Sexual body size and body shape dimorphism of *Testudo hermanni* in central and eastern Serbia

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Abstract. Hermann's tortoise (*Testudo hermanni*) is widely distributed in western and southern Europe. Most populations in the western part of the distribution range (e.g. Spain, France, Italy) are severely reduced, and relatively well studied, whilst the species is still abundant in eastern areas (i.e. the Balkans). However, essential biological information (e.g. main morphological, ecological, and behavioural characteristics) for the Balkans are still extremely limited. As reptiles exhibit strong geographic variation in most morphological, as well as life history traits, gathering data from distant areas is important. We present data from two populations of *T. hermanni* in Serbia, focusing on sexual dimorphism in body size and body shape. We found that almost all of the 43 morphological traits analysed were significantly different between sexes and that sexual size and sexual shape dimorphisms were not expressed in similar ways. Notably, sexual size dimorphism (SSD) was more pronounced than sexual shape dimorphism (SShD). Our analyses suggested that SShD is more stable than SSD, and that the scale of the focus (i.e. whole body proportions versus morphological details) is a key factor to test this notion. When general measurements were considered, the expected consistency of SShD between populations was verified; nevertheless, when more specific morphological attributes were considered, substantial variations were observed. These results provide a baseline for comparisons between populations to further examine geographic variation of sexual dimorphism.

Keywords: morphology, sexual dimorphism, *Testudo hermanni boettgeri*.

Introduction

Most species exhibit geographic variation among distant populations, and this variation, partly induced by environmental factors, has often an adaptive value (DeWitt and Scheiner, 2004). Among vertebrates, reptiles display pronounced physiological, behavioural and morphological phenotypic plasticity and flexibility (i.e. environmentally induced phenotypic variations) (Bonnet et al., 2001a; Zera and Harshman, 2001; Aubret, Bonnet and Shine, 2007); marked inter-individual and inter-population variations have been documented for almost all life history traits (Hailey and Willemsen, 2000; Niewiarowski, Angilletta and Leaché, 2004; Shine, 2005). Such variability and flexibility are key biological factors that must be taken into account to better understand evolutionary processes, and to assess population viability in a context of rapid environmental changes. Therefore, it is important to examine life history variation over large geographic scales, at least for species characterized by large distribution ranges. We studied sexual dimorphism in eastern populations of a widely distributed but threatened species, the Hermann's tortoise (*Testudo hermanni*).

Sexual dimorphism is usually explained as the result of divergent reproductive roles between the sexes. Males and females differ in the benefits and costs associated with the respective attributes (morphological structures, physiology and behaviour) involved in resources acquisition/allocation processes, mating strategy, gamete and offspring production (e.g. Fairbairn, 1997). Sexual dimorphism can also emerge as

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a result of intersexual niche divergence (Shine, 1989; Fairbairn, 1997). Both types of processes (niche divergence versus sexual selection) can generate complex life history trait patterns, and disentangling their influences is often a challenging task (Bonnet et al., 2011). In chelonians, the direction and the degree of sexual size dimorphism are influenced by various factors such as life style, habitat, reproductive and mating system (Berry and Shine, 1980; Dodd, 1997; Bonnet et al., 2001b, 2010; Willemsen and Hailey, 2003; Loehr, Henen and Hofmeyr, 2006). Selective pressures can act in the same or in the opposite directions, and, for instance, sexual size dimorphism (SSD) can be male- or female-biased. Such instability in the direction of SSD has notably been documented between chelonian species of the *Testudo* genus (Willemsen and Hailey, 2003; Ben Kaddour et al., 2008; Gosnell, Rivera and Blob, 2009).

Disregarding the differences in body size per se and focusing on body proportions, some morphological traits are usually more developed in one sex than in the other, a phenomenon referred to as sexual shape dimorphism, SShD (Bonnet et al., 1998, 2001b). In contrast to SSD, sexual body shape dimorphism appears to be more consistent and systematically oriented in the same direction across lineages (Bonnet et al., 2001b, 2010; Ben Kaddour et al., 2008). Several traits, such as the greater relative shell volume of females compared to males, have been explained in the light of selective forces that shape the respective morphology of females and males: fecundity selection in females versus sexual selection (male to male competition) in males (e.g. Bonnet et al., 2001b, 2010; Willemsen and Hailey, 2003; Ben Kaddour et al., 2008).

Sexual dimorphism in body size and body shape of *Testudo hermanni* was thoroughly investigated in Greek populations (Willemsen and Hailey, 2003). It has been shown that the direction of SSD was consistent among different populations from Greece; but that mean body size values varied substantially, suggest-

ing a strong influence of environmental factors on growth rate and other life history traits (Willemsen and Hailey, 1999). Unfortunately, comparable data from other parts of the distribution range are lacking. The most recent studies in neighbouring countries were conducted more than 30 years ago, but they were restricted to few basic morphological data (Meek, 1984, 1985). The goal of the present study was to extend the geographic area and the list of morphological characteristics in order to better describe geographic variation (or lack of variation) in the direction and degree of both sexual size and sexual shape dimorphism. We studied two populations of *T. hermanni boettgeri* from the central Balkan Peninsula (i.e. Serbia). Because Serbia represents one the northernmost parts of the distribution range of this subspecies, we expected some particularities in morphometric features compared to the populations in the central and southern parts of the distribution area. We hypothesized that although absolute body size and SSD may differ between populations (due to variations in food availability for instance), SShD should be relatively stable, because the respective forces acting on each sex should not strongly diverge between populations. In addition, we aimed to put emphasis on prosperous populations of this threatened species (Filippi et al., 2010). The rationale for such additional objective is that there is little chance to protect populations that would remain otherwise unknown whilst well-studied populations have greater chances to attract attention and protection.

