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# The shell measurements that best describe sexual dimorphism in the spur-thighed tortoise *Testudo graeca* from Algeria

Benelkadi Hadj Aissa[1,*], Roberto C. Rodríguez-Caro[2,3,4,5], Mansour Amroun[1], Eva Graciá[2,3]

[1] Faculty of Biological and Agricultural Sciences, University of Tizi-Ouzou, Tizi-Ouzou 15000, Algeria.
[2] Departamento de Biología Aplicada, Universidad Miguel Hernández. Avda. de la Universidad sn, 03202 Elche (Alicante), Spain.
[3]Centro de Investigación e Innovación Agroalimentaria y Agroambiental (CIAGRO-UMH), Univ. Miguel Hernández, Elche, Spain.
[4] Department of Zoology, Oxford University, 11a Mansfield Road, OX1 3SZ, Oxford, England, UK.
[5] Departamento de Ecología, Universidad de Alicante. Carretera de San Vicente del Raspeig s/n. 03690 San Vicente del Raspeig, Alicante, Spain.

*Correspondence: b_aissa1976@yahoo.fr.

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Due to phenotypic plasticity and sex-biased selective pressures, intraspecific variation in tortoise morphology is usually assessed by studying sexual dimorphism. However, inferences may differ based on the choice of shell size measurements for analyses. In this work, we identified linear measurements that best describe sexual dimorphism for the spur-thighed tortoise *Testudo graeca whitei*. We assessed 34 carapace and plastron measurements in 67 individuals (24 males, 43 females) in a population at the natural Mergueb site located on the central limit of the Algerian steppe. Twenty-two out of 34 measurements significantly showed sexual size dimorphism in ANOVA tests. When analyzing sexual shape dimorphism with ANCOVAs, nine measurements showed no shared allometry with the measurements used as covariates to correct by size. Meanwhile, 17 out of the remaining 23 measurements showed significant differences in shape. PCA analyses similarly described *T. graeca*'s sexual dimorphism. In general, females tend to be bigger than males, especially in central scutes what is probably linked with clutch sizes commitments. On the other hand, males are larger-sized in anterior and posterior scutes, probably as a result of courtship, male fighting and copulation. Some of the analyzed measurements are revealed as being especially adequate for further studying the geographical variation of sexual dimorphism in *Testudo graeca.*

***Key words*****:** Biometry; morphological divergence; morphometry; M'Sila; phenotypic plasticity; sexual shape dimorphism; sexual size dimorphism.

Phenotypic plasticity makes chelonians particularly prone to the morphological studies that explore the interactions of selection, life history traits and local conditions (Fritz *et al.*, 2007; Ceballos-Fonseca, 2010). On tortoises of the genus *Testudo* (with a broad southwestern Palearctic distribution), morphometric studies have assessed morphological divergence between and within subspecies (Carretero *et al.*, 2005), have explored Bergmann's or Rensch's rules (Sacchi *et*

DOI: http://dx.doi.org/10.1116/bah.217 Supplementary material available online *al.*, 2007; WERNER *et al.*, 2016), compared sexual size and shape dimorphism (SSD and SShD, respectively; e.g.: DJORDJEVIC *et al.*, 2011) or evaluated the sex-biased impact of disturbances like commercial export and overharvesting or fires (e.g., KADDOUR *et al.*, 2006; LJUBISAVLJEVIĆ *et al.*, 2011; RODRÍGUEZ-CARO *et al.*, 2013). In this genus, sex-biased selective pressures result in female-biased SSD being bigger than males (e.g. LAGARDE *et al.*, 2001; WILLEMSEN & HAILEY, 2003, KADDOUR *et al.*, 2008; DJORDJEVIC *et al.*, 2011; MACALE *et al.*, 2011). Larger females tend to lay bigger clutches (RODRÍGUEZ-CARO *et al.*, 2021), while males' marked locomotion necessity is favored by smaller sizes (WERNER *et al.*, 2016). The majority of morphological studies on chelonians address their sexual dimorphism, with differences in SSD and/or SShD being dependent on the choice of shell measurements used for analyses (e.g. CARRETERO *et al.*, 2005). However, no consensus has been reached about which and how many measurements are to be employed (studies range from 7 to 40 measurements; e.g. PIEH & PERALA, 2004; CARRETERO *et al.*, 2005; LABUS *et al.*, 2016).

