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Righting time versus shell size and shape dimorphism in adult Hermann's tortoises: Field observations meet theoretical predictions

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Abstract

We investigated the relation between righting time (RT) and carapace morphology in 303 adult Hermann's tortoises (*Testudo hermanni* Gmelin, 1789) from two geographically close localities. Their size, shape and body mass, adjusted for size, were significantly different between males and females. Righting time differed among the populations and was related to the ambient temperature and the relative body mass and carapace shape. However, analysis showed that the impact of carapace "form" (shape plus relative body mass) alone had only moderate influence on the variation in righting time ("function"). Both "form" and "function" did not contribute much to the segregation of individuals in geometric space, based on either sex or locality. An interesting detail was that tortoises with a height/width ratio of the shell contour higher than 0.75 had quite a short righting time (less than 100 seconds), which is in accordance with the proposed theoretical model of energy balance of righting in chelonians. We suppose that interactions between general carapace "form", specific components of shell structure, physiological parameters and local environments shape variation in righting response in this species. An interdisciplinary approach combining geometric modeling with traditional biological disciplines would be needed to support this hypothesis.

Keywords

Body mass condition; righting time; sexual shape dimorphism; sexual size dimorphism; shell geometry model; *Testudo hermanni*

Introduction

For chelonians, especially for terrestrial tortoises, their rigid shell is an advantage as well as a limitation. If, for any reason, a tortoise turns on its back, its inability to return to its feet will inevitably lead to death, not only due to dehydration and

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loss of energy, but also from difficulties in breathing and regulation of its body temperature (Stancher et al., 2006). This situation occurs either after falling down from the top of a slope to the foothills in hilly areas, or (exclusively to males) during rival fights and attempts to copulate (Bonnet et al., 2001; Corti & Zuffi, 2003; Willemsen & Hailey, 2003). Righting ability or, more precisely, righting time (RT), is thus a highly adaptive and efficiently performed response for tortoises (Bonnet et al., 2001; Corti & Zuffi, 2003; Stancher et al., 2006).

Domokos & Varkonyi (2008) found that the relation between carapace height and width in chelonians constitutes an important factor regarding their ability to recover prone position. Limb length could be important as well, but has been relatively rarely addressed in morphometric studies (see in Đorđević et al., 2011). Although important for survival (e.g., protection against predators, dehydration, uncomfortable environmental temperatures, or contribution to more efficient digging) (elaborated in Domokos & Varkonyi, 2008), the morphology of the chelonian shell has been mostly used for describing body size and the extent of sexual size and shape dimorphism – SSD and SShD, respectively (Carretero et al., 2005; Loehr et al., 2006; Bonnet et al., 2010; Đorđević et al., 2011). Within the terrestrial genus *Testudo*, sexual differences in the overall shell morphology were interpreted as the outcome of different selection pressures predominantly acting on opposite sexes (Bonnet et al., 2001; Carretero et al., 2005; Ben Kaddour et al., 2008; Đorđević et al., 2013). In *T. hermanni* (the Hermann's tortoise), both SSD and SShD have already been analyzed in detail (Willemsen & Hailey, 2003; Vetter, 2006; Zuffi & Plaitano, 2007; Đorđević et al., 2011), but few studies on the relation between aspects of adaptive shell morphology and RT have been published so far (Zuffi & Plaitano, 2007; Bonnet et al., 2010; Golubović et al., 2013).

Body condition could also be important for the efficient righting of a chelonian. It has been evaluated using many different parameters (elaborated by Bonnet et al., 2001; Willemsen & Hailey, 2002; and others); among them, body mass (BM) is considered as the most practical for field biologists (Jackson, 1980). When scaled by size, BM can provide "an integrative nutritional index", individual mobility parameter (Bonnet et al., 2010), or a reflection of the body mass condition (BMC). If BMC reflects the status of body reserves, then it provides indirect information about habitat quality and reproductive output (Stevenson & Woods Jr., 2006) and could be a decisive factor in righting success (Jackson, 1980; but see in Jacobson et al., 1993). Besides, the potential impact of robustness (contribution of bone and shell elements to body mass), rather than body condition itself, should be considered when interpreting BMC (Carretero, personal communication).

