

Estimates of Growth of the Atlantic Rain Forest Freshwater Turtle *Hydromedusa maximiliani* (Chelidae)

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ABSTRACT.—Demographic studies on long-lived organisms are uncommon, largely because of the long time periods necessary to collect even the most basic data. We report results of the first long-term growth study of a non-Amazonian Neotropical freshwater turtle, the chelid *Hydromedusa maximiliani*. Differences were detected among males, females, and juveniles. Juveniles had higher growth rates (body size and mass) than adult males and females. A significant negative relationship existed between growth rate and mean body size of males and females, which was best defined by linear equations. Growth constants (k) estimated from the von Bertalanffy model were 0.094 for females and 0.073 for males, and the parameter b was 0.75 for females and 0.77 for males. Based on the von Bertalanffy equation, estimated age at sexual maturity was 14 yr (11.6–16.6 yr) for males and 9 yr (5.7–11.9 yr) for females, whereas longevity was estimated at about 100 yr for both sexes. This represents the greatest expected life span reported for a chelid turtle. Because the geographical distribution of *H. maximiliani* is restricted to mountainous regions of the Atlantic rain forest, one of the world's biodiversity hotspots, and because the species is long-lived and late maturing and appears to have a set of life-history traits unique among chelid turtles, a conservation program that extends beyond existing conservation units may be necessary to ensure its survival.

Because most turtle species are long-lived and late maturing, long-term studies are necessary to accurately estimate life-history characteristics (Gibbons, 1990; Iverson, 1991; Tucker and Moll, 1997). Growth is an important population parameter given the trade-off between body size, age, and clutch size in most species (Wilbur and Morin, 1988; Spencer, 2002; Litzgus, 2006). Growth is driven by extrinsic (e.g., habitat temperature and resources) and intrinsic (e.g., physiological) processes (Chen and Lue, 2002) and the effects of variation in growth rates have a cascading effect on life-history traits.

Research on turtle growth has shown growth patterns common among many reptiles and other vertebrates, with rapid growth from hatching to juvenile followed by a declining growth rate as individuals reach maturity (Wilbur, 1975; Shine and Iverson, 1995; Magnusson et al., 1997; Chen and Lue, 2002). Such differential growth patterns presumably reflect distinct age-group strategies mediated by age-specific priorities in energy allocation; juveniles invest most energy in growth whereas adults invest most energy in reproduction (Georges et al., 1993; Spencer, 2002). Natural selection favors rapid growth in juveniles because their carapaces are soft as a result of the incomplete

ossification process rendering them most vulnerable to predation (Wilbur and Morin, 1988; Congdon and Gibbons, 1990; Georges et al., 1993; Spencer, 2002).

Differential growth patterns detected between adult male and female turtles within populations (Kennett, 1996; Chen and Lue, 2002; Spencer, 2002) result in body size sexual dimorphism (Berry and Shine, 1980; Lindeman, 1998; Lovich et al., 1998). Sexual size dimorphism (SSD) is strongly linked to reproductive behavior and sexual selection (Freedberg and Wade, 2004). Larger females produce more and sometimes larger eggs, whereas larger males may enjoy an advantage in competition for mates (Berry and Shine, 1980; Gibbons and Greene, 1990; Freedberg and Wade, 2004; Wilson and Ernst, 2005).

Growth models are useful tools for understanding life histories of turtles because they allow quantification of important demographic parameters such as age at maturity or differential growth patterns among age groups and sexes (Frazer et al., 1990). Data from such studies can be used to predict responses of populations to environmental change and should be most useful in areas such as the Atlantic rain forest, in which environmental change is occurring at a rapid rate. The greatest diversity of South American turtles exists in the family Chelidae; yet little information on the

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ecology and life histories of these turtles exists (Souza, 2004). Growth data exist for only a single species, the Amazonian Red Side-Necked Turtle, *Rhynemys rufipes* (Magnusson et al., 1997).

