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Growth, age at maturity and sexual dimorphism in the geometric tortoise, *Psammobates geometricus*

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Capture-recapture data from a natural population of the geometric tortoise, *Psammobates geometricus*, were used to determine size-based annual growth rates. Juveniles and sub-adults (<90 mm CL) grow at 10.45 ± 8.3 mm CL/yr. At 80 to 90 mm CL, males can for the first time be sexed with confidence using developing secondary sexual characteristics. Adult males grow at 1.70 ± 1.9 mm CL/yr, while adult females grow at 1.56 ± 1.2 mm CL/yr. Using Fabens' (1965) growth interval method and hatchling size (28.13 ± 1.01 mm CL), a preliminary species growth model was constructed by fitting the general form of the Von Bertalanffy growth equation to the data. Independently modelled male and female asymptotic sizes agree closely with the mean sizes of the 20 largest males and females respectively. The model suggests that geometric tortoise adults may reach ages of approximately 30 years. Development of secondary sexual characteristics in males predicts their age at maturity as approximately 5.9 years. Female age at maturity remains inconclusive. Sexual size dimorphism in geometric tortoises is pronounced; females are significantly larger and heavier than males. Consistently larger female body size in *P. geometricus* underscores the hypothesis that natural selection for larger size in females may result in higher fecundity.

Introduction

Chelonian growth and sexual size dimorphism have been studied and reviewed extensively (e.g. Berry & Shine 1980; Frazer & Ehrhart 1985; Moskovits 1988; Gibbons & Lovich 1990; Frazer et al. 1991; Iverson 1991; Iverson et al. 1991; Stamps 1993; Mushinsky et al. 1994). The study and quantification of these and related parameters enable ecologists to understand the underlying concepts of population structure and dynamics, and supply useful data to model age-size relationships of species. Growth models are used for a variety of purposes including the estimation of age and size at maturity and to study differences in life history characteristics between sexes, and among populations and species (Frazer et al. 1990).

The geometric tortoise *Psammobates geometricus* is an endangered terrestrial tortoise that is endemic to the Western Cape Province of South Africa (Greig 1984; Branch 1988; Baard 1993), and it has gained prominence as a result of its critical conservation status (Baard 1988, 1989). It is confined to approximately 5 000 ha or ± 20 mi² of a severely fragmented habitat type, locally known as renosterveld, where it survives in at least 31 isolated localities (Baard 1993). The largest remaining population of this species has been studied since 1986 (Baard 1990) in an attempt to quantify and qualify certain life history parameters fundamental to its continued survival in the natural state. Apart from preliminary studies by Rau (1971) and Greig (unpublished), growth and sexual dimorphism in the geometric tortoise have not been

studied intensively. Rau (1971) and Boycott & Bourquin (1988) supply limited data for hatchling growth up to the age of one year, as well as anecdotal information on sexual dimorphism.

This paper attempts to describe and quantify growth and sexual dimorphism in *P. geometricus* as a base-line for further studies and to provide a preliminary growth model for the species. In this study capture-recapture data of individual tortoises of all sizes were used to compute a growth model for the study population. Morphometric data on adult specimens were used to quantify and describe sexual dimorphism.

Methods

Study site

Research was conducted at the Elandsberg Private Nature Reserve, Hermon, South Africa (3319AC Tulbagh; 33°24'S; 19°01'E) where approximately 1 000-2 000 ha of renosterveld habitat remain in a natural state. This habitat type is defined as small-leafed, low to medium-high shrublands where renosterbos *Elytropappus rhinocerotis* is co-dominant with other asteraceous species (Moll et al. 1984). Similar to central Florida sandhill habitat (Mushinsky et al. 1994), structural diversity and species composition of this fire-prone habitat are influenced by fire interval. The study site is situated within the Mediterranean climate zone of South Africa, receiving the bulk of its rain (approximately 600 mm/year) during winter (May through August).

