

Body size development of captive and free-ranging African spurred tortoises (*Geochelone sulcata*): high plasticity in reptilian growth rates

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In captivity, tortoises often grow faster than their conspecifics in the wild. Here, we document growth (measured as change in body mass) in three individual *Geochelone sulcata* over an exceptionally long period of nearly 18 years and use growth data (measured as change in carapace length) from the literature on free-ranging animals for comparison. Body lengths almost reached a plateau in the animals due to the long observation period. After transformation of body length to body mass for data from wild animals, logistic growth curves were successfully fitted to all data. The resulting functions yielded a 1.4–2.6 times higher intrinsic growth rate in captive than in wild individuals. The logistic growth model estimated the inflexion point of the growth curve at 6–9 years for the captive animals. This coincided with age at sexual maturity, respectively observations of first egg-laying of a female and the masturbation of a male. The inflexion point of the growth curve for free-ranging individuals was estimated at 15 years. Raising tortoises on intensive feeding regimes in captivity may considerably shorten generation times during the breeding stage of restocking programmes, and slow-growing animals are more likely to thrive after release into the wild. Investigations on the health of offspring from fast-growing parents are lacking.

Key words: ectotherm, body mass, body length, diet, conservation

Among breeders, it is well known that captive tortoises often show growth rates exceeding those of animals in the wild. Nevertheless, literature providing evidence for this assumption is rare. An excessive growth rate is suspected to lead to pathological consequences such as obesity, high mortality, gastrointestinal illnesses, renal diseases, “pyramiding”, fibrous osteodystrophy, metabolic bone disease or dystocia (Lambert et al., 1988; Häfeli & Schildger, 1995; McArthur, 2004; McArthur & Barrows, 2004; Lapid et al., 2005; Donoghue, 2006; Hatt, 2008;

Hänse et al., 2010). To our knowledge, age-related growth in captive/intensively kept versus free-ranging/extensively kept herbivorous tortoise species has so far been compared only for Greek tortoises (*Testudo hermanni*; Zwart et al., 1997), Galapagos giant tortoises (*Geochelone nigra*; Furrer et al., 2004), spur-thighed tortoises (*Testudo graeca*; Lapid et al., 2005) and leopard tortoises (*G. pardalis*; Ritz et al., 2010). Whenever such data were presented, it was for growing animals that had not been observed up to adulthood and cessation of growth; therefore, differences in growth rates and their consequences for the age at which sexual maturity was reached could not be reliably modelled. Despite the potential negative consequences of excessive growth, there may be one positive effect. Because sexual maturity is a function of body size, an accelerated growth rate might lead to earlier sexual maturity and thus offspring could be produced faster (Diez et al., 2009). This might help reduce the time required for restocking populations, and therefore be particularly relevant to endangered species.

The problem of an enhanced growth rate may occur in captive individuals of the African spurred tortoise *G. sulcata*. Although this species is widely distributed in Africa south of the Sahara from Senegal to Ethiopia (Loveridge & Williams, 1957; Wermuth & Mertens, 1961; Stearns, 1989; Iverson, 1992), no age-related data on body mass development in free-ranging animals are available. The only age-related data from wild African spurred tortoises are for total length (straight carapace length), given by Hailey & Lambert (2002). Here, we compare these data to data from captive individuals from a private breeding facility to test for differences in growth rates between captive and wild African spurred tortoises.

The African spurred tortoises were kept in outdoor enclosures with natural vegetation of grasses and shrubs during the summer and indoors on hemp in winter. They were fed on fresh grass, wet hay, rarely salad and occasionally vegetables. In their first years of life carp (fish) food was offered as well, as was common practice at the time. The three individuals, two males (A and B) and one female (C), were weighed regularly over a period of almost 18 years.

To test our hypothesis of differing growth rates in captive and wild tortoises, we estimated the growth rates of the three captive individuals studied and compared them with published data for wild individuals. Using data from Hailey & Lambert (2002; read from the graph), we used the individual measurements of age and body mass obtained from different free-ranging individuals as one sample. This generated an average individual (D) of the populations studied in the Sahel by these authors. Due to the fact that for the free-ranging individuals only carapace length measurements were available, whereas only body mass data were available for the captive individuals, we applied the allometric relationship of Lambert (1993; $BM = 0.000922 L^{2.755}$, BM in grams, L in mm) to each of the length measurements in free-ranging animals. Lambert (1993) showed that this relationship does not significantly

