

Sexual size dimorphism in steppe tortoises (*Testudo horsfieldi*): growth, maturity, and individual variation

Frédéric Lagarde, Xavier Bonnet, Brian T. Henen, Johanna Corbin, Ken A. Nagy, and Guy Naulleau

Abstract: Age and size at maturity are determined through complex interactions among size at birth, growth rate, maturation, and survival. We studied sexual size dimorphism and growth rate and maturation patterns in a long-lived organism, the steppe tortoise (*Testudo horsfieldi*), using the scute lamina number and width as age and growth measures. There was no sexual difference in the juvenile growth rate, but females matured later and hence were larger at maturity than males. We also observed considerable inter-individual variation in age and size at maturity. In both sexes, precocious animals grew faster during the juvenile phase but matured at a smaller body size than did tardy animals. Consequently, maturity did not seem size-dependent per se but rather was determined by growth rate. The strong variation between and within the sexes in age and size at maturity suggest that different growth trajectories and maturation schedules depend upon sex and individual responses to resource availability.

Résumé : L'âge et la taille à maturité sont déterminés par des interactions complexes entre la taille à la naissance, le taux de croissance, l'âge à la maturité et la survie. Nous avons étudié le dimorphisme sexuel de taille et les patterns de croissance et de maturation chez un organisme longévif, la Tortue des steppes (*Testudo horsfieldi*), en utilisant le nombre et l'épaisseur des anneaux de croissance situés sur les écailles comme indicateurs de l'âge et de la cinétique de la croissance. Les femelles atteignent leur maturité sexuelle plus tardivement que les mâles, mais nous n'avons pas détecté de différence dans les taux de croissance des juvéniles des deux sexes. Ainsi, les femelles sont plus grandes que les mâles. Nous avons mis en évidence de fortes variations inter-individuelles de l'âge et de la taille à la maturité. Chez les mâles comme chez les femelles, les animaux précoces se caractérisent par une croissance juvénile plus rapide mais atteignent la maturité sexuelle à une plus petite taille que les individus tardifs. La maturité sexuelle ne semble donc pas dépendante de la taille per se, mais est plutôt déterminée par la cinétique de la croissance. Les fortes variations d'âge et de taille à la maturité entre les mâles et les femelles et au sein de chaque groupe semblent traduire la diversité des réponses individuelles à la disponibilité des ressources.

Introduction

Size divergence is one of the most conspicuous differences between males and females, and such dimorphism has been intensively studied in a wide range of animals (Darwin 1871; Bristowe 1929; Pietsch 1976; Clutton-Brock et al. 1977; Berry and Shine 1980; Shine 1989, 1994; Anderson 1994; Vollrath 1998). Most studies of sexual size dimorphism (SSD)

have focused on differences in mean and maximum adult body size, and on the ultimate causes of these differences. They provided pertinent evolutionary explanations at broad taxonomic levels. However, selective pressures that act on adult body size are multiple, complex, and sometimes synergistic or antagonistic, hence obscuring the SSD explanation at the species level (Shine 1988, 1989, 1994; Hedrick and Temeles 1989). For example, both fecundity and survival may covary with foraging abilities, and their respective influences are thus inextricably mixed (Bonnet et al. 2001).

Many factors may affect the direction and intensity of SSD: size at birth, juvenile and adult growth rates, age and size at maturity, and survival. Because each of these traits may be a distinctive target of natural selection, SSD is a central issue in evolutionary biology. The actual SSD observed in a given population results from a combination of these factors, and there are a myriad different possible scenarios (Stamps and Krishnan 1997). Environmental fluctuations can also influence growth rate and survival, further complicating the situation (Shine 1990; Berrigan and Charnov 1994). Overall, the respective influences of different selective forces (e.g., sexual selection, selection for fecundity, ecological selection) on each sex are often inextricably mixed. For example, in species in which juvenile and adult phases differ considerably in morphology and ecology (e.g., holometabolous insects), adult body sizes can result from completely differ-

