Variation in allometric shell growth and relationship with sexual size dimorphism in repatriated Indian star tortoises (*Geochelone elegans*) (Reptilia: Testudinidae)

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This study assesses the rate and pattern of variation of allometric shell growth in Indian star tortoise *Geochelone elegans*. Morphometric measurements of 83 Indian star tortoises were taken over 6 months. The anal notch measurements correctly classified the sex of the individuals based on the results of multiple regression analysis and chi-square test. Discriminant analysis clustered the growth rates into three age groups. The shell growth across sexes varied with age and morphometric measurements of the shell characters (length in males; width in females). The increase in straight carapace width and plastron length (PL) was significantly different across sexes (females > males and males > females respectively) in 5–7 years age class only. A pronounced increase in PL in males and overall width in females only in the age class of 7–9 years may indicate the influence of sexual selection. The difference in allometric shell growth (in males and females) may thus lead to sexually dimorphic adults.

Keywords: *Geochelone elegans*, morphometric differentiation, sexual dimorphism, shell growth.

IN some animal species, variation in size with growth is often associated with a proportional change in the body shape. Allometry is the study of this relationship of body size to various aspects of anatomy, physiology and even behaviour. Chelonian shell shows allometry and thus becomes an ideal group/system to conduct morphometric studies[1]. These studies have been used for investigating taxonomy[2–4], describing the intra-specific distinction between closely related species or subspecies[5–7], and assessing morphometric variation among and within populations[8–10].

Another aspect of the chelonian shell is sexual size dimorphism (SSD): the size difference between males and females of the same species (steppe tortoises (*Testudo horsfieldi*)[3], slider turtle (*Trachemys scripta*)[11], African tortoise (*Geochelone pardalis*)[12], angonoka tortoise (*Geochelone yniphora*)[13], etc.). SSD is known to be driven by the following: (1) sexual selection – size and shape will provide better reproductive success[14]; (2) fecundity selection – favours larger female size allowing them to have more offspring[15], and (3) competitive displacement – size related to resource use to reduce intersexual competition[15–17]. This in turn is affected by the genetic make-up, physiological requirements and environmental factors. In case of chelonians, SSD occurs in both extremes with individuals of either sex being larger than those of the opposite sex[18,19]. Allometric growth in shell is closely associated with SSD and this association can be used to explain the direction and intensity of SSD. For example, in *Malayemys macrocephala*, Brophy[15] observed that while females grew proportionally with respect to most of the shell characters, males selectively grew longer, wider and higher giving them flat and narrow shell compared to that of females.

The tortoise shell serves a variety of physiological (thermoregulation, fat and water reserves, mating and reproduction) and environmental (self-righting, locomotor performance and physical protection) functions. Its shape and size is governed by both intrinsic (genetic and physiology) and extrinsic (environmental) factors[20]. The plastron itself is known to be highly variable with respect to its shape, which makes the overall shell shape variable as well[21,22]. This versatility of morphometric/phenotypic variation is due to the complexity and interaction of the genetic make-up that is under pressure from both natural and sexual selection. Analysis of this variation of shell shape can: (a) provide precise quantification; (b) provide information about the pattern of inheritance and genetic variation (indirectly the effect of sexual selection), and (c) act as a proxy for determining the ability of a population to adapt to external stress (indirectly indicating influence of natural selection)[21].

The present study aims at assessing the inter-relationship of SSD and allometry in one chelonian species, the Indian star tortoise (*Geochelone elegans*). This is a terrestrial member of Testudinidae and one of the four known species of tortoises found in the drier regions of the Indian subcontinent. It is distributed in three regions: northwest India (Rajasthan, Gujarat continuing to Pakistan),

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southern India (Tamil Nadu, Karnataka, Kerala and Andhra Pradesh), and Sri Lanka[23,24], and is primarily found in dry deciduous and scrub forests, grasslands and coastal scrublands[23,25]. Although common in its range, the population is declining due to habitat destruction and, more importantly, illegal collection for pet trade[26]. *G. elegans* is protected under schedule IV of the Wildlife (Protection) Act 1972, amended in 2005 in India. Internationally, it is included in Appendix II of CITES and placed in 'Vulnerable' category in the IUCN Red List. In spite of this, the approximate estimate of annual harvest taken from the wild from the Indian population is 10,000–20,000 individuals[27]. Morphologically, female-biased SSD (i.e. females being appreciably larger than males) is well-documented in Indian star tortoises[23].