Materials and methods

Study species

The Hermann's tortoise, *Testudo hermanni* is a medium-sized (adult size about 20 cm) species, with females typically being larger than males (Vetter, 2006). Its natural distribution range is large; it includes Mediterranean areas of France, the Iberian, Apennine, and Balkan Peninsulas, some islands in the surrounding seas, as well as the European part of Turkey (Gasc et al., 1997; Türkozan et al., 2005). On the Balkans it is found south of the Danube River (Arnold and

Ovenden, 2002). The activity period extends from March to October-November, with variations between localities (Vetter, 2006). Mating occurs throughout the activity period, but is usually more frequently observed in spring (March-May), and to a lesser extent in autumn (August–September; Vetter, 2006). In Greece, however, the most intensive courtship activity was recorded in autumn (Willemsen and Hailey, 2003). Sex ratio is generally skewed, but in variable direction across populations, either towards males or towards females (Hailey, 1990; Hailey and Willemsen, 2000). Such remarkable variation between populations could be the result of differential recruitment, mortality, and growth rates, as well as the consequence of differential incubation temperature regimes due to divergent nesting site selection for instance (Dalrymple, Hampp and Wellins, 1985; Hailey, 1990; Dodd Jr., 1997; Janzen and Morjan, 2001).

Study sites and sampling

Although Serbia shelters large populations of this species, no studies have been conducted in this area yet. We sampled two populations of *T. hermanni* from Serbia. Our first study site is located near the city of Trstenik in central Serbia (43°37′N, 21°0′E, elevation 170 m). Trstenik lies in the valley of the Zapadna Morava River, which is surrounded by (largely inhabited) hills, mostly covered with deciduous forests, with patches of conifer plantations, and meadows. This site was visited from the end of May until the beginning of July 2009. The measurements were recorded directly in the field; all the animals were permanently marked using a code of notches on the marginal scales, and immediately released at the place of capture (Stubbs et al., 1984). According to meteorological data for June 2008, average daily temperature was 20.1°C (with the extremes of 10.5°C and 35.5°C), and total precipitation 93.9 mm.

The second study site is situated in the vicinity of the city of Aleksinac in eastern Serbia (43°33′N, 21°41′E, elevation 180 m). Climate data for June 2008: average daily temperature 22.6°C, min. 12.2°C, max. 36.2°C; total precipitation 15.8 mm. The tortoises from this area were legally collected, with the permission of the Ministry of Environment of the Republic of Serbia, to constitute the officially declared parent "herd" to produce juveniles which then can be used in the pet trade. Animals were collected in May 2008, and brought to the farm near Novi Sad (northern Serbia). Therefore, the adult individuals measured were the only representatives of the wild populations, and are not ment for selling or export. We used this opportunity to obtain morphological data, and we measured the captive adult tortoises shortly after their capture in autumn 2008.

In both populations, we focused on adult tortoises. In some reptile species differences between the sexes are set at birth (e.g. Tomović et al., 2010), but determining the sex of juvenile tortoises is often impossible (Burke et al., 1994; Eendebak, 1995; Hailey, 2000). In *Testudo hermanii*, the sex is recognisable in individuals larger than 10 cm straight carapace length (SCL) (Hailey, 1990). We included only individuals where the sex was accurately determined, and for the assignment of the animals to adult category we used threshold values of 13 cm SCL for males and 15 cm

SCL for females, respectively (see Hailey, 2000). Gender was determined on the basis of shell shape and tail size: males have concave plastron, wider anal notch, more curved supracaudal scute(s), and longer tail (with a long horny "claw" on the tip) than females (Willemsen and Hailey, 2003). We processed a total of 260 adults (150 females and 110 males): 162 animals from central Serbia (100 females and 62 males) and 98 animals from eastern Serbia (50 females and 48 males).

Morphological measurements

To describe body size and body shape, and to enable comparisons with other studies, we recorded general morphological traits (i.e. measurements describing the overall dimensions of the shell) used in previous studies on SSD and SShD (e.g. Bonnet et al., 2001b; Carretero et al., 2005): straight carapace length (SCL, straight line from the front edge of the nuchal plate to the rear supracaudal edge – or to the tangent when the supracaudal is curved); curved carapace length (CCL, from the anterior tip of nuchal to the posterior tip of supracaudal); mid-body carapace width (MCW, straight width of the carapace, at the level of the 6th marginals); maximal carapace width (MaxCW, width of the carapace at the widest point, usually at the level of the 8th marginals); curved carapace width (CCW, width of the carapace at the level of the 6th marginals, between the sutures of the carapacial and plastral horny plates); midline plastron length (MPL, length of the plastron along the midline, from the notch between gular plates to the notch formed by anal plates); maximal plastron length (MaxPL, length of the plastron from the tips of gulars to the tips of anals); plastron width at the level of the 6th marginals (PW6); maximal plastron width (MaxPW); total longitudinal circumference (TLC, perimeter of a shell along the longer axis); mid-body circumference (MBC, perimeter of a shell along the shorter axis, at the level of the 6th marginals); shell height (SH) and body mass (BM).

