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Variations in righting behaviour across Hermann's tortoise populations

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Abstract

In terrestrial animals with rigid protective structures, the ability to upright after being overturned can make the difference between life and death, especially in suboptimal thermal conditions or in the presence of predators. This trait is assumed to be under strong selection. Different factors can influence righting ability, body dimensions and body mass for instance. As these morphological traits diverge among populations, inter-population variability in righting ability is expected. Previous studies on tortoises were performed within single populations and they usually focused on juveniles raised in captivity, precluding an assessment of the inter-population variability in a natural (realistic) context. In the current study, we quantified the righting performance in four populations of free-ranging adult tortoises. We found strong differences in righting success among populations and between genders, suggesting possible adaptations to local conditions. For instance, the topography (e.g. slopes) of each study site varied markedly. On average, males were more successful in righting themselves than females. Body size did not influence righting performances in males, but larger females were less successful compared to smaller ones. The success in righting was positively correlated with carapace domedness (height) and short bridges.

Introduction

Righting ability (returning oneself to an upstanding position after having been overturned) is an important characteristic for armoured animals belonging to various lineages – notably insects (Delcomyn, 1987; Faisal & Matheson, 2001; Frantsevich, 2004), crustaceans (Silvey, 1973) and chelonians (Bonnet *et al*., 2001; Steyermark & Spotila, 2001; Delmas *et al*., 2007). Heavily armoured individuals flipped onto their dorsum are vulnerable. They cannot easily escape predation; they are exposed to dehydration, overheating or freezing (Penn & Brockmann, 1995; Bonnet *et al*., 2001; Corti & Zuffi, 2003), and their mating success can be affected (Penn & Brockmann, 1995). Righting response has been considered as an indicator of fitness by different authors (Burger *et al*., 1998; Steyermark & Spotila, 2001; Ashmore & Janzen, 2003; Corti & Zuffi, 2003; Freedberg *et al*., 2004; Delmas *et al*., 2007; Zuffi & Plaitano, 2007).

However, no study has yet investigated the consequences of variations in righting ability on fitness-relevant traits: survival, reproductive success or growth, for instance. Therefore, although intuitive, the importance of righting ability on individual fitness remains an open question. Comparisons between populations offer a means to address this issue. Assuming that righting ability is subjected to selection, variations among populations are expected.

Terrestrial chelonians (i.e. tortoises) are suitable organisms to examine the importance of variations in righting ability. These reptiles are relatively heavy when adult, their body is enclosed into a rigid shell, they posses short yet powerful limbs; such body plan does not allow high manoeuvrability. Overturned tortoises face severe difficulties to right themselves; in large species, heavy individuals can fail to flip back on their legs despite vigorous efforts.

Free-ranging tortoises may be flipped on their back accidentally during displacements by predators, rivals or uncooperative females during sexual interactions (Bonnet *et al*., 2001). In flat habitats, the risk of being flipped on the back is presumably low compared to uneven habitats where individuals must move across steep slopes and over various obstacles (e.g. steps; Golubović *et al*., 2013). Therefore, overturning ability might be influenced by topography. Several other factors are likely determinants, notably body size and body shape (Bonnet *et al*., 2001; Domokos & Varkonyi, 2008). As differences between sexes in mean body size (sexual size dimorphism, SSD) and body shape have been documented across tortoise populations (e.g. Willemsen & Hailey, 2003; Djordjević *et al.*, 2011), differences in righting ability between males and females are also expected.

Righting performances have been examined in juvenile freshwater turtles (Burger, 1976; Miller, Packard & Packard, 1987; Brooks *et al.*, 1991; Janzen, 1993; Finkler, 1999; Demuth, 2001; Steyermark & Spotila, 2001; Du & Ji, 2003; Freedberg *et al.*, 2004) but rarely in terrestrial species or adults (Bonnet *et al.*, 2001; Mann, O'Riain & Hofmeyr, 2006; Stancher *et al.*, 2006). Furthermore, previous investigations were usually conducted in captivity, that is, under standardized conditions; rare are those performed under natural conditions (Bonnet *et al.*, 2001) and none compared different environments. Overall, we still have very incomplete information on the variability of righting performances in free-ranging tortoises. The current study reports the first comparative data that aim to explore if environmental conditions, bodily dimensions and sex influence righting performances in adult tortoises from four populations.