In this study, we explore those measurements that best describe SSD and SShD in a widely distributed tortoise species, the spur-thighed tortoise (*Testudo graeca* LINNAEUS, 1758). Its Western Palearctic distribution range includes North Africa, the Middle East, Asia Minor, southeastern Europe, and some isolated and small Western European populations of North African origin (IVERSON, 1992; BUSKIRK *et al.*, 2001; GRACIÁ *et al.*, 2017a; JAVANBAKHT *et al.*, 2017). As a result of the wide variety of habitats and phenotypic plasticity, morphological-based taxonomic studies suggest that the *T. graeca* complex is not monophyletic, and that up to 20 distinct taxa exist (HIGHFIELD & MARTIN, 1989a,b; HIGHFIELD, 1990; PIEH, 2000; PERÄLÄ, 2002a; PERÄLÄ, 2002b; PIEH & PERÄLÄ, 2002, 2004). Only 10 of these morphologically defined taxa were later confirmed by molecular means, and the monophyly and conspecificity of the *T. graeca* complex have been definitively described (FRITZ *et al.*, 2007; 2009; GRACIÁ *et al.*, 2017a; Fig. 1). The old divergence of Eastern and Western spur-thighed tortoises traces back to 7.95–3.48 Mya (GRACIÁ *et al.*, 2017a), and it has been reported that morphological patterns, such as Bergmann's and Rensch's rules, differ among lineages probably as a consequence of differential selective pressures (WERNER *et al.*, 2016).

Within the five lineages of the Western clade, one of the most distributed and adequate for phenotypic studies is *T. g. whitei*. The nomenclature of this subspecies has been recently revisited, being *T. g. whitei* attributed to the subspecies present in North Algeria, NE Morocco and Spain (previously named *T. g. graeca*; TURTLE TAXONOMY WORKING GROUP, 2021). Two facts make this subspecies especially suitable for phenotypic studies: first, because this subspecies inhabits a wide variety of habitats from arid to humid climates in Morocco and Algeria (ANADÓN *et al.*, 2015); and second, because unlike North African populations that are ancient, the European populations of this subspecies are recent in phylogeographical terms (prehistoric in the case of SE Spain and introduced in historic times to Doñana and Majorca; GRACIÁ *et al.*, 2017a,b). To the best of our knowledge, no comprehensive studies have addressed differences in the morphology of this taxon. Note, for example, CARRETERO *et al.*, (2005), and KADDOUR *et al.*, (2008), studied the lineage attributed today to *T. g. graeca* in southern Morocco (previously named *T. g. soussensis*; Turtle Taxonomy Working Group, 2021). The present study provides basic information for such further studies. It particularly characterizes the morphology of a well-preserved *T. graeca* population in Algeria, and evaluates 34 of the carapace and plastron measurements used by CARRETERO *et al.* (2005) to find those that best describe SSD and SShD in *T. graeca*.

## MATERIALS AND METHODS

### *Fieldwork and studied measurements*

We conducted this study at the natural Mergueb site in North Algeria in the central region of M'sila. It consists of a steppe ecosystem that covers an area of 16,481 ha at an altitude of 634 m (latitude: 35° 36'12,6''N - 35°35'05,7''N; longitudes 03° 56'23,8''E - 03°58'08,7''E) (Fig. 1). At this natural site, vegetation is characterized by formations of *Artemisia herba-alba, Artemisia campestris, Salsola vermiculata, Anabasis articulata* and *Zizyphus lotus* (ADJABI *et al.*, 2019). Soil has sandy clay-loam and sandy -loam structures. The monthly variation in temperature is wide in this study area, with the minimum temperatures in Febru-