General morphological traits not directly determined by the shell (head, limbs, tail) were measured as follow: forelimb length, left and right (FLL-L, FLL-R, length of the front limbs, from elbow to palm); hind limb length, left and right (HLL-L, HLL-R, length of the hind limb, from knee to foot); head length (HL, from the tip of the snout to the rear edge of the jaw); skull length (SL); head width (HW) and head height (HH), and tail length (TL, from the anterior edge of cloaca to the tip of the tail).

In the current study, we recorded additional traits to better assess the shape of the shell, notably several traits that contribute to the shape of specific body, and shell parts (some of them have also been used in previous studies). We measured: anal notch width (ANW, distance between the tips of anal plates); analia to supracaudalia junction (ASJ, distance between the suture of the anals and the tip of supracaudal); the width of the 2nd, 3rd and 4th vertebral plate (WV2, WV3, WV4); posterior shell height (SHP, distance from the point of cross-junction of anals and femorals, to the front edge of an initial, hatchling scute on the 5th vertebral plate; see fig. 1); horizontal distances from the tangent to supracaudal(s) to the four points on the 5th vertebral
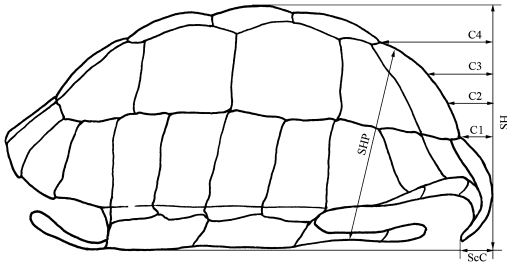
Figure 1. New measurements on *T. hermanni* shell: C1-C4 – estimators of the 5th vertebral plate curviness; ScC – curviness of the supracaudal plate; SHP – posterior height of the shell.

plate (C1, C2, C3 and C4, see fig. 1); supracaudal curviness (ScC, from the tangent to supracaudal(s) to its tip; fig. 1); plastron concavity (PC); lengths of all midline sutures between plastral plates: gulars (GSL), humerals (HSL), pectorals (PSL), abdominals (AbSL), femorals (FSL) and anals (AnSL); bridge length, left and right (BL-L, BL-R), and claw length (CL, length of the horny "claw" on the tip of the tail).

Linear measurements were taken by a calliper (precision 0.02 mm), and curvilinear dimensions by a flexible measuring tape (precision 1 mm); body mass was measured with a digital scale (precision 1 g). All the measurements were performed by the same person (S.D.), to limit undesirable variation in the measurements.

Analyses

Each individual was represented in the data set only once (no recapture included). Importantly, our investigations were limited to the direction and degree of SSD and SShD for various (often correlated) morphological traits. Therefore, we did not use integrative measurements of body size or body shape. Indeed, using a single descriptor of body size (e.g. via PCA) precludes the possibility to examine (notably subtle) differences in body shape between the sexes, which is in opposition to our objectives. More sophisticated methods using landmarks on the shell (Stayton, 2009) are extremely valuable and powerful, but unfortunately time consuming, not routinely applicable in the field, and not appropriate for large numbers. Overall, for our purposes we relied on classical ANOVAs and ANCOVAs (with sex as factor). We therefore adopted a straightforward approach to analyse SSD and to examine, for instance, if a given size-corrected morphological trait was sexually divergent or not (SShD). We used straight carapace length (SCL) as a covariate to control for body size for most measurements, and several other covariates for other body dimensions. For instance, for head width, we used head length as a covariate (see results for other covariates). Substantial size overlapping between the sexes enabled us to use linear models straightforwardly to perform comparisons between the sexes (Barron, 1997). All the tests were performed using Statistica 5.1. The direction and the degree of sexual dimorphism were calculated according to Willemsen and Hailey (2003).

Our relatively comprehensive set of measurements could have generated some inflation of the results. Consequently, for several analyses of SShD where multiple comparisons were possible through the use of different co-variables, we adopted a step by step approach, notably to present the results in the tables. We firstly examined the general shape of the shell (i.e. carapace and plastron) as well as free body parts (head, limbs and tail). Secondly, we examined the dimensions of several more specific elements of the carapace and of the plastron. We made, for instance, the distinction between straight carapace length (SCL) that serves as a broad descriptor of the longitudinal dimension of the carapace versus the width of separate vertebral plates (i.e. WV2, WV3, WV4) or supracaudal curviness (ScC), that represent only small parts of the shell. Such distinction in the analyses was fundamental for two reasons. Firstly, a substantial modification of one part of the shell, e.g. the length of abdominal plates, can be profoundly divergent between the sexes (see Results), without affecting deeply the overall dimension of the plastron. Therefore, the exact questions that can be addressed using midline plastron length versus the length of individual plastral plates are not equivalent: they are intended either towards the specific role of one plate or towards the general role of the whole plastron. Secondly, a subtle modification of the proportion of the carapace or of the plastron can affect differently each separate element. Typically, it could be envisaged that a modest increase (i.e. less than 1%) in the length of the shell relative to shell width may affect specifically few front shell-bones (and hence only few partly overlapping plates), generating strong variations on few plates only (i.e. more than 50%), whilst the plates of the rear part of the shell remain unaffected. Consequently, we distinguished the results related to overall dimensions of the tortoises (carapace, plastron, head, limbs, and tail) from the detailed dimensions of the various plates we measured.