If RT affects survival, then the extent of SSD and SShD related to RT could be constrained by the frequency of righting occurrence and could depend on the dynamics of righting events in local environments. Having at our disposal Hermann's tortoises from somewhat different environments, we were interested to 1) examine the consistency of SSD and SShD in general carapace morphology (including size-corrected BM) in two populations; 2) check for sexual differences in the relation between RT and parameters of general carapace morphology; 3) look for possible inter-population differences regarding the relation between RT and SSD/SShD of the carapace and 4) compare the observed relation between RT and the height/width ratio of the shell contour (R) with the proposed theoretical model of energy balance of righting in chelonians (Domokos & Varkonyi, 2008).

Methods

Species and study sites

The Hermann's tortoise (*Testudo hermanni*) is distributed in Mediterranean Europe, from the coastal area of northeastern Spain in the south-west to European Turkey in the south-east (Gasc et al., 1997). The species is assigned as near threatened in Europe (van Dijk et al., 2004).

Sampling and testing were performed on two wild populations, assigned as P1 and P2 throughout this research. P1: Adult tortoises were collected within 23 ha of a hilly area with steep slopes (average steepness 20%) near Kunovica village (43°18′N; 22°04′E; 324-467 m altitude), in the vicinity of the city of Niš in South-Eastern Serbia. The village is almost completely abandoned, but some orchards and vineyards are still actively maintained by their owners. The study site mostly consists of deciduous forest *Quercetum farnetto-cerris* (Ranđelović et al., 1996), partially degraded into orchards, vineyards and arable land (25%), then pastures and fields (16%) (Turnšek, 2006). The basic substrate is reddish-brown acid soil on red sandstone (Tanasijević & Nikodijević, 1972). Since 2010, this study site has been regularly monitored twice a year for the population dynamics of the Hermann's tortoise. The sample consisted of individuals collected in the second half of May and July in two consecutive years (2010-2011). In both months, females were sporadically seen laying eggs or mating. P2: Adult individuals were collected and measured on a landscape in the form of a natural terrace with a steepness of 0-3%, situated some 70 km south of P1 (43°02′N; 21°52′S; 300-370 m altitude), in the vicinity of Leskovac, a town in Southern Serbia. The locality is an abandoned vineyard, previously run for over 30 years by a big national enterprise, with a total area of 20 ha and with a soil substrate consisting of noncalcareous smonitsa on dacite (Antonović, 1982). These tortoises were collected and measured in the second half of May and in July of 2009, within the scope of a pilot study. The two localities are separated also by the main state highway.

At both localities, the same number of working days per year was dedicated to sampling, with the same number of researchers engaged. At P1, approximately 20 tortoises were seen per day per person, in comparison to 1 tortoise per day per person at P2.

Measurements

The tortoises collected in the field were sexed, weighed and marked at the capture spot with waterproof markers. The unique numbers were written on their plastrons for further recognition until permanent marking was done. After being tested for RT and measured for body size parameters, the tortoises were permanently marked upon first capture, and released on the same day. Adult individuals were recognized on the basis of growth ring patterns on their carapace scutes (Castanet & Cheylan, 1979; Andrews, 1982; Germano, 1988, 1998; Bertolero et al., 2005; Attum et al., 2011). Males were distinguished from females by having a longer and wider tail, curved supracaudal plate and concave plastron (Willemsen & Hailey, 2003). Also, their minimum body sizes were above the threshold values recommended by Hailey (1990) as 130 mm and 150 mm for adult males and females, respectively. Permanent marking was done by filing notches in the marginal scutes by a procedure modified from Stubbs et al. (1984) (see in Đorđević et al., 2011).

Morphometric variables related to body condition included straight carapace length (horizontal straight distance between the front and rear of the carapace with the plastron flat on the substrate) – SCL, and body mass – BM. Additional measurements included curved carapace length – CCL, mid-body carapace width (carapace width at the 6th marginal scute) – MCW, maximum carapace width (carapace width app. at the 8th marginal scute) – MAXCW, and maximum height of the shell – MAXSH. These measurements were described by Bonnet et al. (2001) as descriptors for the general size and shape of a tortoise's shell. Curvilinear measurements were taken using a plastic rope (1 mm precision), while linear ones were taken using a caliper (0.02 mm precision), except MAXSH, which was measured by a device with 1 mm precision. All measurements were done by the same researcher (D.S.). Body mass (BM) was measured on an electronic scale (precision 0.5 g). The general problem here with BM, which could vary up to 100 grams (depending on their current metabolic status), was overcome by letting the tortoises stay in the enclosure for at least 15 minutes before the measuring procedure. All of them expelled their gut and bladder contents either there, or just prior to testing, when handled.