Methods

Species description

The Hermann's tortoise, *Testudo hermanni*, is a medium-sized species, with females typically being larger than males (e.g. Vetter, 2006). This species is distributed in the Mediterranean parts of the Iberian, Apennine and Balkan Peninsulas, as well as in some Mediterranean islands and the European part of Turkey (Türkozan *et al.*, 2005; Fritz *et al.*, 2006).

Study sites

We sampled four populations in the central Balkans (Serbia and Former Yugoslav Republic of Macedonia). Strong differences exist among the four localities in terms of configuration of the terrain (see Table 1).

Field protocol

We processed 481 adults directly in the field: 184 females and 297 males. The following morphological measurements were recorded: straight carapace length (SCL, in millimetres); body mass (BM, in grams); shell height (SH); anal notch width (ANW); bridge length, left (BL L); bridge length, right (BL R); forelimb length, left (FLL L); forelimb length, right (FLL R); hind limb length, left (HLL L); and hind limb length, right (HLL R, all in millimetres; for details see Djordjević *et al.*, 2011). Females larger than 15 cm SCL and males larger than 13 cm were considered as adults (Hailey, 2000).

Each animal was turned on its dorsum and placed on the nearest flat surface, then it was given 10 min to turn back on its legs; the test was interrupted in case of failure and the tortoise was manually redressed. Righting performance was coded as follows: righting success (RS: whether an animal managed to right itself or not Y/N); reaction time (RT: time from the start of the test until the first leg, head or tail movements, in seconds); latency time (LT: time from the first reaction until the first furious waving of legs, head or tail, in seconds; as in Delmas *et al.*, 2007); and net time to right (NT: time elapsed from the first furious waves of legs, head or tail until righting, in seconds). Data from animals that failed to right themselves were discarded from several analyses (e.g. NT comparisons). Regardless of the righting success, each animal was tested only once.

All individuals were immediately released at the place of capture after being measured and tested.

Statistical analyses

Two-factor analyses of variance (ANOVAs; with sex and locality as factors) and *post hoc* tests were used to examine differences in body size (SCL). Similar analyses (with RS and locality as factors) were used to test whether body size (i.e. SCL and BM) influenced RS among localities considering genders separately. In order to check for the influence of different morphological traits (SH, ANW, BL_L, BL_R, FLL_L, FLL_R, HLL_L and HLL_R) on RS regardless of overall body size, we used two-factor analysis of covariance (ANCOVA), with sex and RS as factors, morphological traits as dependent variables and SCL as covariate.

As the data were not normally distributed, differences between genders and among localities in RT, LT and NT were analysed using non-parametric Mann–Whitney *U*-test and Kruskal–Wallis ANOVA, respectively.

Differences between genders and among localities in RS were examined using χ^2 tests.

Results

Inter-population differences in body size and SSD

Two-factor ANOVAs (with sex and locality as factors) revealed significant differences among sexes and localities in body size (SCL – sex effect $F_{1,478} = 155.24$, $P < 0.001$,

Table 1 Configuration of the terrain and numbers of successful and unsuccessful females and males in each locality

Locality	Golem Grad island	Konjsko village	Pčinja River Valley	Trstenik
Configuration of the terrain	High cliffs, rocky terrain	Gentle slopes, with scattered rocks	Gentle slopes, with scattered rocks	Gentle slopes, without rocks
Righted (F/M)	9/51	34/51	37/91	26/29
Failed (F/M)	8/21	17/6	35/37	18/11

Table 2 *Post hoc* (Tukey's unequal N HSD) test between sexes and among populations