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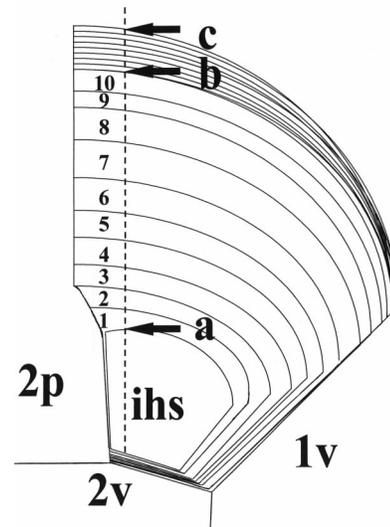
ent selection pressures on larval and adult stages. Larvae are larger than adults in some species (e.g., *Titanus giganteus*, *Gyrostigma* sp.), but the reverse also occurs (e.g., some chalcid larvae) (Wootton 1984). Although interesting, these life-history patterns certainly complicate SSD analyses and it may be easier to study species with direct development. Focusing on species with little or no sexual divergence in ecology (e.g., food habits, activity period, predation pressures) or morphology (e.g., extravagant characters, colours), we can remove most of the confounding effects due to ecological differences and allometry (Hill 1950; Medawar 1950; Gould 1966, 1974; McGowan 1994; Fairbairn 1997; Bonnet et al. 1998, 2001). The absence of parental care should facilitate characterisation of the relative importance of selective pressures on the body size of each sex. In such cases, the differences in reproductive roles are obvious. Male reproductive success increases with the ability to fertilize females and female reproductive success increases with the ability to produce eggs, creating a large divergence in the context of selection between sexes. Studying long-lived species increases statistical power for evaluating relationships among factors influencing growth and adult body size (through trade-offs amongst growth, age and size at maturity, reproduction and survival) because long-lived species often exhibit considerable inter-individual variation in growth rate and maturation patterns (Madsen and Shine 2000). The major disadvantage to this approach is logistical because considerable time and effort is necessary to undertake such studies, but this obstacle can sometimes be surmounted if the subjects display detectable records of growth pattern, growth rate, and sexual maturity on incremental growth markers (i.e., bone lamellae, fish scale rings, otolith rings, wood rings) (Castanet 1975, 1978; Harper 1977; Castanet and Cheylan 1979; Zug 1991). Age at maturity (Andrews 1982) can be determined with reasonable accuracy if a phase of rapid juvenile growth is followed by a marked decrease of growth after maturation, presumably as a consequence of the allocation of resources to reproduction. Together, these criteria will enable biologists to characterize growth rate and age and size at maturity in a straightforward way, and will help to examine the influence of proximate factors on SSD within a given species. In this paper, we evaluate the relationship between growth, age at maturity, adult body size, and SSD in the steppe tortoise (*Testudo horsfieldi* Gray, 1844).

Materials and methods

Study area

We studied a natural population of *T. horsfieldi* at the Djeiron Ecocenter of Bukhara, in the Republic of Uzbekistan (40°N, 65°E). This arid region neighbours the Kyzyl Kum desert and the climate is typical for extreme continental regions (Pereladova et al. 1998). From 1994 to 1998, daytime air temperature was $1.6 \pm 1.5^\circ\text{C}$ in January and $28.8 \pm 0.62^\circ\text{C}$ in July. Mean annual rainfall is 175 mm a year, with almost all (96%) falling between November and May. The summers are extremely hot and dry, and the primary food source for these tortoises (fresh annual plants; F. Lagarde, personal observation) is available for consumption only from March until the end of May.

Fig. 1. Simplified drawing of the first left-pleural scute of *Testudo horsfieldi*. 1v, the first vertebral scute; 2v, the second vertebral scute; 2p, the second left-pleural scute; ihs, the initial hatchling layer of first left-pleural scute; a, the initial edge of first pleural scute at hatching; b, the outer edge of pleural scute lamina prior to maturation; c, the current lateral edge of the first pleural scute. Within b, scute rings are wide and easily distinguishable, but outside of b, scute rings are less than 1 mm wide and more difficult to discriminate. In this example, 10 (1–10) scute rings can be counted from birth (a) to the “growth shift” (b), so we estimated that the age at maturity was 10 years.



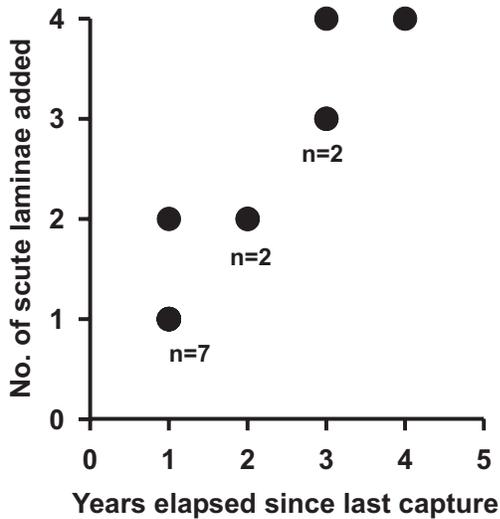
Biological model

In *T. horsfieldi*, there is no strong ecological niche divergence between the sexes. Males and females live in the same biotope, eat the same annual plant species (F. Lagarde, X. Bonnet, J. Corbin, B. Henen, K. Nagy, and B. Mardonov, in preparation), and are active at the same time of the year (Lagarde et al. 1999). The harsh climate limits activity to only 3 months a year, from mid-March to mid-June. During the other 9 months, *T. horsfieldi* remain buried in the sandy soil. From 1996 to 1999, 747 juvenile and adult *T. horsfieldi* were caught by hand. Animals were individually marked with scute notches and painted with numbers for behavioural observations. We recorded the midline carapace length (MCL) of each animal, using vernier calipers (accurate to 0.1 mm).