The animals were tested for RT (overturning, flipping) prior to morphometric measurement, in order to avoid additional stress. The righting test was done *in situ*, on a flat, clean surface in the shade, within one hour after collection. Additionally, the air temperature (T_{ext}) referring to the date and hour of the righting test was recorded (http://weatherspark.com/). Every specimen was turned on its back, with its head oriented in the same direction. It is important to underline that the RT recorded in this study summarized two measures of righting response – latency time (time elapsed until the first move after being placed upside-down) and the time to right (duration of the active righting response) (see Bonnet et al., 2001; Delmas et al., 2008). Individuals which did not return to their feet within 15 minutes comprised a relatively small and unbalanced number of tortoises of both sexes (11% of males and 21% of females from P1 and 3% of females from P2) and thus were excluded from further analyses.

In total, 303 records were available for statistical analyses: 90 adult males and 138 adult females from P1, as well as 45 adult males and 30 adult females from P2. Repeated measurements were not included in this data set.

Statistical analysis

The normal distribution of all variables was tested prior to analysis and data were log transformed afterwards. Differences in general body size between sexes and populations were tested by Two-Way Analysis of Variance (ANOVA) on SCL. To exclude doubts that females collected in two seasons may have significantly different BM due to their supposed distinct reproductive status, we also applied an Analysis of Covariance (ANCOVA), with the females' BM as a dependent variable, the population and season as factor variables and SCL as a covariate.

To compare differences between the variability of the altitudes in the two habitats, we used the nonparametric Levene test, which utilizes the method of ranks (Nordstokke & Zumbo, 2010). Altitude data were a priori recorded for each sampled specimen.

For every variable, ANCOVA with sex and population as factors and SCL as a covariate were used to get information about the degree of SShD. For morphometric variables, the significant effect of population would indicate that shape differs among the populations (both sexes). The significant effect of the tortoises' sex (both populations) would be indicative of SShD. If interaction between both factors was significant, then SShD would vary between the populations (McCoy et al., 1994). As there were four defined groups (two sexes × two populations), Scheffé's post hoc tests were performed to determine which groups were different (procedure applied also in Carretero et al., 2005 for three populations of *T. graeca*).

Sexual differences in size and shape, e.g. SSD and SShD were calculated for individual parameters following Willemsen & Hailey (2003) to provide information about the degree and direction of sexual dimorphism.

Forward Stepwise Discriminant Analysis (with tolerance set as 0.005, according to Carretero et al., 2005) was applied to size-corrected morphometric traits and BM for selection of the variables which significantly contribute to overall shape discrimination between sexes and populations. The selected variables were then subjected to Canonical Variate Analysis to produce squared Mahalanobis distances between sexes and populations and thus to obtain quantification of the degree and significance of the overall SShD within the populations (see details in Carretero et al., 2005).

An ANCOVA was performed to test the relation between righting performance (RT as a dependent variable) and general carapace morphology plus ambient temperature (continuous predictor variables: SCL, CCL, MCW, MAXCW, MAXSH, BM, T_{ext}). The effect size of sex and population (i.e., importance of factors) was based on eta-squared (η^2). The eta-squared value, which can range from 0 to 1.0 and is a measure of effect size (Garson, 2009), indicates that variables can have weak ($\eta^2 = 0.01$), intermediate ($\eta^2 = 0.06$) or strong effect ($\eta^2 = 0.14$) on RT (Cohen, 1988).

To increase the statistical power in determining the eventual relationship between carapace morphology and righting ability, we performed a Canonical Correlation Analysis (CCA) with morphological descriptors of general carapace shape & relative BM (residual values of linear morhometric traits and BM regressed on SCL) as the first variable set and residuals of RT regressed on T_{ext} as the second, keeping sex and population as accessory variables (see Kaliontzopoulou et al., 2012). In that way we were able to analyze the relations between “form” (carapace shape & relative BM) and “function” (righting) while keeping the identity and origin of individuals in a multivariate space. The positions of individual canonical correlation scores were then plotted in a two-dimensional space of “function” (x-axis) and “form” (y-axis).