Data collection

During the initial two years of the study (1986-1987) search teams comprising 10-15 people surveyed three transects, each measuring 100x400 m, every second month. Tortoises were captured, measured, individually marked according to Honegger's (1979) method and released at the point of capture. Supplementary transect and *ad hoc* surveys were conducted in the autumns of 1990 and 1993. During 1986 through 1987 a total of 370 captures and recaptures were made of 232 individuals. Based on prior descriptions of sexual dimorphism in this species (Rau 1971), 113 individuals were classified as adults (55 males and 58 females) and 119 as juveniles or sub-adults. A characteristically deepened plastron concavity, long tail and bulging supracaudal were used to identify males.

Straight carapace length (CL), shell height (SH), carapace width (CW) and body mass (MASS) were recorded for individual tortoises. Three counts of the number of visible growth rings on the third vertebral shield were averaged to yield growth ring number. For further quantification of sexual dimorphism the distance between the posterior midline notch of the plastron and the edge of the supracaudal shield (the anal notch, AN), the distance between the distal points of the anals (the anal width, AW), and the depth of the plastron concavity (PC), measured straight down from a straight edge along the longitudinal midline of the plastron, were obtained. Lengths were recorded with calipers to the nearest 0.1 mm and mass to the nearest g with Pesola spring balances. Measurements and measure of variability are presented as mean plus/minus Standard Deviation. Capture dates and carapace lengths were recorded for 70 individual tortoises at first and last capture. These provided growth rates which were converted to annual rates. Fourteen females ranging from 75-148 mm CL were radiographed to establish at which size they first start producing eggs.

Data analysis

The general form of the Von Bertalanffy equation (Fabens 1965), with carapace length as the measure for size, and generated by non-linear regression using STATGRAPHICS Ver. 4.0 (Statistical Graphics Corporation 1989), was used to describe growth for the geometric tortoise study population:

$$L_t = a(1 - be^{-kt}) \quad (\text{Equation 1})$$

where L_t is carapace length at age t , a is asymptotic length, b is a variable related to size at birth, e is the base of the natural logarithms, k is an intrinsic growth rate variable related to the shape of the curve, and t is age (see Frazer & Ehrhart 1985, and Frazer et al. 1990 for further details on the application of this equation). However, since individual age (t) could not be determined, non-linear regression modelling of Fabens' (1965) growth interval method (a rearranged form of the Von Bertalanffy

equation) was employed to define asymptotic size (a) and intrinsic growth rate (k). The rearranged equation is:

$$L_r = a - (a - L_c)e^{-kd} \quad (\text{Equation 2})$$

where L_r is length at recapture, L_c is length at first capture, d is the time interval between first and last recapture, and the other variables as for Equation 1. Equation 2, however, does not contain variable b , a variable required to construct the Von Bertalanffy model, and which may be calculated only if mean size at a particular age (t) is known (see Frazer et al. 1990). Therefore, at hatching (t_0):

$$L_{t_0} = a(1 - b), \text{ and} \\ b = (1 - L_{t_0}/a)$$

Since data could not be successfully transformed to meet assumptions of normality and homogeneity of variances, the non-parametric Mann-Whitney U -test was used for hypothesis testing and differences were considered significant at the $P < 0.05$ level.

Results

Growth

Mean geometric tortoise hatchling size is 28.13 ± 1.01 mm CL ($n=10$). Juveniles and sub-adults up to 90 mm CL (first signs of sexual dimorphism) grow at 10.45 ± 8.3 mm CL/yr ($n=28$).

