

Morphological divergence among populations of *Testudo graeca* from west-central Morocco

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Abstract—Morphometric analyses were carried out on *Testudo graeca* from west-central Morocco, and compared to previously published mitochondrial DNA sequence variation. We measured 41 characters on 244 tortoises from three localities, including one population of *T. g. soussensis* from Souss Valley. All three populations could be statistically differentiated in a multivariate space using these characters. The population from the Jbilet mountains was the most differentiated (no overlap), those from Essaouira on the coast and from Admine showed limited overlap (5%). Sexual size dimorphism (males < females) remained constant between sites. Sexual shape dimorphism was prominent in all populations, but the degree of dimorphism differed for some characters when corrected for size. Tortoises from Jbilet living under harsher conditions (low precipitation, high thermal amplitude, low plant cover) were smaller, lighter, more flattened and less dimorphic in shape than the others. Although the Admine population (currently assigned to *T. g. soussensis*) was morphologically distinct, its distinctiveness was less supported than in the case of Jbilet; several other qualitative traits previously considered as defining this subspecies were also questionable. Moreover, this morphological variation contrasted with the available genetic evidence (12S rRNA mtDNA) which did not reveal significant variation between any of the populations. This implies that morphological differences have either arisen very recently or can be attributed to phenotypic plasticity. This should be taken into account when using morphological traits for taxonomic considerations and conservation management.

Keywords: body shape; body size; geographic variation; Morocco; sexual dimorphism; *Testudo graeca*; tortoises.

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INTRODUCTION

Testudo graeca L., the Mediterranean spur-thighed tortoise, inhabits a vast area across the Mediterranean region, and also the semi-arid plains of Turkey and Iran, usually associated with dry, open scrub (Iverson, 1992). *Testudo graeca graeca*, the Moorish tortoise, is native to North Africa from Morocco through Algeria and Tunisia to Libya (Schleich et al., 1996). Populations also exist in southwest Spain and several Mediterranean islands, although these have probably been introduced (Álvarez et al., 2000). In Morocco an additional subspecies, *T. g. soussensis*, has recently been described from the Souss Valley based on scutellation and some relative measures and qualitative morphological characters (Pieh, 2000).

Testudo g. graeca occurs in a variety of different habitats in Morocco, from the seacoasts and the edges of the Sahara desert up to 2000 m above sea level in the High Atlas mountains (Bons and Geniez, 1996). Populations are declining in the majority of habitats, partly due to extensive collection for the pet and tortoise-derived souvenir trade to tourists (Highfield and Bayley, 2003), and also due to habitat destruction as a result of agricultural intensification, overgrazing, and deforestation (Bayley and Highfield, 1996). Because of this, *T. g. graeca* is officially considered to be globally threatened, and is listed in Annex II of the Washington Convention and considered 'vulnerable' by the CITES (Baillie and Groombridge, 1996). A precise assessment of variation within Moroccan populations is particularly needed as large numbers are still illegally exported to Europe each year (Highfield and Bayley, 2003). Some of those impounded by customs officials are then returned to Morocco (Álvarez, 2001). This could have a huge effect on local populations if these are genetically substructured or if there are morphological differences due to adaptations to local environment. A detailed assessment of morphological variation is also essential to determine the variation that is typical within genetically distinct lineages. Historically, taxonomic units have been described purely based on morphological differences. However, tortoises are known to be extremely variable (Germano, 1993; Packard et al., 1999), and so there is considerable debate as to which forms should be recognised as species or subspecies. Our aim was to compare morphological variation between and within accepted subspecies in west-central Morocco, where genetic variation has already been assessed through sequencing of the mitochondrial 12S rRNA gene (Harris et al., 2003).

Several hypotheses for explaining morphological variation and sexual dimorphism in *Testudo* based on the combined actions of natural and sexual selections have been recently proposed. Previous studies analysed the shape and size variation between species (Willemsen and Hailey, 2003, for *T. hermanni*, *T. graeca iberica* and *T. marginata*), the size variation between populations of the same species (Willemsen and Hailey, 1999, 2001, 2002, for the same three species) or the size and shape variation within the same population (Bonnet et al., 2001; Lagarde et al., 2001, for *T. horsfieldii*). However, shape variations between populations of the same species have remained ignored. Thus, an additional aim was to test whether these general

predictions were also applicable to *T. graeca graeca* and whether they could explain the inter-population variation found in Morocco.

We chose three populations to be analysed; these included two very different habitats for *T. g. graeca*: i) an inland population living in an area with low plant cover and hard substrate, and ii) a coastal population inhabiting sand dunes; and also iii) a population assigned to *T. g. soussensis*. Differences in growth patterns and asymptotic sizes between these populations have been recorded although sexual size dimorphism (SSD) remained constant between them (Znari et al., in press). In this paper, we specifically tested 1) if body shape (carapace morphology) changed with locality; 2) if there was any sexual shape dimorphism (SShD); and 3) if SShD varied among populations.

We hypothesise that open areas, especially if combined with dominant hard substrates, will provide less shelter and food, leading to less dense populations of tortoises. On the other hand, extreme climates may not limit population size but will reduce time available for activity and growth of tortoises. Thus, we would expect that the relative contributions of natural selection and sexual selection to the morphology of *T. graeca* would change between localities depending on environmental conditions (i.e., climate and habitat).

METHODS

We collected 244 adult tortoises from three widely separated populations in southwest Morocco (fig. 1): the Central Jbilet Mountains ($n = 82$), the Admine Forest ($n = 70$) and Essaouira ($n = 92$). Jbilet is a hilly area located 25 km north of Marrakech at 560 m a.s.l. The climate is arid with typically temperate winters (Le Houerou, 1989). Annual precipitation averages 242 mm but amounts vary widely from year to year. Continental influences result in extreme thermal amplitude (0°C in January to 39°C in July). Substrate is dominated by rocks (schists) with separated spaces of superficial sand; vegetal cover is scarce (see Znari et al., 2000). Admine is a region of low relief bordering the Chtoucka Plain in the Souss Valley, 30 km east of Agadir. Climate is arid with warm winters (Le Houerou, 1989). Mean annual precipitation (239 mm) is similar to Jbilet but thermal amplitude is more moderate due to the Atlantic influence (12°C in January to 31°C in July). Mature soils alternate with deposits of Aeolian sands, and abundant aquifers provide water supply for vegetation dominated by Argan forest with bushes in the most open, sandy areas. In the last 50 years, important sections of forest have been destroyed by overgrazing (Mellado, 1989), and many open areas transformed into irrigated cultures (Bailey and Highfield, 1996) creating a patchy habitat. Finally, Essaouira is a coastal locality approximately 150 km north of Admine. The climate is semi-arid with warm winters (Le Houerou, 1989). Mean annual rainfall is slightly higher than the other two localities (270 mm) and thermal amplitude reaches the lowest value in Morocco (25°C in July to $>10^{\circ}\text{C}$ in January) (Bons and Geniez, 1996). The col-

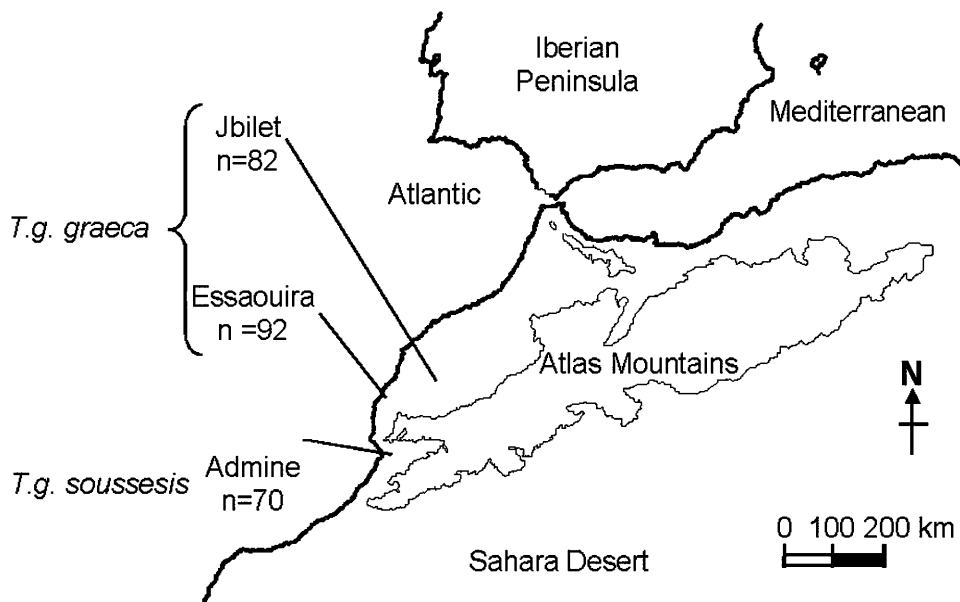


Figure 1. Location of the three study sites in Morocco.

lection site is a coastal dune area dominated by loose sands and covered by sparse psammophilic vegetation.

