

## Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*

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Growth in the wood turtle (*Clemmys insculpta*) is described using the von Bertalanffy growth model and nonlinear regression. Growth in both sexes is similar until about 160 mm plastron length. Males grew at a faster rate after this size. Males appear to mature at a larger size and later age than females, although age-specific body size is highly variable. Sexual size dimorphism, in carapace length, is pronounced, with males attaining mean body sizes significantly larger (1.07–1.10 times) than those of adult females. Plastron length is an inappropriate measure of sexual size dimorphism because of the development of plastral concavity in males. Females tend to predominate in samples, possibly owing to differential maturity of the sexes. The direction of sexual size dimorphism may be maintained by intrasexual competition among males for access to females. Data for several adults captured at intervals of from 9 to 20 years support the concept of indeterminate growth.

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Le modèle de croissance de von Bertalanffy et une régression non linéaire ont servi à décrire la croissance chez la tortue *Clemmys insculpta*. La croissance est semblable chez les deux sexes jusqu'à ce que le plastron mesure 160 mm. Les mâles croissent plus rapidement par la suite. Les mâles semblent atteindre leur maturité à une taille plus grande et à un âge plus avancé que les femelles, mais la taille du corps en fonction de l'âge reste un rapport très variable. Le dimorphisme sexuel, tel qu'exprimé par longueur de la carapace, est très marqué et la taille moyenne chez les mâles atteint des valeurs significativement plus élevées (1,07–1,10 fois) que chez les femelles adultes. La longueur du plastron n'est pas une mesure adéquate du dimorphisme sexuel quant à la taille, car le plastron devient concave chez les mâles. Les femelles tendent à être plus nombreuses dans les échantillons, probablement à cause de la maturité différentielle des sexes. Il est possible que la tendance directionnelle du dimorphisme sexuel quant à la taille soit maintenue par compétition entre mâles pour l'accès aux femelles. Des données sur de nombreux adultes capturés à intervalles de 9–20 ans corroborent le concept de la croissance indéterminée.

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Turtles have been the subject of numerous growth studies (see reviews in Auffenberg and Iverson 1979; Bury 1979; Galbraith and Brooks 1987; Stott 1988). Indeed, several features appear to be predispose them for this type of research. First, the age of many species can easily be determined while they are young by counting annual rings of epithelial tissue on the scutes (Gibbons 1976, 1987). Second, turtles can be given identification marks (Cagle 1939; Ernst et al. 1974) that are visible for many years. Once marked at a known age, individuals can be accurately aged many years after annual rings have been obscured. Third, given the potential longevity of turtles (Gibbons 1976, 1987; Gibbons and Semlitsch 1982), it is often possible to obtain several separate measurements per individual over a relatively long period of time. Finally, the conspicuous shell provides a rigid structure with well-defined landmarks (Bookstein et al. 1985) for taking reliable measurements of body size.

The wood turtle (*Clemmys insculpta*) is well suited for growth studies because growth rings are highly reliable indicators of age in wild specimens as old as 15–20 years (Harding 1985; Harding and Bloomer 1979). Our objectives in this study were (i) to compare the growth rates of male and female *C. insculpta* from Pennsylvania, and (ii) to quantify sexual size dimorphism (SSD). The direction of sexual size differences is interpreted in light of current theories for the evolution of sexual size dimorphism in turtles (Berry and Shine 1980; Gibbons and Lovich 1990).

### Material and methods

Data were collected from two wild populations and 55 museum specimens of *C. insculpta*. A total of 254 captures, representing 87 individuals, was made between 1965 and 1988 at the White Oak Bird Sanctuary, Lancaster County, Pennsylvania. The study site has previously been described by Ernst (1971a). Another 25 individuals were captured between 1984 and 1988 at the Fraser Preserve in Fairfax County, Virginia, during a study of activity patterns using radiotelemetry. Museum specimens were examined from several states (a list of these is available on request). Greatest straight-line carapace (CL) and plastron lengths (PL) were measured with dial calipers accurate to 0.1 mm. CL was not measured on live turtles in the Pennsylvania population. Age was determined from live specimens by counting growth annuli and each turtle was permanently marked for future identification. Each annulus was assumed to represent 1 year of growth. Turtles were sexed using characters outlined in Ernst and Barbour (1972). Sexually mature males had longer precloacal tail lengths and exhibited plastral concavity. Growth parameters of the Pennsylvania population were estimated for each sex using the von Bertalanffy growth model and nonlinear regression. The form of the von Bertalanffy equation used was