Sex & LOC	F GG	F KO	F PV	F TS	M GG	M KO	M PV	M TS
F GG		0.001	0.000	0.000	0.912	0.995	0.996	0.997
F KO	0.020		0.977	0.694	0.000	0.000	0.000	0.000
F PV	0.003	0.979		0.994	0.000	0.000	0.000	0.000
F TS	0.000	0.551	0.972		0.000	0.000	0.000	0.000
M GG	0.958	0.000	0.000	0.000		0.980	0.001	0.989
M KO	0.969	0.000	0.000	0.000	1.000		0.093	1.000
M PV	1.000	0.000	0.000	0.000	0.022	0.090		0.302
M TS	0.649	0.000	0.000	0.000	0.966	0.947	0.011	

Upper right part of the table – body mass; lower left part – straight carapace length.
F, females; GG, Golem Grad; KO, Konjsko; M, males; PV, Pčinja Valley; TS, Trstenik.

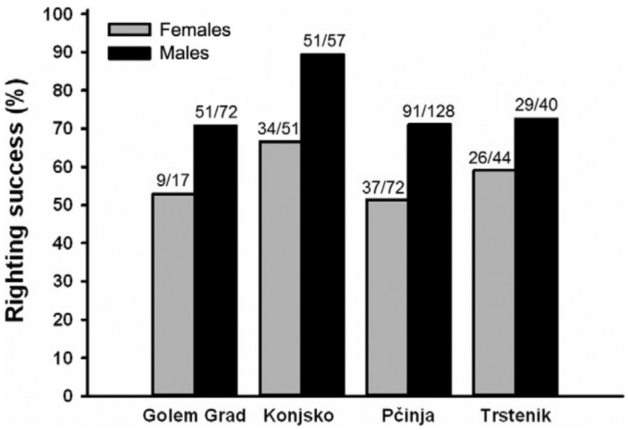

Figure 1 Percentage and numbers of individuals that managed to right themselves (of totals) per gender and locality: males (χ^2 test = 9.39, d.f. = 3, $P = 0.025$) and females (χ^2 test = 3.08, d.f. = 3, $P = 0.380$).

locality effect $F_{3,478} = 13.02$, $P < 0.001$, interaction $F_{3,478} = 9.74$, $P < 0.001$; BM – sex effect $F_{1,478} = 176.51$, $P < 0.001$, locality effect $F_{3,478} = 19.73$, $P < 0.001$; interaction $F_{3,478} = 7.89$, $P < 0.001$). *Post hoc* (Tukey's unequal N HSD) test was performed in order to provide more precise information about the above-mentioned differences (Table 2). For instance, sexual dimorphism in body size was recorded in three populations but not in the fourth (Golem Grad). In addition, females from Golem Grad were smaller compared to the three other populations.

Influence of sex and body size on righting performances

We found strong difference between the sexes in RS (localities pooled). Males were more efficacious in righting themselves (74.7%, 222 of 297 total) compared with females (57.6%, 106 of 184 total; $\chi^2 = 15.39$ d.f. = 1, $P < 0.001$; Table 1 and Fig. 1). Females and males did not differ in any of the other righting response components assessed (RT, LT and NT; Mann–Witney *U*-test, $P > 0.05$ in all cases; Table 3).

Because we found strong differences in body size between the sexes and among populations, we performed two-factor ANOVAs with body size as the dependent variable and RS and locality as factors in each sex separately. The results showed that females that managed to right themselves were smaller ($F_{1,175} = 10.85$, $P = 0.001$) and that size diverged among localities (locality effect: $F_{3,181} = 11.60$, $P < 0.001$, interaction $F_{3,182} = 0.25$, $P = 0.863$; Fig. 2). Analyses of BM provided similar results (RS effect $F_{1,174} = 13.07$, $P < 0.001$; locality effect: $F_{3,181} = 15.53$, $P = 0.000$; interaction $F_{3,182} = 0.52$, $P = 0.667$). We did not find size differences between 'successful' and 'unsuccessful' males either using SCL (RS effect: $F_{1,289} = 0.36$, $P = 0.547$; locality effect: $F_{3,296} = 9.75$, $P < 0.001$; interaction $F_{3,296} = 1.61$, $P = 0.187$) or BM ($F_{1,289} = 1.06$, $P = 0.304$; locality effect: $F_{3,296} = 10.90$, $P < 0.001$; interaction $F_{3,296} = 1.85$, $P = 0.138$).

