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Moving in the real world: tortoises take the plunge to cross steep steps

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Despite exhibiting low velocity and limited agility, many tortoises undertake large scale movements and must overcome various obstacles, notably in populations living in hilly or rocky habitats. Although crucial, studies exploring how tortoises move in complex and irregular environments are scarce. In this context, we examined an important behavioural trait: how tortoises (*Testudo hermanni*) deal with step-like obstacles. In their natural habitat, individuals were positioned in a challenging situation: they were placed on a bench approximately 50 cm high, and were observed over a 10-min period. We compared the behaviour of the tortoises (taking a risk to 'jump' or waiting) from two populations living in contrasted habitats: flat versus rugged (crisscrossed by cliffs and rocky steps). Individuals from the flat habitat were reluctant to jump, whereas most tortoises from the rugged habitat jumped. Immature tortoises were less willing to jump compared to larger and more experienced adults. These results suggest that challenging habitats increase boldness. In addition to fundamental findings, these results may have conservation value and assist in improving translocation strategies for endangered tortoise populations.

ADDITIONAL KEYWORDS: behaviour – jumping – locomotor performance – ontogenetic shift – *Testudo hermanni*.

INTRODUCTION

Although many vertebrates rely on discretion, velocity or agility to escape predation, several groups have developed a different anti-predator strategy: they possess an armour (e.g. armadillos, pangolins, and chelonians). These animals are generally slow-moving and not particularly secretive. Protection against predators is provided by the plates (or indurated tegument parts) of the dorsum, head, limbs, and tail. The advantages of the armour are offset by reduced mobility and high energetic costs, at least in terrestrial environments where the mass of an efficient shield becomes a burden. Body shape is also constrained: armoured animals are heavy bodied, inflexible (hence poor agility), and are characterized by short, thick limbs.

These morphological traits pose serious locomotor challenges on uneven surfaces where individuals can easily lose equilibrium. Therefore, most armoured terrestrial vertebrates typically inhabit flat environments. However, even flat habitats are not free from obstacles. For example, abrupt steps and fallen trees represent challenging difficulties for robust animals with poor agility. Consequently, key processes such as dispersal, migration, reproduction, and access to resources can be impeded unless individuals overcome physical obstacles.

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When facing a positive obstacle (e.g. wall, log, upward slope), individuals can decide to retreat and turn back, climb over the obstacle or walk around it to find an alternative pathway. Facing a negative obstacle (e.g. steep downward slope), animals have an additional option: they can take the plunge and risk of falling to cross the step. These decisions are not similar in terms of consequences: retreating or turning around is usually not hazardous, whereas falling from a cliff can have fatal consequences. This inequality is reflected by the prudence exhibited by animals when they are on the edge of a cliff (Sloane *et al.*, 1978). Precocial species (e.g. goats, chicks) avoid stepping over the edge of a precipice (Gibson & Walk, 1960; Walk & Gibson, 1961; Walk, 1966; Bradley & Shea, 1977). Experimental studies revealed that, in altricial species (e.g. humans), depth perception develops simultaneously with the acquisition of locomotor autonomy (Walk & Gibson, 1961; Emlen, 1963; Gibson, 1969).

Tortoises are suitable organisms to test above mentioned notions: they are slow, armoured animals. Although typical plain inhabitants (Arnold & Ovenden, 2002), many tortoises live in hilly areas and undertake long-distance movements in complex and uneven environments (Calzolai & Chelazzi, 1991; Longepierre, Hailey & Grenot, 2001; Lagarde *et al.*, 2012). Importantly, tortoises exhibit the ability to appraise features of a cliff (Patterson, 1971). This behavioural trait provides a background to examine the variability of behavioural patterns expressed in hazardous situations.