$$PL = \alpha(1 - \beta e^{-k(\text{age})})$$

where PL is plastron length at an estimated age,  $\alpha$  is asymptotic length,  $\beta$  is a parameter related to hatchling size,  $e$  is the base of natural logarithms, and  $k$  is the intrinsic growth rate. In this model the rate of growth at a particular age is directly proportional to the amount of growth yet to be achieved (Draper and Smith 1981). Previous studies of growth in turtles have shown that the von Bertalanffy model provides a better fit than logistic or Gompertz models (Frazer and Ehrhart 1985;

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Bjorndal and Bolten 1988). Growth data for each sex were analyzed using all captures and recaptures of specimens that could be sexed by secondary sexual characters and all captures and recaptures of immature (sex undetermined) specimens. In other words, the data for sexually immature specimens are the same for both male and female growth curves. The number of recaptures varied between 0 and 10 for any one individual; thus the data are "mixed longitudinal" (Cock 1966; Ricklefs 1983). Since the reliability of growth rings has been questioned in *C. insculpta* older than 20 years (Harding 1985; Harding and Bloomer 1979), another model was estimated after removing all records for specimens older than this at first capture. Nonlinear estimation procedures were executed using STATGRAPHICS (STSC Inc. 1986). A sexual dimorphism index (SDI) was calculated using the method of Gibbons and Lovich (1990), where

$$SDI = \frac{\text{mean size of larger sex}}{\text{mean size of smaller sex}}$$

with the result arbitrarily defined as positive when females are larger than males and negative in the converse situation. Mean size differences between the sexes were tested for statistical significances using Student's *t*-tests. Only specimens with PL > 160 mm were used to examine sexual dimorphism. Harding and Bloomer (1979) found that secondary sexual characters were unreliable in a Michigan population of *C. insculpta* until turtles exceeded about 160 mm CL. Our criterion based on PL is likely to be conservative since CL is greater than PL in any given individual. All data discussed in the following sections of this paper pertain to the Pennsylvania population unless specified otherwise.

**Results**

The mean PL of hatchlings (*n* = 8) was 26.6 mm with a range of 25.9–27.1 mm. No evidence of overwintering behavior (Gibbons and Nelson 1978) was observed in the Pennsylvania population. All hatchlings were found in September and October. Since *C. insculpta* began hibernation as early as October at this site (Ernst 1986), opportunity for growth was limited until after spring emergence in March or early April. Growth was very rapid until a PL of between 140–160 mm was attained (Fig. 1). Males and females exhibited similar growth rates until about 160 mm PL. After this size, males grew at a faster rate. Increase in CL relative to PL was greater in males than in females (Fig. 2). The mean ratios of PL/CL in males ( $\bar{x}$  = 0.91, *n* = 11) and females ( $\bar{x}$  = 0.97, *n* = 14) from the Virginia population were significantly different (ANOVA, based on  $\sin^{-1} \sqrt{PL/CL}$ : *F* = 47.7; *df* = 1, 23; *P* < 0.001). The asymptote of the growth model for males was almost 20 mm greater than that for females (Table 1). Removal of data for specimens older than 20 years at first capture resulted in lowered asymptotic estimates and increased estimates of the intrinsic rate of growth, *k* (Table 2). Mean individual growth rate of specimens exceeding 160 mm PL at first capture was 0.8 mm/year (Table 3).

