



When carapace governs size: variation among age classes and individuals in a free-ranging ectotherm with delayed maturity

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Received: 27 October 2017 / Accepted: 8 February 2018
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Abstract

Juvenile growth strongly impacts life-history traits during adulthood. Yet, in juveniles with delayed maturity, elusiveness has hindered age-specific studies of growth, precluding any detailed research on its consequences later in life. Different complex growth patterns have been extracted from captive animals, suggesting species-specific trajectories occur in free-ranging animals. How pronounced are growth and body size variation (VBS) throughout a long-lived ectotherm's life? Is VBS constant among age classes prior to maturity, or do compensatory and/or cumulative effects driven by long-lived-animal-specific strategies create distinct VBS cohorts, to ensure survival? To tackle the issue, we modelled growth data from continuous and dense annual capture–mark–recapture sampling (5096 body measurements of 1134 free-ranging individuals) of both immature and mature, long-lived Hermann's tortoises. We analysed population, cohort, and individual-based growth and VBS. Growth ring inferred ages were cross validated with annual recaptures in 289 juveniles. Analyses unravelled an S-shaped growth curve and identified three age cohorts across which VBS increases in a step-wise manner. Neonate-specific constraints and compensatory effects seem to control VBS until 4 years of age, possibly promoting survival with size. Subsequently, a hardened carapace takes over and cumulative effects fuelled by faster growth progressively increase VBS. Whereas ungulates are in a hurry to attain adult size before growth ceases (minimizing VBS), indeterminately growing tortoises can shape individual asymptotic sizes even after growth decelerates. Tortoise size is clearly shaped by age-specific ecological constraints; interestingly, it is likely the carapace that conducts the strategy, rather than maturity per se.

Keywords Cohorts · Indeterminate growth · Longevity · Tortoise · VBS

Introduction

Growth rate during early life is a major determinant of adult body size, especially in species with delayed maturity (Stearns 1992; Madsen and Shine 2000); body size, in turn, has ubiquitous impacts on life history traits (Peters 1983). Selective forces that control variation in body size (VBS) over time are omnipresent. VBS at birth (static heterogeneity) can either be countered by compensatory effects of growth, or fuelled by the cumulative effects of the environment and create “dynamic heterogeneity” (Tuljapurkar et al. 2009). The constant face-off between these effects can generate cohort VBS, and theory suggests that longer generation times should correlate with lower initial VBS and a faster decline throughout life and vice versa (Gailard and Yoccoz 2003); ungulates neatly follow this rule (Hamel et al. 2016). Consequently, in the pursuit to better understand growth variation and VBS, accurate descriptions

Communicated by Raoul Van Damme.

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of (individual/cohort) growth curve shapes are necessary, and prolonged immaturity mandates that they rely on large datasets that include long-term monitoring of individuals across all age classes. Alas, immature individuals tend to escape observation (Paradis et al. 1993; Pike et al. 2008), precluding detailed descriptions of (individual) juvenile growth curves. In long-lived species with delayed maturity, complex, species-specific juvenile growth curves have only been obtained from humans, few mammal species in captivity (Setchell et al. 2001), and sea turtles (Chaloupka and Zug 1997; Chaloupka 1998). In humans, although growth is not yet fully characterized (Gliozzi et al. 2012), there are two periods of accelerated growth that occur, respectively, after birth and several years later during adolescence (Davenport 1926; Leigh 1996). A very different pattern was observed in laboratory rats where growth rate progressively rises after birth and then exhibits a gradual decline prior maturity (Hughes and Tanner 1970). Sea turtles display two growth spurts taking place just after birth and then a few years later. This is the only example from free-ranging animals, yet it is based on relatively small and sparse samples and indirect skeletochronological ageing techniques, and should thus be considered with care (Chaloupka and Zug 1997; Chaloupka 1998). Nonetheless, differences in growth curve shapes, driven by variation of critical period(s), may well be species specific, and should be scrutinized.

Substantial perturbations occurring during critical phases of rapid growth are expected to have a strong definitive impact on adult size (Roselló-Díez and Joyner 2015). Multiple interactions between the sexes, the genes, and the environment mediated by complex physiological regulations underpin the resulting inter-individual (or between cohorts and inter-population) variability in growth rate (Badyaev 2002; Lui and Baron 2011; Roselló-Díez and Joyner 2015). Lummaa and Clutton-Brock (2002) reported various negative effects of unfavourable conditions (e.g. nutritional stress) during early development on many human adult traits. Nevertheless, the expected impact on adult body size was less documented. Overall the possible influence of environmental factors on the most sensitive periods of juvenile growth is an open question in free-ranging animals.

Thus far, mark–recapture studies performed on free-ranging individuals belonging to different taxa have provided extremely valuable information (Dietz et al. 1994; Lenihan and Van Vuren 1996). However, in most cases the juvenile sample size was limited to few observations and precise analyses were hampered by long intervals between recaptures before maturity; only crude juvenile growth patterns were inferred. The paucity of data explains why usually a linear, or a simple asymptotic growth curve was extracted (Congdon and Loben Sels 1991; Dietz et al. 1994; Lenihan and Van Vuren 1996; Zug and Parham 1996; Beaupre et al. 1998; Dodd and Dreslik 2007; Scott et al. 2012;

Rodríguez-Caro et al. 2013) and rapid ontogenic changes in growth velocity may have been missed. To our knowledge growth spurts have been directly identified from dense and continuous repeated records only in humans, captive primates and in industrially raised animals, only when the time elapsed between successive measurements was reduced (Jobling et al. 1994; Noy and Sklan 1997). Perhaps other taxa display effectively simpler growth patterns? However, it would be remarkable to observe that the kinetic of growth exhibits complex patterns only in those species where juveniles have been intensively monitored through regular recaptures of known individuals.