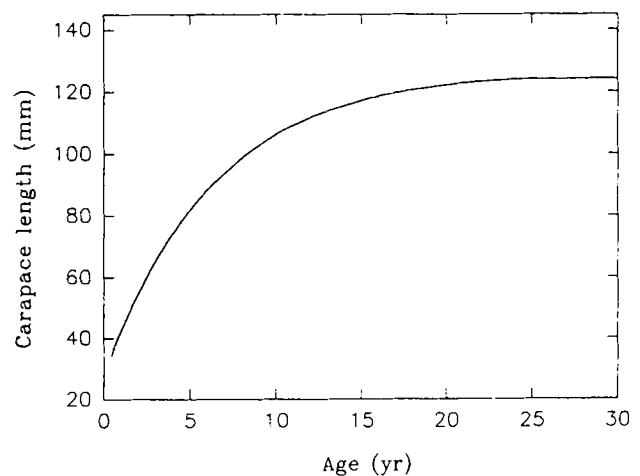


Figure 1. Relationship of annual growth rate (mm CL/year) and straight-line carapace length (mm) in geometric tortoises, *Psammobates geometricus*, from Elandsberg Private Nature Reserve. See text for descriptive equation.

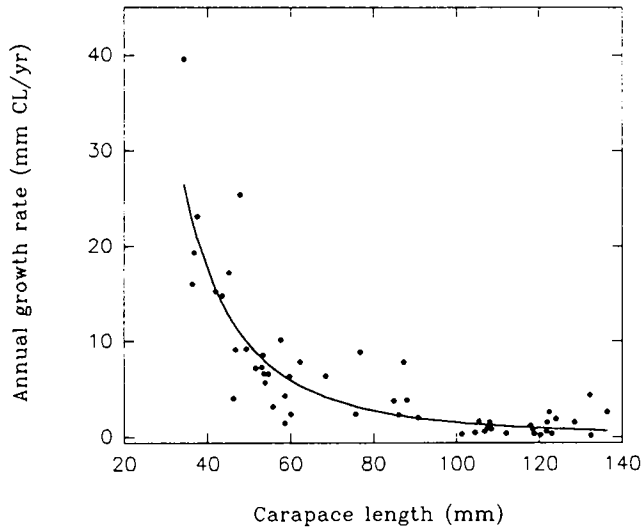


Figure 2. Preliminary curve for growth in straight-line carapace length (mm) in geometric tortoises, *Psammobates geometricus*, at the Elandsberg Private Nature Reserve, from non-linear regression of Von Bertalanffy growth interval equations. See text for descriptive equation.

Males >90 mm CL, grow at a rate of 1.70 ± 1.9 mm CL/yr ($n=14$), while females >90 mm CL grow at a rate of 1.56 ± 1.2 mm CL/year ($n=11$). There is no significant difference between male and female annual growth rate ($Z=0.11$; d.f.=23; $P>0.05$). Time between recaptures ranged from 0.25 to 7.00 yr and annual growth rate (mm CL/yr) ranged from 39.62 (a juvenile) to 0.17 (an adult female) (Figure 1).

Fabens' (1965) growth interval method yielded the following equation when fitted to the capture-recapture data:

$$L_r = 126.2 - (126.2 - L_c)e^{-0.16d}$$

(d.f. = 68; $F=18994.9$; $P<0.05$; $R^2=0.98$).

Using the estimate for a , and mean hatchling size at t_0 , the value of $b=0.78$, and the descriptive Von Bertalanffy equation for *P. geometricus* becomes:

$$L = 126.2(1 - 0.78e^{-0.16t}) \text{ (Equation 3).}$$

From this age-size relationship model (Figure 2) it is concluded that adult geometric tortoises may reach ages of approximately 30 years (based on the calculated age of the largest males and females). Individual male (116.8 mm CL; $n=20$) and female (133.2 mm CL; $n=18$) asymptotic sizes (modelled independently with Fabens' growth interval method) correspond closely with the mean size of the 20 largest males and females (116.2 ± 3.7 and 134.8 ± 3.01 mm CL), respectively. Table 1 provides the estimated values of parameters for the individual male and female Von Bertalanffy growth equations.