In the present study, we assessed the willingness of tortoises to move forward when confronted with a negative obstacle: a 50-cm high step. We compared individuals from two nearby populations, one situated in a relatively flat and smooth environment versus one from an area bordered by steep cliffs and crisscrossed by rocks. We expected that strong differences in habitat structure would be associated with marked behavioural divergences. However, the direction of potential divergences was not predictable; each habitat may favour prudence or promote boldness, depending upon the respective benefits and costs of the magnitude of these behaviours. For example, tortoises rarely confronted by the injury risk of falling might be naive and thus imprudent; conversely, tortoises from a more challenging habitat might be experienced and more willing to take risks with the aim of not remaining trapped by obstacles.

Differences in behavioural characteristics (e.g. locomotor performances) related to sex in chelonians are well documented. For example, males can right themselves more rapidly when flipped onto their backs compared to conspecific females (Bonnet *et al.*, 2001). This greater manoeuvrability might also be associated with a more pronounced boldness of tortoises in uneven substrates. We also expected an ontogenetic effect, with older and heavier tortoises being more prudent to cross obstacles. Offspring are small, light, and possess comparatively elastic shells compared to conspecific adults, and are thus less exposed to injury risk when falling from a step. To address these issues, we examined (1) does boldness to 'jump' from (i.e. walk off/take the plunge) a steep step vary between populations living in contrasting habitats and (2) do body size and sex affect this behavioural trait?

MATERIAL AND METHODS

Species description

Hermann's tortoise (*Testudo hermanni*, Gmelin, 1789) is a medium-sized (adult size of approximately 20 cm) tortoise distributed in the Mediterranean parts of the Iberian, Apennine, and Balkan Peninsulas, as well as on some Mediterranean islands (Gasc *et al.*, 1997). The activity period of this species spreads from March to October, with peaks in April and September (Hailey & Loumbourdis, 1988). Females are larger and less mobile than males (Willemsen & Hailey, 2003).

Study populations

We studied two populations from the Prespa Lake region, in Galičica National Park, FYR of Macedonia. The two populations are separated by less than 4.5 km, although they are completely isolated from each other. One population inhabits an island (Golem Grad; GG), whereas the other lives on the mainland (Konjsko village; KS).

Golem Grad (18 ha) is characterized by a plateau encircled by vertical cliffs (height 15–30 m) and surrounded by narrow beaches (Fig. 1A). The beaches are covered by fallen rocks and large boulders, up to 300 cm in diameter, and less than 5% of the area is flat. Approximately 30–40% of the plateau is covered with large rocks, with a mean diameter of 50 cm. The island is crisscrossed by major obstacles for tortoises. Tortoises are able to move between the plateau and the beaches (radiotracking and recapture data; A. Golubović and X. Bonnet, unpubl. data), and are regularly observed on the few narrow and steep paths that connect these two zones.

The second study site (approximately 15 ha) is situated at the Konjsko village, where the main habitats are represented by a beach and a soft hill (Fig. 1B). The beach, covered with gravel and small stones, gradually continues to the hill by gentle slopes. There are no steep steps and few isolated rocks are scattered in the area; consequently, there are no physical obstacles that might complicate locomotion by the tortoises.