All tortoises were collected by hand between mid-May and early July and immediately transported to the laboratory in Marrakech for measurement. Body weight was recorded to the nearest 0.1 g, and 41 carapace measures were taken to the nearest 0.1 mm with dial callipers (fig. 2). After processing, tortoises were returned to where they were caught.

Discriminant Analysis (using the forward stepwise procedure, tolerance = 0.005) and Canonical Variate Analysis on regression residuals of each variable against carapace length were used to derive a matrix of Mahalanobis distances that allows comparison of overall sexual dimorphism between localities (Rohlf and Bookstein, 1987; McArdle, 1988; LaBarbera, 1989; Tome, 2001; but see Monteiro et al., 2000, for a non-linear approach) and production of an MDS (Multidimensional Scaling, Kruskal and Wish, 1989) plot of localities and sexes. Multiple analysis of variance (MANOVA) was used to compare overall morphological variation between localities and sexes in the same way, entering carapace length as a covariate and the other variables as dependent. Those not entering in the forward stepwise process were excluded.

For each variable, analysis of covariance (ANCOVA) with locality and sex as factors was used to determine shape variation with carapace length as a covariate in order to correct by size. A significant effect of locality would indicate that shape differs among populations (both sexes). Similarly, a significant effect of sex (all localities) would be indicative of SShD. Finally, if interaction between both factors

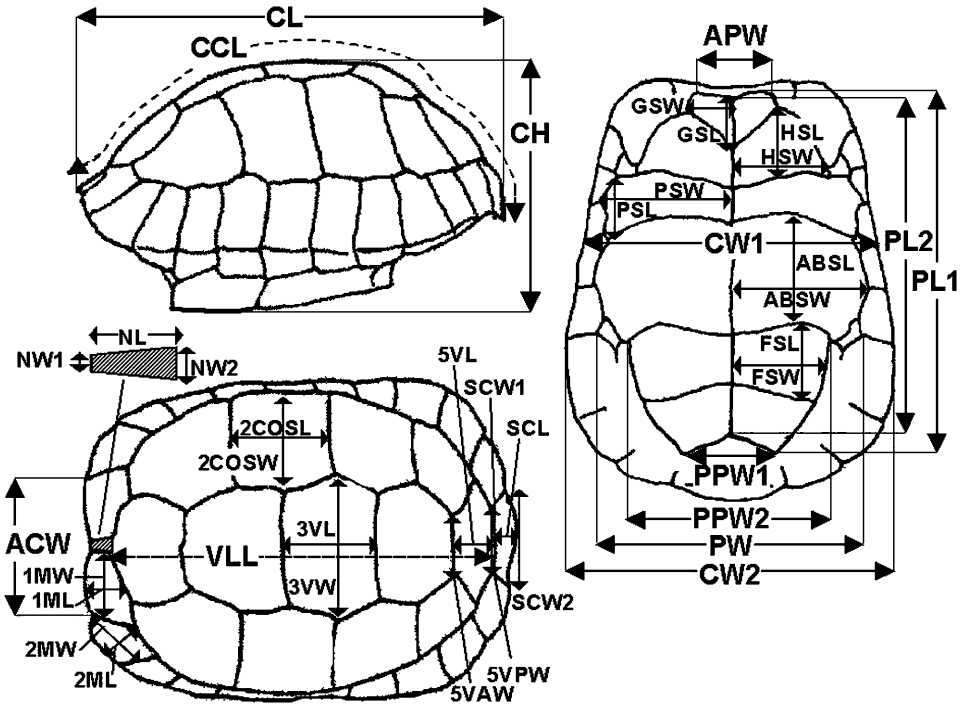


Figure 2. Diagram showing the morphometric variables measured in the specimens of *Testudo graeca* from Morocco. CL: greatest carapace straight length; BW: body weight; CCL: greatest curvilinear carapace length; CW1: medial carapace width; ACW: anterior carapace width (between the right and left seams between the first and the second marginal scutes); CW2: greatest carapace width; PL1: greatest plastron length (from the tip of the right gular scute to that of the right anal scute); PL2: medial plastron length (the medial seam length of all plastral scutes); PW: greatest plastron width (at the level of the seam between pectoral and abdominal plastral scutes); APW: greatest width of the anterior plastral lobe; PPW1: posterior plastron width between the tips of anal scutes; CH: carapace height (at the level of the seam between vertebrals 2 and 3); VLL: vertebral curvilinear length (the medial line across all the five vertebral scutes); NW1: shortest width of nuchal scute; NW2: greatest width of nuchal scute; NL: greatest nuchal scute length; 3VL: third vertebral scute length; 3VW: third vertebral scute width; 5VAW: fifth vertebral scute anterior width; 5VPW: fifth vertebral scute posterior width; 5VL: fifth vertebral scute length; SCW1: shortest width of supra-caudal scute; SCW2: greatest width of supra-caudal scute; SCL: medial length of the supra-caudal scute; 2COSL: second costal scute length; 2COSW: second costal scute width; 1ML: first marginal scute length; 1MW: first marginal scute width; 2ML: second marginal scute length; 2MW: second marginal scute width; PPW2: greatest width of the posterior plastral lobe; GSL: greatest length of gular scute; GSW: greatest width of gular scute; HSL: greatest length of humeral scute; HSW: greatest width of humeral scute; PSL: greatest length of pectoral scute; PSW: greatest width of pectoral scute; ABSL: greatest length of abdominal scute; ABSW: greatest width of abdominal scute; FSL: greatest length of femoral scute; FSW: greatest width of femoral scute.

were significant, then SShD varied between populations (McCoy et al., 1994). When significant, Scheffé's post hoc tests were performed to determine which groups were different. Variables were log-transformed and normality and homocedasticity were assessed prior to the analyses.

RESULTS

Variables APW, VLL, 5VPW, 1MW, GSW, HSL and ABSW were excluded in the forward stepwise procedure of Discriminant Analysis. Multivariate comparisons using the rest of the size-corrected variables revealed overall shape variation between localities and sexes as well as interaction between these two factors (MANCOVA, locality Wilk's $\lambda_{66,320} = 0.13$, $P < 0.0001$; sex Wilk's $\lambda_{33,160} = 0.34$, $P < 0.0001$; locality*sex Wilk's $\lambda_{66,320} = 0.21$, $P < 0.0001$). Percentages of correct classification of discriminant functions using shape variables were high (males: 100% from Jbilet, 91% from Admine and 95% from Essaouira; females: 100% from Jbilet and Essaouira and 95% from Admine). Consequently, there was no overlap in Jbilet and just a small amount of overlap between Admine and Essaouira (fig. 3). Overall SShD was lower in Jbilet than in Admine and Essaouira (table 1). In the last two localities, SShD was greater than site variation whereas the opposite occurred in Jbilet, which was the most distinct population (fig. 4).

Carapace length of the tortoises was smaller in Jbilet than in Admine and Essaouira but these two populations were not different from each other (see appendix). Females were about 20% larger than males but SSD did not differ significantly between localities (Jbilet 21.5%, Admine 21.1%, Essaouira 17.5%; table 2). An analysis restricted to the ten biggest individuals of each population and sex provided the same results (2-way ANOVA, site $F_{2,54} = 111.47$, $P < 0.0001$; sex $F_{1,54} = 488.16$, $P < 0.0001$; site*sex $F_{2,54} = 2.20$, $P = 0.12$). Females were also heavier than males of the same size and differences between the three localities in relative weight were found for both sexes, Admine population being intermediate in relative weight between Jbilet and Essaouira (Scheffé's post hoc tests, $P < 0.05$).

After size correction (ANCOVA), all variables except ACW, NW1 and NW2 proved to be sexually dimorphic at least in one locality and all except NW1 and NW2 differed between localities ($P < 0.01$ in all cases, see appendix). Of the former, APW, PPW1, NL, 3VL, 3VW, 5VAW, SCW2, SCL, PSL, FSL and FSW also showed changes in SShD with locality ($P < 0.001$). In others (CCL, 5VL, 2COSL, 1ML, 2ML, 2MW, GSL and GSW) site variation in SShD was also significant when considered isolately ($P < 0.05$) but it would not be if tests were to be evaluated simultaneously and Bonferroni correction applied.