In September 2011, 600 individuals of *G. elegans* were confiscated at a Malaysian airport and repatriated to Chennai, India for rehabilitation and release back into the wild. Although common in its range, no information is available on the direction and intensity of SSD and allometric shell growth in *G. elegans*, which necessitated this study.

Materials and methods

Of the initial consignment of 600 tortoises, only 497 survived, repatriated and were taken in for rehabilitation. They were housed in separate enclosures, divided based on body weight (Figure 1) and appropriate husbandry and veterinary interventions were provided as mentioned in the literatures[28,29]. Each individual was measured (straight carapace length (SCL), straight carapace width (SCW) and plastron length (PL) using a digital Vernier calliper to the nearest 0.1 mm), marked with paint (a unique number which was painted on top of the carapace for identification) and weighed (using a digital weighing machine to the nearest gram). Each individual was also sexed by examining the concavity of the plastron (male: concave; female: flat), length of tail (male > female) and shape of the anal notch[30–32]. Additionally, the anal notch length (ANL; distance between the vertex of the anal notch to the midpoint of an imaginary line joining the distal-most points of the anal shield) and the anal notch width (ANW; distance between the distal-most points of the anal shield (between the posterior-most points of the anal scute)) were also measured. Using this the angle of the anal notch/vertex (ANA) was calculated (utilizing the principle of calculation of vertex of an isosceles triangle) (Figure 2).

Prior to the release, 83 individuals were randomly selected using a random number selector and SCL, SCW, PL, weight were again measured to assess individual growth rate and pattern. Additionally, the number of scute annuli was counted to estimate the approximate age[33,34]. Although the reliability and predictability of scute annuli for age determination in chelonians have been tested and calibrated in a limited manner, many studies on other desert tortoises like *Gopher* sp. have used this principle as a proxy to obtain the approximate age, especially when the precise measurement of age is not required[34]. The difference in the morphometric measurements (shell growth) over a period of six months was calculated. Growth in overall body size was calculated as the geometric mean of increase of each shell measurement as indicated above[22]. Summary statistics was used to describe the rate and pattern of change in these measurements. Spearman's coefficient of correlation between

Figure 1. *Geochelone elegans* feeding on fruits of *Oppuntia* and *Tridax procumbens*.

Table 1. Body measurements and estimated age of individuals at the end of the study, classified by sex

	Male (n = 36)		Female (n = 47)	
Attribute	Mean	SE	Mean	SE
SCL (mm)	85.93	2.58	83.04	2.03
SCW (mm)	63.12	1.65	60.52	1.06
PL (mm)	73.29	2.262	70.98	1.788
Body mass (g)	158.42	11.913	153.02	9.907
Approximate age (years)	5.50	0.249	5.60	0.275

SCL, Straight carapace length; SCW, straight carapace width; PL, Plastron length.

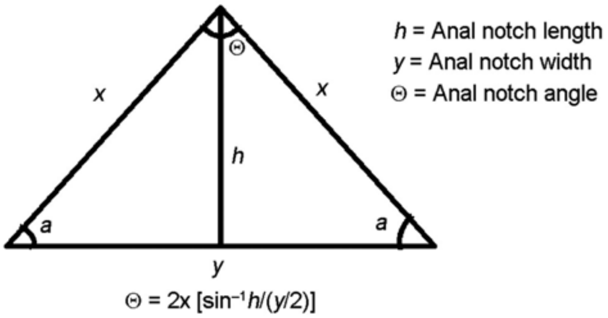

Figure 2. Calculation of the anal notch angle (ANA) using the principle of calculation of vertex of an isosceles triangle.