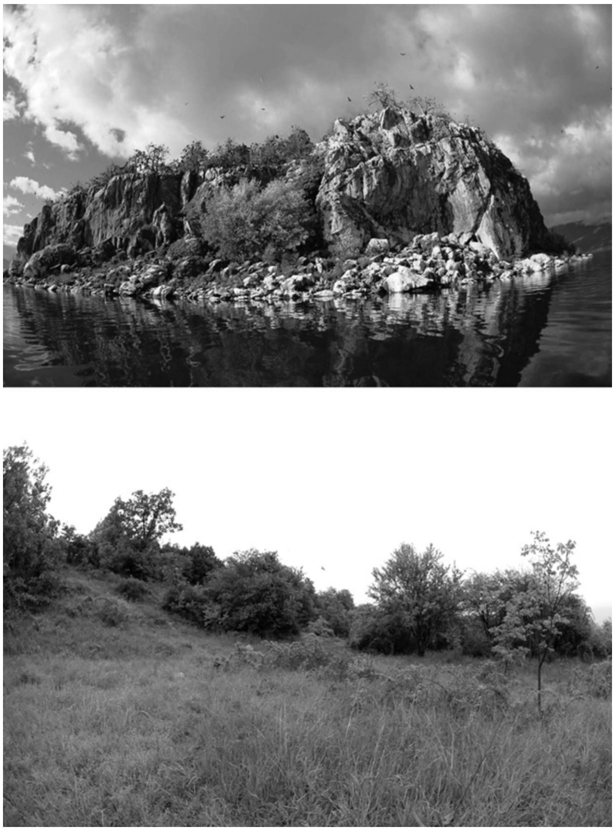

Figure 1. The two study sites, Golem Grad island (A) and Konjsko village (B), exhibit contrasted habitats and configurations: crisscrossed by cliffs and rocky steps (GG) versus flat and gentle slopes (KS).

Field procedure

The tortoises were captured by hand. Each individual was measured (straight carapace length), weighed, marked and released at the exact place of capture (Stubbs *et al.*, 1984). Individuals larger than 13 cm were sexed; smaller individuals were considered as juveniles (Hailey, 2000).

Behavioural test

In spring 2011 (23 April to 6 May) we tested 149 tortoises: 73 from Golem Grad (12 adult females, 27 adult males, and 34 juveniles) and 76 from Konjsko (23 adult females, 23 adult males, and 30 juveniles). Each individual was placed on a wooden bench (height 47 cm, width 28 cm, length 83 cm). The height of the bench mirrored steps that tortoises from Golem Grad must cross during daily movements. The bench was positioned in a shady environment to avoid overheating. We placed a 5-cm thick sponge at the foot of the bench to alleviate tortoises' falls, and we covered it with leaves to imitate the natural substrate. Each subject was placed on the bench facing its one end, whereas the observer was standing 5 m behind the subject; hence, the tortoises could not see the observer. We recorded the time elapsed from the placement of the subject on the bench until the plunge. If the tortoise was motionless, the test was interrupted after 5 min; if the tortoise moved but remained on the bench, the test was terminated after 10 min. No animal was injured during the experiment.

During the test, the parameters recorded were: whether the tortoise walked off the ledge (Y) or not (N); the time elapsed from the start of the test until the first detectable movement of the limbs or head (time to move; TM); the time elapsed from the start of the test until the jump, if any (total time; TT); the time elapsed between the first movement and jumping (net time to walk off the ledge; NT). The last measurement provided an index of time during which the tortoises actively searched for an alternative option before taking the plunge.

Statistical analysis

Influences of discrete variables (habitat, sex, and age) on jumping decision were examined using chi-squared tests. The influences of continuous variables (body mass and straight carapace length) were tested using analysis of variance (ANOVA). The different time durations recorded (TM, NT, TT) were not normally distributed; for these tests, we used nonparametric Kruskal–Wallis ANOVA.

RESULTS

Effect of habitat, sex, and age on jumping decision

Most tortoises (pooled sample) from Golem Grad took the plunge (70%), whereas tortoises from Konjsko were more reluctant (39% walked off the ledge; Fig. 2) ($\chi^2 = 13.86$, d.f. = 1, $P < 0.001$). Similar results were obtained focusing on separate age classes (adults: $\chi^2 = 9.53$, d.f. = 1, $P = 0.002$; juveniles: $\chi^2 = 7.07$, d.f. = 1, $P = 0.008$). Adults from both localities were more willing to take the plunge than juveniles (Golem Grad: $\chi^2 = 3.78$, d.f. = 1, $P = 0.052$; Konjsko: $\chi^2 = 3.48$, d.f. = 1, $P = 0.062$). We found no differences in jumping willingness between the sexes (adults from both localities included; $\chi^2 = 0.14$, d.f. = 1, $P = 0.708$).