Scute rings as growth-pattern indicators

In tortoises, the rings ornamenting each scute of the carapace correspond to successive growth episodes (Castanet and Cheylan 1979; Fig. 1). In *T. horsfieldi*, as with other terrestrial tortoises, two main types of rings are distinguishable, namely the inner rings that are the first to appear and the outer rings that develop later. In our population, the inner rings were >1 mm in width and regular, although there was substantial variation among rings. The outer rings were much narrower (only 0.1–0.5 mm), very irregular, and consequently difficult to count and (or) characterize. The abrupt decrease in ring width from the inside to the external margin of each scute (outside of point b, Fig. 1) indicates a sudden decrease in growth rate (Fig. 1; see also Germano 1994; Willemsen and Hailey 1999; Hellgren et al. 2000). Such virtual cessation, or at least marked decrease, of growth rate is usually interpreted as a shift in the allocation among the competitive demands of growth and reproduction; in a very large range of organisms (including tortoises), resources are massively invested in reproduction at the onset of maturity

Fig. 2. Relationship between the number of subsequent scute laminae of the first (i.e., anteriormost) left-pleural scute and the number of activity periods (i.e., years) between capture and recapture in *T. horsfieldi* ($r_s = 0.93$, $p < 0.001$, $N = 14$). The sample size is indicated under the symbols when different from one, and one individual was first identified in early 1996, hence it was studied for four growth periods.



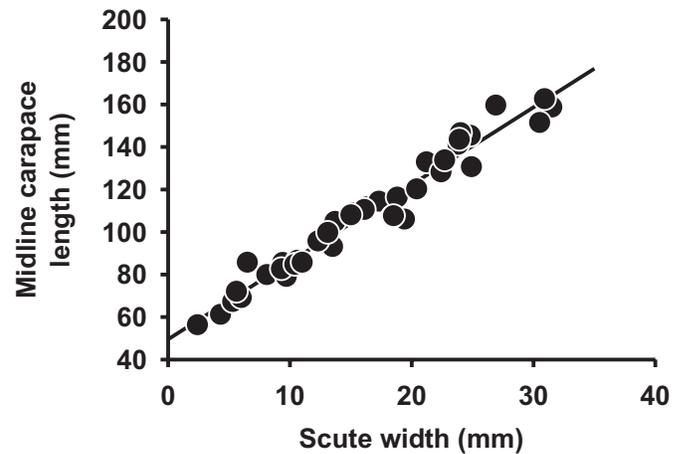
(Andrews 1982; review in Stearns 1992). We used the limit between the wide inner rings and the narrow outer rings as an indicator of sexual maturity (Kuchling 1999). In support of this, we never observed any tortoise exhibiting only the large inner rings (0%, $N = 115$) involved in sexual activity (i.e., courting, fighting, mating, etc.), whilst such behaviours were frequently recorded in tortoises with the two types of scute rings (43%, $N = 59$).

Age estimates

We counted the rings of the first left-pleural scute. The first left-pleural scute was chosen because it had less wear than other shell scutes. Erosion was due to the strong propensity for digging in *T. horsfieldi*. We counted only those rings that formed around the entire scute and only the large inner scute rings (wider than 1 mm), corresponding to the growth episodes that occurred prior to maturity. We confirmed our ability to accurately count inner scute rings by comparing our counts with those from the right-pleural, abdominal, and marginal scutes. In 49% of the specimens, erosion of the carapace precluded multiple counting. In the absence of a method to check the accuracy of a single counting, we decided not to include them in the analyses. In the remaining 51%, no conflict arose among multiple countings and we are confident of the validity of the scute-ring number.

In the course of the 4-year study, we recaptured 14 immature tortoises for which the initial scute number was known. We detected a strong positive correlation between the number of additional inner scute rings (or laminae beyond the initial hatchling scute) and time elapsed among years in the immature tortoises we recaptured over these 4 years (Spearman's ranked correlation, $r_s = 0.93$, $p < 0.001$, $N = 14$; Fig. 2). The sample size was relatively small because the cryptic behaviour of immature individuals makes them extremely difficult to capture and recapture, as is typical for other reptiles (Bonnet et al. 1999; Madsen and Shine 2000). This result demonstrates that in immature steppe tortoises, growth was highly seasonal, occurring during the spring and leading to the deposit of a single inner ring per year. Therefore, we felt confident that the number of scute rings provided an accurate age estimate prior to maturity, at least in our study population.