The most evident shape variation affected the curvilinearity of the carapace (expressed as the relative CCL vs. CL). Females were more domed than males in all three populations, specimens from Jbilet were more plated than those in the other two localities and, interestingly, SShD for this character was much more accentuated in this locality (16% in Jbilet vs. 2.3% and 1.4% in Admine and Essaouira, respectively; see table 2). Vertebral curvilinear length (VLL) followed a similar pattern although differences were less marked (table 2).

Medial and greatest widths of the carapace (CW1 and CW2), indicating the roundness of the rear half of the body, were relatively larger in females than in males. In contrast, the anterior width of the carapace (ACW) did not show SShD

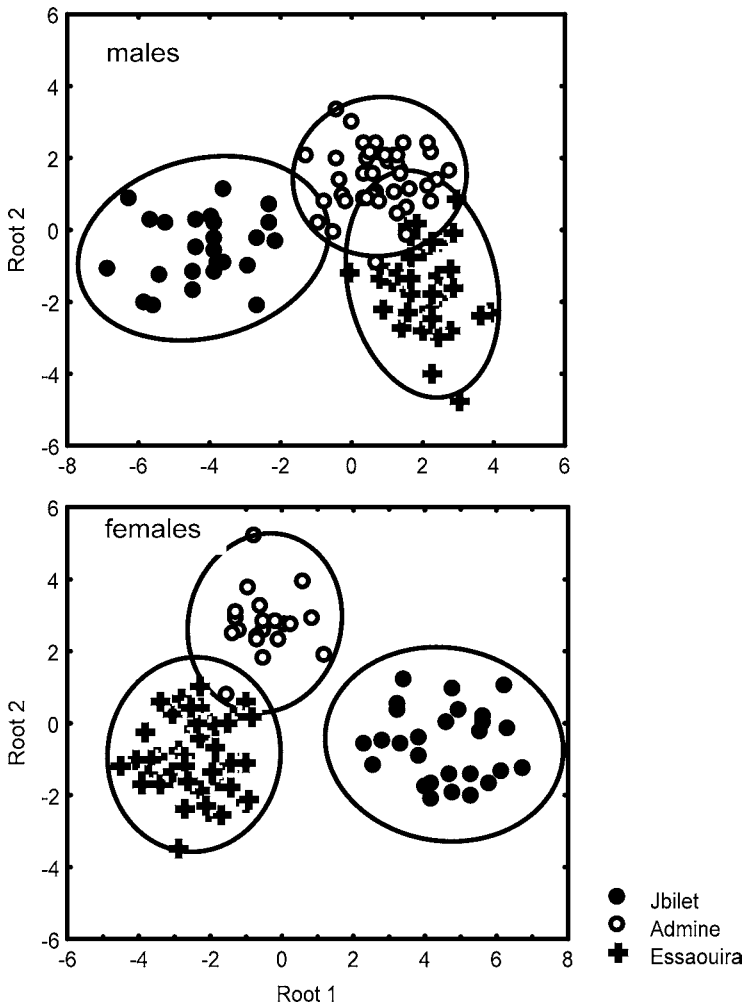


Figure 3. Results of the canonical analyses of morphometric variables (size-corrected) of *Testudo graeca* from Morocco performed separately for each sex.

Table 1.

Mahalanobis distances in carapace shape (size corrected) between the populations and sexes of *Testudo graeca* from Morocco; in bold distances indicating sexual shape dimorphism (SShD).

	Jbilet males	Jbilet females	Admine males	Admine females	Essaouira males
Jbilet females	10.50				
Admine males	33.37	20.54			
Admine females	26.61	34.99	34.44		
Essaouira males	25.72	17.22	9.95	34.09	
Essaouira females	25.99	34.04	41.41	8.93	27.98

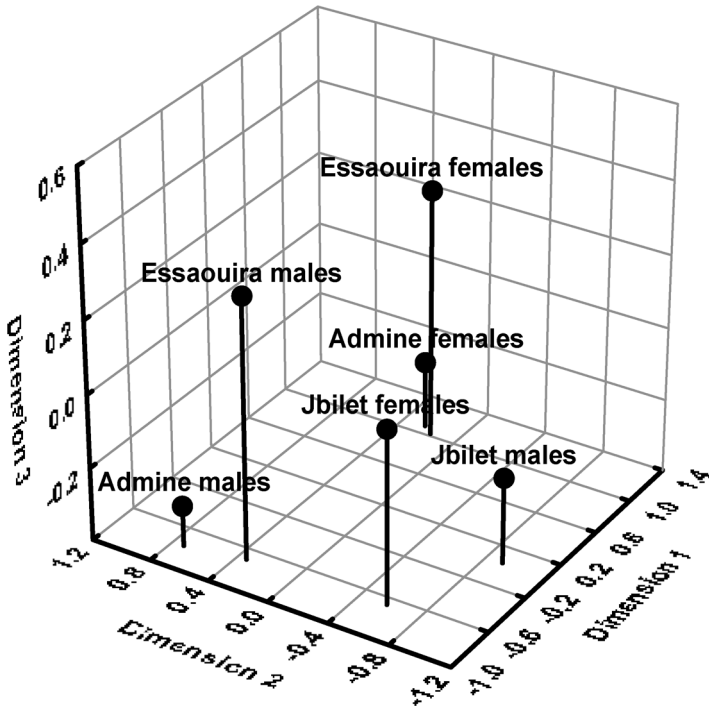


Figure 4. MDS tridimensional plot based on the Mahalanobis distances between localities and sexes of *Testudo graeca* from Morocco in table 2. Stress <math>< 10^{-6}</math>.

(table 2). For all three measures, Jbilet tortoises were less rounded than the others (Scheffé's post hoc tests, $P < 0.05$) but SShD did not differ between localities.

Plastron measures (PL1, PL2, PW and PPW2) also showed SShD (males with shorter and narrower plastron than females) and site variation (Jbilet individuals with smaller plastron than the others) but not any interaction between them. Anterior and posterior plastral lobes (APW and PPW1) were significantly narrower in males than in females but just in Jbilet; in both sexes both measures were lower in Jbilet than in Admine and Essaouira (Scheffé's post hoc tests, $P < 0.05$).

Carapace height (CH), reflecting both domed carapace and bellied plastron, also showed site variation and SShD but no interaction; males and Jbilet specimens carrying relatively lower carapaces (Scheffé's post hoc tests, $P < 0.05$).

Regarding the remaining scutellation characters; all showed site variation (with Jbilet being significantly lower than the other sites) and could be classified into several groups depending on the pattern of SShD. The first contained those variables with constant SShD favourable to females (5VPW, 2COSL, 2COSW, 1MW, 2MW, GSL, HSL, HSW, PSW, ABSL, ABSW, FSL); the second included those variables showing significant SShD only in Jbilet (NL, 5VL, SCW1, SCW2, SCL); the third grouped those variables with significant SShD in Admine and Essaouira but not in Jbilet (3VL, 3VW, PSL, FSW); the fourth included those variables showing SShD

Table 2.

Adjusted means of the morphometric variables by the carapace length for the three populations of *T. graeca* from Morocco analysed separated by sexes. The percentage of sexual dimorphism is calculated as $100*((\text{female}-\text{male})/\text{male})$.