Mean male and female PL (Table 4) did not differ significantly when comparing museum specimens, all specimens from Pennsylvania that exhibited secondary sexual characters (two-tailed *t*-test: *t* = 0.49, *df* = 65, *P* = 0.63), or all males and females greater than 160 mm PL (two-tailed *t*-test: *t* = 0.30, *df* = 18, *P* = 0.77). In the Pennsylvania population, the largest female was 240 mm PL and the largest male was 195 mm PL. Males were significantly larger than females in Michigan and New Jersey samples based on CL (Harding and Bloomer 1979; see Table 4). The SDIs based on asymptotic values reported in Tables 1 and 2 are -1.12 and -1.09, respectively. The mean age of all males ( $\bar{x}$  = 18.4, *n* = 36) and females ( $\bar{x}$  = 17.3, *n* = 29) was not significantly different (ANOVA: *F* = 0.53; *df* =

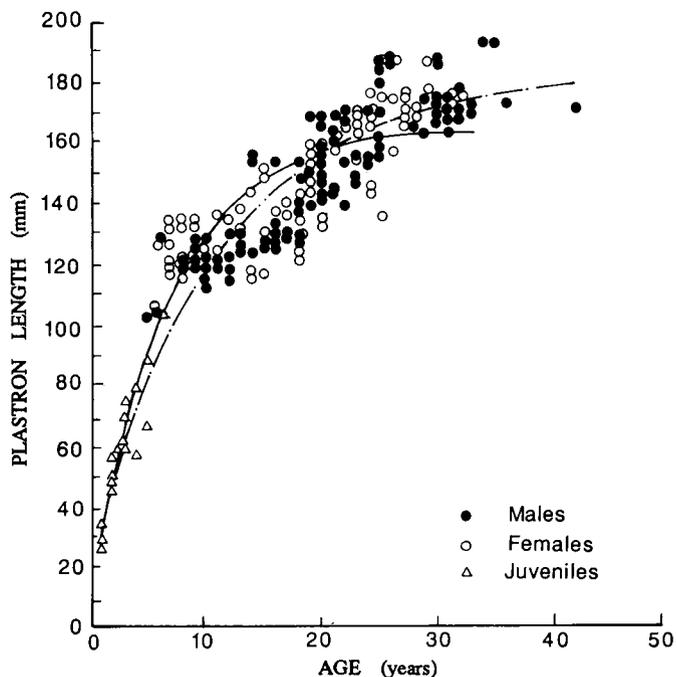


FIG. 1. Growth data and fitted curves for male (---) and female (—) *Clemmys insculpta* from Pennsylvania. Data points for female 17 (Table 3) were considered to be influential outliers and are not included. There are 62 hidden observations.

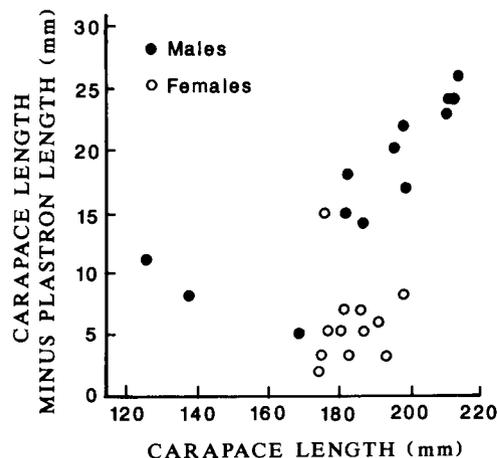


FIG. 2. Relationship between plastron length and carapace length in male and female *Clemmys insculpta* from Virginia (*n* = 25) and Pennsylvania (*n* = 2) at first capture. Two observations are hidden.

TABLE 1. Estimated parameters of the von Bertalanffy growth model for male and female *Clemmys insculpta*

Parameter estimates	Males ( <i>n</i> = 143)	Females ( <i>n</i> = 127)
<i>A</i>	184.956 (3.658)	165.029 (2.812)
<i>B</i>	0.872 (0.019)	0.921 (0.030)
<i>k</i>	0.087 (0.006)	0.142 (0.011)
<i>R</i> <sup>2</sup> (%)	93	91

NOTE: Standard errors of estimates are in parentheses. Parameter estimate convergence for males and females was attained after four and five iterations, respectively.

TABLE 2. Estimated parameters of the von Bertalanffy growth model for male and female *Clemmys insculpta* after removal of all records for specimens older than 20 years at first capture

Parameter estimates	Males ( <i>n</i> = 99)	Females ( <i>n</i> = 105)
<i>A</i>	165.566 (4.440)	151.937 (2.337)
<i>B</i>	0.899 (0.025)	0.984 (0.035)
<i>k</i>	0.121 (0.012)	0.192 (0.015)
<i>R</i> <sup>2</sup> (%)	93	92

NOTE: Standard errors of estimates are in parentheses. Parameter estimate convergence for males and females was attained after three and five iterations, respectively.