Several reptile species combine delayed maturity, long-life expectancy, and wide ranges of body sizes (Andrews 1982; Stearns 1984; Dunham and Miles 1985; Berrigan and Charnov 1994). In these organisms, adult body size responds to environmental factors with cascading effects on most life history traits (Madsen and Shine 2000; Niewiarowski and Roosenburg 1993; Caley and Schwarzkopf 2004). Chelonians provide excellent examples of extremely delayed maturity that leaves plenty of room for complex growth trajectories to establish idiosyncratic routes during a prolonged and substantial increase in size. Immediately after hatching, individuals are naïve and must find appropriate resources. Exploring novel environments can defer growth. Indeed, small tortoises are extremely vulnerable and they must intensively use shelters, trading foraging for safety (Ballouard et al. 2013). Over time, the protective value of the shell increases and larger, more experienced immature individuals can escape predation more easily. A shift in their time budget may promote foraging and exploitation of thermal resources, potentially accelerating growth and increasing VBS. Yet, other factors like dispersal or ontogenic changes in their diets may blur or invalidate this scenario. Thus far, field studies have described simple patterns for most chelonians, but they were based on limited numbers of infrequent recaptures (Congdon and Loben Sels 1991; Zug et al. 1995; Zug and Parham 1996; Hailey and Coulson 1999; Lagarde et al. 2001; Dodd and Dreslik 2007; Živkov et al. 2009; Scott et al. 2012). Applying the necessary growth function can reveal a more realistic complex growth pattern even on small datasets [see Chaloupka's (1998) reanalysis of Zug et al.'s (1995) dataset]. However, in the lack of validation from a CMR framework, results based on indirect skeletochronological ageing techniques on limited data can be questionable. Clearly, accurate field data based on abundant and frequent recaptures are required to further explore these issues.

We benefited from a 9-year-long capture–mark–recapture (CMR) study of a very dense population of Hermann's tortoises (*Testudo hermanni*, Gmelin 1789). The study population was unusual in that it provided abundant recaptures of both immature and adult individuals. This very peculiar situation allowed for solid inferences regarding early tortoise

life, age at maturity, sexual size dimorphism, and asymptotic size. Analyses of both individual trajectories and population means were based on large samples.

The three main objectives of this study were:

1. To examine if the mean growth curve follows a simple pattern (e.g. linear) in juveniles, or conversely if distinct growth periods can be characterized.
2. To appreciate the range of variation of individual trajectories around a mean curve. This objective adds weight to the first objective, since inter-individual variation in size should to a large extent be a consequence of varying environmental effects during critical phases of immature growth. Further, it is important to appraise if and to what extent individuals deviate from a mean pattern.
3. To track the trend of VBS throughout the extremely delayed maturity of tortoises. If juveniles (younger than ~ 10 years) display simple linear growth, and belong to a uniform ecological class before maturity, we would not expect any age- or cohort-specific VBS patterns. However, if different age cohorts face different selective pressures due to varying ecological or genetic constraints on size and growth, VBS shifts would be evident. In long-lived animals VBS is expected, and has been observed to progressively decrease before maturity (Hamel et al. 2016). We examined whether indeterminate growth can have a profound impact on such trends in a long-lived, phenotypically plastic, armoured ectotherm.

Materials and methods

Studied species and study site

The Hermann's tortoise (*T. hermanni*) is widely distributed in the Balkans, occurring in a wide range of habitats (Sterijovski et al. 2014). During 9 years (2008–2016), we studied a very dense (~ 67 adults per hectare, Bonnet et al. 2016) population on Golem Grad Island (Prespa Lake, Macedonia, ~ 18 ha; N 40°52'; E 20°59'). Each year the area was intensively patrolled (2–12 observers). Overall, 19 field sessions adding up to 169 searching days enabled us to process 1830 individuals and to collect 13,115 recaptures. Every captured individual was sexed when possible (small individuals are seldom sexually dimorphic), measured (straight carapace length), permanently marked using a notch code on the marginal scutes, and aged when possible. During resightings, tortoises were recaptured to check identity and were measured again. Individuals were rapidly released at the place of capture (Bonnet et al. 2016).

The age was estimated using growth ring counts on the shell, a method validated in Mediterranean *Testudo* species where the activity period is intersected by a prolonged