Annual growth rate is negatively related to body size (CL) by the power curve: $\text{Annual growth rate} = 246964.5CL^{-2.62}$ (d.f.=52; $R^2=0.67$; $F=107.2$; $P<0.05$) (Figure 1), and MASS is related to CL by the power equation: $\text{Mass} = 0.0003CL^{2.91}$ (d.f.=335; $R^2=0.98$; $F=27742.6$; $P<0.05$), or alternatively if CL is treated as dependent variable: $CL = 16.51\text{Mass}^{0.34}$ (d.f.=335; $R^2=0.98$; $F=27742.6$; $P<0.05$) (see Meek 1982). Adult male geometric tortoises average 105.2 ± 9.4 mm CL (range 84.7-123.4; $n=80$) and 208.3 ± 44.1 g MASS (range 124-320; $n=80$), while adult females average 123.2 ± 9.4 mm CL (range 88.6-142.5; $n=89$) and 410.4 ± 86.8 g MASS (range 161-680; $n=89$).

Number of rings on the third vertebral shield could not be used with confidence to age individuals initially. An analysis of the number of rings in young *P. geometricus* indicated that a range of 1-6 rings ($n=18$) may be deposited in any year (Baard 1990). Further illustration of this variation is the fact that an individual of 120 mm CL may have from 11 to 23 growth rings. Because of shell wear and growth ring bevelling, no more than 26 growth rings could be counted in adult specimens. When the carapace lengths of a subsequent, independent sample ($n=129$) of geometric tortoises from the same locality were converted into ages using Equation 4 (see below), and regressed against number of growth rings (Figure 3), the resulting regression model yielded the equation:

$$\text{Number of growth rings} = 3.02\text{Age}^{0.67}$$

(d.f. = 127; $F=1034.2$; $P<0.05$; $R^2=0.89$)

which may not necessarily age all individual tortoises accurately, but which may be employed to construct reasonably accurate population age structures.

Age at maturity

During this study, the development of secondary sexual characteristics in males (deepening plastron concavity, lengthening of the tail and bulging supracaudal shield) was taken as an indication of the onset of sexual maturity. To estimate mean age at maturity in males, Equation 3 for males (Table 1) was solved for t as follows:

$$t = (1/k)[\ln(ab/a - L_t)] \text{ (Equation 4),}$$

and based on the mean size (L_t) of the 10 smallest mature males (88.4 ± 1.9 mm CL). This results in an estimated age at maturity of 5.9 years. However, this model cannot age tortoises larger than asymptotic size i.e. when L_t exceeds a . Natural variation in age at maturity may explain the fact that individuals as small as 84.7 mm CL (age 5.3 yr) may be classed as males. Males therefore appear to reach sexual maturity at 5.3 to 5.9 years of age.

The absence of developing sexual characters in females prevented their use to estimate age at female sexual maturity. However, the smallest radiographed female containing eggs had a CL of 120 mm, a size

Table 1. Estimated values of parameters for the Von Bertalanffy and growth interval* equations for male and female geometric tortoises, *Psammobates geometricus*. See text for explanation of parameters.

Parameter	a	b	k
Males	116.8	0.76	0.19
Females	133.2	0.79	0.16

*Male growth interval model: $L_r = 116.8 - (116.8 - L_c)e^{-0.19d}$ (d.f.=20; F=22478.7; P<0.05; R²=0.93)

*Female growth interval model: $L_r = 133.2 - (133.2 - L_c)e^{-0.16d}$ (d.f.=18; F=10350.3; P<0.05; R²=0.94)