Effect of habitat, sex, and age on the time to move and activity time before walking off the ledge

Males and females from both localities did not differ in the amount of time elapsed from the start of the test until the first detectable movement (time to move: TM, Tables 1, 2). Juveniles and adults from Konjsko village needed similar time to move, whereas immature animals from Golem Grad moved earlier than adults.

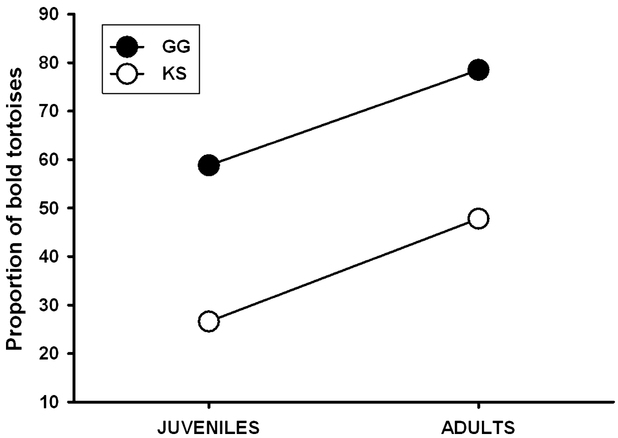

Figure 2. Percentage of tortoises that decided to jump from an approximately 50 cm high step (i.e. bold tortoises) compared to individuals that did not. Juveniles and adults from two habitats: rocky habitat at Golem Grad (GG, black circles) versus flat habitat in Konjsko, (KS, open circles) are plotted. For sample sizes and statistics, see text.

Differences (age classes and sexes) in the time from the first movement to jumping (net time to walk off the ledge: NT) were more pronounced. Females from Golem Grad spent significantly less time in searching for an alternative option before taking the plunge than males. The pattern was opposite in males and females from Konjsko, although the difference was not significant (Tables 1, 2). At both localities, immature individuals hesitated longer before jumping than adults (Tables 1, 2).

Influence of body size on jumping decision

We performed the analyses separately for age classes. Body size had no influence on jumping willingness in adults at both localities. However, in Konjsko, immature individuals that decided to jump were significantly larger than those that did not take a plunge (Table 3) Similar analyses were not performed on Golem Grad as a result of small sample sizes.

DISCUSSION

The present study is based on the comparison between two tortoise populations separated by less than 4.5 km, situated at similar elevations and experiencing similar climatic conditions. The fact that

Table 1. Mean ± SD duration of different behaviours recorded in females, males, and juveniles from Golem Grad (rocky habitat) and Konjsko (flat habitat)

		TM (mean ± SD)	NT (mean ± SD)	TT (mean ± SD)
Golem grad	Females	132.7 ± 82.98	111.2 ± 87.90	243.9 ± 155.16
	Males	95.7 ± 51.05	209.2 ± 121.64	304.9 ± 136.66
	Juveniles	31.3 ± 32.89	265.9 ± 130.15	297.2 ± 146.55
Konjsko	Females	60.9 ± 82.55	159.9 ± 163.43	226.9 ± 184.66
	Males	55.4 ± 44.77	131.2 ± 161.03	186.6 ± 163.33
	Juveniles	51.6 ± 45.51	333.3 ± 163.52	384.9 ± 180.84

TM, time to move; NT, net time to walk off the ledge; TT, total time.

Table 2. Results from Kruskall-Wallis tests to compare the duration of different behaviours exhibited by female versus male and adult versus juvenile tortoises from Golem Grad (rocky habitat) and Konjsko (flat habitat). Bold values denote statistical significance

		TM		NT		TT	
		H	*P*	*H*	*P*	*H*	*P*
Golem grad	Sex	1.30	0.254	5.21	**0.023**	1.61	0.281
	Age	18.90	**0.000**	5.77	**0.016**	0.01	0.923
Konjsko	Sex	0.13	0.716	0.05	0.833	0.05	0.833
	Age	0.03	0.869	6.44	**0.011**	4.40	**0.036**

TM, time to move; NT, net time to walk off the ledge; TT, total time.