TABLE 3. Change in plastron length (PL) of selected adult *Clemmys insculpta* in Pennsylvania. Only specimens with an initial PL greater than 160 mm are shown

Turtle No.	Sex	PL (mm)		Years	mm/year
		Initial	Final		
7	Male	161.3	173.0	14	0.8
10	Male	171.9	173.9	20	0.1
17	Female	227.0	240.0	16	0.8
19	Male	187.0	195.2	10	0.8
47	Female	162.5	177	9	1.6

1.63; *P* = 0.48), nor was it different for males ( $\bar{x}$  = 24.4, *n* = 13) and females ( $\bar{x}$  = 23.0, *n* = 7) that were greater than 160 mm PL (ANOVA: *F* = 0.06; *df* = 1,19; *P* = 0.81).

Secondary sexual characters were not apparent in turtles below 103 mm PL. Two of 87 Pennsylvania turtles were incorrectly sexed as females at 121 and 127 mm PL. Subsequent recaptures confirmed them to be males. The minimum age of turtles with well-developed secondary sexual characters was 5 years. Of five males observed courting or copulating in Pennsylvania and Virginia, the smallest was 141 mm PL. The smallest female of the same courting or copulating pairs was 134 mm PL. The smallest nesting female (*n* = 7) was 136 mm PL. The mean PL of courting or mating males (168 mm) was significantly greater than that of their partners (143 mm) (one-tailed *t*-test: *t* = 2.16, *df* = 6, *P* < 0.05) but was not significantly larger than the mean PL of nesting females (156 mm) (one-tailed *t*-test: *t* = 1.10, *df* = 9, *P* > 0.10). Mean PL of nesting females was not significantly greater than that of courting or mating females (one-tailed *t*-test: *t* = 1.53, *df* = 9, *P* > 0.05). Courting or mating males had plastron lengths 5–45 mm larger than their partners in four of five reproductive encounters observed in Virginia and Pennsylvania. In the remaining case the male had a plastron length that was 6 mm shorter than that of the female.

### Discussion

The results of our analysis suggest that growth in *Clemmys insculpta* can be adequately described using the von Bertalanffy growth model. However, examination of Fig. 1 reveals considerable variation in body size in any age interval. In addition, the model tends to underestimate body size of the largest females. There are two major sources of variation in the predictive ability of the model (Dunham and Gibbons 1990). First, the models are stationary (Dunham 1978) and the growth trajectories do not include the effect of seasonal variation in growth rate. This is important since individual growth rates of temperate species of

turtles are lower during colder months (Galbraith and Brooks 1987). Second, the predictive power of the model is further reduced because of the yearly age interval. For example, specimens captured between age *X* and age *X* + 1 are categorized as exactly age *X* regardless of when they were captured during that interval. More precise within-year age data would enhance the agreement between predicted and observed growth rates. It is also possible that some of our age estimates are unreliable. Unfortunately, we are unable to test the accuracy of our estimates. Ages assigned at recapture were based on the sum of estimated age at first capture and the elapsed time interval between captures. Germano (1988) found that growth rings were reliable indicators of age in *Gopherus agassizii* only during their first 20–25 years. The reliability of growth ring analysis was confirmed by Galbraith and Brooks (1987) for juvenile *Chelydra serpentina*. Harding and Bloomer (1979) and Harding (1985) suggested that growth annuli in *Clemmys insculpta* are unreliable estimators of age in specimens older than 15–20 years. In our Pennsylvania sample, 25% (*n* = 22) of the specimens were older than 20 years at first capture.