hibernation (Lagarde et al. 2001; Bertolero et al. 2005). Growth rings were large and thus easily counted before maturity. Following maturity, a sharp reduction of ring width posed difficulties for accurate counting. Hatchling tortoises were identified by their very small size, lack of cumulative growth rings, a very soft shell, and most of the time a visible umbilical scar. This category included those individuals captured in spring that underwent first hibernation, indeed hatching occurs in late summer/early autumn, before substantial growth. In the course of recaptures, age was re-estimated blindly (i.e. without checking previous estimate). Recaptures of hatchlings over years provided an absolute age. To minimize possible error while ageing individuals from growth rings, we considered that one growth ring was deposited per year. Then, considering recaptures over years, we corrected each count following the most parsimonious approach (e.g. if an individual was captured in 2008, 2009 and 2015 and aged as 1, 2 and 7 years, respectively, we would correct the last instance to 8 instead of modifying the first two). Very small, 1- to 3-year-old tortoises were easily aged. However, since counting became more ambiguous over time, when considering older individuals, we only retained those that had been recaptured at least twice without significant discrepancies among estimated ages. In practice, all the individuals where the error margin added up to more than 5 throughout all recaptures, were removed, and this occurred in two instances only. A subsample of individuals initially placed in the immature cohort had reached maturity during the study period and could thus be sexed with certainty. Overall, in juveniles and presumably young adults ageing combined both indirect (growth ring count) and direct (recapture) techniques. In many large and presumably old individuals the surface of the shell was smooth, the age was not estimated.

Growth analyses

In an attempt to follow the trends in VBS prior maturity, we engaged in a visual exploration of the frequency distribution of individual SCLs for each of the first nine age classes (see Table 1 for a breakdown of each used individual and observation).

The comparison between age-specific distribution curves of SCLs allowed for the detection of shifts in VBS among age cohorts, e.g. a lack of change in VBS would generate a succession of broadly identical curves, whereas a constant decrease/increase in VBS within the population would produce a progressive and regular change (e.g. linear/curvilinear). Since tortoises can reach maturity at various sizes (Willemsen and Hailey 1999) we assumed that VBS increases towards maturity and will generate successively flatter (wider and shorter) curves (unlike ungulates where VBS at maturity is very small [Hamel et al. 2016]). Whether

Table 1 Breakdown of observations (Obs) and individuals (Ind) obtained from free-ranging Hermann's tortoises of known age (289 juveniles or young adults)

Age	Obs	Ind	O-F	I-F	O-M	I-M	SCL <i>F + M</i>	SCL <i>F</i>	SCL <i>M</i>
1	104	95	2	1	6	6	41.3 (3.9)	41.9 (2.9)	44.3 (1.8)
2	110	97	6	6	13	12	49.8 (4.7)	48.3 (3.1)	51.6 (5.5)
3	118	86	11	9	26	20	58.0 (4.8)	57.4 (5.8)	60.8 (4.6)
4	99	75	9	6	40	29	66.1 (5.3)	64.2 (3.6)	68.2 (4.8)
5	108	79	9	5	55	39	76.2 (6.8)	78.2 (9.8)	78.1 (6.9)
6	108	82	17	13	69	21	88.8 (8.1)	90.3 (8.2)	87.9 (6.5)
7	120	101	24	17	58	50	96.9 (8.7)	99.9 (11.2)	97.6 (7.4)
8	97	81	19	16	51	40	106.7 (9.9)	110.8 (10.0)	108.3 (9.2)
9	58	52	16	15	32	28	114.5 (10.8)	121.6 (11.8)	112.3 (8.9)
10	56	50	10	9	40	35	123.3 (10.2)	123.6 (3.8)	124.3 (11.2)
11	35	31	3	3	30	27	128.0 (9.1)	127.1 (7.6)	129.2 (8.5)
12	27	23	6	6	21	17	142.0 (12.1)	140.7 (13.5)	142.3 (12.0)
13	11	10	3	3	8	7	146.1 (8.9)	154.0 (7.7)	143.1 (7.8)
14	8	8	2	2	6	6	150.6 (16.8)	170.5 (19.1)	144.0 (10.6)
15	7	6	2	2	5	4	153.6 (3.9)	158.5 (0.7)	151.7 (2.4)
16	5	4	0	0	5	4	157.6 (7.1)		157.6 (7.1)
17	1	1	0	0	1	1	167 (0)		167 (0)
Total	1072	289	139	28	466	85			

O-F and I-F stand, respectively, for observations and numbers of females, idem for males (O-M and I-M). SCL means straight carapace length (mm), both sexes pooled (SCL *F + M*) and separately for females and males (SCL *F*, SCL *M*). Means are provided \pm their standard deviation (in brackets, σ). The proportion of tortoises that could be sexed increased with age

such change is progressive, or characterized by non-regular steps at crucial ages, creating sets of curves facing different ecological and/or genetic constraints, was an open question.

Subsequently, we analysed growth patterns and asymptotic size in two ways: the dataset was split to distinguish those individuals whose age had been estimated from those whose age could not be estimated (thereafter referred as individuals of known age vs. individuals of unknown age). Individuals of known age constituted the younger class and involved 1- to 17-year-old tortoises (for a detailed breakdown, see Table 1). Individuals of unknown age comprised all individuals that were supposedly adults (Bertolero et al. 2011) and thus measured ≥ 130 mm straight carapace length (SCL). In most of them growth rings could not be counted unambiguously or at all (Bertolero et al. 2011), yet they were easily sexed using morphological characters (Djordjević et al. 2013).

Both groups of tortoises were used to estimate population and sex-specific mean asymptotic sizes, yet the approach diverged. In individuals of known age, we plotted size against age, whereas in individuals of unknown age we used incrementing body size measurements in function of the successive dates of captures and recaptures.