Results

Sexual size dimorphism

Considering absolute values, females were larger than males for almost all traits in both populations (tables 1a and 1b). Reverse patterns were observed in some specific traits: anal notch width (ANW), supracaudal curviness (ScC), plastron concavity (PC), tail length (TL) and claw length (CL). For several traits, we did not find any significant differences between the sexes: length of the suture between femoral plates (FSL, in both populations), head length (HL, population from the eastern Serbia) and the 4th point of the 5th vertebral scute curviness measurements set (C4, population from the central Serbia) (table 1b).

Table 1a. Descriptive statistics (mean, sample size, SD; measurements in mm) of the general morphological traits of male and female Hermann's tortoises from central (Trstenik) and eastern Serbia (Aleksinac) (ANOVA with sex as the factor, larger sex indicated in boldface, all P < 0.001). The abbreviations are the same as in the text.

	General measurements of the shell and body			
	Population 1 (Trstenik)		Population 2 (Aleksinac)	
	Females (*n* = 100)	Males (*n* = 62)	Females (*n* = 50)	Males (*n* = 48)
Trait	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Shell				
SCL	**199.2 ± 13.5**	167.1 ± 14.0	**215.8 ± 11.2**	187.5 ± 8.9
CCL	**251.8 ± 14.7**	223.9 ± 17.2	**266.6 ± 13.7**	248.2 ± 13.3
MCW	**147.4 ± 8.2**	131.7 ± 10.5	**156.7 ± 7.9**	143.7 ± 7.6
MaxCW	**159.7 ± 10.2**	147.3 ± 14.1	**167.3 ± 8.0**	159.9 ± 9.3
CCW	**262.7 ± 13.7**	226.5 ± 17.5	**280.5 ± 15.2**	250.3 ± 12.7
MPL	**162.7 ± 9.3**	124.8 ± 8.8	**173.9 ± 8.3**	138.2 ± 6.2
MaxPL	**179.7 ± 10.3**	143.4 ± 10.7	**192.3 ± 9.1**	157.1 ± 7.6
PW6	**130.2 ± 8.0**	118.8 ± 10.1	**138.1 ± 7.0**	128.7 ± 6.4
MaxPW	**134.8 ± 8.1**	124.6 ± 11.2	**142.1 ± 7.0**	134.5 ± 7.0
TLC	**493.8 ± 29.4**	420.3 ± 33.1	**531.1 ± 25.6**	466.9 ± 20.9
MBC	**399.3 ± 20.7**	354.2 ± 27.5	**424.6 ± 20.7**	386.5 ± 18.8
SH	**97.2 ± 5.4**	81.8 ± 5.8	**105.1 ± 6.2**	90.5 ± 4.8
BM	**1586.5 ± 262.0**	1027.9 ± 228.7	**1866.7 ± 249.8**	1288.9 ± 152.5
Limbs				
FLL-L	**46.5 ± 2.8**	43.4 ± 4.0	**50.9 ± 2.9**	48.6 ± 2.7
FLL-R	**46.5 ± 3.1**	43.4 ± 3.9	**50.6 ± 3.2**	48.3 ± 2.8
HLL-L	**56.0 ± 3.3**	51.4 ± 4.8	**60.2 ± 3.0**	56.7 ± 2.9
HLL-R	**55.9 ± 3.2**	51.3 ± 4.6	**60.4 ± 3.0**	57.1 ± 2.8
Head				
HL	**32.3 ± 1.5**	30.9 ± 2.1	**34.1 ± 1.7**	33.5 ± 1.8
SL	**26.2 ± 1.7**	24.9 ± 1.8	**26.7 ± 2.0**	25.9 ± 1.5
HW	**27.3 ± 1.4**	25.8 ± 1.9	**28.7 ± 1.2**	27.8 ± 1.4
HH	**21.0 ± 1.1**	20.0 ± 1.3	**22.3 ± 1.0**	21.6 ± 1.0
Tail				
TL	34.0 ± 5.0	**50.2 ± 7.4**	32.9 ± 5.4	**55.1 ± 5.9**

Sexual dimorphism in body shape

In both populations, size corrected body traits (ANCOVAs with SCL as covariate) showed that broadly half of the traits examined were relatively larger in females and half were larger in males (tables 2a and 2b). For instance, the following traits were relatively larger in one sex: mid-body (MCW) and maximal carapace width (MaxCW), plastron width at the level of 6th marginal plates (PW6), maximal plastron width (MaxPW), anal notch width (ANW), front and hind limbs (FLL, HLL), plastron concavity (PC), head and tail dimensions, and curviness of the supracaudal plate (ScC). Using other covariates, we detected additional differences between the sexes (sometimes in the opposite direction compared to the results obtained with SCL as the covariate), for instance, in head proportions or relative dimensions of the limbs (tables 2a and 2b).

Consequently, a somewhat complex situation aroused from the examination of the multiple possible comparisons (tables 1 and 2). However, focusing on the general dimensions of the tortoises, general trends were apparent both considering SSD and SShD.

General trends in SSD and SShD

1) Females were larger in absolute size, but they were not relatively heavier.
2) Males exhibited relatively greater rims around their shell. For instance, males

Table 1b. Descriptive statistics (mean, sample size, SD; measurements in mm) of the specific traits analysed of male and female Hermann's tortoises from central (Trstenik) and eastern Serbia (Aleksinac) (ANOVA with sex as the factor, larger sex indicated in boldface, all P < 0.05). The abbreviations are the same as in the text.