	Jbilet		Admine		Essaouira		% sexual dimorphism		
	males	females	males	females	males	females	Jbilet	Admine	Essaouira
BW	609.0	623.4	624.3	641.2	635.8	666.7	2.4	2.7	4.9
CCL	134.3	155.7	194.0	198.4	194.1	196.7	16.0	2.3	1.4
CW1	79.9	87.3	106.2	112.7	104.1	111.0	9.3	6.1	6.6
ACW	31.4	34.7	40.6	41.5	40.8	40.7	10.6	2.1	-0.2
CW2	81.1	89.9	112.3	116.6	108.9	113.3	10.8	3.8	4.0
PL1	94.7	106.7	130.0	144.5	127.2	139.0	12.7	11.2	9.3
PL2	87.4	97.2	118.3	134.4	116.1	129.9	11.2	13.6	11.9
PW	72.6	80.1	96.9	103.1	96.3	102.0	10.3	6.4	6.0
APW	20.7	22.6	26.6	25.5	25.2	24.6	9.2	-3.9	-2.1
PPW1	25.3	30.5	41.8	33.8	40.5	32.8	20.4	-19.2	-18.9
CH	56.4	63.5	74.5	81.8	74.4	80.3	12.7	9.9	7.8
VLL	107.7	121.5	147.8	159.9	148.4	157.6	12.7	8.2	6.2
NW1	2.8	3.1	3.0	3.1	2.9	3.1	10.3	3.2	6.9
NW2	4.1	4.4	5.0	5.3	4.8	5.4	8.7	7.0	11.8
NL	8.3	10.4	11.7	11.0	13.1	11.9	25.5	-6.0	-8.6
3VL	23.7	22.1	26.3	30.6	27.7	31.8	-6.6	16.3	14.9
3VW	36.1	34.8	41.5	47.3	40.4	46.4	-3.5	13.9	15.0
5VAW	13.3	15.8	22.8	20.7	20.4	21.0	18.4	-9.3	2.9
5VPW	30.2	34.2	43.0	46.3	43.6	44.0	13.3	7.6	1.0
5VL	21.7	24.4	34.1	33.3	33.4	32.3	12.2	-2.2	-3.4
SCW1	15.4	17.6	23.0	24.2	22.0	22.0	14.4	5.3	0.1
SCW2	25.7	31.7	44.0	38.7	41.6	36.5	23.3	-12.0	-12.3
SCL	15.0	19.5	28.1	22.5	26.5	22.6	30.5	-20.0	-14.7
2COSL	21.2	22.1	25.5	30.3	26.7	31.2	4.5	18.9	16.8
2COSW	33.0	35.7	41.7	44.9	42.6	46.3	8.3	7.6	8.5
1ML	15.8	18.3	23.2	22.8	22.3	22.9	16.0	-2.1	2.9
1MW	14.9	16.7	20.0	20.3	19.7	20.1	11.9	1.3	1.7
2ML	16.4	18.9	24.4	24.0	24.2	24.6	15.5	-1.7	1.5
2MW	16.6	19.0	23.6	23.8	23.6	23.8	14.6	0.8	0.7
PPW2	68.8	73.2	92.3	98.8	90.5	95.3	6.4	7.0	5.3
GSL	12.1	14.2	18.5	19.1	18.4	18.6	18.0	3.0	0.9
GSW	10.6	11.6	13.5	13.0	13.0	13.1	9.3	-3.8	0.3
HSL	14.0	16.0	19.5	21.3	19.1	20.1	14.8	8.9	5.4
HSW	26.1	29.4	35.6	36.6	34.3	36.2	12.7	2.9	5.7
PSL	8.8	7.5	10.4	12.9	10.0	11.7	-15.1	23.7	17.5
PSW	35.4	39.4	47.3	51.2	46.3	49.4	11.5	8.2	6.8
ABSL	31.2	34.6	41.1	47.9	41.9	47.2	10.8	16.6	12.6
ABSW	11.4	12.7	15.4	15.4	15.2	15.6	12.2	0.4	3.1
FSL	24.7	27.3	33.8	37.0	32.5	36.1	10.6	9.6	11.2
FSW	12.0	12.9	14.9	20.0	13.6	19.0	7.5	34.6	40.4

in Jbilet and Essaouira but not in Admine (5VAW, 2ML, GSW); and, finally, the fifth with one variable showing SShD in Jbilet and Admine but not in Essaouira (1ML).

DISCUSSION

Natural and sexual selection

Hypotheses put forward to explain SSD and SShD in reptiles include sexual selection (Shine, 1978; Berry and Shine, 1980; Anderson and Vitt, 1990) and natural selection including selection for fecundity (Bonnet et al., 1997; Olsson et al., 2002), and resource partitioning between sexes (Herrel et al., 1999; Andersson, 1994; Shine et al., 2002). Shell morphology of Moroccan *Testudo graeca* clearly showed both SSD and SShD. Most of our results agree with the predictions already demonstrated in other tortoises of genus *Testudo* (Bonnet et al., 2001; Willemsen and Hailey, 2003), namely that shell morphology derives from a balance between natural and sexual selection. Natural selection constrains shell size and shape, enhancing survivorship in both sexes and increasing reproductive output in females; and sexual selection 'designs' male and female shells assuring successful mating with partners (Bonnet et al., 2001; Willemsen and Hailey, 2003). In the absence of other selective pressures, natural selection will promote large females and hence increase fecundity, whereas sexual selection will promote small, mobile males for mate searching (Bonnet et al., 2001). However, this assumes that other factors, such as courtship behaviour (Willemsen and Hailey, 2003), population density (i.e., available partners and potential sexual competitors), duration of activity season or predation intensity should not show relevant differences between populations. We have no information on these parameters but we could make some new predictions at the intraspecific level based on the literature.

We have shown that females are larger than males for *T. graeca* in Morocco, similar to previous findings for *T. g. iberica*, *T. hermanni boetgeri* and *T. horsfieldii* but not for *T. marginata* (Lagarde et al., 2001; Willemsen and Hailey, 2003). The degree of SSD remained constant across populations in *T. graeca* from Morocco, which has also been found for *Testudo hermanni boetgeri* from Greece (Willemsen and Hailey, 1999) indicating short-term stability for this trait. However, the degree of SSD in Moroccan *T. graeca* (17-20%) is larger than in all other *Testudo* studied: *T. g. iberica* 9%, *T. hermanni boetgeri* 11%, *T. marginata* 2% (Willemsen and Hailey, 2003), and *T. horsfieldii* (sometimes placed in the separate genus *Agriomenys*, Khozatsky and Mlynarski, 1966) 2% (Bonnet et al., 2001).

Znari et al. (in press), studying the same Moroccan populations, concluded that growth trajectories in both sexes did not differ except in duration: females matured later than males and then reached larger asymptotic sizes. Similar results have been found in *T. hermanni* and *T. horsfieldii* (Willemsen and Hailey, 1999; Lagarde et al., 2001, respectively). Willemsen and Hailey (2003) showed that SSD was not scaled with female relative clutch mass in three Greek *Testudo* and found important intra-specific differences in male courtship behaviour. Thus, they concluded that sexual

selection in males was more important than selection for fecundity in females for developing SSD. We lack similar information for the Moroccan tortoises but relative clutch mass in a Spanish population of *T. g. graeca* (4.9%; Díaz-Paniagua et al., 1997) was similar to that in *T. g. ibera* (5.5%; Hailey and Loumbourdis, 1988). Tortoise size in Spain was similar to Admine and Essaouira but larger than Jbilet, and SSD was similar for all (Braza et al., 1981; Andreu et al., 2000). Therefore, assuming that courtship behaviour does not differ among populations of *T. graeca*, we suggest that that relative contribution of selection for fecundity to dimorphism in Iberian and Moroccan *T. graeca* would not differ from that reported for *T. g. iberica* in Greece.

General shape trends identified are also consistent with the same predictions. Although the same size, females were heavier, higher, more domed and rounded than males, and carapaces were enlarged posteriorly (but not anteriorly) as expected if a capacity for carrying eggs (i.e. fecundity) was favoured. It is noteworthy that these differences do not occur in *T. graeca graeca* (Willemsen and Hailey, 1999). On the other hand, small, concave plastrons of males facilitate mobility for mate searching, righting in eventual combats and copulation (Bonnet et al., 2001). Similar general shape patterns are found in other species of *Testudo* with low aggressive courtship behaviour and, unlike *T. g. ibera* and *T. hermanni*, not facing other strong environmental constraints (Willemsen and Hailey, 1999). However, SShD was large, affected different body parts and was even inverse in comparison with other species. *Testudo marginata*, which inhabits densely covered habitats and has males that bite competitors severely, lacks SSD and shows no sexual differences in doming (Willemsen and Hailey, 1999). *Testudo horsfieldii*, under extremely severe temporal and spatial constraints, showed a low degree of SShD with males more mobile, but more domed than females (Bonnet et al., 2001; Lagarde et al., 2002).

In an evolutionary context, patterns of SSD and SShD in *Testudo* were clearly homoplastic at the species level. *Testudo graeca* is morphologically closer to *T. hermanni* but different from the less dimorphic *T. marginata* and *T. horsfieldii*, whereas molecular analysis (van der Kuyl et al., 2002) indicates closer phylogenetic relationships between *T. graeca*-*T. marginata* and *T. hermanni*-*T. horsfieldii*, respectively.

