that of the Gompertz model (i.e.  $m=1$ , Table 2).

Growth was fast during the juvenile years, but slowed at 12-13 years in both sexes (Fig. 1, Table 3), approximately at the projected time of maturation, 8-13 years, of *Terrapene c. carolina* (Stickel & Bunck, 1989). By the ages of 17 years in males and 16 years in females growth had plateaued (Table 2). By age 20 growth had nearly ceased in both sexes, averaging < 1 mm per year (Table 3).

Allometric analyses of various carapacial and plastral dimensions showed that males grew proportionally more in length than in either height (Fig. 2, Table 4, ANCOVA  $df=1$ ,  $F=49.75$   $P<0.0001$ ) or width

TABLE 4. Allometric relationships of adult *Terrapene carolina bauri*. Slopes are all significantly ( $P<0.001$ ) different from zero.

x vs. y	Sex	N	Linear relation:	
			$y=a+bx$ (in mm)	$R^2$
CL vs. CH	F	42	$y=3.67+0.50x$	0.82
	M	34	$y=15.05+0.36x$	0.61
CL vs. CW	F	43	$y=-5.80+0.76x$	0.85
	M	36	$y=13.17+0.58x$	0.72
CL vs. PL	F	43	$y=-7.51+1.01x$	0.94
	M	35	$y=8.61+0.87x$	0.95
PL vs. CH	F	42	$y=8.51+0.48x$	0.84
	M	34	$y=11.89+0.42x$	0.61
PL vs. CW	F	43	$y=3.11+0.72x$	0.84
	M	35	$y=10.38+0.65x$	0.71
CW vs. CH	F	42	$y=15.83+0.57x$	0.71
	M	34	$y=22.96+0.45x$	0.43

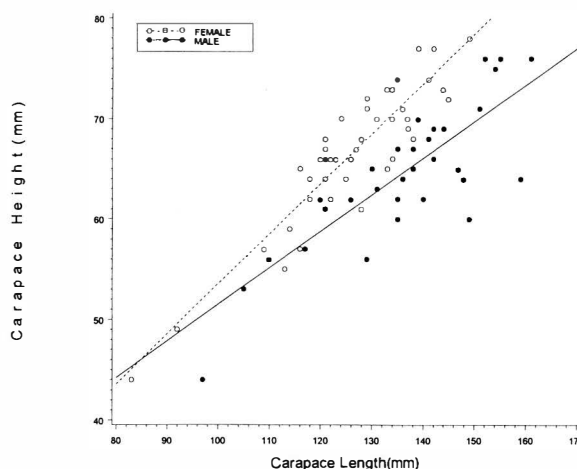


FIG. 2. Allometry of sexually dimorphic carapace height plotted as a function of carapace length and sex. (Female:  $CH = 3.67 + 0.499CL$  and Male:  $CH = 15.04737 + 0.364CL$ ; ANCOVA:  $df = 1$ ,  $F=49.75$ ,  $P < 0.0001$ )

(Fig. 3, Table 4, ANCOVA  $df=1$ ,  $F=14.28$   $P<0.0003$ ). In addition, width increased more than height, producing a longer, flatter carapace than that of females. Allometric growth in females produced a higher, more vaulted, and slightly wider carapace, possibly as an adaptation for shelled-egg storage before oviposition. The plastral hinge was functional in all specimens examined.

The cervical scute and all vertebrae have a greater width: length ratio in juveniles, but this ratio decreases as the scutes grow faster in length than in width while the carapace lengthens (Table 5). However, these scutes increase in length at different rates, resulting in the cervical scute becoming long and narrow, vertebral 1 longer than wide, and vertebrae 2-5 remaining wider than long, although narrowing with age. In adults, vertebrae 2 and 5 are widest, vertebral 4 is the most narrow, and vertebral 3 eventually becomes the shortest in length.

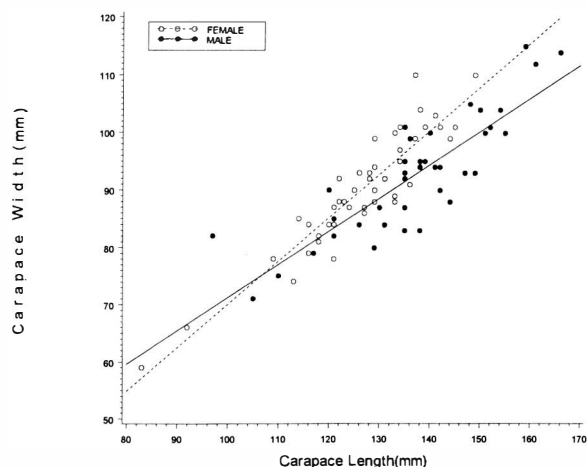


FIG. 3. Allometry of sexually dimorphic carapace width plotted as a function of carapace length and sex. (Female:  $CH = -5.796 + 0.758CL$  and Male;  $CH = 13.172 + 0.580CL$ ; ANCOVA:  $df = 1$ ,  $F = 14.28$ ,  $P < 0.0003$ )

#### DISCUSSION

The allometric patterns, in which mature male *T. c. bauri* are generally larger in all dimorphic carapace dimensions and grow to produce a longer, flatter carapace than that of the females, are normal for turtles of the genus *Terrapene* (Legler, 1960; Brown, 1971).