Our results also indicate that adult *C. insculpta* exhibit significant sexual size dimorphism in which males are larger than females. This is supported by (i) data based on the mean CL of large samples from two widely separated populations and (ii) asymptotic body sizes estimated using the von Bertalanffy growth equation based on PL data from a third population. The SDIs calculated from the two approaches are similar and suggest that adult males may be 1.07–1.12 times as large as adult females. We are cautious in our interpretation of SSD based on asymptotes and prefer the range of significant body sizes, based on CL, in Table 4 (1.07–1.10). As Knight (1968) pointed out, an asymptote may not be an accurate estimate of the actual size at which growth slows appreciably. In addition, we do not assume that the asymptote defines maximum attainable size. Our data clearly show that some individuals exceed these values. Instead, the asymptote represents an "average maximum" PL (Knight 1968). In spite of these shortcomings, our estimates of asymptotic body size are realistic when compared with estimates of mean body size (Table 4). Removal of data for specimens older than 20 years at first capture resulted in underestimated asymptotic values less than mean PL (Tables 2 and 4). This problem likely stems from the resulting truncated data set as does the significant increase in estimates of *k* (Knight 1968). Based on this we believe that inclusion of older animals results in a more accurate portrayal of growth.

It is important to note that SSD is statistically significant only when mean CL is used as a measure of body size (Table 4). We conclude that differential linear growth rates of CL and PL between the sexes are responsible for this phenomenon (Fig. 2). Male *C. insculpta* develop pronounced plastral concavity as they mature (Ernst and Barbour 1972). Development of this feature appears to occur at the expense of linear increases in PL. The result, in males, is that linear CL increases more rapidly than linear increases in PL. This situation clearly illustrates the importance of selecting an appropriate measure of body size for studies of SSD (Gibbons and Lovich 1990). In the case of *C. insculpta*, linear measurement of CL is a better measure of body size than PL.

In a previous review of sexual size dimorphism (SSD) in turtles, Berry and Shine (1980) interpreted the direction of SSD in terms of mating strategy. They concluded that males were larger than females when large male body size evolved as an adaptation to increase success in male combat for females.

TABLE 4. References on body size of male and female *Clemmys insculpta*

Location	Measure of size	Males	Females	SDI	Source
Michigan	CL	200 (86)	182 (105)	-1.10*	Harding and Bloomer 1979
New Jersey	CL	178 (311)	165 (464)	-1.08*	Harding and Bloomer 1979
Virginia	CL	196 (11)	183 (14)	-1.07*	This study
Pennsylvania	PL	173 (13)	172 (7)	0	This study
Virginia	PL	178 (11)	178 (14)	0	This study
Miscellaneous museum species	PL	172 (31)	172 (24)	0	This study

NOTE: Sample sizes are given in parentheses. Only specimens with a plastron length greater than 160 mm were used. Abbreviations and symbols are as follows: CL, carapace length; PL, plastron length; SDI, sexual dimorphism index; \*,  $p < 0.05$ . We tested the statistical significance of measurements reported by Harding and Bloomer (1979) by using an estimate of the standard deviation based on the range of measurements divided by 6.

Evidence in support of this hypothesis was reported by Moskovits (1988) for *Geochelone denticulata*. Aggressive interactions between male *C. insculpta* have been reported in captivity and under natural conditions. Dominance hierarchies, based on size, sex, and maturity were observed among captive specimens by Dinkins (1954), Harding and Bloomer (1979), and Harless (1970). Aggressive interactions between males under natural conditions were also reported by Barzilay (1980). In one instance, the larger male appeared to have been the "winner." In the other case, the smaller male was judged by the author to be the "victor." Barzilay hypothesized that aggression was related to spatial defense of territory. Kaufmann (1988) reported that 85% of 381 encounters between wild males were agonistic. The outcomes revealed a linear dominance hierarchy that persisted unchanged for 4 years. Copulating males were typically challenged by other males, regardless of rank, but dominant males were less likely to be dislodged from the female. Dominant males were more likely to replace subordinate males they interrupted. Differences in body size between dominant and subordinate males were not reported.