Current knowledge of South American turtle biology in general has centered on Amazonian species (Souza, 2004) despite considerable turtle species richness outside of this region (Souza, 2005). *Hydromedusa maximiliani* is a small (<200 mm straight-line carapace length; <520 g body mass) freshwater turtle species endemic to Atlantic rain forest mountainous regions from southeastern and southern northeastern Brazil, inhabiting primary forest streams above 600 m elevation with clear, cold water and sandy or rocky bottoms (Souza, 2005). Prior studies on these turtles have been short term, from one to two years in duration (Yamashita, 1990; Guix et al., 1992; Souza, 1995b). We present growth data for a *H. maximiliani* population that has been continuously studied over the last decade by traditional capture-recapture methods. We confirm distinct differences among males, females, and juveniles, and this study represents the first long-term study of a non-Amazonian chelid turtle.

MATERIAL AND METHODS

Turtles have been hand-collected and trapped since 1993 in five streams from an approximately 250 of 37,000 ha area encompassed by the Parque Estadual de Carlos Botelho, PEBC (24°00'–24°15'S, 47°45'–48°10'W), São Paulo State, southeastern Brazil, as part of a long-term project on the ecology of *H. maximiliani*. The PEBC is a conservation unit of intact tropical mountain rain forest, at an altitude ranging from 30–970 m with annual rainfall around 1,900 mm. A cold and dry period from May to August and a hot and wet one from September to April characterize the local climate. Vegetation is typical tropical rain forest, with large canopy trees and an understory of small tree species (Souza, 1995b; Souza and Abe, 1998). Captured animals were marked by notching marginal scutes for individual identification (Cagle, 1939) and released at the point of capture. Turtles were grouped by sex, based on their external body characteristics (color, plastron concavity, tail length) and body size (Souza, 1995a; Souza and Abe, 1997, 1998). Small, unmarked individuals not exhibiting adult body characteristics were regarded as juveniles. For each captured turtle, body size (plastron midline suture length; PL) was measured with calipers to the nearest 0.1 mm, whereas body mass was measured with spring scales to the nearest 0.1 g. Intensive fieldwork was carried out from July 1993 to July 1994 by

monthly sampling (3–4 days/month) and from October 2003 to December 2005 by sampling every 3–4 months. Turtles captured in occasional searches during November of 1999 and January of 2003 also were included in analyses. Thus, growth records for turtles span more than a decade. Turtle growth (G ; mm/yr) was calculated as absolute plastron growth, $G = PL_{recapt} - PL_{capt} / \Delta T$, where PL_{recapt} = plastron length at recapture, PL_{capt} = plastron length at capture, and ΔT = time interval in years between PL_{recapt} and PL_{capt} . Body mass gain (g/yr) was calculated similarly. Adult male, female, and juvenile growth and body mass gain were compared by analysis of variance (Zar, 1999). The relationship between annual growth and turtle body size was verified by simple linear regression between the exponential growth (EG) rate $EG = \log_e PL_{recapt} - \log_e PL_{capt} / \Delta T$ and the geometrical mean size (GS) $GS = \sqrt{PL_{recapt} \times PL_{capt}}$ to minimize time interval effect between recaptures (Magnusson et al., 1997). The same set of juveniles was included in both male and female data for regression analyses (Spencer, 2002). Thus, we make the assumption that juvenile males and females have similar growth rates. Individuals with observable plastron scute wear were excluded from samples. We ignore seasonal variation in growth rates as in other studies (Magnusson et al., 1997; Chen and Lue, 2002; Spencer, 2002).