	Specific measurements of the shell and body			
	Population 1 (Trstenik)		Population 2 (Aleksinac)	
	Females ($n = 100$)	Males ($n = 62$)	Females ($n = 50$)	Males ($n = 48$)
Trait	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Shell				
ANW	39.7 ± 3.9	**54.5 ± 6.3**	41.2 ± 4.8	**58.8 ± 4.4**
ASJ	**33.4 ± 6.0**	31.4 ± 5.0	**39.1 ± 4.6**	35.3 ± 3.7
WV2	**39.7 ± 2.8**	33.0 ± 2.2	**41.7 ± 3.6**	36.0 ± 2.0
WV3	**45.9 ± 3.5**	37.1 ± 2.9	**49.3 ± 4.0**	40.3 ± 2.5
WV4	**40.1 ± 3.4**	36.3 ± 3.3	**43.2 ± 4.3**	39.4 ± 3.1
SHP	**69.4 ± 4.3**	64.5 ± 6.1	**76.5 ± 3.3**	72.6 ± 3.2
C1	**14.7 ± 4.6**	10.1 ± 2.8	**18.5 ± 4.0**	12.5 ± 2.7
C2	**21.9 ± 5.3**	17.2 ± 4.0	**27.7 ± 4.4**	21.2 ± 3.3
C3	**29.8 ± 5.9**	25.7 ± 4.8	**37.1 ± 5.2**	31.1 ± 3.9
C4	41.2 ± 6.8	38.7 ± 6.9	49.8 ± 5.5	46.7 ± 5.0
ScC	0.6 ± 1.3	**8.3 ± 2.9**	0.1 ± 0.4	**8.7 ± 2.7**
PC	1.4 ± 1.2	**5.6 ± 1.4**	1.7 ± 1.4	**6.1 ± 1.4**
GSL	**24.7 ± 2.5**	20.3 ± 3.5	**26.8 ± 2.2**	22.6 ± 2.3
HSL	**26.2 ± 2.5**	22.1 ± 2.3	**28.2 ± 2.8**	24.2 ± 3.0
PSL	**12.6 ± 2.1**	9.9 ± 2.2	**13.9 ± 2.5**	11.3 ± 2.0
AbSL	**59.7 ± 4.5**	42.6 ± 3.8	**61.7 ± 6.5**	45.8 ± 4.5
FSL	11.0 ± 2.3	10.4 ± 2.2	13.4 ± 2.2	12.5 ± 2.5
AnSL	**25.2 ± 3.0**	16.0 ± 1.6	**25.9 ± 3.6**	17.5 ± 2.1
BL-L	**85.5 ± 5.3**	60.8 ± 4.1	**91.6 ± 6.1**	66.6 ± 3.8
BL-R	**84.8 ± 5.0**	60.7 ± 4.1	**91.0 ± 6.0**	66.7 ± 3.3
Tail				
CL	11.2 ± 2.4	**16.0 ± 3.2**	11.6 ± 2.3	**15.8 ± 4.0**

had an almost skirt-like posterior part of the carapace, due to the lateral extensions of their marginal scales and, particularly, longer supracaudal scale. Overall, this contributed to relatively greater maximal width (MaxCW) and curvilinear length of the shell (CCL) of males.

3) Female shells were relatively higher than the males', suggesting a more voluminous shell in this sex.

4) Male shells were more open, due to a relative reduction of the plastron associated with its deeper indentations: for example, both bridges and plastron length (midline and maximal) were longer in females (absolutely and controlled for SCL), but the anal notch width was substantially greater in males.

5) Males had relatively longer limbs.

6) Males exhibited relatively larger head.

We also observed several pronounced, although more specific differences between the sexes. For example, males exhibited more concave plastron and longer tail claw. On the other hand, females had substantially larger abdominal and anal sutures lengths.

Considering SSD and SShD, we generally observed:

a) Strong SSD: the divergences in body size between the sexes were often pronounced. The average values of the degree of sexual dimorphism (Willemsen and Hailey, 2003) were 36.8 and 30.0 for central (Trstenik) and eastern Serbia (Aleksinac), respectively.

b) Small SShD in the general morphology: the divergences between the sexes in the general body proportions were often

Table 2a. Comparisons of size-corrected general body traits (body shape) of female and male Hermann's tortoises from central (Trstenik) and eastern Serbia (Aleksinac) (ANCOVA with sex as the factor, larger sex is in boldface, all P < 0.05). The abbreviations are the same as indicated in the text.

General traits		Adjusted means			
		Population 1 (Trstenik)		Population 2 (Aleksinac)	
Trait	Covariate	F	M	F	M
Shell shape					
CCL	SCL	235.0	**241.5**	249.7	**264.6**
CCL	TLC	233.3	**242.4**	249.7	**265.1**
MCW	SCL	137.8	**141.3**	148.3	151.8
MaxCW	SCL	147.9	**159.9**	156.9	**169.7**
MaxCW	MCW	150.5	**156.5**	161.4	**165.8**
CCW	SCL	**247.3**	242.3	264.0	266.1
TLC	SCL	458.9	456.0	499.1	498.0
MBC	SCL	374.5	379.2	400.9	**409.3**
SH	SCL	**91.8**	87.3	**99.2**	96.3
Openings					
MPL	SCL	**153.2**	134.3	**165.3**	146.4
MPL	MaxPL	**147.6**	140.1	**160.2**	151.8
MaxPL	SCL	**168.3**	154.6	**181.8**	167.2
PW6	SCL	121.0	**127.9**	130.8	**135.8**
MaxPW	SCL	125.2	**134.3**	134.5	**141.8**
Body condition					
BM	SCL	1321.4	1293.2	1606.6	1540.9
BM	MCW	**1389.3**	1225.1	**1720.7**	1434.9
BM	TLC	1305.6	1308.8	1606.2	1549.4
Head proportions					
HL	SCL	30.8	**32.4**	33.0	**34.6**
SL	SCL	25.0	**26.1**	25.7	26.9
HW	SCL	25.8	**27.3**	27.4	**29.0**
HH	SCL	19.9	**21.1**	21.4	**22.3**
HW	HL	**26.8**	26.3	**28.5**	27.9
Limb proportions					
FLL-L	SCL	43.4	**46.6**	48.4	**51.1**
FLL-R	SCL	43.3	**46.8**	47.6	**51.3**
HLL-L	SCL	52.4	**55.2**	57.1	**59.8**
HLL-R	SCL	52.6	**54.9**	57.6	**59.9**
HLL-L	FLL-L	**54.5**	53.0	**59.4**	57.6
HLL-R	FLL-R	**54.5**	52.7	**59.7**	57.8
Tail size					
TL	SCL	29.6	**54.9**	29.1	**58.7**