Finally, we calculated the individual height/width ratios of the shell contour (R = MAXSH/MAXCW) following the theoretical shell geometry model by Domokos & Varkonyi (2008), and plotted the values against RT to examine the variation in overturning time within subsequent R classes.

Statistical analyses were processed by Statistica 5.0 and SPSS version 15.0 software.

Results

In the sample of females from P1, differences in relative BM between years and seasons were not detected (ANCOVA – season: MS = 0.003, $F_{1,133} = 2.441$, $P = 0.121$; year: MS = 0.0003, $F_{1,133} = 0.252$, $P = 0.617$; interaction season × year: MS = 0.002, $F_{1,133} = 1.845$, $P = 0.177$). Consequently, we treated all these records as one sample in consecutive statistical procedures. Moreover, females with the same SCL but from different populations had similar BM in the two seasons (ANCOVA – season: MS = 0.0019, $F_{1,163} = 1.392$, $P = 0.240$). There were differences regarding population (ANCOVA – population: MS = 0.0056, $F_{1,163} = 4.199$, $P = 0.042$), but no significant interaction between season and population (ANCOVA – interaction season × population: MS = 0.0006, $F_{1,163} = 0.413$, $P = 0.522$).

The nonparametric Levene test revealed that the habitat of P1 significantly differed ($F = 63.964$; $P < 0.0001$) from the habitat of P2 because of its higher variability in altitude.

Two-way ANOVA on SCL with sex and population as factors pointed to significant SSD and SShD (table 1). Sexual size dimorphism was female oriented: values of the degree and direction of SSD were 13.0 and 16.2 for SCL, and 47.4 and 50.2 for BM (calculated for P1 and P2, respectively). Righting time was not dependent on general body size ($F_{1,298} = 0.223$, $P = 0.64$).

The direction of SShD was also consistent between populations: Parameters CCL (−1.5, −4.6), MCW (−1.9, −2.6) and MAXCW (−4.8, −4.6) were more male oriented, while MAXSH (3.7, 3.1) and relative BM (11.1, 5.8) were more female oriented (P1 and P2, respectively). Males from P1 had more voluminous shells, but males from P2 had more domed (curvilinear) ones. Furthermore, females from P2 had more domed and less rounded shells.

Table 1.
Descriptive statistics for the morphometric variables (measures are in mm, except body mass which is in g) and RT (measures in s) and AN(C)OVA comparisons for site and sex; all but the first using SCL as a covariate.

Variable	P1		P2		AN(C)OVA (sex, site, sex × site)		
	Males $N = 90$	Females $N = 138$	Males $N = 45$	Females $N = 30$	*F*	*df*	*P*
SCL	175.1 ± 1.2	197.9 ± 12.2	171.1 ± 10.2	198.8 ± 19.2	220	1, 299	<0.0001
	146.4-198.2	161.6-225.1	148.1-195.2	151.9-245.7	1	1, 299	0.26
					2	1, 299	0.18
CCL	232.9 ± 1.6	254.3 ± 14.9	228.6 ± 14.7	247.4 ± 21.0	26.75	1, 298	<0.0001
	180.0-262.0	198.0-285.0	190-257	204.0-304.0	10.74	1, 298	0.001
	(243.7)	(240.0)	(243.9)	(232.7)	11.69	1, 298	0.0007
MCW	135.6 ± 0.8	145.6 ± 7.5	133.7 ± 8.0	145.4 ± 10.7	19.20	1, 298	<0.0001
	117.0-151.0	124.5-162.9	113.0-156.6	122.1-174.2	0.08	1, 298	0.78
	(141.1)	(138.4)	(141.5)	(137.80)	0.76	1, 298	0.38
MAXCW	144.7 ± 0.9	151.0 ± 8.0	144.7 ± 10.4	154.3 ± 10.9	64.57	1, 298	<0.0001
	119.6-160.3	127.4-173.1	115.8-174.6	130.0-182.8	15.48	1, 298	0.0001
	(150.7)	(143.40)	(153.2)	(146.2)	0.08	1, 298	0.77
MAXSH	91.0 ± 0.6	102.0 ± 1.0	88.2 ± 5.7	99.8 ± 7.6	14.06	1, 298	0.0002
	70.0-105.0	83.0-120.0	77.0-100.0	87.0-120.0	9.05	1, 298	0.003
	(94.1)	(97.60)	(92.5)	(95.3)	0.20	1, 298	0.66
BM	1089.9 ± 19.9	1606.5 ± 26.6	1052.8 ± 178.2	1580.6 ± 323.8	31.92	1, 298	<0.0001
	615.0-1507.0	932.0-2135.0	629.0-1592.0	910.0-2475.0	0.21	1, 298	0.64
	(1223.0)	(1358.6)	(1246.7)	(1319.4)	4.94	1, 298	0.03
RT	252.1 ± 21.3	277.8 ± 19.1	119.3 ± 128.3	148.3 ± 143.8	0.42	1, 298	0.52
	10.0-859.0	5.0-897.0	9.0-587.0	7.0-495.0	36.10	1, 298	<0.0001
	(168.3)	(186.2)	(70.2)	(80.8)	0.02	1, 298	0.89