Data obtained in individuals of known age were fit with both the Bertalanffy growth model [$SCL_t = SCL_A - ((SCL_A - SCL_0) e^{-kt})$] 'Eq. 1' and with a logistic growth model [$SCL_t = SCL_A / (1 + e^{b-kt})$] 'Eq. 2', whereas data obtained in individuals of unknown age were

fit with Fabens' method of fitting the Bertalanffy growth model [$SCL_t = SCL_A - ((SCL_A - SCL_0) e^{-kt})$] 'Eq. 3' (Fabens 1965). In the equations above, SCL_A is the population mean asymptotic size, SCL_0 is length at time 0, SCL_1 and SCL_2 are observed straight carapace lengths in successive years, k is a growth rate constant and t is age in growth days (GD). The estimates of the growth constant k , SCL_A , and SCL_0 were obtained through an iterative non-linear regression (R v 0.99.879, R Core Team 2014), using our own data to find suitable start values for the non-linear model ($k = 0.0005$, $SCL_A = 220.0$ mm, $SCL_0 = 32.7$ mm). Even though SCL_0 is not a parameter in Fabens' method of fitting Bertalanffy's growth model, it could be estimated analytically as described in King et al. (2016), using SCL at birth (smallest individual captured on the island SCL = 32.7 mm) and $t = 146.3$ (the estimated GD needed to obtain 32.7 mm of SCL according to the best fit model of growth).

Since growth coincides with the period of active thermoregulation (Bertolero et al. 2005), we excluded hibernation from growth calculations. The onset and the end of hibernation were obtained in the field from ten individuals fitted with temperature data loggers in late summer in 2010 and 2011 and recaptured the following spring (unpublished data). On average, the duration of hibernation was 190 days. We considered that the activity period elapsed from the 22nd of April to the 14th of October (175 days).

Exploring individual and age-specific size variation

Using non-parametric bootstrapping, we randomly resampled our dataset of individuals of known age 10,000 times and estimated mean asymptotic size for each resample. We suggest that differences in asymptotic size between resamples would have been driven by shifts in individual trajectories from the original sample picked up more frequently by chance by the bootstrap procedure.

As for the individuals of unknown age, a smaller subsample of tortoises that had been encountered and measured during at least five consecutive years was used to build individual-based growth curves and estimate individual-based asymptotic SCLs. This way we could truly appreciate the population's full potential for growth variation. After sexual maturity Hermann's tortoise growth decreases linearly as a direct function of size, a pattern that fits well to Bertalanffy's model (Hailey and Coulson 1999). We, therefore, used 'Eq. 3' where individual estimates of SCL_A were obtained through an iterative non-linear regression using the sex-specific value for the growth constant k (from the analyses of individuals of unknown age) as constrained value. The first capture occasion was treated as growth day zero, thus the estimate of SCL_0 represented the expected size of the individual at the day of first capture.

Results

Among 1830 marked individuals, 289 were aged (of which 113 could a posteriori be sexed—28 females, 85 males) providing 1072 body size measurements (of which 605 belonged to individuals that could a posteriori be sexed—139 females, 466 males). This subsample constitutes the individuals of known age group. In the unknown age group, 845 marked tortoises were recaptured once or more, providing a total of 4024 body size measurements (2012 annual size increments). Among them, 55 females and 790 males, respectively, provided 122 and 1890 incremental measurements. Some of these individuals ($N = 97$, 8 females, 89 males) had been encountered for at least five consecutive years and could thus be used to build individual-based growth trajectories. Mean adult male SCL = 171.4 mm (median = 173.3 mm) and mean adult female SCL = 173.6 mm (median SCL = 173.0 mm). The largest individual measured was a male of 218.2 mm SCL; the largest female measured 211.1 mm SCL. Both of these individuals are part of a subsample of 121 individuals with extremely smooth shells (i.e. very old), the smallest being 155.5 mm long. The smallest individual on the island measured 32.7 mm.

Growth analyses

Visual exploration of the frequency distribution of individual SCLs for each of the first 9 years of life revealed two abrupt shifts in VBS separating three groups of juveniles: very young individuals measured during their first year of life (the first shift occurs between 1 and 2 years), young 2- to 4-year-old individuals (the second shift occurs between 4 and 5 years), and then individuals older than 5 years (Fig. 1, see Table 1 for shifts in σ between age classes). This step pattern suggests that VBS increases with age in a non-regular step-wise way.

The von Bertalanffy and logistic growth models fitted on the known age group yielded drastically different outcomes (Table 2). Nevertheless, both models showed similar broad fitting (Bertalanffy $R^2 = 7.5$; Logistic $R^2 = 7.2$), but due to the overly generous estimates of the von Bertalanffy model (Hermann's tortoises cannot reach 500 mm in SCL) we retained the logistic model for the sex-specific analyses. This subset contained 1- to 15-year-old individuals of both sexes and proposed similar asymptotic sizes in females and males ($SCL_A \pm 1$ standard error [SE] = 178.1 ± 8.0 mm vs 172.4 ± 4.6 mm, respectively; Fig. 2), suggesting that before maturity and during the first years after its onset, body size and growth rate do not differ considerably between the sexes.

In individuals of unknown age, the three-parameter von Bertalanffy growth equation yielded SCL_A and SCL_0 of 180.7 ± 0.9 and 34.6 mm, respectively. These values were closer to the logistic model of the known age group compared to the output of the Bertalanffy model, suggesting that the growth patterns of juveniles and adults differ. Sex-specific analyses of the individuals of unknown age indicated that females should attain a larger size than males, both considering hatchling (SCL_0) and asymptotic adult sizes: 38.7 mm versus 33.9 mm at hatching, and 188.7 ± 6.3 mm versus 179.9 ± 1.9 mm asymptotic SCL (Table 2).