Differences between populations

Differences between sexes in relative weight derive from the extra organs (follicles, eggs) contained in the body of females (Bonnet et al., 2001) but appear to be invariant between populations within each *Testudo* species (see above). In contrast, inter-population variation may be attributable to differences in body condition (Willemsen and Hailey, 2002). In our case, relative weight was scaled with precipitation and thermal amplitude for both sexes in the localities studied (Jbilet < Admine < Essaouira). In arid climates, primary production mainly depends on precipitation (Pianka, 1986) and thermal amplitude restricts periods available for trophic activity (long hibernation and aestivation have been recorded in Jbilet; Znari, pers. obs.). In fact, growth rate of juvenile tortoises was lower in Jbilet

than in Admine and Essaouira (Znari et al., in press). Furthermore, other sources of adult size variation (Jbilet < Admine = Essaouira), such as age distribution and longevity, were similar between localities (Znari et al., unpubl.). All this evidence strongly suggests that food (and water) supply constrains the ecology of juvenile and adult *T. graeca* in SW Morocco.

Digging ability is positively selected in tortoises living in open areas (Bonnet et al., 2001). The more flattened habitus of the carapace in Jbilet tortoises may improve penetration into the soil in habitats with very limited shelter, as in *T. horsfieldii* from the steppes of Uzbekistan (Bonnet et al., 2001). Nevertheless, SShD for this trait in Moroccan *T. graeca* was the opposite (and slightly more pronounced in Jbilet) of that found in *T. horsfieldii*. This can be due to different mating behaviour, rarely involving combat in *T. graeca* (Willemsen and Hailey, 2003).

Similarities of Jbilet population with *T. horsfieldii* also involved other characters. Nuchal and supra-caudal scutes were smaller and plastral lobes were narrower leaving wider openings for head and limbs in both sexes. It has been demonstrated that the size of shell openings is correlated with limb length and mobility (Bonnet et al., 2001). However, those traits were more dimorphic in Jbilet than in the other localities, which suggests that not only natural selection (i.e., movement between shelters, food search) but also other selective forces, acting differentially on both sexes, are present.

The adaptive value of other characters seems less obvious, namely, changes in relative size and shape as well as in dimorphism of scutes depending on the population (see results). Most variation derived secondarily from the domed carapace and enlarged openings following similar trends for the whole body. However, others could be non-adaptive and due to local variation (Willemsen and Hailey, 2002). When the combined effects of all factors are considered, a general picture of the morphological variation of Moroccan *T. graeca* arises: the three localities were different but Jbilet was especially distinct and overall dimorphism was marked but lower in this locality, as would be expected if natural selection were more important than in the other populations (Willemsen and Hailey, 2003).

In conclusion, evidence for *Testudo* suggests that SSD and SShD at the species level derive from sexual and natural selection and are not following phylogenetic relationships. Our results demonstrate that SSD in *T. graeca* remains stable at the species level but that SShD changes within species under similar pressures responding rapidly to selection. Hence, the method for analysing SShD for separate characters (Bonnet et al., 2001) seems applicable at intra-specific level.

Taxonomic implications

In our analysis, the Admine population currently assigned to *T. g. soussensis* was morphologically distinct in shape (but not in size) from Jbilet and Essaouira populations considered to belong to *T. g. graeca*. However, distinctive status is less supported by morphometric analysis for this population than for Jbilet. Pieh (2000)

separated *T. g. soussensis* from *T. g. graeca* based on lack of spurs, divided anal and the relative proportions of pectorals and vertebrae. However, these traits were questionable in the Admine population since just 23% of individuals lacked spurs, only 7% had a divided anal, and relative size of the third vertebral did not differ between Admine and Essaouira (see results). Similar differences have been found in regional populations of other tortoise species with no call for subspecific status (i.e., *Gopherus agassizii*, Germano, 1993).

On the other hand, morphological variation did not parallel the available genetic evidence based on partial 12S rRNA gene sequences (Harris et al., 2003) which do not support the distinction of *T. g. soussensis* and which reveal low divergence between Moroccan, Algerian and Iberian populations. It could be argued that morphological variation is still genetic but results from short-term evolution and thus is not recorded by mtDNA markers. If true, further analysis using more rapidly evolving genetic markers such as microsatellites should find geographically consistent genetic variation between populations (Harris et al., 2003). Alternatively, changes could be environmental resulting from a tortoise's phenotypic plasticity at the egg or juvenile stage (see reviews by Gotthard and Nylin, 1995; Via et al., 1995; for tortoises see Packard et al., 1999). Experiments involving cross-translocation or manipulation of the incubation environment have been applied successfully for testing similar hypothesis in other reptiles (Shine et al., 1997; Qualls and Shine, 1998, 2000) although the long generation time and the conservation problems involved would pose serious difficulties in this case.

Considering both the conflicting morphological evidence and the lack of genetic distinctiveness between the populations analysed, current intra-specific subdivision of *Testudo graeca* in Morocco must be regarded as unsatisfactory. In the near future, a parallel morphometric and genetic survey based on extensive sampling, including populations from other areas and living under different climate regimes, would help to clarify the status of this species not only in Morocco, but in the whole of North Africa.

Implications for conservation

Finally, ongoing conservation measures should take into account present results in the framework of the evolutionary significant unit (ESU) criteria (see review by Crandall et al., 2000). The studied populations showed almost no mtDNA differences (Harris et al., 2003), suggesting full genetic inter-changeability. However, their strong morphological differences involving clear functional implications make them non-interchangeable ecologically. Until information on other populations, geographically or ecologically intermediate, becomes available, these populations should be treated as separate conservation units independent of their taxonomic status (Crandall et al., 2000). The same principle may be applicable to other, similar, *Testudo* populations and no translocation or mixing of individuals should be recommended without both genetic and morphological assessment.

ACKNOWLEDGEMENTS

This work was funded by projects from Fundação para a Ciência e a Tecnologia, FCT (Portugal), SFRH/BPD/5702/2001 and POCTI/41912/BSE/2001 as well as by an ICCTI-CNCPRST international cooperation award (Portugal-Morocco). The comments of an anonymous reviewer contributed to improve the early draft of the manuscript.

REFERENCES

- Álvarez, A. (2001) Doscientas tortugas moras son devueltas a Marruecos. *Quercus*, 190, 19.
- Álvarez, Y., Mateo, J.A., Andreu, A.C., Díaz-Paniagua, C., Diez, A. & Bautista, J.M. (2000) Mitochondrial DNA haplotyping of *Testudo graeca* on both continental sides of the Straits of Gibraltar. *J. Hered.*, 91, 39-41.
- Andersson, M. (1994) Sexual size dimorphism. In: J.R. Krebs & T. Clutton-Brock (Eds.), *Sexual Selection. Monographs in Behaviour and Ecology*, pp. 246-293. Princeton University Press, Princeton, New Jersey.
- Anderson, R.A. & Vitt, L.J. (1990) Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia*, 84, 145-157.
- Andreu, A.C., Díaz-Paniagua, C. & Keller, K. (2000) *La Tortuga Mora (Testudo graeca L.) en Doñana. Monografías de Herpetología, vol. 5*. Asociación Herpetológica Española, Barcelona.
- Baillie, J. & Grommbridge, B. (Eds.) (1996) *1996 IUCN Red List of Threatened Animals*. IUCN Gland, Switzerland and Cambridge, UK.
- Bayley, J.R. & Highfield, A.C. (1996) Observations on ecological changes threatening a population of *Testudo graeca graeca* in the Souss Valley, Southern Morocco. *Chelonian Conserv. Biol.*, 2, 36-42.
- Berry, J.F. & Shine, R. (1980) Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia*, 44, 185-191.
- Bonnet, X., Lagarde, F., Henen, B.T., Corbin, J., Nagy, K.A., Naulleau, G., Balhoul, K., Chastel, O., Legrand, A. & Cambag, R. (2001) Sexual dimorphism in steppe tortoises (*Testudo horsfieldii*): influence of the environment and sexual selection on body shape and mobility. *Biol. J. Linn. Soc.*, 72, 357-372.
- Bonnet, X., Shine, R., Naulleau, G. & Vacher-Vallas, M. (1997) Sexual dimorphism in snakes: different reproductive roles favour different body plans. *Proc. R. Soc. Lond. B*, 265, 179-183.
- Bons, J. & Geniez, P. (1996) *Amphibians and Reptiles of Morocco*. Asociación Herpetológica Española, Barcelona.
- Braza, F., Delibes, M. & Castroviejo, J. (1981). Estudio biométrico y biológico de la tortuga mora (*Testudo graeca*) en la Reserva Biológica de Doñana, Huelva. *Doñana, Act. Vert.*, 8, 13-41.
- Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M. & Wayne, R.K. (2000) Considering evolutionary processes in conservation biology. *Tree* 15 (7), 290-295.
- Díaz-Paniagua, C., Keller, C. & Andreu, A.C. (1996) Clutch frequency, egg and clutch characteristics, and nesting activity of spur-thighed tortoises, *Testudo graeca*, in Southwestern Spain. *Can. J. Zool.*, 74, 560-564.
- Germano, D.J. (1993) Shell morphology of North American tortoises. *Am. Midl. Nat.*, 129, 319-335.
- Gotthard, K. & Nylin, S. (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos*, 74, 3-17.
- Hailey, A. & Loubourdis, N.S. (1988) Egg size and shape, clutch dynamics, and reproductive effort in European tortoises. *Can. J. Zool.*, 66, 1527-1536.
- Harris, D.J., Znari, M., Mace, J.C. & Carretero, M.A. (2003) Genetic variation in *Testudo graeca* from Morocco estimated using 12S rRNA DNA sequencing. *Rev. Esp. Herpetol.*, 16, 5-9.

- Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. (1999) Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.*, 13, 289-297.
- Highfield, A.C. & Bayley, J.R. (2003) *The trade in tortoise-derived souvenir products in Morocco*. Tortoise Trust. Report <http://www.tortoisetrust.org/articles/banjo.html>
- Iverson, J.B. (1992) *A Revised Checklist with Distribution maps of the Turtles of the World*. Richmond, Indiana: Privately Published.
- Khozatsky, L.I. & Mlynarski, M. (1966) *Agrionemys* — nouveau genre de tortues terrestres (Testudinidae). *Bull. Acad. Pol. Sci., Cl. II*, 14, 123-125.
- Kruskal, J.B. & Wish, M. (1989) *Multidimensional Scaling*. Sage University Paper series on Quantitative Applications in Social Sciences. 11. Sage Publications. Beverly Hills, London.
- Labarbera, M. (1989) Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Syst.*, 20, 97-117.
- Lagarde, F., Bonnet, X., Henen, B.T., Corbin, J., Nagy, K.A. & Naulleu, G. (2001) Sexual size dimorphism in steppe tortoises (*Testudo horsfieldii*): growth, maturity, and individual variation. *Can. J. Zool.*, 79, 1433-1444.
- Lagarde, F., Bonnet, X., Nagy, K.A., Henen, B.T., Corbin, J. & Naulleu, G. (2002) A short sprint before a long jump: the ecological challenge to the steppe tortoise (*Testudo horsfieldii*). *Can. J. Zool.*, 80, 493-502.
- Le Houerou, H. (1989) Classification écoloclimatique des zones arides (s.l.) de l'Afrique du Nord. *Ecol. Mediterr.*, 15, 95-144.
- McArdle, B.H. (1988) The structural relationship: regression in biology. *Can. J. Zool.*, 66, 2329-2339.
- McCoy, J.K., Fox, S.F. & Baird, T.A. (1994) Geographic variation in sexual dimorphism in the collared lizard *Crotaphytus collaris* (Sauria: Crotaphytidae). *Southwest. Nat.*, 39, 328-335.
- Monteiro, L.R., Bordin, B. & Furtado dos Reis, S. (2000) Shape distances, shape spaces and the comparison of morphometric methods. *Tree*, 15, 217-220.
- Mellado, J. (1989) S.O.S. Souss: Argan forest destruction in Morocco. *Oryx* 23(2), 87-93.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002) Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56, 1538-1542.
- Packard, G.C., Miller, K., Packard, M.J. & Birdchard, G.F. (1999) Environmentally induced variation in body size and condition in hatchling snapping turtles (*Chelydra serpentina*). *Can. J. Zool.*, 77, 278-289.
- Pianka, E.R. (1986) *Ecology & Natural History of Desert Lizards*. Princeton University Press, New Jersey.
- Pieh, A. (2000) *Testudo graeca soussensis*, eine neue Unterart der Maurischen Landschildkröte aus dem Sousstal (Südwest-Marokko). *Salamandra*, 36, 209-222.
- Qualls, F.J. & Shine, R. (1998) Geographic variation in lizard phenotypes: importance of the incubation environment. *Biol. J. Linn. Soc.*, 64, 477-491.
- Qualls, F.J. & Shine, R. (2000) Post-hatching environment contributes greatly to phenotypic variation between two populations of the Australian garden skink, *Lampropholis guichenoti*. *Biol. J. Linn. Soc.*, 71, 315-341.
- Rohlf, F.J. & Bookstein, F.L. (1987) A comment on shearing as a method of size correction. *Syst. Zool.*, 36, 356-367.
- Schleich, H.H., Kästle, W. & Kabisch, K. (1996) *Amphibians and Reptiles of North Africa*. Koeltz Scientific Publishers, Koenigstein.
- Shine, R. (1978) Sexual size dimorphism and male combat in snakes. *Oecologia* 33, 269-277.
- Shine, R., Elphick, M.L. & Harlow, P.S. (1997) The influence of natural incubation environments on the phenotypic traits of hatchling lizards. *Ecology*, 78, 2559-2568.
- Shine, R., Reed, R.N., Shetty, S. & Cogger, H.G. (2002) Relationships between sexual dimorphism and niche partitioning within a clade of sea-snakes (Laticaudinae). *Oecologia* 133, 45-53.

- Tome, S. (2001) Sexual dimorphism in Italian wall lizard (*Podarcis sicula* Rafinesque-Schmaltz, 1810). In: P. Lymberakis, E. Valakos, P. Pafilis & M. Mylonas (Eds.), *Herpetologia Candiana*, pp. 121-125. Societas Europaea Herpetologica, Natural History Museum of Crete, Irakleio, Greece.
- van der Kuyl, A.C., Ballasina, D.L.P., Dekker, J.T., Maas, J., Willemsen, R.E. & Goudsmit, J. (2002) Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from 12S rRNA gene sequences. *Mol. Phylogenet. Evol.*, **22**, 174-183.
- Via, S., Gomulkiewicz, R., De Jong, G., Scheimer, S., Schlichting, C. & Van Tienderen, P. (1995) Adaptive plasticity: consensus and controversy. *Tree*, **10**, 212-217.
- Willemsen, R.E. & Hailey, A. (1999) Variation in body size of the tortoise *Testudo hermanni* in Greece: proximate and ultimate causes. *J. Zool.*, **248**, 379-396.
- Willemsen, R.E. & Hailey, A. (2001) Variation in adult survival rate of the tortoise *Testudo hermanni* in Greece: implications for the evolution of body size. *J. Zool.*, **255**, 43-54.
- Willemsen, R.E. & Hailey, A. (2002) Body mass condition in Greek tortoises: regional and interspecific variation. *Herpetol. J.*, **12**, 105-110.
- Willemsen, R.E. & Hadley, M.E. (2003) Sexual dimorphism of body size and shell shape in European tortoises. *J. Zool.*, **260**, 353-365.
- Znari, M., El Mouden, E.H., Benfaida, J. & Boumezzough, A. (2000) Partage des ressources spatiales et trophiques au sein d'un peuplement de lézards insectivores des Jbilettes centrales (Maroc occidental). *Rev. Ecol. (Terre Vie)*, **55**, 141-160.
- Znari, M., Germano, D.J. & Macé, J.C. (in press) Growth and population structure of the Moorish tortoise (*Testudo graeca graeca*) in westcentral Morocco: possible effects of overcollecting for the tourist trade. *J. Arid Environ.*

APPENDIX

Descriptive statistics of the morphometric variables for the three analysed populations of *T. graeca* from Morocco and AN(C)OVA comparisons for site and sex; all but the first using CL as covariate. Numbers indicate mean \pm SE, range and sample size.