Growth curves for *H. maximiliani* were assigned independently for males and females based on the nonlinear von Bertalanffy equation (Fabens, 1965) $PLt = a(1 - be^{-kt})$, where t is the age (in years), a is the asymptotic or maximum body size, b is the parameter related to the size at the birth, e is the natural logarithmic base, and k is the growth constant. This growth model has been applied to other freshwater turtle species (Dunhan and Gibbons, 1990; Kennett, 1996; Chen and Lue, 2002; Spencer, 2002). Fabens (1965) reformulated the von Bertalanffy equation for those cases where the growth parameters a and k could be obtained from animals with unknown ages (as the case of *H. maximiliani*). This equation modification allows estimation of these parameters from the capture-recapture data as $PL_{recapt} = a - (a - PL_{capt})e^{-kd}$ where d is the time interval (in years) between capture-recapture events (Shine and Iverson, 1995; Spencer, 2002). The FiSAT II software (Gayanilo et al., 2005) was employed to estimate growth parameters a and k . FiSAT routines compute the growth function by estimating the parameter a or substituting the maximum size recorded for a species or group of individuals (Gayanilo et al., 2005). This

approach must be performed when estimates of a differ from empirically derived values. Because parameters a and k are proportionally inverse, underestimating a overestimates k (Kulmiye and Mavuti, 2005). In this study, the a value estimates from the Faben's method were lower for both males (131.3 mm) and females (117.4 mm). Thus, we used the a -value used the larger body size (PL) recorded for species in the studied area (139.4 mm for males and 128.1 mm for females) to compute the growth curves.

The parameter b (size at the birth) can be obtained by rearranging the von Bertalanffy model if hatchling body size is known (Frazer and Ladner, 1986). Assuming $t = 0$ at birth, the von Bertalanffy equation can be simplified to $PL_0 = a(1 - b)$. The reproductive behavior of free-ranging *H. maximiliani* is unknown, and even after one decade of population monitoring, neither mating nor nesting behavior has been observed at PECB or any other locality. However, x-rays and photographs report females containing ellipsoid eggs approximately 35–42 mm long (Guix et al., 1992; Winkler, 2006). Also, recruitment at PECB occurs between September and January (Souza, 1995b; Souza and Abe, 1997). Throughout the more than 10 years of study, four small individuals with plastron lengths ranging from 31.2–34.7 mm were sampled during this five-month recruitment period. These turtles had typical hatchling characteristics, including soft shells and presence of yolk sac scars (Souza, 1995a; F. I. Martins, pers. obs.). Based on these observations, we estimate a $PL_0 = 32.9$ mm to represent mean plastron length of the four small *H. maximiliani* individuals.

The von Bertalanffy growth functions were calculated separately for males and females with juvenile growth records included in both estimates. Without inclusion of juveniles, the von Bertalanffy model underestimates the parameter a (when it is not fixed) and k , resulting in incorrect age estimates (Spencer, 2002). After obtaining the parameters a , b , and k , the parameter t (age, in year) was estimated based on the original von Bertalanffy equation, resulting in the species' growth curve estimates (Zug et al., 1997; Spencer, 2002).

RESULTS

From 1993 to 2006, 42 capture-recapture events were recorded for *H. maximiliani* including 11 males, 25 females, and six juveniles. Mean recapture interval was 6.26 yr, ranging from 1–12 yr. Growth rate was significantly higher for juveniles than for adult males and females for both body size (approximately three times higher; $F_{2, 41} = 38.65$; $P < 0.05$) and body

TABLE 1. Absolute growth (mm/yr) and body mass (g/yr) rate of male, female, and juvenile *Hydromedusa maximiliani* recaptured between 1993 and 2006 at the Parque Estadual de Carlos Botelho, São Paulo State, southeastern Brazil. Only ≥ 1 yr recapture interval was considered for analyses. Values are expressed as mean \pm SD.