Exploring individual and age-specific size variation

Bootstrapping the original sample of individuals of known age and estimating asymptotic size of each bootstrap suggests that even though there is a clear population mean asymptotic size, there exist early-age, likely immature individuals (predominantly 1- to 10-year-olds; Table 1) with idiosyncratic trajectories. Such individuals have driven the estimated SCL_A values of 10,000 bootstraps to range from 162.8 ± 6.2 to 189.4 ± 6.4 mm.

The asymptotic sizes based on the 97 particularly well-monitored (consecutive annual recaptures ≥ 5) individuals ranged between 152.5 ± 6.3 and 212.4 ± 9.0 mm in males, and between 180.5 ± 4.0 and 223.8 ± 12.3 mm in females (Fig. 3).

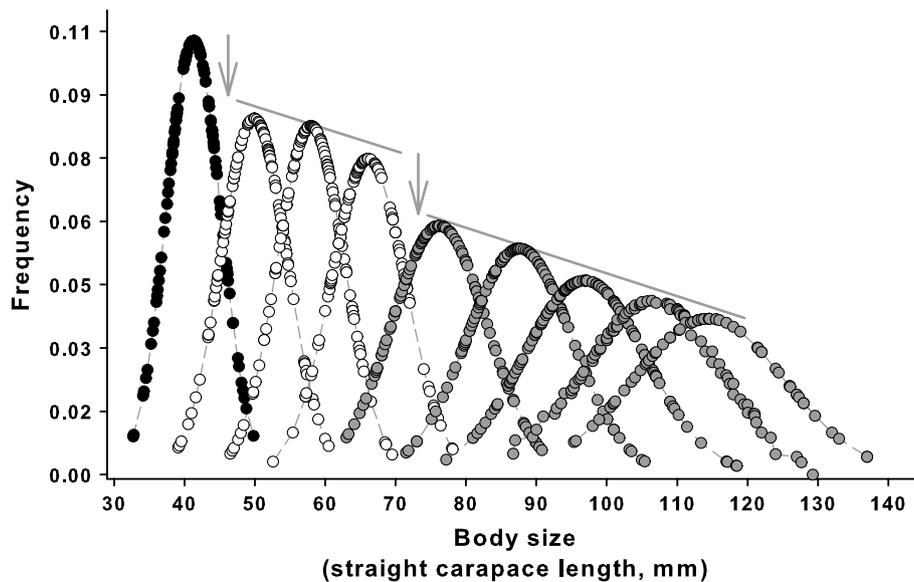


Fig. 1 Distributions of body sizes (straight carapace length, mm) within each of the first 9 years of Hermann's tortoise (*Testudo hermanni*) life from Golem Grad Island. Each curve stands for one age class from 1- to 9-year-old individuals (from left to right). Each circle represents the measurement collected in individuals of known age

(several individuals were recaptured over years and are represented in more than one cohort, see text for details). Two distribution shifts (arrows) separate three main age cohorts. They are, respectively, indicated in black (1-year-old individuals), white (2- to 4-year-old individuals), and grey (5- to 9-year-old individuals)

Table 2 Population and cohort (sex) mean estimates of growth parameters obtained via growth models (Bertalanffy and logistic) built on the known age and unknown age datasets of Hermann's tortoises from Golem Grad Island

Source	<i>n</i>	<i>k</i>	SCL_A	SCL_0	R^2
Unknown age	2034	0.0003	180.7 ± 0.9	34.6^*	2.23
Unknown age <i>F</i>	123	0.0005	188.7 ± 3.2	38.7^*	2.36
Unknown age <i>M</i>	1911	0.0003	179.9 ± 1.0	33.9^*	2.20
Known age, logistic	1072	0.001	175.3 ± 2.7	32.8	7.24
Known age, logistic <i>F</i>	107	0.001	178.1 ± 8.0	29.2	8.92
Known age, logistic <i>M</i>	423	0.001	172.4 ± 4.6	34.0	7.61
Known age, Bertalanffy	1072	0.0001	511.8 ± 75.5	25.9	7.45

Sample size is indicated (*n*). *F*, *M*, *k*, SCL_A , SCL_0 and R^2 denote female, male, growth rate, asymptotic SCL (mean \pm SE), SCL at birth and coefficient of determination, respectively. Analytically obtained SCL_0 values are denoted with an asterisk (*)

Although females exhibit the largest estimated asymptotic size, they were actually not consistently larger than males. In both sexes, asymptotic size varied greatly; the magnitude of variation was 59.9 mm in males, and 43.3 mm in females. On average, the estimated asymptotic size \pm 1 SE of any given adult differed from 49% of other individually analysed adults ($SCL_A \pm 1SE$). Although our population-wide analyses predicted that tortoises from Golem Grad Island should converge to a single asymptotic size (Fig. 2), 60.6% of individual asymptotic sizes \pm their respective 1SE fell out of the 1SE interval around the mean SCL_A estimated

from individuals of known age; this proportion was 61.7% considering individuals of unknown age (Fig. 3). Finally, the individual-based growth trajectories showed that regardless of SCL at first capture, mature tortoises can still end up at different asymptotic size (Fig. 4). The range of projected growth from capture to asymptotic size spanned between 0.0 and 40.3 mm.