Numbers within P1 and P2 columns indicate mean ± standard error, minimum and maximum values. Adjusted means are presented in parentheses. Abbreviations of variables are defined in the manuscript. N = sample size.

Although not significantly different, RT was consistently longer in females (table 1). This difference was more pronounced in P2 (the degree and direction of sexual difference for RT, using adjusted means from ANCOVA, was 10.6 and 15.2 for P1 and P2, respectively). Righting time was not considered sexually dimorphic, but it differed between populations: the tortoises from P2, on average, were taking less time to flip back (table 1).

Forward Stepwise Discriminant Analysis showed that variable MCW was not significantly involved in a model describing carapace shape. The traits most contributing to SShD were MAXCW, then BM, CCL and MAXHS. The overall SShD, represented by squared Mahalanobis distances between sexes within the sam-

Table 2.
P values of the post-hoc Scheffe's test, performed on adjusted means from ANCOVA with sex and population as factors and SCL as a covariate variable.

	P1		P2	
	M	F	M	F
Size-corrected CCL				
P1M		<0.0001	0.03	<0.0001
P1F	<0.0001		<0.0001	0.001
P2M	0.03	<0.0001		<0.0001
Size-corrected MCW				
P1M		<0.0001	0.06	<0.0001
P1F	<0.0001		<0.0001	0.97
P2M	0.06	<0.0001		<0.0001
Size-corrected MAXCW				
P1M		<0.0001	1.000	<0.0001
P1F	<0.0001		<0.0001	0.02
P2M	1.000	<0.0001		<0.0001
Size-corrected MAXSH				
P1M		<0.0001	0.008	<0.0001
P1F	<0.0001		<0.0001	0.18
P2M	0.008	<0.0001		<0.0001
Size-corrected BM				
P1M		<0.0001	0.16	<0.0001
P1F	<0.0001		<0.0001	0.51
P2M	0.16	<0.0001		<0.0001
Size-corrected RT				
P1M		0.76	<0.0001	0.02
P1F	0.76		<0.0001	0.002
P2M	<0.0001			0.88

ples (P1 = 1.47, P2 = 1.44), was statistically highly significant ($df = 4, 296$; $P < 0.0001$ in both cases). Post-hoc Scheffe's tests from CVA (table 2) proved the presence/absence of SShD in characters, already presented in table 1.

The ANCOVA revealed that RT was significantly longer for specimens in population 1 than in population 2 (tables 1 and 3). In addition, 4 out of 6 morphological covariates included in the ANCOVA as well as T_{ext} had a significant effect on RT. These factors explained the different proportions (η^2) of the observed variability of RT with the removed effect of population (table 3). The effect size of carapace shape components, relative BM and T_{ext} on variation in RT was low but significant. Only the population factor showed an intermediate effect on righting time.

Canonical correlation analysis confirmed a significant but low relation ($r = 0.30$, $df = 5$, $P = 0.00004$) between "form" (first variable set) and "function" (second

Table 3.
ANCOVA with RT as a dependent variable, population and sex as fixed factors and SCL, CCL, MAXCW, MAXSH, BM and T_{ext} as predictor variables.