Influence of other morphological traits on righting performances

We tested the potential influence of other morphological traits (SH, ANW, BL_L, BL_R, FLL_L, FLL_R, HLL_L and HLL_R) on the RS of males and females. The results showed that only SH ($F_{1,338} = 4.2$, $P = 0.040$) and BL R ($F_{1,338} = 8.5$, $P = 0.004$) influenced RS (Table 4). However, morphological traits differed between the sexes ($P < 0.001$ in all cases), suggesting significant sexual dimorphism in body shape. Females had significantly higher mean values of the BL and SH, while males exhibited relatively longer front and hind legs and wider ANW ($P < 0.001$ in all cases). Raw and adjusted means of the morphological traits are given in Table 4.

Inter-population differences in righting success

Pooling the sexes, we found differences in RS among localities (χ^2 test = 7.81, d.f. = 3, $P = 0.050$). A closer inspection of the data revealed that RS differed among localities in males (χ^2 test = 9.39, d.f. = 3, $P = 0.025$) but not in females (χ^2 test = 3.08, d.f. = 3, $P = 0.380$; Table 1, Fig. 1). As we found no size effect on righting response in males, it was not necessary to control for this factor.

Table 3 Mean values ± SD and sample sizes (N) of reaction time (RT in seconds), latency time (LT in seconds) and net time to right (NT in seconds) in females and males of *Testudo hermanni* from four populations

Locality	Sex	RT	N	LT	N	NT	N
Golem Grad	Females	13.8 ± 14.44	9	4.1 ± 5.99	9	299.6 ± 166.05	9
	Males	23.7 ± 32.83	51	23.8 ± 29.38	51	215.0 ± 154.84	51
Konjsko	Females	65.4 ± 71.93	34	40.2 ± 49.43	34	114.1 ± 113.55	34
	Males	53.7 ± 52.07	51	34.6 ± 62.70	51	80.9 ± 98.00	51
Pčinja Valley	Females	27.6 ± 27.65	37	15.6 ± 15.34	16	253.2 ± 144.27	37
	Males	31.8 ± 28.94	91	27.9 ± 34.69	67	226.1 ± 140.65	91
Trstenik	Females	46.9 ± 36.80	26	39.8 ± 51.80	26	184.3 ± 131.85	26
	Males	49.7 ± 72.04	29	44.5 ± 53.84	29	185.8 ± 137.04	29

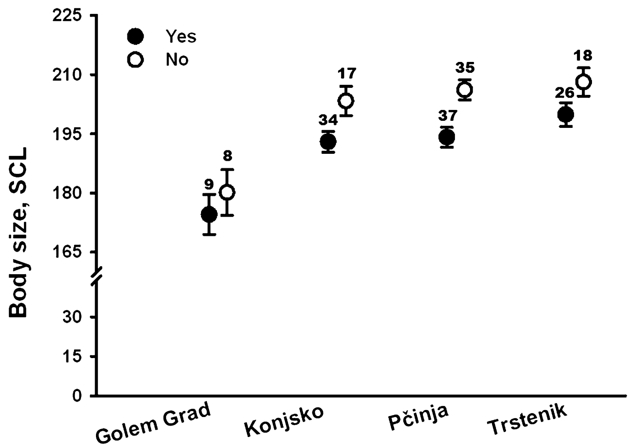

Figure 2 Mean values and sample sizes (N) of straight carapace length (SCL in mm) of females that righted themselves or not at each locality. Righting success effect ($F_{1,175} = 10.85$, $P = 0.001$) locality effect ($F_{3,181} = 11.60$, $P < 0.001$).