Discussion

Many studies have reported that environmental fluctuations can strongly influence juvenile growth with long-term consequences during adulthood (Madsen and Shine 2000; Metcalfe and Monaghan 2001; Lummaa and Clutton-Brock 2002; Taborsky 2006). However, juveniles were usually grouped into relatively homogenous cohorts (e.g. years) while possible strong differences among age classes (e.g. 1-year-old *versus* older juveniles) or among individual trajectories before maturity were not acknowledged. In other terms, the existence of stages of juveniles independently from environmental fluctuations has been overlooked. Our study model's long immature phase revealed non-uniform growth patterns before maturity in a long-lived free-ranging species. Three main stages of juveniles could be distinguished. Analyses also revealed strong inter-individual variations of growth trajectories; most individuals did not fall into the 1 SE interval around the population mean. Overall our results diverge from the classical schematics where

Fig. 2 Estimated mean (solid line) and sex-specific (dashed lines) growth trajectories and mean asymptotic sizes (± 1 SE, indicated with light grey circles) superimposed against raw individual sizes (dark grey circles) of Hermann's tortoises of known age. The horizontal grey dashed line denotes size at maturity obtained from the literature (Bertolero et al. 2011)

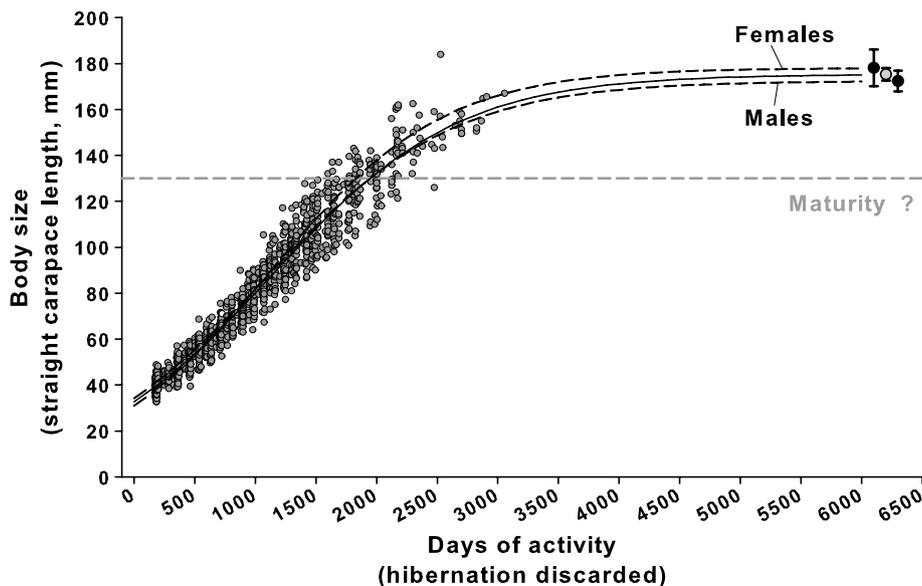
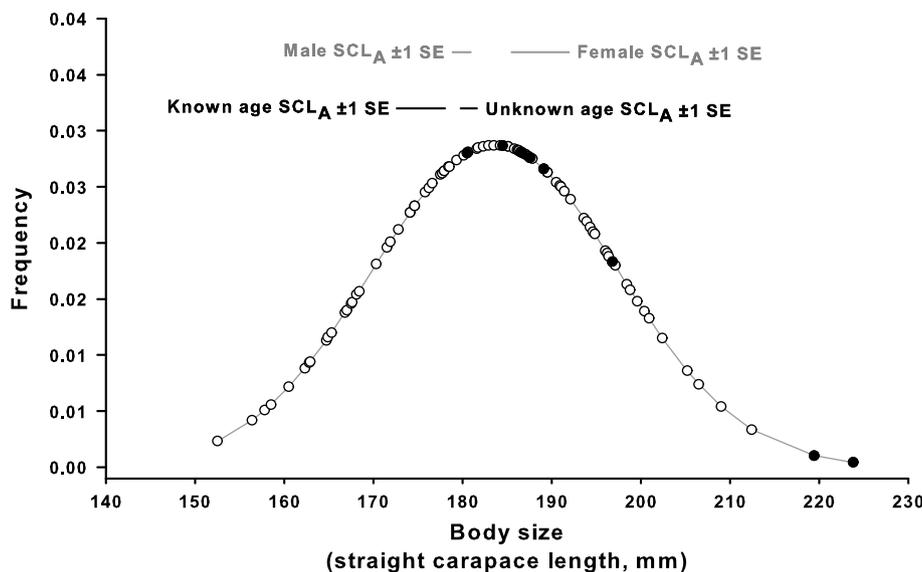


Fig. 3 Distribution of estimated individual asymptotic sizes of Hermann's tortoises from Golem Grad Island against estimated population and sex-specific mean asymptotic sizes from Table 2. Females are marked with filled circles and males with open circles. To facilitate comparison, ranges of population and cohort mean asymptotic sizes are displayed with four horizontal lines above the bell curve. These lines encompass a limited range of variation, accentuating the wide potential for individual asymptotic sizes