In a more recent review of SSD in turtles, Gibbons and Lovich (1990) concluded that sexual size differences in turtles were determined to a large extent by sex-specific maturity patterns as influenced by natural and sexual selection. They hypothesized that the earlier maturing sex would remain the smallest throughout life and that that sex would predominate numerically. Our data show that mean PL of courting or copulating males, a very conservative estimate of overall body size in this sex, is significantly larger than that of their female partners, thus suggesting that males may mature later at larger body sizes. Similar data were reported by Harding and Bloomer (1979). However, it is also possible that males may court sexually immature females. Interpretation of our data is complicated by small sample sizes and the extreme variation in size of maturity in turtles (Carr and Goodman 1970; Gibbons et al. 1981). Our predicted growth curves clearly show that male *C. insculpta* have the potential to reach larger body sizes than females. Data reported by Harding and Bloomer (1979) and summarized in Table 4 suggest that females predominate in large samples, thus supporting the hypothesis offered by Gibbons and Lovich (1990). We realize that there are alternative explanations for the perception of skewed sex ratios in turtles. Ream and Ream (1966) reported that sex ratios varied according to collection method. In their study, baited traps yielded predominantly males, basking traps yielded predominantly females, and hand collecting produced an even sex ratio. In addition, many turtles exhibit environmental sex determination,

so it is possible that the influence of temperature on incubating eggs can produce skewed sex ratios. Seasonal and microgeographic effects on hatchling sex ratios were reported by Vogt and Bull (1982, 1984) for several species of turtles. Since *C. insculpta* has nontemperature-dependent sex determination (Bull et al. 1985), the latter explanation is not applicable to our results.

The actual size at which maturity is attained may vary among populations as well as within populations. In the Pennsylvania population we studied, the mean PL of courting or copulating males was 168 mm. The mean PL of nesting females was 156 mm. Breckenridge (1944) suggested that *C. insculpta* in Minnesota matured at carapace lengths between 152 and 178 mm. Harding and Bloomer (1979) reported that maturity was attained at about 165 mm CL in New Jersey populations. The smallest female observed in courtship activity by Harding and Bloomer (1979) in a Michigan population was 158 mm CL; the smallest courting male was 192 mm CL. The significance of interpopulation variability in attainment of maturity is difficult to assess at this time owing to the use of different measures of body size among published studies and small sample sizes at some localities.

Finally, we turn to the question of growth following maturity. Although growth in mature reptiles has been considered to be indeterminate by some (Porter 1972; Wilbur 1975), others have questioned this assumption (Andrews 1982; Halliday and Verrell 1988). Brisbin (1990) suggested that abbreviated natural life-spans would produce the appearance of indeterminate growth. Based on data from crocodylians, he concluded that captive specimens eventually ceased linear growth under circumstances promoting artificially long life-spans. Others have shown that variation in growth rate prior to maturity is a more significant source of variation in body size than age (Carr and Goodman 1970; Halliday and Verrell 1988) and that this situation can also lead to the appearance of indeterminate growth. Confirmation of the existence of indeterminate growth is further confounded by measurement error or an inappropriate measure of "size." For example, it is conceivable that an organism could show determinate growth in some linear dimension but show indeterminate growth in weight or some other variable.

Our data demonstrate that growth continues in some *C. insculpta* even after attainment of a very conservative estimate of body size at maturity. The mean annual growth rate of adult *C. insculpta* listed in Table 3 (0.8 mm) is intermediate between values reported for other turtle species. Wilbur (1975) reported that adult painted turtles (*Chrysemys picta*) exhibited a mean annual growth rate of 0.55 mm. Gibbons (1968) and Ernst

(1971*b*) found that *C. picta* grew an average of just over 1 mm/year following attainment of sexual maturity. In the congeneric *Clemmys guttata* and *C. muhlenbergii*, mean annual adult growth rate is approximately 2.9 mm (Ernst 1975, 1977). Adult growth rates of these species may seem insignificant at first; however, given the potential longevity of turtles (Gibbons 1987) a significant increase in body size is possible over time. The phenomenon of indeterminate growth may be maintained because of sexual selection (Gibbons and Lovich 1990). If large body size in male turtles enhances access to females as predicted by Berry and Shine (1980), then continued growth following maturity would be selectively advantageous. Similarly, female turtles generally attain a fecundity advantage with increased body size (Gibbons et al. 1982), thus favoring indeterminate growth. Later maturity at larger body sizes in male *C. insculpta*, relative to females, is apparently sufficient to maintain the male size advantage in spite of continued growth in females.

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