Fig. 3. Relationship between midline carapace length (MCL) and scute width ($W = a - c$ distance of the first, left-pleural scute in Fig. 2) in *T. horsfieldi*. The line represents the regression (MCL = $49.51 + 3.63W$, $r^2 = 0.95$, $p < 0.001$, $N = 40$).



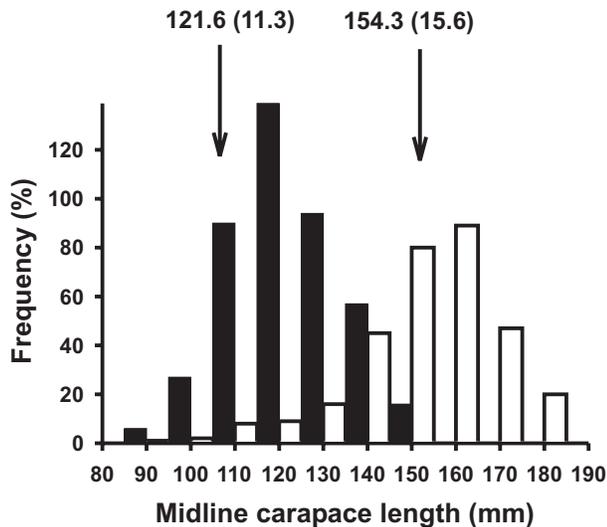
Females from this population laid eggs in May and June of 1998 (Lagarde et al. 1999; Henen et al. 2000), so hatchlings would probably benefit by avoiding the hot, dry climate and scarce food conditions of summer and fall, and emerging from their nests the following spring when the climate is mild and their food (fresh winter-annual plants) is plentiful. This activity pattern of hatchlings is consistent with statements of Ernst and Barbour (1989). Consequently, the first growth period and scute growth ring (1 in Fig. 1) probably occur in the spring following oviposition and hatchling. Thus the growth rings indicated in Fig. 1 should correspond to annual increments since hatching. The use of scute lines as an estimator of tortoise age is still under discussion, notably because several growth episodes sometimes occur within a given year in some species, leading to a bias in the age estimate, at least in adults (Germano and Bury 1998). However, our results should not suffer from such methodological problems for two reasons. First, we focused on inner scute rings, which are easily counted and correspond to growth episodes before maturity. Second, the short 3-month activity period of *T. horsfieldi* enables the growth of a unique inner ring each year.

Age and size at sexual maturity

Age at maturity was estimated by counting the inner rings before the growth shift in scute width. In Fig. 1, for example, we estimated that the age at maturity was 10 years. We measured each growth-ring width and the incremental scute widths (distances from a to b and a to c ; Fig. 1) with a digital caliper (to 0.01 mm) along the line projecting laterally from the caudomedial corner of the initial hatchling scute ("ihs"; Fig. 1). Our data also enabled us to estimate the size at maturity in adult individuals despite the fact that they continued to grow thereafter. We found a strong linear correlation between MCL and the total scute width (Fig. 3). We estimated MCL at maturity from the equation in Fig. 3.

To reinforce the notion that the shift between large inner and small outer scute rings is a signature of the acquisition of sexual maturity, we used the direct criterion of sexual maturity based on behavioural observations recorded in the field. We noted the behaviour for each tortoise ($N = 1819$ observations) spotted in the field from 1996 to 1999. Males were considered to be mature if they displayed a combination of characteristics: a typical adult male's tail morphology (Bonnet et al. 2001) along with male-male combat and (or) courtship and copulation with females. The criteria we used to determine female maturity were a typical female's tail morphology (Bonnet et al. 2001) along with the acceptance to copulate

Fig. 4. Size distribution in male (solid bars, $N = 430$) and female (open bars, $N = 317$) *T. horsfieldi*. Arrows indicate mean carapace length with standard deviation in parentheses for males and females.



and (or) presence of shelled eggs in the oviduct detected by X-rays (Henen et al. 2000). We found 102 males and 34 females that met these criteria for maturity. We also used these data to determine the respective sizes of the smallest adult male and smallest adult female of the population.

Annual growth rate estimates

For a given individual, the mean width (mm) of subsequent rings prior to the estimated maturity corresponds broadly to the mean annual juvenile growth rate (mm/year).