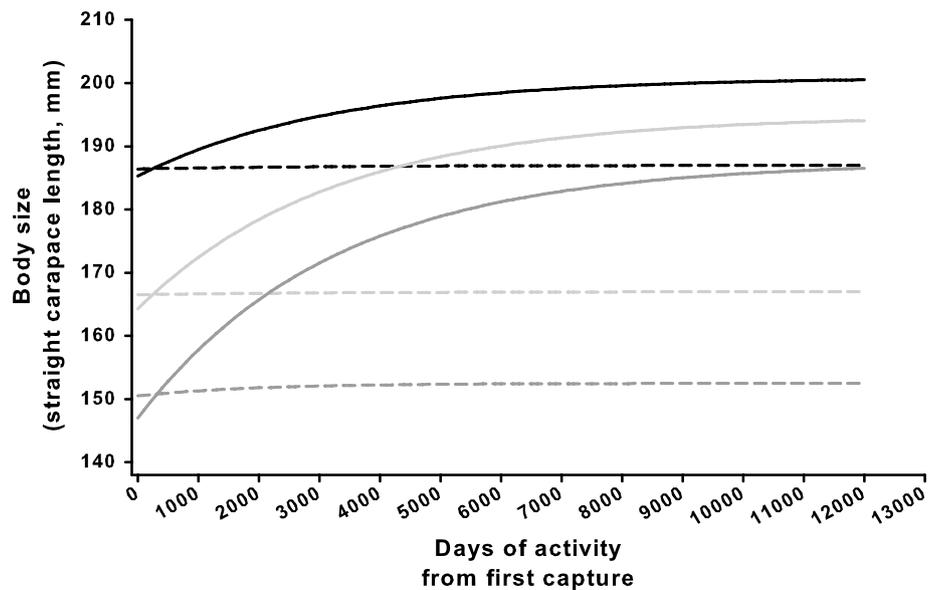


simple growth rates and a lack of variation of individual trajectories are considered before maturity. Abundant information combined with frequent recaptures suggested that pooling all juveniles aged 1 through 10 into a single category is an inappropriate approach. The discrepancy between the current versus previous studies is likely due to divergent recapture rates of juveniles under field conditions; with small juvenile sample sizes, simple growth curves were deemed appropriate for young Hermann's tortoises (e.g. 10 mm/year in Willemsen and Hailey 2001).

Juveniles are rarely captured and even less often recaptured, but we benefited from a favourable setting. The closed island system of Golem Grad allowed us to accumulate and delve into a remarkably dense dataset of annual size measurements of free-ranging tortoises. Consequently, it was

possible to combine frequent recaptures with data from annual growth rings to obtain the age and growth of individuals. The long and non-uniform immature phase of long-lived chelonians likely reflects ecologically distinct phases of life. If humans experience accelerated growth immediately after birth and then during adolescence (Davenport 1926; Leigh 1996), the fit of the S-shaped logistic growth curve we observed suggests the opposite pattern for our tortoises: first, growth rate is slow, then it gradually increases, becoming more rapid in the intermediate class of juveniles, and later slows down before reaching asymptotic size (Tsoularis 2001; Fig. 2). From such results we could extrapolate that, where humans benefit from parental nourishment and thus experience fast growth immediately after birth, hatchling tortoises have only themselves to rely on. Fully

Fig. 4 Estimated individual growth trajectories of three pairs of adult Hermann's tortoises of unknown age from Golem Grad Island with similar straight carapace lengths at the time of first capture, monitored during at least five consecutive years. Each pair is indicated with a colour pattern (black, light and dark grey) and with two line types (solid vs dashed)



independent neonates may require a 'grace period' during the first 500 days (~ 2.5 years; Fig. 2) of life during which they gradually learn where to find key resources. Hatching tortoises are small (estimated SCL_0 from both datasets ranges between 32.8 and 33.9 mm), possess a soft shell, and thus are vulnerable to environmental fluctuations or predators (Keller et al. 1998; Barje et al. 2005). It is thus expected that they adopt a secretive life, foraging only when necessary; the systematically meagre representation of this demographic in other tortoise studies (e.g. Zug et al. 1995; Živkov et al. 2009; most localities in Willemsen and Hailey 1999) supports this notion. Strong ecological constraints along with morphological constraints on egg size in chelonians (Macip-Ríos et al. 2013) translate into low static heterogeneity illustrated in the tall and narrow bell curve of size distribution within the first year of tortoise life (Fig. 1). Nevertheless, with size come safety and a harder carapace, thus successive acceleration of growth is imminent. An increase in VBS marks the first obvious departure towards dynamic heterogeneity, likely fuelled by individual differences in growth potential. This marks the onset of the second age cohort (2- to 4-year-old; Fig. 1) during which compensatory effects seem to maintain the uniformity in VBS; smaller individuals are stimulated to exploit any available resources and compensate with faster growth to ensure survival, or they can likely selectively disappear (Plard et al. 2015). Between 60 and 70 mm of length (~ 600 GD/3.5 yrs) faster linear growth begins (Fig. 2), likely supported by a firmer shell and familiarity with the environment. Subsequently, experience and boldness allow for more intense and possibly more efficient utilization of environmental resources marking the onset of the last identified age cohort (≥ 5 years; Fig. 1) at which point dynamic heterogeneity seems to take over. This stage