Contingency tests with sex and locality as the independent variables and RS as the dependent variable showed that sexes did not differ in RS in the Golem Grad island (χ^2 test = 2.00, d.f. = 1, $P = 0.157$) and Trstenik (χ^2 test = 1.67, d.f. = 1, $P = 0.197$), but males from the Pčinja River Valley (χ^2 test = 7.77, d.f. = 1, $P = 0.005$) and Konjsko village (χ^2 test = 8.35, d.f. = 1, $P = 0.004$) righted themselves more frequently than females (sample sizes are provided in Table 1).

Pooling the sexes, the mean RT differed among localities (Kruskal–Wallis ANOVA, $H_{3,454} = 16.81$, $P < 0.001$), with the higher mean values observed in Konjsko and the lower in Golem Grad (Table 3). Mean NT also differed among localities (Kruskal–Wallis ANOVA, $H_{3,328} = 72.06$, $P < 0.001$), with the shortest time in Konjsko and the longest in Golem Grad and Pčinja Valley (Table 3). LT did not differ among localities.

Discussion

This study reports the first results revealing significant variations of righting performance across free-ranging tortoise populations, supporting the notion that this trait could be subjected to selection in different habitats or conditions (e.g. sex ratio, population density).

Inter-population differences in body size and SSD

SSD, with larger females, and geographic variations of this trait have been documented across populations of Hermann's tortoises (e.g. Willemsen & Hailey, 2003; Djordjević *et al.*, 2011). This study therefore confirms previous results. The lack of SSD in one population, Golem Grad, was remarkable however. Females from this locality were relatively small compared with other populations, that is, averaged similar size as males. The strong variations in body size and SSD we observed across populations were possibly due to contrasted food and thermal conditions, an issue out of scope of the current study (Willemsen & Hailey, 1999).

Influence of sex and body size on righting performances

Males were smaller and more successful in righting than females. Although any tortoise can be overturned accidentally (e.g. during displacements), adult males are far more exposed to this risk compared with all the other age/sex categories (e.g. juveniles, adult females). Indeed, only males can be flipped onto their back during male-to-male combats or by reluctant females (Lagarde *et al.*, 1999, 2002; Bonnet *et al.*, 2001; Mann *et al.*, 2006). Therefore, the greater ability of males to right themselves was expected, and this effect has been documented in other species (Bonnet *et al.*, 2001). Nonetheless, we did not observe any sex difference in the other characteristics of the righting response: RT, LT and NT. These latter elements describe the willingness of the individuals to escape from a perilous (at least uncomfortable) situation. This suggests that individuals of both sexes exhibited similar 'motivation' to right themselves, but that males were more agile to achieve this manoeuvre.

We found a strong effect of body size on RS in females. This study shows that smaller females may have an advantage over larger ones if accidentally overturned. On the other hand, the larger mass of bigger females confers stability. This size effect

Table 4 Means, adjusted means and sample sizes (N) of shell height (SH), anal notch width (ANW), bridge length, left and right (BL_L, BL_R), forelimb length, left and right (FLL_L, FLL_R), hind limb length, left and right (HLL_L, HLL_R; all in millimetres) of females and males, which were successful in righting test (FY, MY) and failed to right themselves (FN, MN), respectively

Group		SH	ANW	BL_L	BL_R	FLL_L	FLL_R	HLL_L	HLL_R	N
FN	Mean	100.2	40.0	88.4	88.1	48.0	47.9	57.1	57.0	71
	Adjusted mean	98.0	39.2	86.3	86.1	47.0	46.9	55.8	55.8	
FY	Mean	96.8	39.3	84.1	83.5	46.0	46.0	54.5	54.5	102
	Adjusted mean	99.0	40.2	86.0	85.4	47.0	47.0	55.8	55.7	
MN	Mean	86.4	56.6	63.7	64.1	46.7	46.4	53.5	53.7	55
	Adjusted mean	85.8	56.0	63.7	64.1	46.6	46.4	53.1	53.2	
MY	Mean	86.1	54.8	62.5	62.4	45.1	44.9	52.1	52.1	177
	Adjusted mean	87.2	55.5	63.4	63.3	45.7	45.6	52.8	52.9	

may also mirror differences in space utilization between females of different size – an issue not yet investigated.