Growth model for single captures of known-age animals

Using the number of inner scute rings and the MCLs of 115 immature individuals, we fitted the age (from scute-ring counts) and carapace length data to Richards' growth model (Richards 1959). Richards' growth model is usually preferred to other fixed-growth models (e.g., Gompertz, von Bertalanffy, or logistic models) because it allows the data to determine the shape of the growth curve (Germano 1994; Lindeman 1997). To derive the theoretical relationship between size and age, Richards' model requires the size at hatching (MCL_0). The MCL calculated on 14 hatchling steppe tortoises was 40.6 ± 3.3 mm (mean \pm SD). To take into account the abrupt decrease in growth at maturity, we fixed the asymptotic size (MCL_A) of males (149 mm) and females (184 mm) using the mean upper decile sizes of each sex (Bradley et al. 1984; Germano 1994). Then, the growth equation used in this study for males and females is

$$MCL = [MCL_A^{(1-m)} - (MCL_0^{(1-m)} - MCL_0^{(1-m)})e^{(-2t/T)(1+m)}]^{1/(1-m)}$$

where T is the growth period equivalent to the age at which 90% of the asymptotic size is reached, t is age, and m is the curve-shape parameter.

Repeatability of measurements

The repeatability of MCLs was estimated by comparing duplicate MCL measurements on 81 individuals. The measurement error was 1.6 ± 2.6 mm, representing a total error of $1.3 \pm 2.2\%$. Simi-

Table 1. Parameter estimates for Richards' growth model in male and female *Testudo horsfieldi*.

	r^2	RMS	m	T
Males ($N = 106$)	0.90	53.48	-0.0004	16.16
Females ($N = 107$)	0.90	85.34	-0.007	20.81

Note: RMS is the residual mean square (sum of the residual squares divided by sample size), r^2 is the explained variance of the nonlinear regression analyses, m is the parameter related to the shape of the growth curve, and T is the growth period (year).

larly, the accuracy of scute-width measurements was estimated by comparing 70 duplicates. The measurement error was 0.17 ± 0.15 mm, corresponding to a error of $9 \pm 7\%$.

Statistics

We used ANOVA to compare body sizes between the sexes. We tested the data for deviations from normality before the ANOVA, although the F test is remarkably robust to deviations from normality and robust against violations of the "homogeneity of variances" assumption (Lindman 1974). Linear regression analyses were used to study the relationship among annual growth rate, age, and size at maturity, but Spearman's ranked correlations were used when sample sizes were small.

We analysed the juvenile growth pattern and the relationships among growth rate, age, and size at maturity using individual growth trajectories based on annual scute ring width measurements. We detected violations of the sphericity assumption (lack of independence) in all of our repeated-measures tests (Mauchly's sphericity tests, $p < 0.01$), so we used repeated-measures analyses of variance (MANOVA) to complete these analyses (O'Brien and Kaiser 1985). All statistical tests were performed using the Statistica 5.1 computer program (StatSoft Inc., Tulsa, Okla.).

Results

Sexual size dimorphism and maturity

In this population, female *T. horsfieldi* had larger MCLs than males (ANOVA, $F_{[1,745]} = 1179$, $p < 0.001$) (Fig. 4). The estimated age at maturity, based on the number of the inner wide rings, was lower in males than in females (males: 10.1 ± 1.6 years, range 7–12 years; females: 12.6 ± 2.0 years, range 9–17 years; ANOVA, $F_{[1,69]} = 33$, $p < 0.001$) and males matured at smaller estimated MCLs than did females (males: 118 ± 99 mm, range 102–144 mm; females: 148 ± 11 mm, range 124–177 mm; ANOVA, $F_{[1,69]} = 135$, $p < 0.001$).

The minimum size at maturity for males, based upon sexual behaviour, was 98 mm ($N = 102$) and for females, based upon their reproductive status (i.e., egg-bearing), was 145 mm ($N = 34$). These values indicate that males and females reached maturity at approximately 66 and 79% of their asymptotic sizes, respectively.

Growth model for animals of known age

Parameter estimates of Richards' model suggest that the growth curve for *T. horsfieldi* is a von Bertalanffy type curve, both in males and in females (m approaching 0; Table 1). The growth period, which is roughly equivalent to the age at 90% of the asymptotic MCL, was delayed by 5 years in females relative to males (Table 1; Fig. 5).

Fig. 5. Richards' growth trajectories as a function of age (from scute-ring counts) and sex in *T. horsfieldi* (mature males (●), mature females (○), and juveniles (shaded)). The dotted lines represent the asymptotic size for males (lower dotted line) and females (upper dotted line).