Table 2. Age cluster-wise description of shell characters and weight

Attribute	Mean	SD	SE	Minimum	Maximum	Mean	SD	SE	Minimum	Maximum
3–4 year age class			Female (n = 18)					Male (n = 8)		
SCL (mm)	1.58	1.88	0.44	–1.00	5.70	2.01	1.51	0.53	0.40	4.20
SCW (mm)	0.15	1.35	0.32	–1.60	2.35	1.59	1.71	0.60	–0.10	4.58
PL (mm)	1.43	1.74	0.41	–1.04	5.15	1.50	0.59	0.21	0.58	2.25
Weight	12.06	11.25	2.65	0.00	43.00	11.25	6.71	2.37	4.00	22.00
Geometric mean	1.34	0.90	0.21	0.29	3.41	1.34	0.86	0.31	0.38	2.61
5–7 year age class			Female (n = 20)					Male (n = 23)		
SCL(mm)	3.17	2.37	0.53	0.20	8.03	3.85	2.23	0.05	0.60	8.90
SCW (mm)	1.91	1.07	0.24	–0.70	3.70	1.14	1.51	0.32	–1.60	3.90
PL (mm)	1.92	2.05	0.46	–0.78	6.82	3.45	1.18	0.25	1.16	6.10
Weight	23.50	15.89	3.55	3.00	66.00	22.61	17.35	3.62	1.00	68.00
Geometric mean	2.15	1.50	0.33	0.00	5.00	2.30	1.33	0.28	0.00	5.00
8–9 year age class			Female (n = 9)					Male (n = 5)		
SCL (mm)	3.56	2.44	0.81	0.00	7.00	4.68	1.70	0.76	3.00	7.00
SCW (mm)	2.11	1.39	0.46	0.40	4.30	0.62	2.32	1.04	–2.06	2.80
PL (mm)	4.19	2.83	0.94	–0.20	7.98	5.12	0.65	0.29	4.24	5.81
Weight	41.33	19.53	6.54	11.00	71.00	30.0	22.78	10.19	3.00	57.00
Geometric mean	2.95	1.69	0.57	0.43	5.61	3.70	0.75	0.34	2.80	4.85

the overall body size and individual shell character measurements, and the number of rings (age) were computed in both sexes[3]. To evaluate the growth of the shell characters and to correctly classify the individuals in different age groups, discriminant analysis was performed with a matrix of coordinates representing each shell character[22,35]. To retrospectively determine the usefulness of the shell character measurements (especially anal notch measurements) in predicting the sex, multiple regression analysis was conducted in each age-class cluster (3–4, 5–7 and 8–9 years). In order to validate this method, 43 adults (23 males and 20 females) with clear sexual characters and SSD were selected. The predictions from the multiple regression analysis done on this group were further tested for difference in observed and calculated values using chi-square test. The response variable in both cases was the sex and the independent variables were the anal notch measurements (ANA, ANL and ANW). A one-way ANOVA was also performed to see the difference in growth of each shell character between males and females for the three age-group clusters and also to analyse the effect of feed consumption on the body size in males and females. Difference of $P < 0.05$ was regarded as statistically significant. All the analyses were done in SPSS 20 and XLSTAT version 2013 for Microsoft Office 2013®.

Results

The shell characters from 83 individuals (47 females and 36 males) were measured. Table 1 shows the mean SCL, age class and weight at the end of six months of rehabilitation. Table 2 shows the number of males and females in each age class. The individuals in the sample size ranged from 3 to 9 years in age, 70–100 mm SCL and 100–200 g body mass.

A multiple regression was run to predict the sex from ANH, ANW and ANA. This method showed validity in case of adults with known sexes as evident by the chi-square values $\chi^2(1, N = 43) = 3.6$, $P < 0.05$. The multiple regression equation correctly classified 86% of the adult individuals, with six males being wrongly classified as females. When applied to the 83 samples in the present study, these variables statistically significantly predicted the gender, $F(3,79) = 9.169$, $P < 0.0005$, $R^2 = 0.258$. Out of the three variables, the ANA/vertex angle and ANW added statistically significantly to the prediction, $P < 0.05$. ANW was positively and ANA was negatively correlated to gender. In other words, it predicted that the anal notch will be more acute and narrow for males compared to females. The general formula for prediction of the gender based on these three variables is

$$\text{Sex of the tortoise} = 8.631 - (0.279 \times \text{ANL}) + (0.205 \times \text{ANW}) - (0.099 \times \text{ANA}),$$

where the value for the sex of female is 1 and for male is 2.