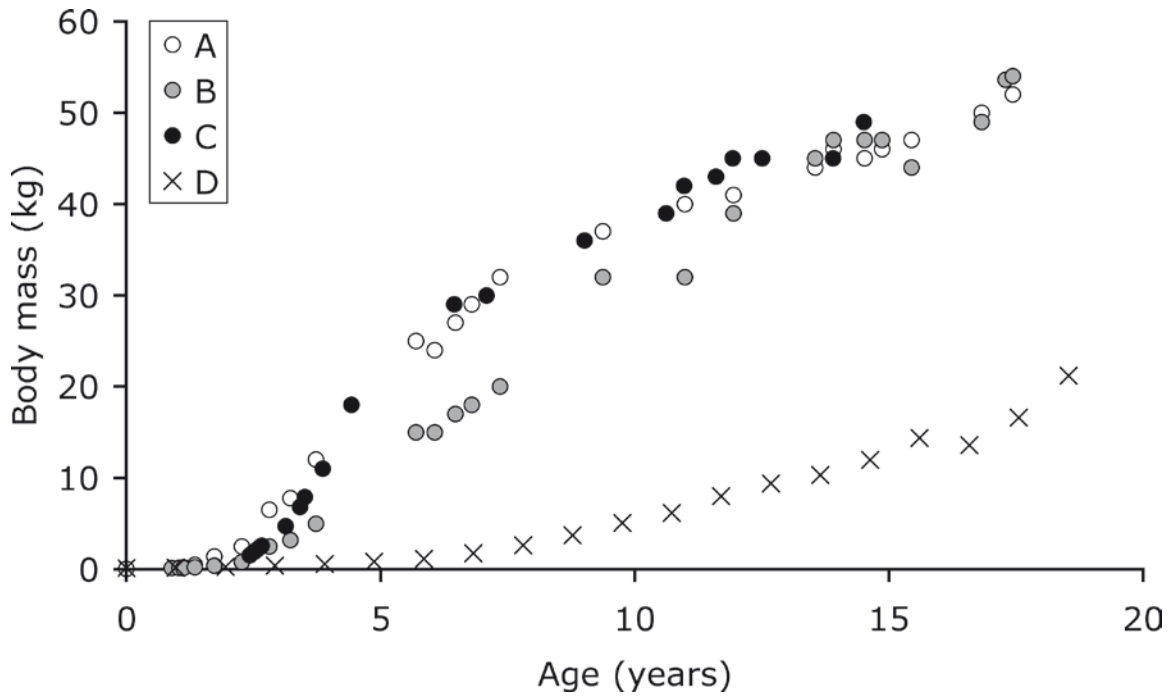


Fig. 1. Relationship of age to body mass development in captive African spurred tortoises (*Geochelone sulcata*) at a private breeding facility (males: A, B; female: C) and in free-ranging animals (D) investigated by Hailey & Lambert (2002). For estimated parameter values of growth models and goodness-of-fit of models, refer to Table 1.

vary between free-ranging and captive African spurred tortoises. The same was observed in leopard tortoises (Ritz et al., 2010).

To find the best growth model for each of the three captive animals and the average wild animal, we considered three mathematical models that relate the mass of an animal $BM(t)$ to its age t . All models used have been suggested for chelonians (Andrews, 1982; Hailey & Coulson, 1999) and consider an initial body mass BM_0 (in grams), an asymptotic mass BM_∞ (in grams), and the intrinsic growth rate g (without units). In particular, we fitted age (in days) versus mass for each individual assuming:

- 1) the von Bertalanffy growth model:

$$BM(t) = ({}^3\sqrt{BM_\infty} - {}^3\sqrt{BM_0}) \cdot \exp(-gt) + {}^3\sqrt{BM_0}$$

according to the Pütter–Bertalanffy equation (Pütter 1920, von Bertalanffy 1938, 1957) that allows for non-zero initial body masses (BM_0);

- 2) the logistic growth model:

$$BM(t) = BM_0 + \frac{BM_\infty}{1 + \exp(-g(t-t_i))}$$

where t_i is the age of the individual that corresponds to the inflexion point of the growth curve and defines the age of sexual maturity of the individual according to the resource allocation model (Stearns, 1992). This model is based on the general Chapman–Richards model (Richards, 1959), but assumes a symmetric inflexion point and a non-zero initial body mass;

- 3) the Gompertz model:

$$BM(t) = BM_0 + BM_\infty \exp(-\exp(-g(t-t_{max})))$$

where t_{max} is the age with the maximal increase in body mass (Medawar, 1940). The general Chapman–Richards

model (Richards, 1959) reduces to this parameterization of the Gompertz model when an inflexion point close to zero or infinity is assumed.

We applied non-linear regression analysis to estimate parameters of growth models for each of the animals. Analyses were conducted with the software STATISTICA 7.1 (StatSoft, Inc., 2005). Goodness-of-fit was assessed by variance explained (R^2).

There was a distinct difference in the growth of the free-ranging and the captive animals (Fig. 1). The growth in the body mass of each of the captive African spurred tortoises and of the average wild animal was best explained by the logistic model (Table 1). Estimated hatchling masses (BM_0) were, at 0.5–2.0 kg, too high compared to actual hatchling masses of 50–110 g. Asymptotic body mass (BM_∞) was estimated at 51–56 kg in the captive individuals. For the collective free-ranging specimens, BM_∞ was estimated at 27 kg, which is close to the 33 kg estimated for this parameter by Hailey & Lambert (2002) using the original data on an individual basis.