	SS	Df	MS	F	P	η^2
Intercept	2.05	1	2.05	10.99	0.001	0.04
log10SCL	0.30	1	0.30	1.63	0.20	0.006
log10CCL	0.20	1	0.20	1.08	0.30	0.004
log10MCW	0.93	1	0.93	4.98	0.03	0.02
log10MAXCW	0.89	1	0.89	4.78	0.03	0.02
log10MAXSH	2.08	1	2.08	11.14	0.001	0.04
log10BM	1.84	1	1.84	9.85	0.002	0.03
log10T_{ext}	1.80	1	1.80	9.66	0.002	0.03
Sex	0.07	1	0.07	0.35	0.55	0.001
Pop	4.84	1	4.84	25.93	<0.0001	0.08
Sex × Pop	0.11	1	0.11	0.60	0.44	0.002
Error	54.54	292	0.19			

variable set). The first variable set described only 11.41% of the overall variance while the second accounted for the remaining 88.59%. It is likely that the "form" predicted 8.11% of the average proportion of variance in "function". The "form" canonical vector of association was most highly correlated with relative BM (0.16) and size-corrected MAXCW (−0.11), followed by size corrected MCW (0.09) and MAXSH (−0.09). Again, relative CCL was very slightly correlated (0.002). Both populations and sexes were apparently overlapping in multivariate space defined by the canonical correlation axes of form (x) and function (y) (fig. 1).

On the plot of R *versus* RT (fig. 2), most of the tortoises (around 76%) fitted into the group of R values between 0.61 and 0.70. The remaining 23% of the entire sample entered either the group with R values between 0.51 and 0.60 or the group with R values between 0.71 and 0.80. Approximately 3% of individuals had an R ratio either less than 0.55 or higher than 0.75.

Discussion

Consistency in the direction and extent of SSD/SShD in Hermann's tortoises

In Hermann's tortoises, the direction of SShD in general carapace morphology has been recognized as quite resistant to the influence of environmental factors (elaborated in Đorđević et al., 2011). Nevertheless, our results suggest a variation in the degree of sexual dimorphism on a small geographic scale, similar to the study by Carretero et al. (2005) on *T. graeca* in west-central Morocco. In our study only CCL and relative BM showed significant variation in the extent of SShD. Curved

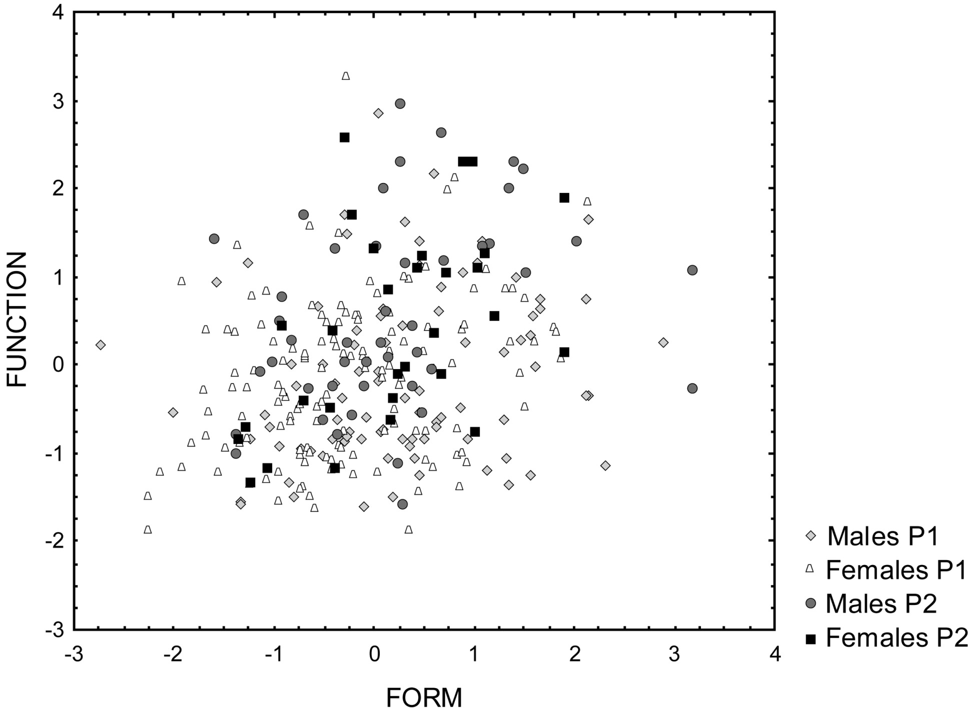

Figure 1. Scatter-plot of individual canonical correlation scores obtained from an analysis of the relation between FORM (carapace shape) on the x-axis and FUNCTION (temperature-corrected RT) on the y-axis. Symbols: P1 males (diamonds), P1 females (triangles), P2 males (circles) and P2 females (squares).