Variable	Jbilet		Admine		Essaouira		AN(C)OVA (site, sex, site*sex)		
	males	females	males	females	males	females	F	df	P
CL	125.3 ± 2.3	152.2 ± 3.7	150.9 ± 2.2	182.7 ± 6.0	144.4 ± 3.0	169.7 ± 5.1	24.43	2, 237	<0.0001
	101.8-172.2	100.4-202.3	115.0-184.4	105.7-226.2	102.8-183.4	100.7-213.5	64.46	1, 237	<0.0001
BW	372.7 ± 21.2	669.2 ± 38.6	636.3 ± 25.7	1145.1 ± 82.2	591.5 ± 34.6	1012.0 ± 69.3	10.68	2, 236	<0.0001
	238.1-924.0	181.4-1305.0	317.9-972.0	240.8-1930.0	221.1-1115.0	175.9-1755.0	8.53	1, 236	0.004
CCL	40	42	44	26	44	47	0.64	2, 236	0.53
	122.0 ± 7.2	155.9 ± 5.9	194.1 ± 2.9	231.2 ± 7.4	187.8 ± 4.0	216.2 ± 6.2	69.13	2, 205	<0.0001
CW1	64.0-219.8	65.2-219.0	156.6-222.4	135.7-284.0	136.1-238.7	125.9-274.5	6.56	1, 205	0.01
	27	29	40	25	44	47	3.77	2, 205	0.02
ACW	72.3 ± 3.6	86.9 ± 2.9	106.3 ± 1.6	130.0 ± 4.0	100.8 ± 1.9	121.2 ± 3.3	62.43	2, 205	<0.0001
	42.1-120.9	43.4-121.3	85.1-126.4	80.2-155.4	77.1-127.7	75.6-149.2	12.00	1, 205	0.0006
CW2	27	29	40	25	44	47	0.22	2, 205	0.80
	28.5 ± 1.4	34.7 ± 1.3	40.9 ± 0.8	47.5 ± 1.4	39.7 ± 0.9	44.2 ± 1.2	36.46	2, 204	<0.0001
PL1	17.3-45.6	16.4-48.3	20.9-50.7	30.3-56.3	28.7-51.0	27.6-58.7	2.93	1, 204	0.09
	27	28	40	25	44	47	2.14	2, 204	0.12
PL2	73.3 ± 4.0	89.6 ± 3.2	112.5 ± 1.8	135.5 ± 4.4	105.3 ± 2.1	124.3 ± 3.5	67.87	2, 205	<0.0001
	41.6-127.3	43.3-129.2	86.5-137.7	82.3-168.4	78.5-130.9	76.0-152.6	7.42	1, 205	0.0007
PW	27	29	40	25	44	47	1.06	2, 205	0.35
	85.8 ± 5.4	106.9 ± 4.3	130.1 ± 2.0	169.9 ± 5.8	122.6 ± 2.4	153.7 ± 4.6	60.80	2, 205	<0.0001
APW	45.3-164.3	44.6-157.4	101.6-157.0	95.7-203.1	93.4-157.7	89.9-189.7	18.22	1, 205	<0.0001
	27	29	40	25	44	47	0.17	2, 205	0.85
PL2	79.5 ± 4.7	97.3 ± 3.8	118.3 ± 1.8	156.6 ± 5.2	112.1 ± 2.1	142.8 ± 4.2	68.69	2, 205	<0.0001
	43.3-150.4	42.9-145.9	93.8-141.0	89.8-186.9	86.8-142.2	84.4-175.1	23.98	1, 205	<0.0001
PW	27	29	40	25	44	47	0.08	2, 205	0.92
	65.6 ± 3.5	79.8 ± 2.8	96.9 ± 1.4	119.4 ± 3.7	93.2 ± 1.9	111.8 ± 3.2	67.04	2, 205	<0.0001
APW	38.2-113.7	38.2-111.9	78.0-111.2	72.5-144.7	70.2-121.4	67.1-139.4	11.70	1, 205	0.0007
	27	29	40	25	44	47	0.41	2, 205	0.66
APW	18.7 ± 0.7	22.4 ± 0.6	26.7 ± 0.5	29.0 ± 0.9	24.5 ± 0.5	26.7 ± 0.7	34.18	2, 205	<0.0001
	14.2-29.2	12.9-27.7	19.2-35.1	19.2-38.6	18.6-31.0	17.5-36.0	0.23	1, 205	0.63
	27	29	40	25	44	47	5.25	2, 205	0.005

Variable	Jbitet		Adminie		Essaouira		AN(C)OVA (site, sex, site*sex)		
	males	females	males	females	males	females	F	df	P
PPW1	23.0 ± 1.6	30.6 ± 1.2	42.1 ± 1.0	40.3 ± 1.5	39.0 ± 0.9	36.4 ± 1.1	45.29	2, 205	<0.0001
	11.2-40.9	11.3-39.8	24.5-54.7	22.3-53.6	24.1-50.9	22.4-51.0	8.13	1, 205	0.005
CH	51.2 ± 2.7	63.7 ± 2.5	74.5 ± 1.1	94.4 ± 2.8	72.0 ± 1.3	87.7 ± 2.4	25.72	2, 205	<0.0001
	26.2-88.4	27.2-91.9	62.1-88.4	58.2-112.0	56.1-88.5	50.5-106.0	56.79	2, 205	<0.0001
VLL	97.9 ± 5.7	121.7 ± 4.7	147.9 ± 2.2	186.3 ± 6.1	143.4 ± 2.9	173.3 ± 5.1	18.12	1, 205	<0.0001
	49.9-175.2	51.0-172.0	122.4-178.0	110.5-231.0	109.0-179.1	101.7-221.5	0.41	2, 205	0.66
NW1	2.8 ± 0.2	3.2 ± 0.2	3.1 ± 0.1	3.3 ± 0.1	2.9 ± 0.1	3.3 ± 0.1	63.82	2, 205	<0.0001
	1.6-5.1	1.6-5.3	2.0-7.3	2.2-5.0	1.8-4.3	2.0-4.6	12.83	1, 205	0.0004
NW2	4.1 ± 0.3	4.9 ± 0.6	5.1 ± 0.3	5.8 ± 0.3	4.8 ± 0.2	5.7 ± 0.2	0.29	2, 204	0.002
	1.9-8.7	1.8-17.4	3.0-11.6	3.7-8.4	2.8-7.5	3.4-8.5	0.28	2, 204	0.07
NL	7.8 ± 0.5	10.5 ± 0.5	12.1 ± 0.4	12.8 ± 0.6	12.8 ± 0.3	13.0 ± 0.4	0.10	2, 204	0.90
	3.9-14.3	3.4-16.7	3.5-17.7	4.7-17.1	7.7-16.7	4.7-16.5	23.36	2, 204	<0.0001
3VL	21.8 ± 1.1	22.6 ± 0.7	26.3 ± 0.4	34.9 ± 1.4	27.0 ± 0.7	34.9 ± 1.1	0.42	1, 204	0.51
	10.3-36.8	10.3-33.5	21.7-31.5	19.8-42.8	19.2-44.2	19.8-48.0	7.88	2, 204	0.0005
3VW	33.2 ± 1.5	35.3 ± 1.0	41.6 ± 0.6	53.4 ± 2.0	39.5 ± 0.9	50.5 ± 1.5	38.71	2, 226	<0.0001
	17.5-50.9	17.7-51.3	34.2-48.6	30.2-65.7	21.9-51.4	30.0-67.4	6.48	1, 226	0.01
5VAW	11.9 ± 0.7	16.0 ± 0.7	22.9 ± 0.5	25.1 ± 1.3	19.8 ± 0.5	23.5 ± 0.8	8.04	2, 226	0.0004
	5.5-19.7	7.3-24.5	15.6-28.8	6.7-32.3	13.3-27.5	14.1-33.5	32.07	2, 227	<0.0001
5VPW	27.5 ± 1.7	34.5 ± 1.4	44.1 ± 1.3	53.9 ± 1.9	42.2 ± 1.0	48.5 ± 1.4	8.77	1, 227	0.003
	13.0-49.8	14.4-49.7	7.8-58.1	32.3-66.2	31.7-56.4	30.0-66.2	6.30	2, 227	0.002
	27	28	38	24	44	47	1.09	1, 201	0.29
							6.22	2, 201	0.002
							42.24	2, 202	<0.0001
							4.57	1, 202	0.03
							1.40	2, 202	0.25