small. The average values of the degree of general sexual shape dimorphism were −4.0 and −4.2 for central (Trstenik) and eastern Serbia (Aleksinac), respectively, albeit oriented in the same direction between populations.

c) Strong SShD for specific traits: focusing on specific traits, we observed strong sexual divergences. The average values of the degree of specific sexual shape dimor-

phism were −11.0 and −7.6 for central (Trstenik) and eastern Serbia (Aleksinac), respectively.

Direction and the degree of sexual dimorphisms: comparisons with previous studies

Body size dimorphism (SSD). We found that both the degree and the direction of SSD were

Table 2b. ANCOVA results (covariates specified) – comparison of size-corrected specific body measurements (body shape descriptors) of females and males from central (Trstenik) and eastern Serbia (Aleksinac) (higher values are in boldface when significant). All the results are significant at P < 0.05. The abbreviations are the same as indicated in the text.

Specific traits		Adjusted means			
		Population 1 (Trstenik)		Population 2 (Aleksinac)	
Trait	Covariate	F	M	F	M
ANW	SCL	36.9	**57.5**	39.5	**60.4**
ANW	MaxPL	35.1	**59.2**	38.5	**61.4**
ASJ	SCL	28.5	**36.2**	36.2	38.1
ASJ	MaxPL	28.2	**36.6**	37.1	37.3
WV2	SCL	**37.6**	35.1	39.4	38.3
WV3	SCL	**42.9**	40.2	**46.3**	43.3
WV4	SCL	37.11	**39.2**	39.8	**42.6**
SHP	SCL	64.8	**68.9**	73.2	**75.8**
C1	SCL	11.6	**13.4**	15.9	15.1
C2	SCL	17.9	**21.5**	24.6	24.4
C3	SCL	25.0	**30.9**	33.6	34.6
C4	SCL	34.8	**45.6**	45.0	**51.3**
ScC	SCL	0.5	**8.5**	−0.3	**9.1**
PC	SCL	0.9	**6.1**	1.3	**6.5**
GSL	SCL	22.9	22.1	**26.1**	23.3
HSL	SCL	**25.3**	23.1	26.3	26.1
PSL	SCL	**12.0**	10.7	**13.5**	11.7
AbSL	SCL	**55.7**	46.2	**56.8**	50.6
FSL	SCL	10.4	11.2	12.9	13.1
AnSL	SCL	**24.0**	17.2	**25.0**	18.3
BL-L	SCL	**80.4**	65.8	**86.3**	71.8
BL-R	SCL	**79.8**	65.5	**85.6**	72.0
CL	SCL	9.7	**17.7**	10.0	**17.5**

variable across populations in *T. hermanni* (table 3). The same trend was observed in *T. hermanni* in Greece, and *T. graeca* in Greece and Morocco. Indeed, the mean values of the main descriptors of body size (straight carapace length and body mass) were highly variable between populations and between the sexes (table 3).

Body shape dimorphism (SShD). The basic descriptors of body shape (general morphological traits) varied modestly between the studied populations, and always in the same direction (table 3).

Specific body shape measurements. Sexual divergences in specific traits were marked and highly variable between populations. However, similar trends in the direction of sexual dimorphism were apparent in *T. hermanni* in Greece, and *T. graeca* in Greece and Morocco (table 3).

Discussion

Our results are consistent with previously published analyses focusing on sexual dimorphism of the *Testudo* genus (Willemsen and Hailey, 1999; Bonnet et al., 2001b; Lagarde et al., 2001, 2003; Willemsen and Hailey, 2003; Ben Kaddour et al., 2008). However, our data (more than 40 traits measured) provided a more comprehensive description of the morphology than previously available ones, enabling us to better assess the generality and subtleties of the sexual dimorphism patterns (Gosnell, Rivera and Blob, 2009).

We sorted out, for the first time, general measurements of the body shape from specific, localised morphological traits. Our main findings reinforce the notion proposed a decade ago which suggested that SSD is likely more variable than SShD (Bonnet et al., 2001b); but our

Table 3. Comparison of the degree and direction of sexual dimorphism in two populations of *T. hermanni* from Serbia (calculated as 100((female − male)/male), Willemsen and Hailey, 2003) and other populations of *T. hermanni* and *T. graeca*. Results for size are means from ANOVA (sex as factor), and for shape are adjusted means from ANCOVA (sex as factor, SCL as covariate).