carapace length is supposed to be driven by sexual selection in males (Bonnet et al., 2001; Willemsen & Hailey, 2003), but it could also be a reflection of natural selection *sensu stricto* (e.g., the importance of thermoregulation, see Sacchi et al., 2007). When considering relative body mass, heavy females imply greater fecundity, while light males suggest more mobility (Bonnet et al., 2001). If the extent of such a sexual dimorphism significantly differs among localities, it could be a reflection of a difference in the quality of the environment.

Alternatively, the differences in the extent of SShD on a small geographic scale may result from phenotypic plasticity effects. In explaining the discrepancy between the low genetic divergence and apparent morphological variation among *T. graeca*, Carretero et al. (2005) proposed environmental impact on early developmental stages as an alternative to direct selection pressure. Experiments on another chelonian, *Chelydra serpentina*, demonstrated the existence of plasticity in SShD and a similar response of both sexes to different environments (Ceballos & Valenzuela, 2011). All this suggests the importance of adding genetic analyses and experimental manipulation in future studies on this topic.

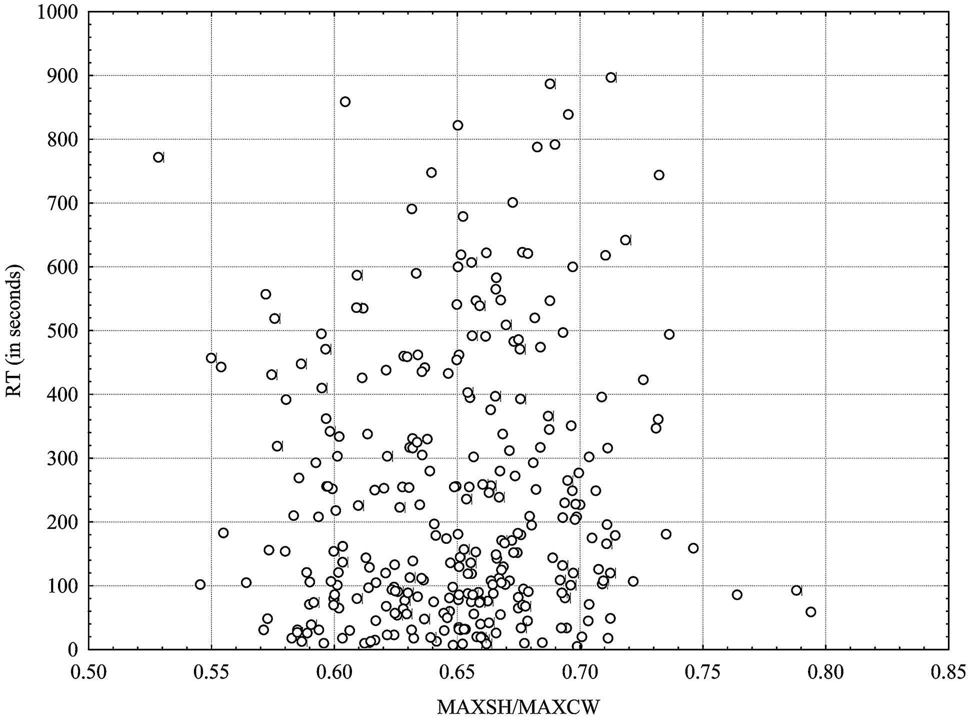

Figure 2. Distribution of individual R-values (R = MAXSH/MAXCW). For abbreviations see *Measurements* subsection.

Relation between RT and parameters of general carapace morphology

Body size was previously recognized as one of the factors affecting righting ability (Burger et al., 1998). However, sexual differences in RT have only been detected so far for certain components of righting response (Bonnet et al., 2001 for *T. horsfieldii* in the field; Delmas et al., 2008 for *Trachemys scripta elegans*, under constant incubation conditions) and recently for overall righting success in four wild populations of *T. hermanni* (Golubović et al., 2013). We found an obvious lack of sexual differences in RT in the two populations of Hermann's tortoise studied, despite observed SSD in general carapace morphology. Additionally, we proved that RT was partially controlled by traits describing both carapace shape and relative BM, but not by body size.