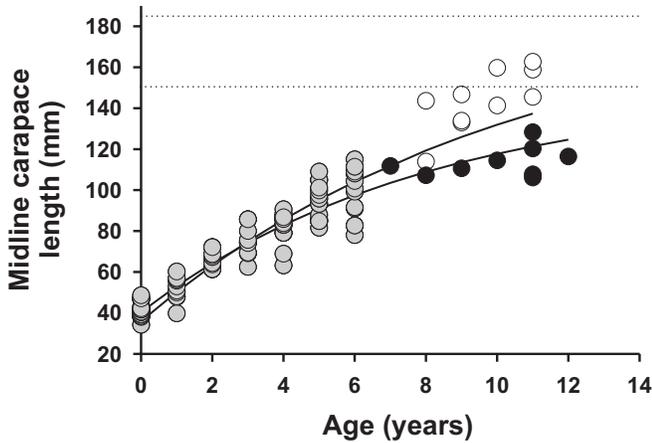
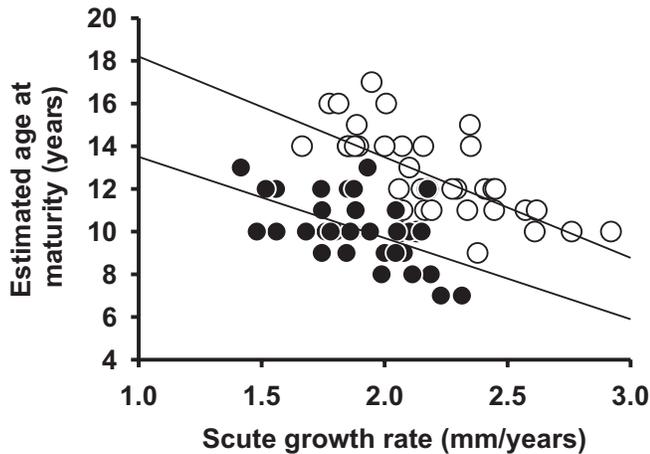


Fig. 7. Relationships between estimated age at maturity and annual juvenile growth rate of scutes in *T. horsfieldi*. The regression equations are $Y = 17.30 - 3.8X$ for males (●; $r_s = -0.49$, $p = 0.003$, $N = 33$) and $Y = 22.92 - 4.7X$ for females (○; $r_s = -0.68$, $p < 0.001$, $N = 38$).



Juvenile growth rate

To compare the juvenile growth rates of males and females, we used their respective scute-ring width as an estimator of annual growth rate (i.e., width along the broken line in Fig. 1). Repeated-measure analysis over time indicated that juvenile growth patterns differed significantly between males and females younger than 12 years (MANOVA with sex as the factor and subsequent scute-ring width as the dependent variable: Wilks' $\lambda = 2.98$, $F_{[12,18]} = 2.98$, $p = 0.017$). A more detailed analysis showed a significant sex effect on growth pattern ($F_{[1,29]} = 15.60$, $p < 0.001$), a significant time effect ($F_{[11,319]} = 3.08$, $p < 0.001$), and a significant interaction between time and sex ($F_{[11,319]} = 2.22$, $p = 0.01$). This difference between sexes was apparent only after the age when we detected the first indication of maturation in males (7 years). Hence, there was no significant difference between the sexes in growth patterns prior to 8 years of age

Fig. 6. Individual male (●) and female (○) juvenile growth trajectories. The arrows indicate the earliest recorded male maturation (left arrow) and female maturation (right arrow), respectively. Values are given as the mean + SD.

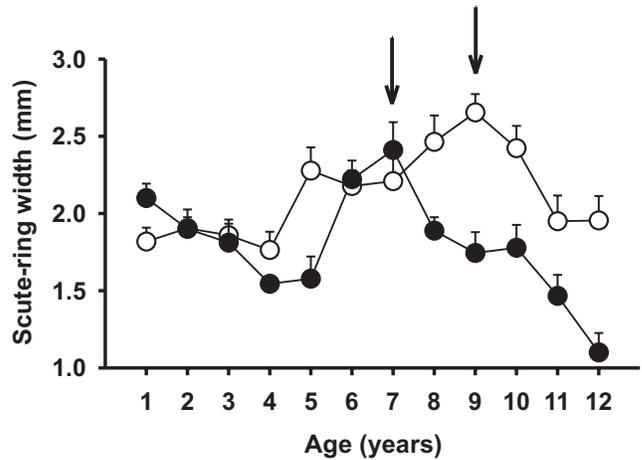
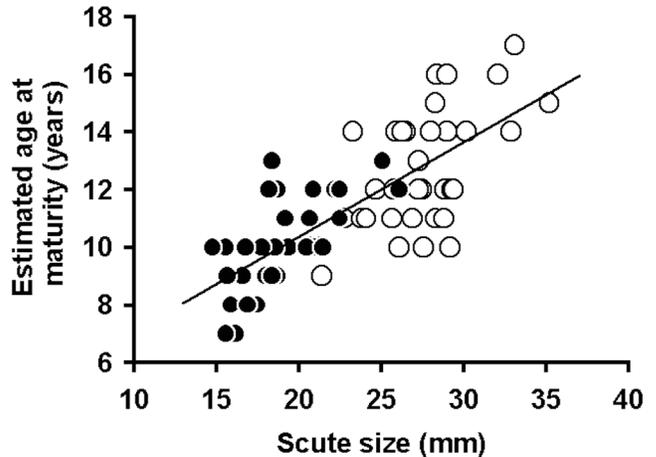