	<i>N</i>	Plastron growth (mm/year)	Body mass gain (g/year)
Males	11	1.6 \pm 1.23	7.63 \pm 7.01
Females	25	1.09 \pm 1.15	6.46 \pm 5.16
Juveniles	6	3.70 \pm 0.40 *	12.27 \pm 4.47 *

* $P < 0.05$.

mass (approximately two times higher; $F_{2, 41} = 7.19$; $P < 0.05$; Table 1). A significant negative relationship existed between exponential growth rate (GR) and geometric mean body size (PL) and was best defined by linear equations ($GR = 0.054 - 0.0004PL$; $R^2 = 0.96$; $P < 0.001$ and $GR = 0.06 - 0.0005PL$; $R^2 = 0.90$; $P < 0.001$ for males and females, respectively; Fig. 1).

Growth constant estimated from the von Bertalanffy model was 22% higher for females ($k = 0.094$) than males ($k = 0.073$), whereas the parameter b was 0.75 for females and 0.77 for males. The growth pattern is described as $PL_t = 139.4(1 - 0.77e^{-0.073t})$ for males and as $PL_t = 128.1(1 - 0.75e^{-0.094t})$ for females (Fig. 2).

DISCUSSION

Long-term research on South American turtles is scant or absent for most of the nonmarine species, including the freshwater turtles in the family Chelidae (Souza, 2004). Such studies provide the opportunity to estimate demographic parameters necessary for conservation and management programs (Edmonds and Brooks, 1996; Hall et al., 1999; Tucker et al., 2001; Henry, 2003). Testing theoretical models that describe relationships between size and age of slow-growing long-lived organisms requires extensive sampling periods and considerable recapture rates (Frazer et al., 1990; Dunham and Gibbons, 1990; Georges et al., 1993; Spencer, 2002).

Hydromedusa maximiliani exhibited the same growth pattern reported for other turtle species, with high growth rates for juveniles, low rates for adults, and decreasing rates associated with increasing body size (Kennett, 1996; Magnusson et al., 1997; Chen and Lue, 2002; Spencer, 2002). The negative relationship between body size and growth rate in association with sexual differences in growth rates can be partially explained by the sexual maturation process (Wilbur and Morin, 1988). As turtles grow and

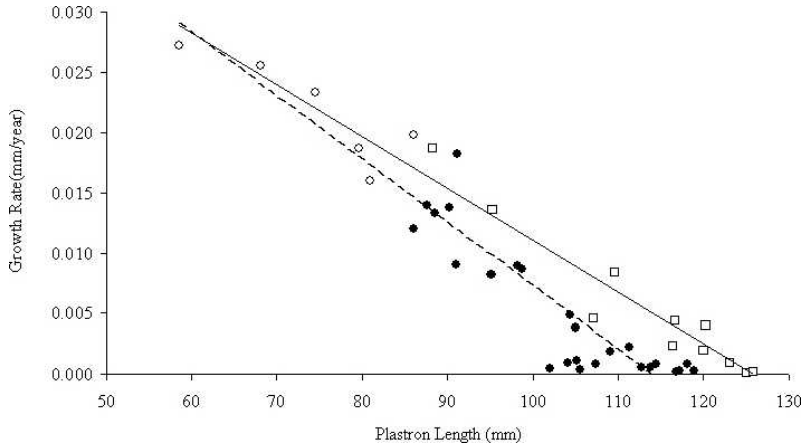


FIG. 1. Relationships between plastron length (geometrical mean size, in millimeters) and exponential growth rate for males (solid line; $R^2 = 0.96$; $N = 17$; $P < 0.001$) and females (dotted line; $R^2 = 0.90$; $N = 31$; $P < 0.001$) of *Hydromedusa maximiliani* at the Parque Estadual de Carlos Botelho, São Paulo State. Empty circles represent juveniles, full circles females, and empty squares males.

attain sexual maturity, energy allocation shifts from growth to reproduction, resulting in a conspicuous decline of growth rates as animals increase in body size or age (Wilbur, 1975; Wilbur and Morin, 1988; Dunhan and Gibbons, 1990).