	T. hermanni central Serbia (Trstenik) (this study)	*T. hermanni* eastern Serbia (Aleksinac) (this study)	*T. hermanni* Greece (Willemsen and Hailey, 2003)	*T. graeca* Greece (Willemsen and Hailey, 2003)	*T. graeca* Morocco (Ben Kaddour et al., 2008)	*T. graeca* Morocco 1 (Carretero et al., 2005)	*T. graeca* Morocco 2 (Carretero et al., 2005)	*T. graeca* Morocco 3 (Carretero et al., 2005)
Size								
SCL	+19.2	+15.1	+10.8	+9.2	+17.7	/	/	/
BM	+54.3	+44.8	+36.5	+32.4	+82.1	/	/	/
Shape – general measurements								
CCL	−2.7	−5.6	−3.3	−9.2	−0.6	+16.0	+2.3	+1.4
MCW	−2.5	−2.3	−3.5	+2.0	+3.8	+9.3	+6.1	+6.6
MaxCW	−7.5	−7.5	−8.1	−1.3	+0.8	+10.8	+3.8	+4.0
CCW	+2.1	−0.8	/	/	/	/	/	/
MPL	+14.1	+12.9	+14.0	+6.7	+5.8	+11.2	+13.6	+11.9
MaxPL	+8.9	+8.7	/	/	+4.1	+12.7	+11.2	+9.3
PW6	−5.4	−3.7	/	/	/	/	/	/
MaxPW	−6.8	−5.1	/	/	/	+10.3	+6.4	+6.0
TLC	+0.6	+0.2	/	/	/	/	/	/
MBC	−1.2	−2.1	/	/	/	/	/	/
SH	+5.2	+3.0	+2.1	+3.6	+5.4	+12.7	+9.9	+7.8
FLL-L	−6.9	−5.3	/	/	/	/	/	/
FLL-R	−7.5	−7.2	/	/	/	/	/	/
HLL-L	−5.1	−4.5	/	/	/	/	/	/
HLL-R	−4.2	−3.8	/	/	/	/	/	/
TL	−46.1	−50.4	/	/	/	/	/	/
HL	−4.9	−4.6	/	/	/	/	/	/
SL	−4.2	−4.5	/	/	/	/	/	/
HW	−5.5	−5.5	/	/	/	/	/	/
HH	−5.7	−4.0	/	/	/	/	/	/
BM	+2.2	+4.3	+5.9	+8.9	+12.0	+2.4	+2.7	+4.9

Table 3. (Continued).

	T. hermanni central Serbia (Trstenik) (this study)	T. hermanni eastern Serbia (Aleksinac) (this study)	T. hermanni Greece (Willemsen and Hailey, 2003)	T. graeca Greece (Willemsen and Hailey, 2003)	T. graeca Morocco (Ben Kaddour et al., 2008)	T. graeca Morocco 1 (Carretero et al., 2005)	T. graeca Morocco 2 (Carretero et al., 2005)	T. graeca Morocco 3 (Carretero et al., 2005)
				Shape – specific measurements				
ANW	−35.8	−34.6	−35.9	−25.6	−20.7	+20.4	−19.2	−18.9
ASJ	−21.3	−5.0	/	/	−29.5	/	/	/
WV2	+7.1	+2.9	+8.7	+8.8	/	/	/	/
WV3	+6.7	+6.9	+10.1	+4.2	/	−3.5	+13.9	+15.0
WV4	−5.4	−6.6	−1.0	+3.6	/	/	/	/
SHP	−6.0	−3.4	/	/	/	/	/	/
C1	−13.4	+5.3	/	/	/	/	/	/
C2	−16.7	+0.8	/	/	/	/	/	/
C3	−19.1	−2.9	/	/	/	/	/	/
C4	−23.7	−12.3	/	/	/	/	/	/
ScC	−94.1	−103.3	/	/	/	/	/	/
PC	−85.2	−80.0	/	/	/	/	/	/
GSL	+3.6	+12.0	/	/	/	+18.0	+3.0	+0.9
HSL	+9.5	+0.8	/	/	/	/	/	/
PSL	+12.1	+15.4	+19.5	−2.8	/	/	/	/
AbSL	+20.6	+12.3	/	/	/	/	/	/
FSL	−7.1	−1.5	−1.6	+2.8	/	/	/	/
AnSL	+39.5	+36.6	/	/	/	/	/	/
BL-L	+22.2	+20.2	/	/	/	/	/	/
BL-R	+21.8	+18.9	/	/	/	/	/	/
CL	−45.2	−42.9	/	/	/	/	/	/

analyses also suggest that the scale of the focus is a key factor to test this notion. When general measurements are considered, the consistency of SShD between populations seems to be verified; however, when more specific morphological attributes are considered, important variations are observed. The effect exerted by selective forces on general body proportions might well be more canalised compared to the effect on more specific morphological traits. For instance, the sex divergence in the relative width of the shell of the tortoises should be more constrained compared to sex divergence in the relative shape of the supracaudal plate. Such differences in the responsiveness of general traits (e.g. body proportion) relative to more specific traits (e.g. supracaudal curviness) are expected. Indeed, the consequences of the putative modification of a single terminal plate, even pronounced, are physiologically modest compared to an important modification of the whole proportions of the body. The same notion may apply considering body size, a trait more flexible in response to environmental factors than general body proportions.