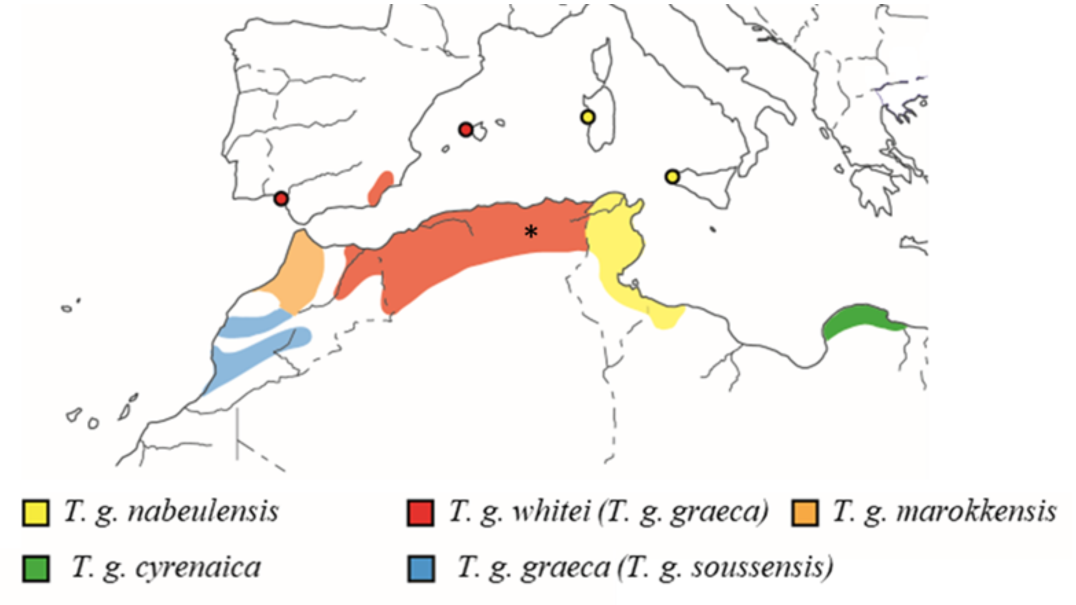

**Figure 1**: Approximate ranges of *Testudo graeca* subspecies according to GRACIÁ *et al.* (2017a) and location of the study area in Algeria (asterisk). Lineage nomenclature prior to the last revision of the TURTLE TAXONOMY WORKING GROUP (2021) is shown between parentheses.

ary (-0.5 ºC) and maximum ones in July (46.2 ºC). The average annual rainfall lies between 121 and 181 mm (ADJABI *et al.*, 2019).

In order to fulfill our goals, we went on approximately two outings per month with two or three prospectors for 2 years in different transects that were far away from one another. In all, 70 adult individuals were captured (25 males, 45 females) and individually identified by photography records (each animal was measured just one time). The found tortoises were measured using a sliding caliper (accuracy = 0.01 mm). A tape was used for the curvilinear measurements. Animals were sexed according to their external morphological characteristics (CARRETERO *et al.*, 2005), and 34 morphometric measurements were taken on dorsal and ventral parts according to previous studies (PERÄLÄ, 2001; CARRETERO *et al.*, 2005; TICHÝ & KINTROVÁ, 2010; TURKOZAN *et al.*, 2018; Table S1, Fig. 2).

Subadults individuals were ruled out for this study. At the end, all the retained individuals (24 males and 43 females) had secondary sexual characters and a straight carapace length (SCL) over 100 mm (as in ROUAG *et al.*, 2007). After taking the measurements, all specimens were finally returned to their habitats.