Chelonians can exhibit differential growth (including intraspecific) in habitats where avail-

able resources (food supply) are variable (Moll, 1976; Brown et al., 1994; Spencer, 2002; Bjorndal et al., 2003). Consequently, comparative studies of free-ranging populations should take resource variation into consideration when interpreting variation in growth rates among individuals. *Hydromedusa maximiliani* is known to be omnivorous (Yamashita, 1990; Guix et al., 1992;

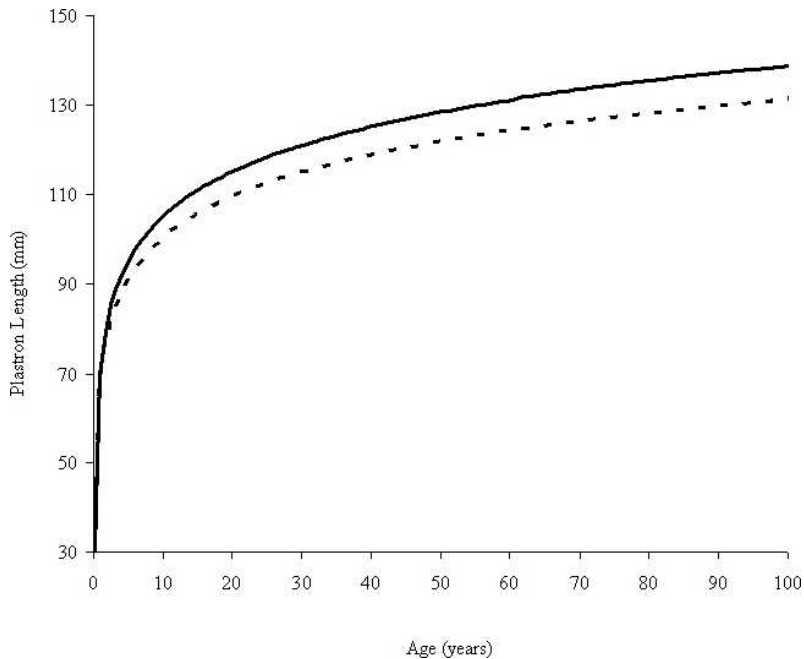


FIG. 2. Relationship between estimated age (years) and plastron length (millimeters) for *Hydromedusa maximiliani* captured between 1993 and 2006 at the Parque Estadual de Carlos Botelho, São Paulo State. Solid line is the growth curve estimated for juveniles and males, $PL_t = 139.4 (1 - 0.77e^{-0.073t})$, and dotted line is the growth curve estimated for juveniles and females, $PL_t = 128.1 (1 - 0.75e^{-0.094t})$.

TABLE 2. Growth parameters estimated from the nonlinear von Bertalanffy model for males and females Chelidae species available records.

Species	<i>a</i>	<i>k</i>	Country	Reference
<i>Chelodina expansa</i>			Australia	Spencer, 2002
Males	308.0	0.07		
Females	318.0	0.07		
<i>Chelodina rugosa</i> *			Australia	Kennett, 1996
Males	197.5	0.41		
Females	246.2	0.29		
<i>Elseya dentata</i> *			Australia	Kennett, 1996
Males	258.1	0.20		
Females	307.2	0.16		
<i>Emydura macquarii</i>			Australia	Spencer, 2002
Males	208.0	0.23		
Females	214.0	0.20		
<i>Hydromedusa maximiliani</i>			Brazil	This study
Males	139.4	0.073		
Females	128.1	0.094		

* denotes parameters estimated from carapace length instead of plastron length.

Souza, 1995b). Nevertheless, juveniles and small individuals ingest more microcrustaceans and more often have full stomachs than adults (Souza and Abe, 1998). Our study showed more pronounced growth and body mass gain for juveniles than adults consistent with the hypothesis that consumption of microcrustaceans during the juvenile life-history stage promotes more rapid growth for juveniles.