On the contrary, body size had no effect on RS in males. In male tortoises belonging to the *Testudo* genus, locomotor performances promote reproductive success, while the risk of being overturned is important under natural conditions (Lagarde *et al*., 1999; Bonnet *et al*., 2001; Willemsen & Hailey, 2003); selection may thus favour relatively smaller body size and enhanced agility in this sex (Berry & Shine, 1980). The combination of these traits (small size and agility) may lead to pronounced righting ability; thus, a possible size effect could be blurred.

Influence of other morphological traits on righting performances

SH and BL played significant role in RS. Tortoises with shorter bridge relative to body size were more successful in righting themselves. Relative BL illustrates a trade-off between mobility and protection; a small bridge provides space for leg movements but also exposes soft tissues to predators (Bonnet *et al*., 2001; Zuffi & Plaitano, 2007). Individuals with a more domed carapace (i.e. greater SH) were more successful to right themselves. Domedness increases instability of overturned individuals and, thus, helps them to flip back on their legs. This result has been documented both in the field and in captivity (Bonnet *et al*., 2001; Domokos & Varkonyi, 2008). Although not novel, these correlations clearly show that our field procedure and measurements were appropriate to assess the relationships between morphological traits and righting ability. However, one expected effect was not observed. Bonnet *et al*. (2001) suggested that in males, relatively longer legs favour righting ability. Although male Hermann's tortoises do also exhibit longer legs (Willemsen & Hailey, 2003; Djordjević *et al*., 2011) and greater righting performances than females, we found no effect of limb length on RS. Perhaps muscular strength or joint flexibility are more important traits for righting performances in this species; further investigations (e.g. on skeletons) are thus required. Additionally, the wide space for the legs and tail movements (provided by ANW and BL), not the limb length *per se*, could be significant to increase righting ability in males (see also Bonnet *et al*., 2001; Mann *et al*., 2006).

Inter-population differences in righting success

We found differences between populations (localities) in RS and in other characteristics of the righting response (RT and net time until righting). We expected that tortoises from uneven habitats would display greater RS compared with tortoises from flat habitats. Instead, the tortoises from Konjsko (gentle habitat) were more successful to right themselves (RS ~ 80%) than those from Golem Grad (uneven habitat, RS ~ 70%). Thus, other important factors must be involved. Sex differences in RS were found in two localities (in Pčinja River Valley and in Konjsko village, males were more successful) but not in two others (Golem Grad and Trstenik). We hypothesize that in Golem Grad, characterized by high and dangerous cliffs and a very rugged environment, risky behaviours, including attempts to flip over the rivals might be counter-selected; in this site, the tortoises of both sexes might be inexperienced and poorly efficient to right themselves (low mean RS and absence of sex difference). We acknowledge, however, that an explicit relationship between righting ability and habitat type was not supported by the patterns we observed. The documented inter-population differences could be the result of different environmental (e.g. predator densities and vegetation) and population characteristics (e.g. sex ratio and population density).

In conclusion, our main results suggest that righting ability is a trait that does not vary randomly and, thus, is likely under selection. RS is influenced by several factors: gender, body size and likely habitat configuration. However, these factors are associated with specific and sometimes antagonistic morpho-functional constraints: agility provided by a light shell trade-offs against protection (Stearns, 1992). Therefore, increasing righting ability competes against other morphological and behavioural traits; this effect should be considered (and measured) to better assess the biology of terrestrial tortoises and possibly other heavily armoured animals.

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