### *Statistical analyses*

In order to describe the general morphometry of males and females, we calcu-

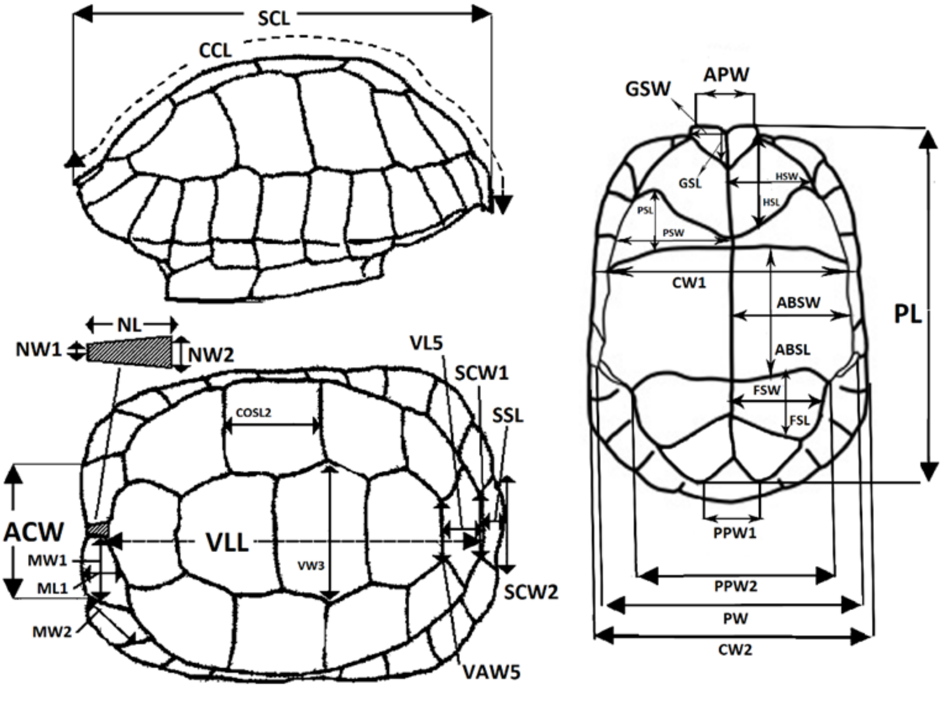

**Figure 2:** Graphical representation of the 34 morphometric measurements assessed for *T. g. whitei.* See Table S1 for their description. Image taken with modifications from CARRETERO *et al.*, (2005).

lated descriptive statistics by sex for all the assessed measurements (mean, range, standard deviation). Moreover, the percentage of sexual dimorphism between sexes was calculated as 100*((female-male)/male), following CARRETERO *et al.* (2005). SSD was estimated by univariate ANOVAs to identify the significant differences in size between males and females. SShD was calculated by ANCOVAs, using the straight carapace length (SCL) or plastron length (PL) as a covariate for the carapace and plastrons measures, respectively. Significant interactions between covariates and sex were explored to discard no shared allometry among measurements, that would impact ANCOVA interpretations (MCCOY *et al.*, 2006). To obtain reliable results in ANOVA and ANCOVA analyses, all the measurements were log-transformed to fit normality and homoscedasticity.

A Principal Component Analysis (PCA) was also conducted for the 34 measurements to identify sexual dimorphism patterns across them. To do so, we used a correlation matrix and only those axes with >5% of explained deviance were retained. Then the relation between the main PC axes with sex was analyzed by ANOVAs. All the statistical analyses were conducted by R project version 4.2.0.

## RESULTS

### *Sexual size dimorphism*

The shell morphology of this population displayed clear differences in size between males and females (Table 1). Twenty-two of the 34 analyzed measurements showed significant sex differences in the ANOVA test (Table 1). Eight of them (SCL, CCL, ML1, MW2, COSL2, VW3, SCW1 and VLL) were carapace measurements, while the remaining fourteen (GSL, HSW, PSL, PSW, ABSL, ABSW, FSL, FSW, PW, PPW1, PPW2, CW1, CW2 and PL) were measurements taken of the plastron. Most measurements were larger for females than males, and the only significative exception was PPW1 (Table 1). Moreover, 94% of the measurement ranges were wider in females than males and around 91% of their standard deviations were higher too.

### *Sexual shape dimorphism*

When analyzing sexual shape dimorphism with ANCOVAs, nine measurements showed no shared allometry with the measurements used as covariates to correct by size (size: sex term in Table 1). Since this violates a prerequisite of ANCOVA, we did not interpret these results. Meanwhile, 17 out of the remaining 23 measurements (10 in carapace, 7 in plastron) proved to be sexually dimorphic. The only exceptions were NW1, NW2, ACW, SSL, GSW and PW (Table 1). Only one significant measurement was larger in males than females after size correction (APW; Table S2 ).

The conducted PCA assessed the multiple interactions among measurements in relation to sexual dimorphism. The results described well the species' morphology with two axes (Fig. 3). The meanings of the retained PC axes were: PC1 (72.44% deviance) revealed the general tortoise size with bigger measurements (like CW2, SCL or PPW2) being associated to higher negative values of this axis; PC2 (5.46%

**Table 1:** Shell measurements by *T. g. whitei* sex at M'Sila (Algeria). Number of studied individuals and mean, range and standard deviation by measurement (in mm). Sexual Size Dimorphism (SSD) was estimated as the percentage of variation between females and males (positive values are linked with bigger females and negative values are linked to bigger males) and the *P* values were estimated by ANOVA analyses after log-transformation. Sexual Shape Dimorphism (SShD) was estimated by ANCOVA using as a covariable SCL and PL for carapace or plastron measurements, respectively.