Although the negative relationship between body size and growth rate is expected among chelonians (see above) the trajectory curves describing this relationship can differ between males and females. A linear relationship between body size and growth rate exists for male *Emydura macquarii* (an Australian Chelidae), whereas female growth is best described by logarithmic equations (males grow slower than females; Spencer, 2002). The relationship was linear for both male and female *H. maximiliani*. Based on our growth estimates, male *H. maximiliani* had a lower growth constant ($k = 0.073$) than did females ($k = 0.094$). Thus, the sexual difference in growth constant for *H. maximiliani* appears not to be influencing the best-fit model (linear for both) in this species.

The growth constants reported for male and female *H. maximiliani* are lower than those reported for other Chelidae species (Table 2). Asymptotic or maximum size was larger for males *H. maximiliani* than for females, an expected result because body-size dimorphism exists with males larger than females (Souza, 1995b; Souza and Abe, 1997), and this growth parameter was fixed (see Material and Methods). In turtle populations where sexual differences among growth parameters are detected,

the sex with the larger asymptotic size is the one with a lower growth rate or smaller k (Kennett, 1996; Chen and Lue, 2002; Spencer, 2002). This was the case in *H. maximiliani*.

Data on sexual maturity and reproductive behavior of *H. maximiliani* are scant and anecdotal, with only two brief reports on free-ranging females with eggs (Yamashita, 1990; Guix et al., 1992). Based on the von Bertalanffy equation for *H. maximiliani*, a 120-mm plastron length female with eggs reported by Guix et al. (1992) would be approximately 26 yr old. Age at maturity for Australian chelid turtles is reported to be 4–11 yr for males and 6–15 yr for females (Kennett, 1996; Spencer, 2002). Based on morphological data for our *H. maximiliani* population, smaller males exhibiting external secondary characters (such as plastron concavity and larger tails) had a mean 101.7-mm straight-line plastron length (range: 93.5–107.6 mm; $N = 10$) and females had a mean 87.9-mm straight-line plastron length (range: 72.2–97.0 mm; $N = 10$). The von Bertalanffy equation estimate ages of 14 yr (ranging from 11.6–16.6) for males and 9 yr (ranging from 5.7–11.9) for females, one of the oldest estimated ages at maturation for chelids (Kennett, 1996; Spencer, 2002).

Understanding the relationships between body size and age at maturity is a critical component of demographical studies of free-ranging populations (Galbraith et al., 1989; Kennett, 1996; Loehr et al., 2004; Litzgus, 2006). Research on reproductive behavior of Australian chelids has shown that females reach maturity later than males and attain larger body size (Georges et al., 1993; Shine and Iverson,

1995; Spencer, 2002; Rowe et al., 2003). Estimated age at sexual maturity was greater for males than females in *H. maximiliani*, the opposite pattern observed for other chelid species (Georges et al., 1993; Shine and Iverson, 1995; Spencer, 2002). Future research on growth and reproductive behavior among Neotropical chelids are necessary to identify evolutionary strategies in life histories for this taxon.

The larger (plastron midline suture length) *H. maximiliani* (139.4 mm for males; 128.1 mm for females) would correspond to ages of approximately 100 yr based on the von Bertalanffy equation, suggesting longer expected life spans for a chelid turtles (Kennett, 1996; Spencer, 2002). However, old animals were uncommon (only five individuals with plastron length above 130 mm were captured throughout more than 10 years of sampling effort). *Hydromedusa maximiliani* has a geographical distribution restricted to Atlantic rain forest mountainous regions, a hotspot of global biodiversity (Myers et al., 2000) and exhibits growth rate, body size dimorphism, and age at maturity that makes the species distinct among the Chelidae. The association between these stochastic (habitat fragmentation) and demographic (population structure, growth) factors may have a negative impact on *H. maximiliani* populations inhabiting areas not contained in conservation unit. These results emphasize the importance of long-term research as conservation and management tools for long-lived organisms.

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