Table 3. Influence of body size on jumping willingness in two main age classes from Golem Grad (rocky habitat) and Konjsko (flat habitat)

Locality	Age	Jumped SCL	Not jumped SCL	*F*	*P*	Jumped BM	Not jumped BM	*F*	*P*
Golem grad	Adults	168.5 ± 12.73	175.0 ± 8.55	1.87	0.180	958.7 ± 189.96	982.1 ± 133.97	0.09	0.761
	Juveniles	–	–	–	–	–	–	–	–
Konjsko	Adults	177.2 ± 18.66	178.8 ± 22.96	0.06	0.803	1138.2 ± 343.44	1219.5 ± 437.18	0.49	0.490
	Juveniles	113.3 ± 22.08	70.0 ± 30.92	10.40	**0.003**	379.5 ± 204.49	145.9 ± 151.78	11.54	**0.002**

Values are given as the mean ± SD. Analyses of variance using straight carapace length (SCL) and body mass (BM) as dependent variables are also provided. Significant values are shown in bold.

these close populations are characterized by markedly different habitat structure offered an interesting situation to assess the relationship between habitat and behaviour. The most prominent difference between the two localities is represented by strong contrasts of the topography: uneven and rocky habitat at Golem Grad versus the relatively flat habitat in Konjsko (Fig. 1). Despite the short distance between the populations, we found strong differences in behaviours involved in crossing obstacles. We acknowledge that our data did not allow us to separate the possible contribution of local adaptation from phenotypic plasticity (a goal beyond the scope of the present study), and that the comparison of only two populations impose strong limitations. However, all the traits measured provided consistent results between the two populations and different age categories. For example, the striking parallelism of the ontogenic behavioural shifts (Fig. 2) suggests that we accurately measured a consistent and possibly important life history trait. In general, tortoises from Golem Grad were more prone to take the plunge when facing a steep step, suggesting a nonrandom association between habitat and behaviour of the tortoises.

Importantly, our experimental design placed the tortoises in a realistic context. Taking a plunge from a height of approximately 50 cm is a challenge that the individuals living on Golem Grad cannot easily avoid. Radiotracking and long-term recapture data (L. Tomović and X. Bonnet, unpubl. data) showed that the free-ranging tortoises sometimes decide to cross far higher steps. In the field, we directly witnessed tortoises ($N = 4$) losing their balance and falling from the cliffs in an attempt to descend very steep slopes; none of them were injured. However, we also found some badly injured and dead tortoises with broken shells at the foot of 15–30-m high cliffs; the individuals were previously observed on the overhanging edge of these cliffs ($N = 10$). Clearly, the tortoises from Golem Grad are exposed to severe risks during movements. In comparison to natural conditions, our experimental design was less challenging, far less dangerous, and representative of the characteristics routinely encountered in an uneven and very rocky habitat. Taking the plunge from a 50-cm step is unlikely to entail injury (although we did not perform the test using hard rocky substrate). The tortoises from Konjsko are not exposed to serious complications during movements and likely have limited experience in terms of crossing steep steps. Accordingly, none of nearly 400 tortoises recorded at this locality had broken shells.

Male tortoises are generally more active (Lagarde *et al.*, 1999, 2002) and more agile than females (Bonnet *et al.*, 2001). However, at both localities, there was no significant difference in jumping willingness between the sexes. We also expected the adults would be more prudent because their body weight increases the risk of being injured when falling from high steps compared to juveniles. Instead, we found the reverse patterns. The young and light individuals (juveniles), or more agile and active sex (males), did not exhibit greater boldness to take the plunge. Tortoises are long-living animals with learning abilities (Spigel, 1964; Berry, 1986). We propose that the difference in behaviours documented in our findings reflects ontogenic shifts driven by experience rather than by variations in morphological characteristics (body size).