| | **Meas.** | **Males** | | | | **Females** | | | | **SSD** | | **SShD (ANCOVA)** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **N** | **Mean** | **Range** | **SD** | **N** | **Mean** | **Range** | **SD** | **%** | ***P*** | **covariate** | ***P*** | **size:sex *P*** |
| Carapace | SCL | 24 | 140.14 | 116.15-166.00 | 12.50 | 43 | 158.18 | 113.20-215.00 | 24.98 | 12.87 | **<0.001** | NA | NA | |
| | CCL | 24 | 176.79 | 147.00-214.00 | 16.69 | 43 | 201.07 | 142.00-266.00 | 32.15 | 13.73 | **<0.001** | SCL | **<0.001** | 0.917 |
| | NL | 24 | 11.14 | 8.50-13.80 | 1.48 | 43 | 11.98 | 9.25-16.50 | 1.89 | 7.54 | 0.067 | SCL | **0.018** | 0.174 |
| | NW1 | 23 | 3.38 | 2.00-5.45 | 0.99 | 41 | 3.19 | 2.00-4.80 | 0.75 | -5.62 | 0.504 | SCL | 0.507 | 0.661 |
| | NW2 | 24 | 5.55 | 2.00-8.30 | 1.68 | 43 | 6.11 | 3.80-10.00 | 1.54 | 10.09 | 0.108 | SCL | 0.113 | 0.622 |
| | ACW | 24 | 41.03 | 30.50-52.15 | 4.92 | 43 | 41.88 | 21.20-56.35 | 6.83 | 2.07 | 0.726 | SCL | 0.652 | 0.316 |
| | ML1 | 23 | 19.80 | 16.70-23.70 | 1.67 | 41 | 22.22 | 16.75-29.60 | 3.40 | 12.22 | **0.001** | SCL | **<0.001** | 0.695 |
| | MW1 | 24 | 22.87 | 18.85-27.85 | 2.49 | 43 | 24.50 | 17.55-30.55 | 3.46 | 7.13 | 0.066 | SCL | **<0.001** | 0.199 |
| | MW2 | 24 | 21.16 | 17.70-27.70 | 2.37 | 42 | 23.76 | 16.65-30.70 | 3.79 | 12.29 | **0.002** | SCL | **<0.001** | 0.787 |
| | COSL2 | 24 | 25.55 | 21.80-31.25 | 2.02 | 41 | 32.67 | 21.05-45.80 | 6.77 | 27.87 | **<0.001** | SCL | **<0.001** | **0.001** |
| | VW3 | 24 | 39.89 | 32.65-47.00 | 3.75 | 41 | 47.23 | 32.75-67.70 | 9.01 | 18.40 | **<0.001** | SCL | **<0.001** | 0.098 |
| | VAW5 | 24 | 20.83 | 14.45-28.95 | 3.87 | 43 | 22.57 | 14.35-33.15 | 4.84 | 8.35 | 0.164 | SCL | **0.020** | 0.114 |
| | VL5 | 24 | 32.17 | 25.00-43.45 | 4.56 | 43 | 34.86 | 22.75-50.30 | 6.13 | 8.36 | 0.083 | SCL | **<0.001** | 0.051 |
| | SCW1 | 24 | 21.37 | 15.55-28.20 | 3.23 | 43 | 23.80 | 16.60-32.00 | 3.92 | 11.37 | **0.014** | SCL | **<0.001** | 0.062 |
| | SCW2 | 24 | 41.75 | 33.15-51.00 | 5.02 | 43 | 42.16 | 28.65-51.25 | 6.39 | 0.98 | 0.897 | SCL | 0.770 | **0.007** |
| | SSL | 24 | 23.82 | 18.70-30.75 | 2.85 | 43 | 23.70 | 17.05-29.50 | 3.55 | -0.50 | 0.788 | SCL | 0.608 | 0.097 |