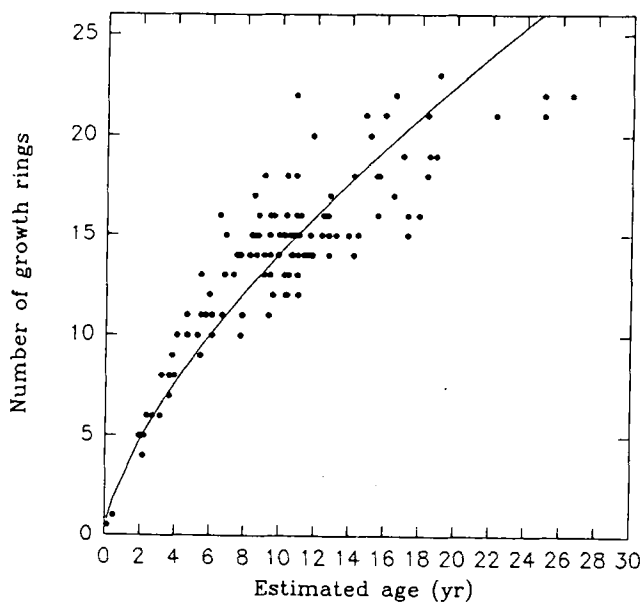


Figure 3. Relationship of number of growth rings on the third vertebral shield and estimated age (yr) for geometric tortoises, *Psammobates geometricus* of Elandsberg Private Nature Reserve. See text for descriptive equation.

corresponding to an age of approximately 17 years by the Von Bertalanffy equation for females in Table 1. However, due to the small sample size of radiographed females (n=14), there is still uncertainty about the size and age at which females begin producing eggs.

Sexual dimorphism

There are significant differences between adult male and female CL (Z=9.38), MASS (Z=10.54), SH (Z=10.79) and CW (Z=10.81); in all cases: d.f.=167 and P<0.05. AW and AN/CL do not differ significantly between the sexes (Z=-0.35 and Z=-0.59 respectively; d.f.=35; P>0.05), but there is a significant difference between male and female AN, PC and AW/CL (Z=2.02, Z=-5.26 and Z=-4.12 respectively; d.f.=35; P<0.05). Dimensions of the biggest male and female are, respectively: CL=123.4 and 142.5 mm; MASS=320 and 680 g; SH=67.9 and 83.4 mm; and CW=80.8 and 105.6

mm. The plastron concavity shows deepening in males as they approach maturity at about 90 mm CL (Figure 4), but is not fully developed until they reach 100-120 mm CL. Individuals >100 mm CL and classified as males had plastron concavities deeper than approximately 2 mm, and all individuals classified as females had concavities of 1 mm and shallower.

Discussion

Growth

Growth in *Psammobates geometricus* can be described using the Von Bertalanffy growth model. However, it underestimates the body sizes of the largest males and females, because male and female asymptotic size in the model represent "a mean asymptotic size for individuals in the population" (Frazer et al. 1990), and thus adults may be expected to be normally distributed around this mean. Further, the model does not quantify variation in the growth process (Gibbons & Lovich 1990), but one has to remember that a mathematical description of any biological process such as growth, attempts to normalize the variation, and the more successful it is, the higher the R² value will be. This gives the model good average predictive value, but evidence of seasonal and interannual variation will be lost. The close agreement of the male and female asymptotes to the mean adult size of the sexes gives confidence to the predictive ability of the *P. geometricus* model, but more data are required to test that confidence.

Age and growth rate determination for *P. geometricus* are further complicated because geometric tortoises remain active throughout the year, with activity levels decreasing during winter (Baard 1990). Reduced activity in chelonians usually results in reduced growth, but unlike some species from the northern hemisphere (see, e.g., Germano 1988; Galbraith & Brooks 1987), more than one growth ring may be laid down during one year in *P. geometricus* (see above). Similar to the desert tortoise *Gopherus agassizii* (Germano 1992), shell wear and growth ring bevelling further conceal the actual number of growth rings. Without long-term extensive mark and recapture studies, there is consequently no meaningful way to relate the real age of *P. geometricus* to number of growth rings on its third vertebral shield, other than to estimate individual age using the preliminary growth