Experience influences behaviour in chelonians and other reptiles (Spigel, 1964; Brodie, 1993; Lind & Welsh, 1994; Irschick *et al*., 2000; Steyermark & Spotila, 2001; Martín & López, 2003; Arthur, Boyle & Limpus, 2008; Okuyama *et al*., 2009). We suggest that young tortoises are initially prudent, their confidence increases through time (i.e. experience), and, eventually, they become able to adequately 'evaluate the feasibility' of walking off a cliff-like obstacle (King, 1970). This possible ability to gauge risks is supported by our observations during the tests. We noticed that, when on the bench, tortoises stretched their necks to examine the basis of the step and moved their heads from one side to another. These movements typically improve the perception of the distances (Ferris, 1972; Goodson, Ritter & Thrope, 1987). Because both depth perception (Walk & Gibson, 1961; Patterson, 1971) and the important role of vision in orientation (Emlen, 1969; Lebboroni & Chelazzi, 2000; López *et al*., 2000) have been documented in tortoises, we assume that the particular visual examination enabled individuals to assess the risk of jumping. When looking downwards, the tortoises spread their front and hind legs, presumably to increase stability during depth gauging. After a short period, they went backwards and searched for another way. In most individuals, this searching pattern was repeated several times. These sequences suggest that the animals hesitated before actual jumping occurred.

The time elapsed from the beginning of the test to the first movement was similar between sexes at both localities (Tables 1, 2). On the other hand, this time was generally shorter in juveniles than in adults (highly significant at Golem Grad). This suggests that juveniles rapidly attempted to find a shelter, probably because their soft shell and small size provide limited protection against the predators (Douglass & Winegraner, 1977; Keller, Diaz-Paniagua & Andreu, 1998). We also found differences in the amount of time during which the tortoises tried to find an alternative before walking off the ledge. Juveniles hesitated more than in adults at both localities. These results, along with the percentage of juveniles that eventually took the plunge (Fig. 2), mirror the fact that immature tortoises were more prudent than adults. Comparing hesitation time between sexes, we observed opposite (and unexplained) patterns at each locality (Tables 1, 2).

The present study provides the first evidence for marked inter-population variability in a major behaviour involved in the capacity of armoured animals to cross over obstacles. Our results revealed a strong association between habitat and behaviour. On Golem Grad, steep cliffs and numerous large rocks pose strong challenges to the tortoises. Tortoises are forced to express a great degree of boldness when facing a step to explore their habitat. By contrast, tortoises from Konjsko live in a flat habitat and do not experience such difficulties. Experience and local adaptation may promote boldness, as suggested by the pronounced ontogenic increase of audacity observed at both localities (Fig. 2). The change in behaviour from juvenile to adult stages might be associated with the ability of tortoises to evaluate the risks/benefits correlated with crossing steep obstacles and, hence, may be under strong selective pressure. Future studies are needed to explore whether habitat shapes key behavioural traits (e.g. boldness) in other populations (Bradley & Shea, 1977).

Our results may also have conservation value. Displacement of individuals from one part of their distribution range to another is increasingly used for the re-establishment (or reinforcement) of populations (Guyot & Clobert, 1997; Kingsbury & Attum, 2009; Attum *et al*., 2010). Management guidelines need to be based on habitat use and movement patterns of translocated animals (Attum *et al*., 2010, 2011). Our data suggest that the habitat selected for translocation should, if possible, mirror the structure of original habitat. In addition, accustom periods (e.g. using large outdoor enclosures) before releasing may help animals to adjust to novel (more challenging) environments. This might be important because the acclimatization of chelonians to novel habitat can last up to 5 years (Meek & Avery, 1988).

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