| | VLL | 24 | 137.85 | 112.00-166.00 | 13.27 | 43 | 164.49 | 113.00-219.00 | 27.46 | 19.33 | **<0.001** | SCL | **<0.001** | 0.995 |
| Plastron | APW | 22 | 21.31 | 16.45-25.25 | 2.25 | 41 | 20.04 | 13.85-24.70 | 2.52 | -5.96 | 0.056 | PL | **0.035** | 0.396 |
| | GSL | 24 | 17.95 | 14.35-23.00 | 2.27 | 43 | 20.17 | 8.40-29.70 | 4.10 | 12.37 | **0.020** | PL | **<0.001** | 0.634 |
| | GSW | 24 | 13.01 | 10.35-15.40 | 1.33 | 41 | 13.12 | 8.55-16.70 | 1.83 | 0.85 | 0.917 | PL | 0.884 | 0.822 |
| | HSL | 24 | 30.88 | 24.60-37.75 | 3.22 | 43 | 32.86 | 22.80-43.30 | 5.50 | 6.41 | 0.118 | PL | **0.036** | 0.201 |
| | HSW | 24 | 32.93 | 26.90-39.00 | 2.85 | 43 | 36.30 | 24.00-45.25 | 5.09 | 10.23 | **0.002** | PL | **<0.001** | **0.010** |
| | PSL | 24 | 25.87 | 22.20-30.30 | 2.51 | 42 | 31.73 | 21.60-45.00 | 5.65 | 22.65 | **<0.001** | PL | **<0.001** | 0.232 |
| | PSW | 24 | 47.65 | 38.60-56.55 | 4.40 | 43 | 53.88 | 37.20-69.45 | 8.39 | 13.07 | **<0.001** | PL | **<0.001** | **0.006** |
| | ABSL | 24 | 40.60 | 31.80-50.00 | 4.13 | 41 | 50.40 | 34.30-70.85 | 9.47 | 24.14 | **<0.001** | PL | **<0.001** | 0.330 |
| | ABSW | 24 | 48.52 | 39.25-55.95 | 4.31 | 43 | 55.13 | 38.90-74.20 | 8.92 | 13.62 | **<0.001** | PL | **<0.001** | **0.041** |
| | FSL | 24 | 30.70 | 24.00-38.10 | 3.25 | 43 | 36.18 | 23.60-47.75 | 6.80 | 17.85 | **<0.001** | PL | **<0.001** | 0.257 |
| | FSW | 24 | 33.80 | 26.50-39.20 | 3.07 | 43 | 37.96 | 27.00-48.00 | 5.77 | 12.31 | **0.001** | PL | **<0.001** | **0.039** |
| | PW | 24 | 90.17 | 71.00-105.55 | 8.47 | 43 | 99.62 | 36.15-136.85 | 18.89 | 10.48 | **0.042** | PL | 0.051 | 0.440 |
| | PPW1 | 24 | 37.67 | 28.20-47.45 | 5.22 | 43 | 32.82 | 21.20-42.25 | 5.16 | -12.87 | **0.001** | PL | **<0.001** | **0.007** |
| | PPW2 | 24 | 66.96 | 52.90-76.30 | 5.72 | 43 | 75.61 | 53.25-96.75 | 11.62 | 12.92 | **<0.001** | PL | **<0.001** | 0.058 |
| | CW1 | 24 | 98.84 | 81.25-116.95 | 9.06 | 43 | 111.75 | 80.90-150.00 | 16.66 | 13.06 | **<0.001** | PL | **<0.001** | **0.006** |
| | CW2 | 24 | 105.05 | 84.15-123.25 | 9.86 | 43 | 117.36 | 81.30-153.75 | 18.28 | 11.72 | **0.002** | PL | **<0.001** | **0.001** |
| | PL | 24 | 123.79 | 101.75-145.35 | 9.79 | 41 | 145.31 | 100.15-199.00 | 25.21 | 17.38 | **<0.001** | NA | NA | NA |