lasts a staggering ~ 8 years (1400 GD; Fig. 2) during which, a tortoise's more relaxed attitude towards its surroundings may lessen the constraints on size variation, promoting idiosyncratic growth trajectories. The wide range of estimated asymptotic sizes (162.8 ± 6.2 to 189.4 ± 6.4 mm) from bootstrapped datasets from the individuals of known age supports this idea. Meanwhile, opportunities, perturbations in the environment, or lack thereof, fuel individual variation in size progressively blurring the size distinctions between age classes—a notion well illustrated in Fig. 1 by the progressive flattening and finally overlapping of bell curves between the ages of 5 and 9. This sudden progressive increase in VBS is surprising for an animal so low on the slow-fast continuum. Long-lived animals invest in survival rather than reproduction (Gaillard and Yoccoz 2003), so smaller more vulnerable individuals are under pressure to grow and catch up with their mates, thus continuously decreasing VBS. However, considering the delayed costs of compensatory growth (Metcalfe and Monaghan 2001), a chelonian's hardened carapace may well compensate for the survival benefits size would otherwise bring at an earlier age. In other words, the survival benefits of a hardened carapace may give young and small (relative to their age) tortoises the option of deterring possibly costly compensatory growth, thus promoting an increase in age-specific VBS. A marked increase in tortoise survival at the age of five (from 68 to 86% followed by a plateau soon after in Fernández-Chacón et al. 2011) remarkably corroborates this idea. Determinate growers, such as ungulates, pay the price to reach a safe size before growth ceases; therefore, they experience an ever-decreasing VBS (Hamel et al. 2016). On the other hand, the Hermann's tortoise can grow significantly after maturity (Fig. 4); accompanied by a solid carapace at the age of five this seems to translate into liberty

in growth regimes regardless of maturity. In sea turtles, indirect skeletochronological ageing techniques suggested similar polyphasic growth before maturity, supposedly driven by diet shifts and changes in foraging areas (Chaloupka and Zug 1997; Chaloupka 1998). Our result based on CMR data provides strong support to these pioneer studies and thus to the fact that complex patterns in chelonian growth before maturity might be more widespread than currently assumed. Aggregating immature individuals and thus neglecting possible rapid non-linear developmental shifts may result in major imprecision when studying the fitness consequences of early life variations. The elusive nature of immature individuals should promote a more systematic approach; for example, in reptiles, artificial shelters and/or specific searching sessions bolster the detection of otherwise uncatchable juveniles (Bonnet et al. 1999, 2014; Ballouard et al. 2013). Precisely on Golem Grad most very small tortoises were found sheltered under stones while larger individuals were found using the classical visual searching technique.

Between the ages of 9–20 years, annual growth rate decreases markedly (Fig. 2) and becomes negligible as observed in other populations (Bertolero et al. 2011). Supposedly this sharp decrease leaves little room for subsequent growth to contribute to individual variation in maximal body size. Willemsen and Hailey (1999) argued that the duration of growth before it decelerates is the only proximate cause of variation in adult size. The SCL range (155.5–218.2 mm) of the oldest individuals (characterized by smooth shells, presumably more than 25 years; close to asymptotic size) should thus be projections of the spectrum of tortoise sizes at their respective times when growth had decelerated. However, not all adults in our population seem to fully conform to this scenario. Figure 4 demonstrates that adult tortoises display a wide range of growth trajectories relatively independently from their body size at first capture. In other words, despite a reduced growth rate, substantial individual variations can be measured in adult tortoises, providing that large sample sizes are continuously monitored on the long term (e.g. 5–10 years). Overall, the duration of growth before it decelerates is a crucial proximal cause of variation in size; however, later interactions between genes and the environment during the long mature life of tortoises may well significantly influence asymptotic size.

Further disentangling the respective contributions of various growth rates before and after maturity on individual size is not easy, but it might be crucial to better understand the actual extensive range of body sizes found in many long-lived ectothermic species (Gotthard 2001). This is an important issue because body size influences many life history traits, for example, mating success during ritual fights in males (Willemsen and Hailey 1999) or fecundity in females (Andersson 1994; Lagarde et al. 2001). On the other hand, selective advantages of smaller size may maintain variation:

early maturing small individuals may invest more resources into reproduction rather than growth, thereby balancing the advantage of a large body size (Stearns and Koella 1986). Additionally, variations in foraging resources may influence the opportunity for individuals to express their own growing potential (Gotthard 2001).

Finally, there is no dearth in reptile growth studies, and for a big part our data conform to existing knowledge. Nevertheless, it has become evident that major gaps still exist, particularly when studying the long immature phase of reptiles with delayed maturity. The complexities that we have pin pointed in this study surely penetrate even deeper into the specific life history characteristics of this phase. Possible consequences on variation in adult traits urge further exploration of interactions between environmental fluctuations and age cohort peculiarities.

Acknowledgements Mitko Tasevski from Konjsko is our most valuable asset in the field, providing hospitality and crucial logistics, such as boat transport for which we are grateful beyond words. We are grateful for the useful comments and encouragement of G. Zug and one anonymous reviewer. The authorities and staff of National Park ‘Galičica’ granted permission (Permit no. 03–246) for the study and provided administrative support. We extend our gratitude to the numerous students and collaborators that helped with data collection throughout the years of study. The present study was partially financially supported by the Ministry of Education and Science of Serbia (Grant no. 173043). All applicable institutional and/or national guidelines for the care and use of animals were followed.

Author contribution statement XB and DA conceived the ideas; DA analysed the data and led the writing of the manuscript; DA, XB, LT and AG substantially contributed to the conception and design of the manuscript. All authors collected the data, contributed critically to the drafts and gave final approval for publication.

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