Variable	Jbilet		Admine		Essaouira		AN(C)OVA (site, sex, site*sex)		
	males	females	males	females	males	females	F	df	P
5VL	19.4 ± 1.1	24.6 ± 1.0	34.2 ± 0.7	39.6 ± 1.5	32.3 ± 0.8	36.0 ± 1.2	85.00	2, 202	<0.0001
	8.7-33.9 27	10.4-36.2 28	27.2-45.3 39	22.4-50.2 24	22.4-45.4 44	20.1-50.4 47	0.54	1, 202	0.46
SCW1	14.0 ± 1.1	17.8 ± 0.8	23.1 ± 0.6	29.0 ± 1.2	21.3 ± 0.6	24.5 ± 0.7	49.19	2, 202	<0.0001
	6.0-30.9 27	6.6-28.4 28	14.4-30.5 39	16.1-38.3 25	13.3-28.2 44	14.7-36.8 47	4.19	1, 202	0.04
SCW2	22.9 ± 1.9	32.2 ± 1.4	44.1 ± 1.1	47.8 ± 1.9	39.9 ± 1.1	41.4 ± 1.4	2.06	2, 202	0.13
	9.9-48.1 27	10.4-44.5 28	30.7-58.8 38	22.7-59.5 25	25.6-54.0 44	21.6-60.6 47	0.28	1, 202	0.60
SCL	13.6 ± 1.1	20.0 ± 0.9	28.1 ± 0.6	27.7 ± 1.0	25.4 ± 0.7	25.7 ± 0.9	15.49	2, 202	<0.0001
	4.8-29.1 27	5.6-28.4 28	19.1-35.7 38	14.9-35.5 25	13.2-34.7 44	13.5-34.1 47	52.79	2, 202	<0.0001
2COSL	19.0 ± 1.0	22.0 ± 0.7	25.4 ± 0.3	35.8 ± 1.4	25.7 ± 0.5	34.6 ± 1.1	1.30	1, 202	0.25
	10.5-32.6 27	10.6-32.6 29	21.7-29.3 43	19.6-55.5 26	19.2-34.0 44	19.3-45.7 47	22.86	2, 202	<0.0001
2COSW	29.9 ± 1.5	35.6 ± 1.2	41.7 ± 0.6	51.7 ± 1.7	41.4 ± 0.8	50.5 ± 1.4	68.07	2, 209	<0.0001
	16.0-49.0 27	16.7-50.1 29	34.6-49.1 43	32.4-67.1 26	30.9-51.5 44	30.8-65.0 47	32.33	1, 209	<0.0001
1ML	14.7 ± 0.9	18.3 ± 0.6	23.4 ± 0.5	25.8 ± 0.8	21.7 ± 0.4	24.7 ± 0.6	0.02	2, 209	0.98
	7.5-24.8 27	7.3-23.9 29	18.9-37.3 39	16.7-33.3 24	16.0-26.0 44	15.8-31.7 47	61.61	2, 203	<0.0001
1MW	13.5 ± 0.7	16.6 ± 0.6	20.0 ± 0.3	23.4 ± 0.7	19.2 ± 0.5	21.9 ± 0.6	4.47	1, 203	0.04
	7.6-22.5 27	8.2-23.2 29	15.6-23.8 40	13.4-28.3 25	13.5-25.5 44	13.4-29.1 47	4.52	2, 203	0.01
2ML	15.2 ± 0.9	19.0 ± 0.7	24.4 ± 0.3	27.5 ± 0.9	23.5 ± 0.5	26.7 ± 0.7	49.66	2, 205	<0.0001
	7.4-26.1 27	7.3-24.7 29	20.9-30.3 39	18.0-35.3 24	17.1-28.6 44	16.9-33.1 47	4.59	1, 205	0.03
2MW	15.1 ± 0.9	19.0 ± 0.7	23.7 ± 0.5	27.8 ± 1.0	22.9 ± 0.5	26.1 ± 0.7	2.48	2, 205	0.09
	7.3-26.3 27	7.5-25.7 29	15.9-28.8 40	17.6-36.9 25	15.7-28.9 44	16.0-33.8 47	73.58	2, 203	<0.0001
						3.64	1, 203	0.05	
						24.29	2, 203	0.01	
						54.17	2, 205	<0.0001	
						3.78	1, 205	0.05	
						3.13	2, 205	0.05	

Variable	Jbilet				Admine				Essaouira				AN(C)OVA (site, sex, site*sex)		
	males		females		males		females		males		females		F	df	P
PPW2	62.2 ± 3.4	73.2 ± 2.9	92.4 ± 1.4	114.7 ± 3.7	87.5 ± 1.7	104.6 ± 3.0	66.62	2, 205	<0.0001						
	35.2-109.9	35.9-107.5	72.2-109.1	66.9-138.2	68.1-112.7	61.6-130.4	7.20	1, 205	0.007						
GSL	11.0 ± 0.8	14.2 ± 0.6	18.7 ± 0.5	22.6 ± 0.8	17.8 ± 0.4	20.6 ± 0.7	0.06	2, 205	0.94						
	5.4-21.3	6.0-19.2	7.3-24.0	12.5-28.0	11.7-22.2	11.4-29.4	60.99	2, 205	<0.0001						
GSW	9.5 ± 0.4	11.5 ± 0.3	13.5 ± 0.2	14.9 ± 0.5	12.7 ± 0.3	14.3 ± 0.4	5.24	1, 205	0.02						
	7.2-15.7	6.6-14.3	10.3-17.1	9.7-20.1	9.5-16.8	8.9-24.9	3.19	2, 205	0.04						
HSL	12.9 ± 0.8	16.2 ± 0.7	19.6 ± 0.4	24.6 ± 1.0	18.5 ± 0.4	21.8 ± 0.6	32.08	2, 205	<0.0001						
	7.2-26.1	6.3-27.8	15.6-25.6	12.7-33.3	12.9-25.2	14.4-29.2	0.82	1, 205	0.36						
HSW	24.0 ± 1.2	29.4 ± 1.0	35.6 ± 0.5	42.1 ± 1.6	33.3 ± 0.6	39.2 ± 1.0	3.93	2, 205	0.02						
	14.4-41.1	13.4-43.0	30.2-41.3	17.8-50.2	26.2-42.5	25.0-48.1	48.12	2, 205	<0.0001						
PSL	9.6 ± 2.4	7.7 ± 0.5	10.5 ± 0.3	15.2 ± 0.7	9.7 ± 0.2	13.2 ± 0.5	11.59	1, 205	0.0008						
	4.0-70.4	4.3-17.6	6.4-15.0	9.8-21.7	7.0-13.5	6.6-20.0	1.06	2, 205	0.35						
PSW	32.1 ± 1.7	39.4 ± 1.4	47.4 ± 0.7	59.0 ± 1.7	44.8 ± 0.8	54.0 ± 1.5	49.57	2, 205	<0.0001						
	18.4-54.7	17.9-55.3	37.9-56.3	36.3-67.9	34.3-53.3	33.3-69.9	8.43	1, 205	0.004						
ABSL	28.3 ± 1.8	34.7 ± 1.5	41.1 ± 0.7	56.5 ± 2.1	40.3 ± 0.8	52.3 ± 1.7	1.44	2, 205	0.24						
	14.6-52.9	14.6-57.1	30.3-49.4	31.3-69.7	30.0-51.9	30.8-69.2	26.01	2, 205	<0.0001						
ABSW	10.4 ± 0.8	12.7 ± 0.4	15.5 ± 0.3	18.5 ± 0.8	14.6 ± 0.4	17.5 ± 0.6	2.95	1, 205	0.09						
	4.1-22.0	4.8-17.3	11.8-19.7	9.4-23.7	10.5-20.1	9.1-25.1	9.08	2, 205	0.0002						
	27	29	40	25	44	47	62.43	2, 205	<0.0001						
							15.35	1, 205	0.0001						
							0.42	2, 205	0.66						
							59.92	2, 205	<0.0001						
							23.94	1, 205	<0.0001						
							0.38	2, 205	0.68						
							28.98	2, 205	<0.0001						
							2.70	1, 205	0.10						
							1.32	2, 205	0.27						

Variable	Jbilet		Admine		Essaouira		AN(C)OVA (site, sex, site*sex)		
	males	females	males	females	males	females	F	df	P
FSL	22.9 ± 1.4	27.8 ± 1.2	33.8 ± 0.5	42.4 ± 1.3	31.5 ± 0.6	39.3 ± 1.1	43.98	2, 205	<0.0001
	9.6-42.3 27	6.5-41.3 29	27.9-40.8 40	26.0-52.8 25	23.8-38.7 44	24.3-50.8 47.0	11.93	1, 205	0.0007
FSW	11.3 ± 0.7	13.2 ± 0.8	15.3 ± 0.8	22.7 ± 0.8	13.2 ± 0.3	20.6 ± 0.6	0.03	2, 205	0.97
	5.1-22.3 27	6.0-26.7 29	9.5-34.6 40	13.9-27.6 25	9.9-16.3 44	12.2-29.1 47.0	33.46	2, 205	<0.0001
						52.07	1, 205		<0.0001
						7.50	2, 205		0.0007