Chelonians continue to grow after reaching sexual maturity (e.g. Germano, 1992; Willemsen and Hailey, 2001). Under favourable environmental conditions (food availability, ambient temperatures), individuals can grow rapidly, whilst unfavourable conditions limit body size and entail a cessation of growth. However, males and females are not subjected to identical reproductive selective forces (Dodd, 1997; Willemsen and Hailey, 2003; Vetter, 2006). For instance, population density can profoundly influence competition between males, and thus body size within this sex (larger individuals may have an advantage in male-to-male encounters; Berry and Shine, 1980), whilst such factor is less important for females. Population density may thus affect SSD, generating various situations where large males (high density and high occurrence of ritual combats) or small males (low density promotes mobility) are respectively advantaged. Therefore we expect impor-

tant inter-individual and inter-population differences in the expression of body size and consequently in SSD. On the other hand, there are no environmental variables yet identified that may strongly alter the general body plan of one sex specifically under different conditions, thereby generating highly variable SShD patterns between populations. Overall, this means that general body size measurements and specific sexually dimorphic shape traits should be more variable compared to the sex differences in general body proportions (broad body shape). We propose to take into account the fundamental difference between general proportions versus specific traits to further study SShD.

In both studied populations, mean body size (SCL), and hence absolute dimensions of most traits, were larger in females, but the related sex differences were important and variable. However, several traits showed higher average absolute values in males (a fortiori when scaled by size). Greater male plastron concavity, wider anal notch width, greater tail length, longer tail claw and marked supracaudal curviness have been previously documented in this species, and in fact these traits are used to determine sex (e.g. Willemsen and Hailey, 2003). Greater concavity of the male plastron seems to facilitate mounting and help maintaining the balance over the domed carapace of the females (Moskovits, 1988; Willemsen and Hailey, 2003). Our data enable us to add relative lengths of the sutures of the certain plastral plates (i.e. abdominals and anals) to the list of sexually divergent traits. Shorter anal plate sutures (with substantially larger ANW) may contribute to larger space available for the movements of the tail during copulation, and may be another result of sexual selection in males (Brophy, 2006). On the contrary, greater value of abdominal sutures length in females could indicate larger volume of abdominal cavity, which provides more space for the eggs (fecundity selection). These results suggest that several specific traits are under strong sexual selection in males. A long, mobile, but well protected tail, along with a con-

cave plastron may well promote sperm transfer. The tail, the surrounding parts of the carapace and of the plastron are likely shaped to enhance mating success in males. These specific elements of the morphology are likely highly variable among species and populations, depending upon the mating strategy, population density and sex ratio. Although we cannot test this hypothesis yet, the results we presented in this paper (high variability in the tail-related traits) provide a preliminary basis. In females, we did not identify any specific morphological trait that could be under similar selection; as a possible result, females always exhibited a compact morphology.

Relative dimensions of the head (controlled for SCL) were larger in males. This can be explained by the role of the head in courting displays or male to male interactions in tortoise species (Hailey, 1990; Bonnet et al., 2001b; Willemsen and Hailey, 2003; Mann, O'Riain and Hofmeyr, 2006). On the other hand, females had relatively wider heads (controlled for HL), which can be explained by the importance of the bite force for feeding efficiency (Bonnet et al., 2001b; Bulté et al., 2008b). Therefore, the observed pattern could be the result of the effects of sexual selection in males versus fecundity selection in females (Bonnet et al., 2001b; Bulté et al., 2008a, b).

Importantly, the degree (percentage) of such differences in general body shape between males and females differed significantly but slightly between the two studied populations from Serbia, whilst the divergences were more marked for SSD and for specific morphological traits (table 3). This observation also applies when comparing other populations of *T. hermanni* and of *T. graeca* (table 3), and it conforms to the conclusions proposed using additional species, *T. marginata* and *T. horsfieldii* (Bonnet et al., 2001b; Willemsen and Hailey, 2003; Mann, O'Riain and Hofmeyr, 2006; Ben Kaddour et al., 2008).

Our main conclusion is that although the direction of SShD is likely very stable across populations and species, whilst SSD is more variable (review in Ben Kaddour et al., 2008), the intensity of SShD varies depending upon the scale of observation. The direction of SShD is predictable (relatively invariable) for most traits, notably for the general body organisation (Bonnet et al., 1998), and this notion may apply also for more specific traits. In terms of intensity of SShD, the issue is more complex, however. Sex divergences in the general body proportions and body plans are likely less variable compared to more specific sexually dimorphic traits, such as ornamentations, weapons or structures that confer, for instance, a specific advantage for copulation (horns, antlers, caudal structures, claws...). For example, the more developed musculature of males relative to females typically belong to the general, relatively invariable body plan (Bonnet et al., 1998), whilst the antlers, tusks, canines in some male mammals, or clawed tail of male Hermann's tortoises, belong to the highly variable specific morphological trait category. Further studies are needed to test such hypotheses.

Finally, this paper presents the first data on sexual dimorphism of *T. hermanni* in the central part of the Balkan Peninsula. We included some measurements that have not been recorded in previous studies. The lack of comprehensive data in tortoise morphology, and thus the necessity to provide more descriptive data to perform thorough comparisons has been recently emphasised by Litzgus and Smith (2010). In accordance, our analyses enabled us to propose new directions to study sexual dimorphism in chelonians (and in other taxa). Notably, to better explore the links between geographic variation of morphology in relation to population structure (sex ratio, density...), behaviour, mating strategy and environmental resources (food, temperature, habitat...), we propose to take into account the variability of SSD and SShD both in terms of general body proportions and of specific morphological structures. We also suggest that field studies are essential to set up conservation plans through a better understanding of the

ecological characteristics of still healthy populations, and by bringing attention to them.

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