deviance) represented the trade-off between developing bigger central scutes or larger scutes at the anterior or posterior part. This axis was positively related to variables like NW2, COSL2, ABSL or VW3 and correlated negatively with others like PPW1, APW or SSL. Both PC1 and PC2 showed significant relation with individuals' sex (*p* = 0.02; *p* < 0.001 in ANOVA tests, respectively). Males were more re-

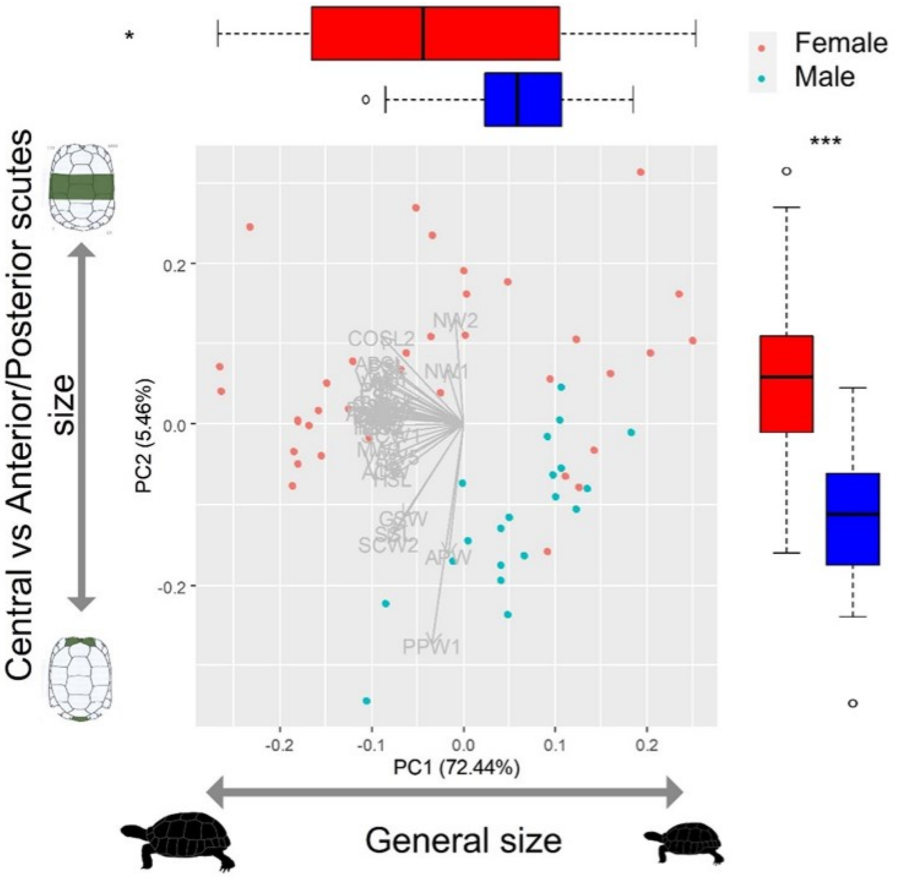

**Figure 3:** *Testudo graeca* morphology can be adequately explained by two main axes of variation: (1) general size of individuals; (2) development of bigger gular and caudal scutes, or bigger central scutes. Morphology traits are defined in Table S1. Principal component analysis (PCA) for the first two axes (PC1 = 72.44 and PC2 = 5.46 percentage of variance absorbed, Table S) for 34 morphometric measures from 60 individuals (with the complete dataset). Individuals, represented by each dot in the 2-D space, are color-coded according to their sex. Arrow lengths indicate the loading of each life history trait on a given principal component axis. PC1 (p = 0.02) and PC2 (p < 0.001) resulted significantly related to sex in ANOVA tests, whereas PC1 is linked to general size and PC2 describes that males develop higher front and posterior shell parts and females develop bigger central parts.

lated to higher values of PC1 (matching their smaller size) and lower values of PC2 (associated with bigger anterior or posterior scutes). Contrarily, females resulted widely distributed across PC1, and more related to positive values of PC2 (associated with bigger central scutes). PC loadings and individual scores are provided as Supplementary Material (Tables S3, S4).

## DISCUSSION

This study contributes to basic knowledge on the spur-thighed tortoise (*T. g. whitei*) in North Africa, particularly in Algeria. To the best of our knowledge, the tortoises studied in the steppe of M'Sila constitute the first biometric records of the subspecies *T. g. whitei* in North Africa. These Algerian tortoises were relatively small in size compared to other Western Mediterranean *T. graeca* populations (Table 2), probably as a result of inhabiting very arid conditions. As regards to size dimorphism, and as expected from previous literature with *T. graeca* (e.g. CARRETERO *et al.*, 2005; ROUAG *et al.*, 2007; KADDOUR *et al.*, 2008; ARAKELYAN *et al.*, 2018), females were around 13% bigger in straight carapace length (SCL) than males. This estimate fits the expectation according to the latitude of M'Sila population and the marginally significant Rensch's rule pattern found in *T. g. whitei* (see WERNER *et al.*, 2016, although noting that the lineages was named *T. g. graeca* then). The shell morphology of *Testudo* tortoises results from a balance between natural and sexual selection. Whereas natural selection promotes large females and, hence, increases fecundity, sexual selection promotes small mobile males for mate