The growth in overall body size showed a significant increase across the different age groups ($\rho = 0.360$, $\alpha = 0.001$). However, males and females showed differential and selective growth of shell characters in different age groups. In males, the increase in PL and SCL showed positive correlation with age ($\rho = 0.734$,

$\alpha < 0.0001$, and $\rho = 0.376$, $\alpha = 0.024$ respectively) (Figure 3 *a*–*c*); whereas in females the increase in SCW showed positive correlation with age ($\rho = 0.446$, $\alpha = 0.002$) (Figure 4 *a*–*c*).

In addition, overall body size (Figure 5), showed two instances of rapid growth (two spikes) at five and eight years. To further explain this pattern, discriminant analysis was performed, which showed separation of the individuals based on the three characters of the shell in three different clusters (3–4, 5–7 and 8–9 years). The discriminant power to the first axis was 78.58%, whereas the second axis was 21.42% (Figure 6).

As seen with ANOVA, in the 5–7 age cluster, there was a significant difference in the increase in SCW in females and males ($F = 6.588$, d$f = 42$, $P = 0.014$), with females showing higher mean growth (2.27 mm, SD: 1.20 mm) compared to males (1.14 mm, SD: 1.52 mm) (Figure 7). In the case of males in the 5–7 age cluster, the increase in PL significantly differed compared to the females ($F = 9.241$, d$f = 42$, $P = 0.004$), with the mean growth of males being higher than females (3.454 mm, SD: 1.171, and 1.92 mm, SD: 2.05 mm respectively) (Figure 8). There was no significant difference in the growth of shell characters between males and females of the other age clusters. Also, there was no significant difference between the weight gain in males and females

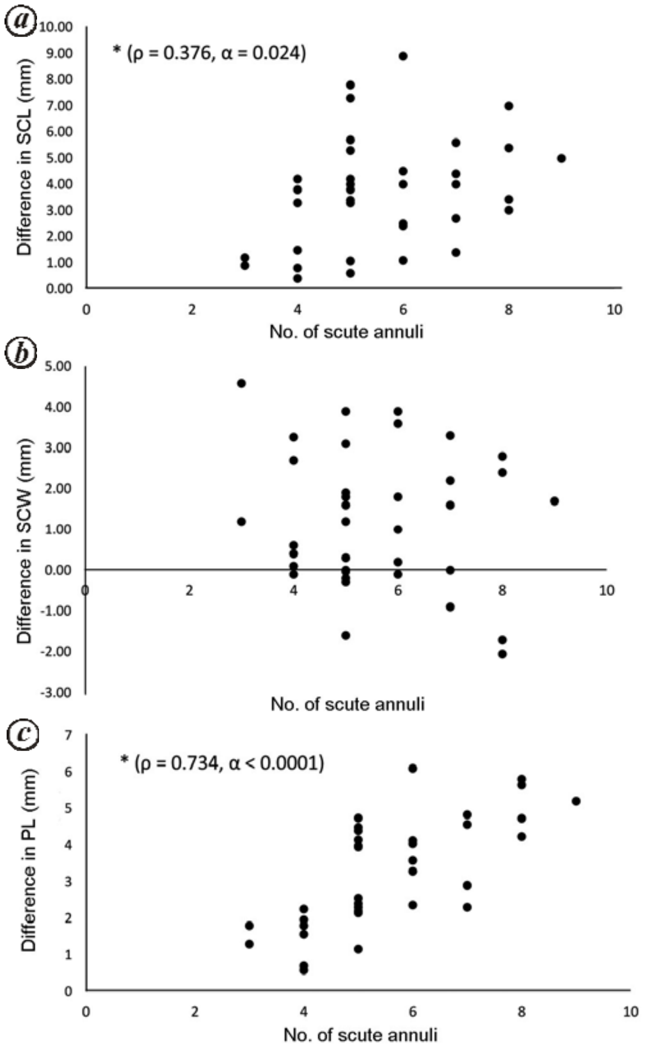

Figure 3. ***a***, Scatter plot showing increase in straight carapace length (SCL) in males across different age groups. Growth of SCL is significantly positively correlated with age. ***b***, Scatter plot showing increase in straight carapace width (SCW) in males across different age groups. There is no correlation between growth and age. ***c***, Scatter plot showing increase in plastron length (PL) in males across different age groups. Growth of PL is significantly positively correlated with age.