Fig. 8. Relationship between scute width at maturity (an indicator of MCL) and age at maturity for males (●) and females (○). The regression equations are $Y = 2.79 + 0.38X$ for males ($r_s = 0.72$, $p < 0.001$, $N = 33$) and $Y = 2.47 + 0.37X$ for females ($r_s = 0.52$, $p < 0.001$, $N = 38$).



(same MANOVA design: Wilks' $\lambda = 0.83$, $F_{[7,55]} = 1.50$, $p < 0.18$), but a strong difference appeared between 8 and 12 years, with male growth rate decreasing and female growth rate increasing until 9 years (MANOVA: Wilks' $\lambda = 0.43$, $F_{[5,25]} = 6.39$, $p < 0.001$; Fig. 6).

Individual growth patterns

In males and females, age and size at maturity were strongly affected by juvenile growth rates. Animals matured earlier if they grew faster as indicated by scute growth rates (Fig. 7), but they also matured at smaller body sizes (Fig. 8). There was no difference between slopes for male and female regression lines relating age at maturity to growth rate (ANCOVA: $F_{[1,67]} = 0.43$, $p = 0.50$; Fig. 7), but females matured later independently of the juvenile growth rate ($F_{[1,68]} = 94.75$, $p < 0.001$; Figs. 7 and 8).

Discussion

Sexual size dimorphism

Testudo horsfieldi shows the same direction of sexual size dimorphism as other species of *Testudo* (Lambert 1982; Willemsen and Hailey 1999), with females being larger than conspecific males (Mlynarski 1966; Brouchko 1981; Michel and Stöck 1996; Ataev 1997; our study). This contrasts strongly with other testudinids in which males are generally larger than females (Berry and Shine 1980; Wilbur and Morin 1988; Lambert 1995; Lambert et al. 1998). Male *T. horsfieldi* (as in other tortoise species) fight frequently and some male–male combat can last more than 1 h (F. Lagarde, personal observations). If male combat success affects access to reproductive females, it may cause males to evolve larger body sizes (Cagle 1950; Auffenberg 1977; Berry and Shine 1980; Stamps 1983; Niblick et al. 1994). On the other hand, selection for fecundity (Darwin 1871) likely exists for females because females exhibit a positive correlation between clutch size, as well as annual egg production, and body size (Henen et al. 2000) as do numerous other chelonian species (Gibbons et al. 1982; Mitchell 1985; Congdon and van Loben Sels 1993; Nieuwolt-Dacanay 1997; Zuffi et al. 1999). Females may become larger to optimize lifetime reproductive output (Congdon and Tinkle 1982; Wilbur and Morin 1988; Gibbons and Greene 1990; Gibbons and Lovich 1990; Forsman and Shine 1995). Therefore, different selective forces (i.e., male combat success and female fecundity) would appear to favour a larger body size for both sexes. In the absence of direct measurement of fitness components to evaluate the importance of these selective forces on body size, assessment of the determinants of SSD in *T. horsfieldi* cannot be done simply. However, the resolution of the SSD question may ultimately benefit from understanding the dynamic process of growth, which determines age and size at maturity.

Male and female growth and maturation patterns

Testudo horsfieldi follows the general growth pattern for chelonians: a rapid juvenile growth phase until maturity followed by a continuous, slow adult growth phase (Andrews 1982; Wilbur and Morin 1988). A slight decrease in growth rate prior to maturation (i.e., prior to 12 years) may indicate physiological preparation for first reproduction, especially for females. The sexual difference in age at maturity is primarily responsible for the sexual size dimorphism in *T. horsfieldi*, with sexual differences in growth rates occurring only late in juvenile development (8–12 years).