**Table 2:** SCL measurement of *Testudo graeca* across its Western Mediterranean distribution as shown in WERNER *et al.* (2016), together with the obtained at this study. See GRACIÁ *et al.* (2017a,b) and TURTLE TAXONOMY WORKING GROUP (2021) for lineages assignation.

| Location | Lineage | Females SCL (mm) | | Males SCL (mm) | | References |
|---|---|---|---|---|---|---|
| | | N | Mean | N | Mean | |
| Souss Valley, Morocco | *T. g. graeca* | / | 184.9 | / | 145 | BAYLEY & HIGHFIELD (1996) |
| Admine, Morocco | *T. g. graeca* | 26 | 182.7 | 44 | 151 | CARRETERO *et al.* (2005) |
| Jbilet, Morocco | *T. g. graeca* | 42 | 152.2 | 40 | 125 | CARRETERO *et al.* (2005) |
| Essaouira, Morocco | *T. g. graeca* | 47 | 169.7 | 44 | 144 | CARRETERO *et al.* (2005) |
| Tetuan, Morocco | *T. g. marokkensis* | 10 | 170.6 | 14 | 174 | PIEH & PERALA (2004) |
| Tarmilete, Morocco | *T. g. marokkensis* | 21 | 138.5 | 17 | 130.4 | PIEH & PERALA (2004) |
| M'Sila, Algeria | *T. g. whitei* | 43 | 158.2 | 24 | 140.1 | This study |
| Tunisia | *T. g. nabeulensis* | 58 | 129.9 | 34 | 121 | PIEH & PERALA (2002) |
| El Kala, Algeria | *T. g. nabeulensis* | 33 | 150.7 | 35 | 138.4 | ROUAG *et al.* (2007) |
| Cyrenaica, Libya | *T. g. cyrenaica* | 14 | 172.4 | 18 | 149.4 | PIEH & PERALA (2002) |
| Doñana, Spain | *T. g. whitei* and *T. g. whitei* x *T. g. marokkensis* | 58 | 166.1 | 133 | 139 | BUSKIRK *et al.* (2001) |
| Doñana, Spain | *T. g. whitei* and *T. g. whitei* x *T. g. marokkensis* | 15 | 175 | / | / | DIAZ *et al* (1996) |

searching (CARRETERO *et al.*, 2005). Our results also reflected a more variable size upon female maturity (as reported in NE Algeria by ROUAG *et al.*, 2007), which probably results from a longer growth period before and after maturity (RODRÍGUEZ-CARO *et al.*, 2013). In this line, differences in female adult sizes have been recently related to differences in their reproductive outcome: bigger females have more offspring with newborns displaying higher survival rates (SEGURA *et al.*, 2021). Hence it would seem beneficial for females to invest in growth, even after reaching maturity.

Our study also identifies key shell measurements to study SSD and SShD. Of the 34 recorded measurements, we found significant SSD in 22 and significant SShD in 17. The main differences between *T. graeca* males and females were found in different shell parts. Males had bigger anterior (gular plates) and posterior sizes (caudal region), whereas females had bigger central shell parts. Once again, the shell structure of *T. graeca* males is a consequence of sexual selection (e.g. CARRETERO *et al.*, 2005; KADDOUR *et al.*, 2008; ZNARI & HICHAMI, 2018; MAKRIDOU *et al.*, 2019). The shell structure of tortoise males generally allows wider movements for their legs to enhance movement capabilities, and the righting ability to avoid the fatal consequences of intrasexual combats (BONNET *et al.* 2001). In the *Testudo* genus, SShD has been even related to the particular features of courtship, which involves the male butting the female's carapace with the thickened gular area of the plastron (WILLEMSEN & HAILEY, 2003). Larger sized abdominal, vertebral and plastral plates in females clearly indicate a direct relation between larger volume and increased clutch size (SEGURA *et al.* 2021).

Altogether, our analyses suggest the interesting potential of particular measurements when conducting sexual dimorphism studies in *T. graeca*. At the same time, we detected 9 measurements that did not conform ANCOVA prerequisites by showing no shared allometry between sexes. Although size-correction is not advisable in such cases (MCCOY *et al.*, 2006), the interaction "size:sex" has been seldom tested in tortoise literature (e.g. CARRETERO *et al.* 2005; DJORDJEVIĆ *et al.* 2011; although see DJURAKIC & MILANKOV, 2019). We, therefore, recommend the standardization of morphometric recording protocols and analytical procedures to generate comparable data and results among research groups.

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