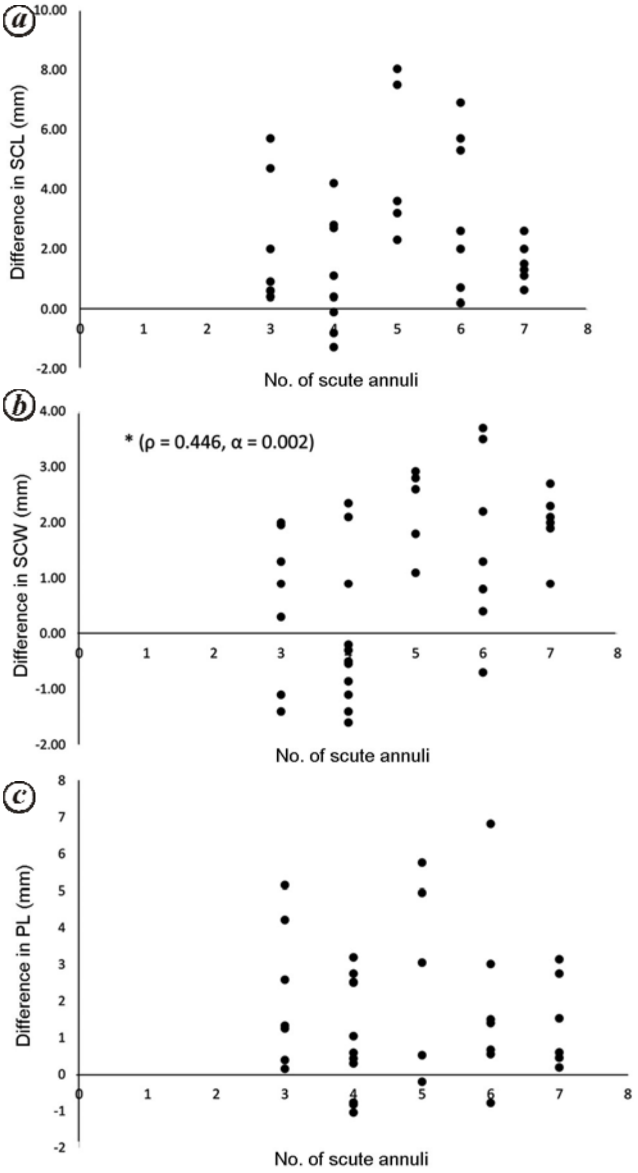

Figure 4. ***a***, Scatter plot showing increase in SCL in females across different age groups. There is no correlation between growth and age. ***b***, Scatter plot showing increase in SCW in females across different age groups. Growth of SCL is significantly positively correlated with age. ***c***, Scatter plot showing increase in PL in females across different age groups.

($F = 0.031$, $df = 42$, $P = 0.862$) which indicated that the difference in growth rate and pattern was independent of the body mass and consequently the individual food consumption.

Discussion

Studies on the growth rate and pattern in chelonians like *T. horsfieldi* suggest that the growth pattern shows a rapid juvenile growth phase until maturity followed by a continuous, slow adult growth phase[36,38]. The present study on the sample of *G. elegans* follows more or less a similar pattern, where the individuals in the age group of 5–7 years show a hypermorphic growth pattern in preparation of entering the breeding pool. Across the various age groups, there are two peak periods of growth, one after four years and the other after seven years. Further supported by the DA, this indicates that the growth in size is differentiated into three clusters 3–4, 5–7 and 8–9 years in ascending order (8–9 > 5–7 > 3–4 years). Additionally, the DA allows the differentiation of 79% of individuals into these respective age groups solely based on the shell size.