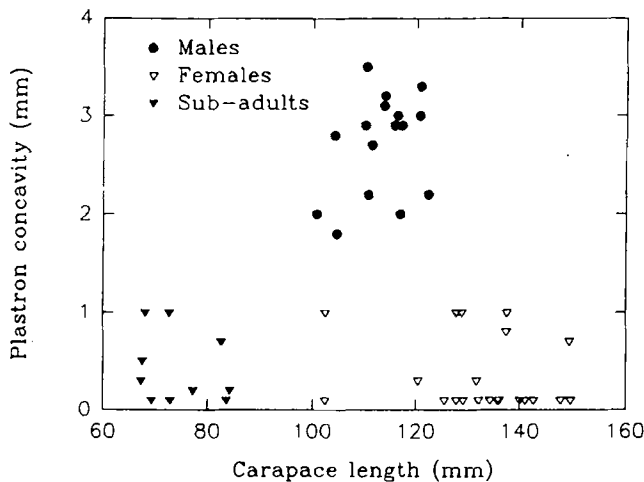


Figure 4. Depths (mm) of plastron concavities of 16 male, 21 female and 10 sub-adult geometric tortoises, *Psammobates geometricus* of Elandsberg Private Nature Reserve. Male sexual maturity is reached at approximately 90 mm CL.

equation and regress that against individual growth ring number (Figure 3). Alternatively, computed "age-size tables" based on accurate annual growth rates and anchored at known hatchling size, appear to provide a working alternative to age animals in an indirect way. It must be pointed out, however, that these results pertain to one population of this species only and may not necessarily reflect growth conditions in other populations.

Age at maturity

Estimated age at maturity depends upon either that size chosen as indicative of first maturity or that size where secondary sexual characteristics for the first time allow the sexing of individuals (Frazer & Ehrhart 1985). Size at maturity must be understood to represent an estimate based on (usually limited) information available at the time, and that variability around the mean size will exist (Gibbons & Lovich 1990). Size of the smallest nesting female may underestimate the mean size at maturity, and Frazer and Ehrhart (1985) suggest that the mean size of all nesting females should be used to approximate this age.

No conclusive data on age at maturity are available for female geometric tortoises, but males appear to reach sexual maturity at approximately 5.3 to 5.9 years. This compares with data from previous authors who estimated age at maturity as either 5 to 6 years (Baard 1989), 5 to 7 years (Rau 1976) or 7 to 8 years (Greig 1982). However, no indication was given by these authors concerning differences in male versus female age at maturity, and more research is required to address this point. The study of female age at maturity is regarded as particularly important in understanding this species' life history and for further modelling of age-size relationships.

Sexual dimorphism

Most chelonian species exhibit sexual dimorphism in size-related characters (see, e.g., Berry & Shine 1980; Gibbons & Lovich 1990), which can be the result of any of a wide array of processes (Roff 1992; Stamps 1993). In *P. geometricus* sexual dimorphism in body size is pronounced, with females reaching considerably larger asymptotic sizes than males. In reptiles, when sexual size differences are the result of sexual selection, it is normally the males that attain larger body sizes, because of the advantages a larger body size would have in male-male aggressive encounters, with resulting greater access to females (Stamps 1983). To date, aggressive behaviour or forced insemination have not been recorded for *P. geometricus*, although pre-coital courtship may take place. The preliminary indications therefore are that the observed sexual dimorphism in *P. geometricus* is not the result of sexual selection.

Where females reach larger asymptotic sizes than males, it is normally attributed to fecundity selection, in that larger females will be able to lay more or larger eggs than smaller females (Fitch 1978, 1981; Gibbons & Lovich 1990). If this is also true for *P. geometricus*, the growth data suggest that males and females grow at more or less similar rates, but that males reach their asymptotic size much sooner than females. Results from this study on sexual dimorphism in *P. geometricus*, however, should be regarded as preliminary, awaiting further research and analysis.

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