Because juvenile chelonians must grow rapidly to reach sizes that minimize predation risk (Wilbur and Morin 1988), we may expect male and female juveniles to have similar growth rates prior to maturity (Gibbons and Greene 1990). Nevertheless, precocial sex differentiation in growth patterns occurs in some ectotherms (Andrews 1982; Nylin et al. 1993) and in some tortoises (Andrews 1982; St.-Clair et al. 1994; Lambert et al. 1998). Females may also face minimal size constraints, potentially greater than predation considerations, on producing optimal clutch size. This appears to be true for female *T. horsfieldi*, which mature later than do males (Brouchko 1981; our study). Direct and indirect estimates of minimum male size at maturity are very similar (98 and

102 mm, respectively), but estimates differed for females (145 and 124 mm, respectively). This discrepancy may have been due to inadequate sampling of females ($N = 34$), especially small females, for radiographic determination of their reproductive condition or because vitellogenic cycling may begin years before ovulation occurs as recorded in other chelonians (Kuchling and Bradshaw 1993; Kuchling 1999). Allocation of resources to reproduction may start before effective reproduction (i.e., laying), leading to the discrepancy between the direct and indirect estimates of age at maturity in females. Taking into account such caveats will reinforce the sex divergence we observed with females maturing even later.

Individual variation

There was a large inter-individual range in age (9–17 and 7–12 years for females and males, respectively) and estimated size at maturity (from 124 to 177 mm in females and from 102 to 144 mm in males). Such variations have been observed in many species of tortoises (e.g., Gibbons and Greene 1990; Congdon and van Loben Sels 1993; Wood and Wood 1993; St.-Clair et al. 1994). It is important to include the variation in inter-individual range in age and estimated size at maturity in the models in order to accurately describe and understand the complex relationships among age, growth rate, size, and age at maturity (Frazer and Ehrhart 1985; Stearns 1992).

Individual variations are due to complex interactions between genotype and environmental conditions (Andrews 1982; Dunham and Gibbons 1990; Madsen and Shine 1993; Berrigan and Charnov 1994), notably in ectotherms that exhibit considerable phenotypic plasticity (Andrews 1982; Bonnet et al. 2001). The benefit for individuals of maturing early is usually manifested through an increase in survivorship (by diminishing random mortality before maturity) and by an augmentation of the number of reproductive episodes, at least in iteroparous species (Lewontin 1965; Hamilton 1966). However, the magnitude of such a benefit depends on the life-history pattern, notably the relationship between age and size at maturity; the advantage of early maturity can be balanced if fecundity (and adult survival) is positively influenced by size as is often observed in animals with indeterminate growth (Stearns 1992).

Stearns and Koella (1986) described four models relating age and size at sexual maturity. In turtles, few studies have been carried out in this field; however, enough data are available to make preliminary comparisons. Female *Emydoidea blandingii* that had slower growth rates matured later at similar mean body size to those with more rapid growth rates, and this pattern seems to be applicable to many species (Congdon and van Loben Sels 1993). Nevertheless, *T. horsfieldi* represents Stearns and Koella's fourth model, which states that individuals that grew slowly delayed maturity and were the larger adults in the population. Such a pattern should occur when juvenile mortality is growth-rate-dependent (Stearns and Koella 1986), which is typically the case in species exhibiting an extended juvenile phase such as tortoises (Iverson 1990; Shine and Iverson 1995). In female *T. horsfieldi*, the loss of early reproduction may well be balanced by a large body size at maturity and a subsequent higher fecundity per reproductive bout because these two

traits are positively correlated (Henen et al. 2000). Similarly, tardy males are larger than precocious ones and may have an advantage during ritual fights (Auffenberg 1977; Cagle 1950; Niblick et al. 1994; F. Lagarde, personal observation). They may also prospect and survey their territory more efficiently (Gibbons and Lovich 1990). Alternatively, males that grow rapidly and mature early may benefit from the low maintenance requirements of small body size. In ectotherms, the field metabolic rate is lower in small individuals than larger ones (Wikelski et al. 1997). In addition, such energy savings can be invested in mate searching or maintenance (Gibbons and Lovich 1990), promoting reproduction and survival (Wikelski and Thom 2000). This benefit may be very important for male *T. horsfieldi* because annual activity (3.5 months) is strongly constrained by the harsh environment.

Our results suggest the existence of a continuum between two individual tactics in growth rate and maturation patterns. In many ectotherm animals, low food quality and (or) availability entails delayed maturity and small body size at maturity. However, a reduction of environmental temperatures (and hence annual activity) entails a delayed maturity but a larger body size at maturity (Berrigan and Charnov 1994; Sinervo and Adolph 1994). Our data fit well with the second scenario. The Uzbek continental climate limits the annual activity period of *T. horsfieldi* to only 3 months. Within this 3-month period, ambient temperatures fluctuate strongly each day (from -10 to $+45^{\circ}\text{C}$), further limiting activity to a total of 360 h per year. Consequently, steppe tortoises can exploit trophic resources only during 16% of the full food-availability period. In our population, steppe tortoises are clearly more constrained by unfavourable environmental temperatures than by food availability.

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