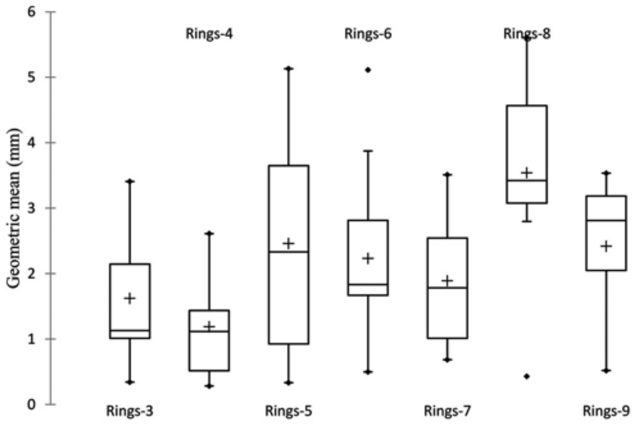

Figure 5. Box plots showing mean growth of body size (geometric mean) in males and females in different age classes. Two peaks at 5 and 8 years indicate hypermorphic growth. The geometric mean is plotted on the *y*-axis and the approximate age/number or rings is plotted on the *x*-axis.

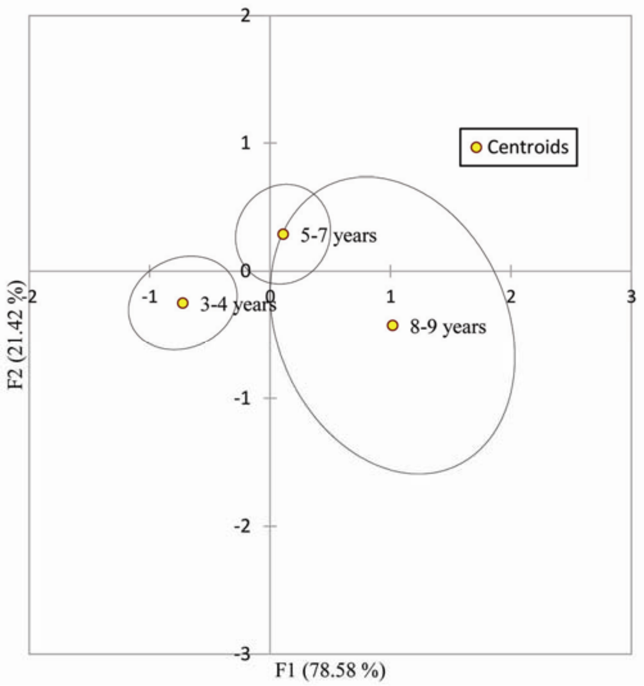

Figure 6. Discriminant analysis showing centroids separating into three age clusters (3–4, 5–7 and 8–9 years) with respect to overall body size (geometric mean).

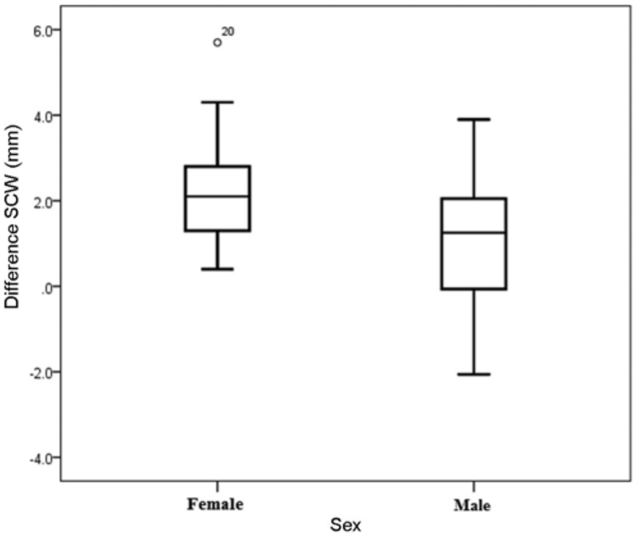

Figure 7. Box plots showing increase in PL in males and females in the age cluster of 5–7 years. The difference is statistically significant with a higher growth in males compared to females.