We demonstrated the overall association between general carapace form and duration of specific performance ability (righting). The combination of a large relative BM and narrow posterior base of carapace, accompanied by the combination of a wide and flattened shell, prolonged overturning. Nevertheless, the moderate power of proposed carapace "form" in explaining the overall variation in RT points out the necessity to include additional parameters in future analyses: limb length, muscle mass, metabolic activity, or more subtle components of carapace shape (Zuffi &

Plaitano, 2007; Golubović et al., 2013). A high association between morphology and function is perhaps expected if both sets of traits express correlated sexual dimorphism (see, for example, Kaliontzopoulou et al., 2012). In our study, moderate, but statistically significant, overall correlation between carapace form and RT could stem from a discrepancy between obvious sexual dimorphism in the body form and the absence of sexual divergence in righting performance.

Inter-population differences in relation between RT and general carapace morphology

We found a significant population effect on variation in RT. Moreover, our observations demonstrate that tortoises from the more open and less steep locality required, on average, less time for overturning. Different environments provoke different selective pressures on populations and it could happen that two populations living in seemingly similar surroundings apparently differ in their quality of nourishment and/or in the microhabitats' attributes (Wiesner & Iben, 2003). Also, differences in phenotypic expression cannot be neglected: the long-lasting effect of incubation temperature on righting behaviour was shown in two emydid terrapin species (Freedberg et al., 2004).

We also looked for differences in association between "form" and "function" in these two populations. Righting time was controlled by several sexually dimorphic traits that also describe the general carapace "form", but we detected only mild inter-population differences in the extent of sexual dimorphism regarding relative BM (the trait which was mostly associated with the overall correlation of carapace "form" to duration of overturning). On the contrary, there was strong between-population difference in the extent of SShD in CCL – the trait not controlling RT. Various sources suggested different adaptive roles of CCL, related to sexual selection (Bonnet et al., 2001; Willemsen & Hailey, 2003), natural selection *sensu stricto* (Sacchi et al., 2007), or perhaps both. In our study, sexual dimorphism in CCL was more pronounced in the environment where we assumed that quick righting more notably contributes to survival. Obviously, CCL may have a more complex role in overall reproductive success in Hermann's tortoises.

Concordance of field observations and theoretical predictions regarding relation of shell shape to RT

Regarding carapace components generally important for the successful righting of a chelonian (Domokos & Varkonyi, 2008), we found that they only partially controlled RT in the Hermann's tortoise. However, surprisingly concordant with the theoretical predictions of Domokos & Varkonyi was the substantially shorter and more uniform RT in tortoises with an R ratio higher than 0.75 compared to those with less domed carapaces. In the theoretical model of Domokos & Varkonyi, which describes the energy balance of overturning, efficient self-righting in relatively short-necked chelonians (which the *Testudo* species are) without exception occurred at R values of 0.74-0.75 or higher. This remarkable concordance between measured field data and theoretical prediction is exceptional, as the latter were based on purely geometrical and mechanical considerations (Domokos, personal communication). Since only three specimens of the group with R values higher than 0.75 were recorded, we could not perform any statistical verification of the displayed RT distribution pattern. This stresses the need for further investigation with more balanced samples which could enable the statistical confirmation of the distribution patterns shown in our study.

In conclusion, RT in this species can be shaped by the interaction of general carapace "form", specific components of shell structure, physiological parameters and local environments. Consequently, there are many external factors summarized as "population effect": climate variation, landscape features, subtle differences in environmental temperatures, quality of nourishment, etc. (Highfield, 1989; Freedberg et al., 2004; Elnitsky & Clausen, 2006; Golubović et al., 2013). Even though sexual difference in RT was not found in this study we assume that RT could be sexually dimorphic depending on the strength and direction of both selection for survival and selection for reproduction in local environments. However, the intriguing question of what shapes the relation between RT and SSD/SShD in chelonians cannot be answered without an interdisciplinary approach combining geometric modeling with traditional biological disciplines. This approach could be important in applied chelonian conservation for recognizing the key features of optimal refugium when translocation of an individual population is considered as the solution for its preservation.

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