Although for all animals the von Bertalanffy models did converge, the estimated hatchling masses (BM_0) were either strongly negative (e.g. –26kg for individual C) or asymptotic body mass was rather unrealistic (>100kg for B and D) for this growth model. The Gompertz model did not converge for any of the individuals. The intrinsic growth rate (g , Table 1) of each of the captive animals was higher than that of the average free-living animal, being 1.4 to 2.6 times higher under the logistic model. Solving the logistic growth equations using the parameters from Table 1 for the year of the highest weight gain (the year that includes the time of the inflexion point), the captive animals had maximum weight gains of 7.7, 5.6

Table 1. Logistic growth models calculated and goodness-of-fit for captive (A, B, C) and free-ranging (D) African spurred tortoises (Hailey & Lambert, 2002). Number of individual measurements (n), parameter values derived from non-linear regression analyses (initial body mass BM_0 , asymptotic mass BM_∞ , intrinsic growth rate g [without unit], inflexion point of the growth curve t_i = age in days that corresponds to sexual maturity), and variance explained (R^2); * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Animal	Sex	n	Parameter estimates				Goodness-of-fit R^2
			BM_0 (g)	BM_∞ (g)	g	t_i (days)	
A	Male	25	1546**	53546**	0.001617***	2174***	0.95
B	Male	25	1659**	55632*	0.001112***	3173***	0.98
C	Female	22	2020*	51020*	0.002080*	2156*	0.96
D	Unknown	20	460*	26891**	0.000788***	5604***	0.99

and 9.4 kg per year, respectively, compared to 1.9 kg per year for the free-ranging animals.

Assuming the resource allocation model (Stearns, 1992), in which sexual maturity coincides with the inflexion point of the growth curve where growth rate decelerates, the logistic model predicted that captive male A reached sexual maturity at an age of about 6.0 years, captive male B at an age of about 8.7 years and captive female C at an age of about 5.9 years (Table 1). It was observed that both males masturbated at between four and five years old (as confirmed by microscopic identification of ejaculate) and that the female laid her first eggs at the age of five years. In contrast, the estimated age of sexual maturity was 15 years (inflexion point) for free-ranging animals.

The results confirm observations in other tortoise species that captive individuals display faster growth than their free-ranging conspecifics. This is most likely due to intensive feeding under captive conditions; it should, however, be noted that this does not automatically imply a nutrient-imbalanced or a nutrient-deficient diet, but can also be the result of a balanced diet offered in high amounts (Furrer et al., 2004; Diez et al., 2009; Ritz et al., 2010).

Our analysis of growth curves of animals revealed that the logistic growth model best described growth in body mass of African spurred tortoises. The Gompertz model and the von Bertalanffy model were not applicable, because the first did not converge and the second revealed biologically unrealistic estimates of growth parameters. Hailey & Lambert (2002) also found in their analysis of four African spurred tortoises that the logistic model fitted the growth of three individuals best, and that the Gompertz model was appropriate for one individual only. The von Bertalanffy model, which is generally suggested for reptiles (Halliday & Verrell, 1988), did not yield applicable results either in this study or in the study by Hailey & Lambert (2002). These observations question the generality of the von Bertalanffy model for reptiles (Halliday & Verrell, 1988) but support the observations of Avery (1994) that mass growth in smaller reptiles and chelonians is best fitted by a logistic model (Chen & Lue, 2002). Further support for the applicability of the logistic

model to African spurred tortoises comes from accuracy of estimated ages at sexual maturity. The captive female tortoise laid her first eggs at the age of five years, which is close to the age of about 5.9 years predicted by the logistic model. We did not observe the first copulation of males, but noticed that they masturbated at an age between four and five years. However, the discrepancy between the estimated and the actual hatchling mass indicates that even the logistic model is not ideal.

Based on the growth-curve-based estimates of sexual maturity, we suggest that faster growing tortoises reach sexual maturity earlier than slower growing individuals, and that generation times in restocking programmes could be distinctly reduced if breeding animals were raised intensively. In the literature for private tortoise breeders, one may find warnings against fast growth, and even warnings that offspring of faster growing animals may be less viable (e.g. Wegehaupt, 2006). To our knowledge, further evidence for these claims is lacking in tortoises, and one might suspect that such effects may be more evident if fast growth is triggered by high amounts of an inappropriate diet rather than by high amounts of an appropriate diet. However, reports that home-bred *Testudo* hatchlings had lower survivorship than hatchlings from free-ranging populations (Lambert et al., 1988), and that faster-growing individual lizards and skinks have lower survival rates in the wild (Bradshaw, 1970, 1971; Olsson & Shine, 2002), indicate that for restocking programmes, it seems prudent to ensure that the generation intended for release in the wild is maintained for a long period, with slow growth. Whether the quality of offspring itself is influenced by the growth rate of the parent animals remains to be investigated.

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