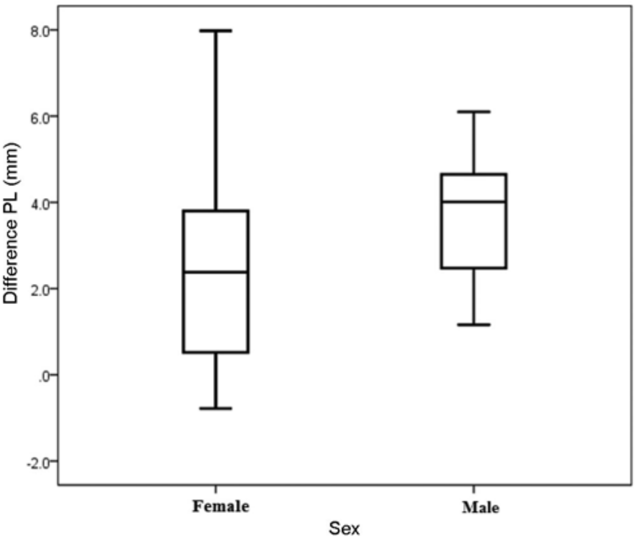

Figure 8. Box plots showing increase in SCW in males and females in the age cluster of 5–7 years. The difference is statistically significant with a higher growth in females compared to males.

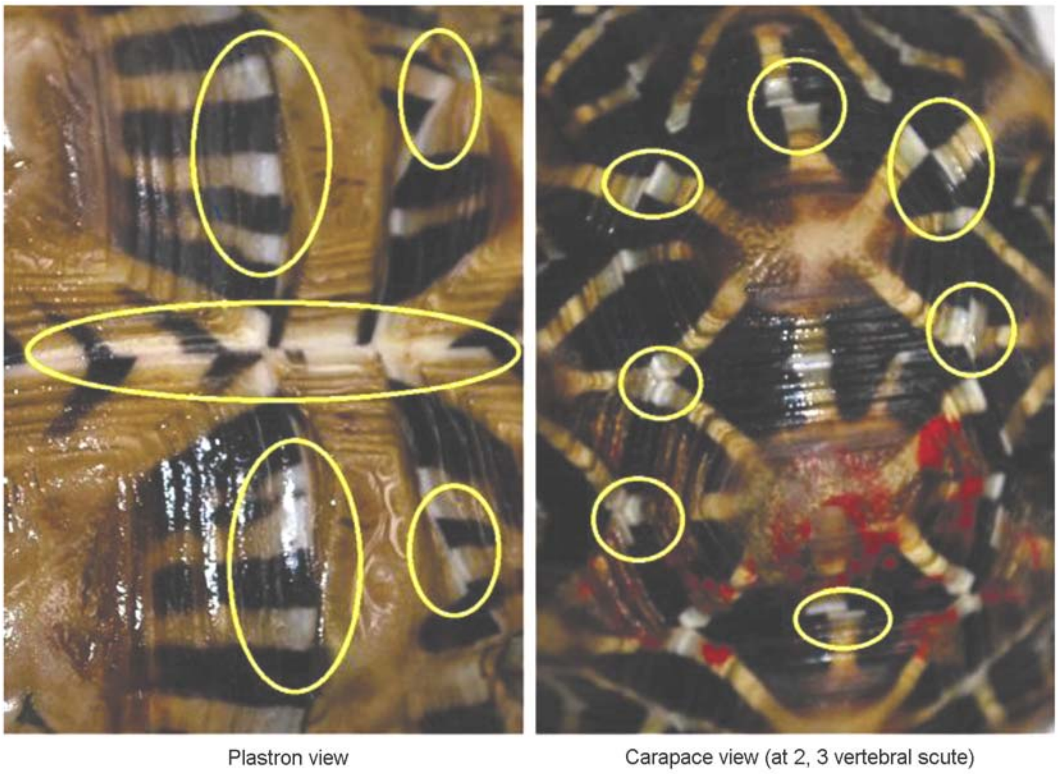

Figure 9. Close-up views of the plastron and carapace showing areas of new growth (circled).