Stickel & Bunck (1989) published the only comprehensive report on growth in *Terrapene carolina*, a study of the subspecies *T. c. carolina* on the Maryland coastal plain (which has a shorter carapace length on average than *T. c. bauri*; Conant & Collins, 1991). Their growth/age relationships were determined by bivariate linear analysis, and therefore cannot directly be compared with our results. However, the expected size at a series of ages was calculated with the complete Richards model for both male and female *T. c. bauri* (Table 2) and the values were used to make a general comparison with growth of *T. c. carolina* in Maryland (Stickel & Bunck, 1989). The rapid growth by approximately 27% in the first year by both male and female *T. c. bauri* (assuming an average hatchling carapace length of 32 mm; Iverson, 1977) is similar to the average annual growth rate of 22.8%/yr for juvenile *T. c. carolina* (assuming an average hatchling carapace length of 31 mm in the Washington, D. C. area; Allard, 1948). At 8 years of age male *T. c. bauri* grew 6.03%/yr, and females grew by an average of 5.4%/yr.

However, by 13 years of age the growth rate of Florida *T. c. bauri* declined to approximately 2.0%/yr for both sexes. The large difference in growth rates for even a relatively short time interval emphasizes the potential problems that may be introduced by assuming indeterminate growth. The carapace length of *T. c. carolina* increased at an average rate of 6.8%/yr for males and 5.3%/yr for females between ages 8-13, which is comparable to the growth of *T. c. bauri* at the beginning of the same interval. Between 14-19 years of

TABLE 5. Allometric relationships of carapace scutes (D) to carapace length for adult *Terrapene carolina bauri*. Slopes are all significantly different from zero ( $P < 0.05$ ).

D	Sex	N	Linear relation:	
			$y = a + bx$ (in mm)	$R^2$
V1L	F	41	$y = 3.83 + 0.18x$	0.53
	M	35	$y = 4.89 + 0.17x$	0.48
V5W	F	39	$y = -1.26 + 0.25x$	0.51
	M	35	$y = 1.54 + 0.22x$	0.66
CVL	F	37	$y = -1.91 + 0.07x$	0.22
	M	36	$y = 5.63 + 0.02x$	0.01
CVW	F	37	$y = 3.39 + 0.00x$	0.00
	M	36	$y = 6.89 - 0.03x$	0.10
V1W	F	41	$y = 1.73 + 0.19x$	0.37
	M	35	$y = 11.41 + 0.11x$	0.21
V2L	F	37	$y = 3.39 + 0.21x$	0.63
	M	33	$y = 1.76 + 0.21x$	0.76
V2W	M	36	$y = 14.22 + 1.16x$	0.29
	F	33	$y = 7.42 + 0.19x$	0.60
V3L	M	35	$y = 1.80 + 0.21x$	0.56
	F	32	$y = -2.39 + 0.23x$	0.70
V3W	M	33	$y = 10.99 + 0.20x$	0.56
	F	32	$y = 5.14 + 0.24x$	0.70
V4L	M	36	$y = -3.57 + 0.28x$	0.62
	F	33	$y = -3.66 + 0.27x$	0.56
V4W	M	36	$y = 8.16 + 0.19x$	0.44
	F	33	$y = -2.55 + 0.26x$	0.63
V5L	M	39	$y = 2.76 + 0.16x$	0.32
	F	34	$y = 4.92 + 0.14x$	0.50

age, male *T. c. carolina* only increased 2.3%/yr in carapace length; female *T. c. carolina*, 3.4%/yr; and both sexes of *T. c. bauri* grew approximately 1.0%/yr (0.5-1.9 mm). After age 19 little measurable growth occurred per year in either subspecies. Ewing (1939) reported an average increase in carapace length of 3.05 mm/yr over a period of 11 years for a female *T. c. carolina* from the vicinity of Washington, D. C. His turtle grew from 93 mm to 126.5 mm, with most of the growth occurring in the first eight years. He estimated the final age of the turtle at 31.6 years.

The pattern of growth shown by both subspecies (rapid juvenile growth, followed by a slowing growth rate once maturity is reached, and a leveling of size increase in later life) is typical for turtles of the genus *Terrapene* (Legler, 1960; Blair, 1976), and North American emydid turtles in general (Cagle, 1946, 1948; Gibbons, 1967; Ernst, 1971, 1975, 1977; Ernst & Ernst, 1973; Lovich *et al.*, 1990; Congdon & van Loben Sels, 1991).

Maturation is an energy-draining process that diverts stored resources, or resources previously available for somatic growth, to gonadal growth and development plus gamete production, formation of secondary sexual structures and sexual behaviours (Bernardo, 1993). In habitats with varying resource availability, the disproportionate allocation of resources to sexual reproduction experienced between males and females may have important implications on the timing of the

development of sexually dimorphic characteristics, such as carapace length. However, because the animals measured in this study were sampled from multiple populations at different times and thus represent an artificial assemblage, it is difficult to make inferences about the factors responsible for the timing of the observed sexual dimorphism, or for that matter any of the other growth parameters estimated. Also, the quantitative comparison of male and female growth trajectories may be limited because juveniles of unknown sex are included in both male and female analyses (Brisbin, 1990). However, the growth pattern may vary only slightly between the sexes during this period (Stickel & Bunk, 1989) and therefore may not greatly influence the estimation of the model parameters.

Studies of *T. c. bauri* analysing the growth of individual populations will be able to address the role of resource limitations on timing of sexual dimorphism as well as other factors responsible for the estimated growth parameters. The study of growth within discrete populations of Florida *T. c. bauri* may also be compared with results presented above, which may represent the average growth pattern experienced by *T. c. bauri*.

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