In chelonians, especially tortoises, the rate and pattern of growth is affected by resource availability, predator size and intensity, thermal environment and water availability[3,11]. For instance, in the case of snail-eating turtle *M. macrocephala*, the pressure of the natural selection favours smaller male body size, as the benefit of early sexual maturity offsets the disadvantages of the smaller body size[15]. In *G. elegans*, the age of sexual maturity is around 6–8 years in males and 7–12 years in females[15,19]. This means that the growth during 3–4 years can probably increase the individual's body size in order to offset the negative environmental stresses in a small body size. In other words, natural selection seems to be driving the growth during this period and probably acts equally in both sexes prior to sexual maturity. Further studies, with larger sample size and longitudinal growth data are required to confirm these trends.

It is a known fact that the compromise between advantage of being able to enter the breeding population early (increased mating chances and success), and the disadvantage of being vulnerable to negative environmental stressors (predation and heat desiccation) in a small size, can determine the pattern of SSD[11]. In some species, with epigamic selection (female prefers males with specific traits like size), the males may delay the age of sexual maturity in order to attain a larger size. The size of the male at sexual maturity will therefore be a negotiation between advantages of a competitive breeder at an early age and higher chance of a female selecting it as a suitable mate[11]. Another advantage of sexually precocious males is the low metabolic requirement in a small size enabling them to expend some of the saved resources in searching and maintenance of a mate, thereby promoting reproduction and survival[3]. However, one should note that in the sexually precocious males, the growth rate is diminished, thereby reducing the maximum adult size[11]. In *T. horsfieldi*, Lagarde *et al.*[3] noted that the SSD is determined by the size of the individual at the time of sexual maturity. On similar lines, in *G. elegans*, the males mature early and at a smaller size, and the adults are considerably smaller than females.

Apart from the overall size, the shell shape in chelonians also determines the ability of the individual to reproduce successfully. In most cases, females tend to grow wider and larger to maximize clutch size, egg size or sometimes both[38]. In contrast, males develop concave plastron for a better fit on the female carapace during mating, with a selective growth of plastron. One can also see a similar pattern in case of *G. elegans*, where males show selective hypermorphic increase in SCL and PL, whereas females show selective increase in SCW with the growth occurring outwards from the sutures connecting each scute (Figure 9). Consequently, the females become larger and the males smaller. Additionally, plastron itself is sexually dimorphic with males having concave plastron due to faster relative growth, similar to a few other species of chelonians[11]. Males may show a slightly pronounced level of such hypermorphic growth enabling them to have increased variation in shell shape during growth compared to females[22].

This selectiveness is evident in the 5–7 age group only, which might indicate that sexual selection is driving the SSD to enable the individuals (especially the male) to enter the breeding population early. The selective growth continues until sexual maturity (8–9 years), after which the growth is more or less slow and will be dependent on feeding habits and partitioning of energy resources for reproduction[3,39]. The pattern in females can show a slight reduction in growth just prior to sexual maturity (8–9 years), to prepare the individual, physiologically, for her first reproductive event[3].

Captive individuals of various size classes sharing the enclosure and common feed were selected as the study sample. In such scenarios, usually the bigger individuals tend to dominate the smaller ones in competition for food. This also happens in the wild population, but due to availability of a larger area for foraging, the smaller individuals also get adequate food resources, with minimum competition. As there was no significant difference in the weight gain in males and females, the effect of feed consumption on the different body sizes of males and females is negligible. Some of the males and females were misclassified while using the anal notch measurements, which may have biased the results. Testing this method on a large sample size might yield more conclusive results.

In conclusion, the growth during 3–4 years in *G. elegans* is to increase the overall body size (probably due to natural selection); growth during 5–7 years is differential in females and males (width and length respectively) and is in preparation for sexual maturity (in response to sexual selection); 8–9 years shows peak growth in males at sexual maturity, whereas in female there is slight reduction, as a preparation for the phase of sexual maturity. The difference in the allometric shell growth between male and female tortoises could be responsible for the sexually dimorphic adults.

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