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ORIGINAL ARTICLE

Locomotor performances reflect habitat constraints in an armoured species

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Abstract
Physical limits of speed performances impose strong selective pressures on animals, influencing important functions such as predator avoidance and foraging success. Armoured herbivorous species such as tortoises represent a peculiar case: features that optimise encounter rate during reproduction, the ability to reach favourable sites for thermoregulation and resting, foraging or nesting sites may be more important than running speed. To explore this issue, we measured three characteristics related to travelling ability but that are independent of running speed: (1) muscular strength, (2) time needed for overturning and (3) jumping from a high step as proxies of the ability to overcome various obstacles. Additionally, reaction times in tortoises placed in a normal or overturned position were measured as a proxy of antipredator response. More than 400 adult Hermann's tortoises from six populations were tested in the field during two seasons. Measures of travelling ability and antipredator response varied markedly among populations, and thus with environmental characteristics such as habitat type, terrain ruggedness and presence of predators. Tortoises from rugged and hot habitats (e.g. Mediterranean macchia) were the most successful and the fastest to accomplish the tests. Overturned tortoises were more reluctant to start moving compared to those in normal position, but this effect was absent in the two localities free from predators. Sex and season had limited effect on the measured performances. Overall, locomotor features essentially varied with environmental constraints. Future environmental studies should explore whether the observed differences among populations are linked to genetic adaptation or phenotypic plasticity.

Significance statement
Locomotor performances crucially influence habitat use, foraging and reproductive success, thus directly affecting individual fitness. Although running speed is often considered as a main indicator of agility, in armoured terrestrial vertebrates some other agility components might be more important. Heavy, rigid armour imposes trade-off between protection of soft body parts and locomotor performances and consequently habitat use. This study compiles three tests of locomotor performance which might be important for overcoming various obstacles present in mosaic habitats of tortoises. Testing adult Hermann's tortoises from six populations with various habitat characteristics, we found significant inter-population differences. The ability of tortoises to complete the tests positively correlates with climatic conditions and topography of their habitats. Additionally, presence of predators in the habitats dramatically affects tortoise's antipredator behaviour. Measured locomotor performances and antipredator behaviour showed surprisingly low level of sexual dimorphism.

Keywords Righting · Jumping · Muscular strength · Antipredator behaviour · Hermann's tortoise · *Testudo hermanni*

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Introduction

Locomotor performances influence fitness in animals in many ways (Jayne and Bennett 1990; Ghalambor et al. 2003; Lailvaux and Irschick 2006). For example, elevated locomotor performances can assist foraging, predator avoidance, finding refuge and breeding sites, mate searching, patrolling territory or fighting off rivals. However, high locomotor performances require substantial energy supplies for the development, use and maintenance of associated morpho-functional traits, creating a trade-off against other important functions such as reproduction (Zera and Harshman 2001). Further, environmental conditions such as terrain ruggedness, ambient temperature or food availability impose strong limitations on locomotor performances (e.g. Miles 1994; Kohlsdorf et al. 2004; Goodman et al. 2008; Lailvaux and Husak 2014). These issues have been intensively studied, both in captivity and in the field, in animal species in which running or jumping performances occupy a central place (Kohlsdorf et al. 2004; Goodman et al. 2008; Rubin et al. 2016). Except for several laboratory studies examining the energetic aspects of locomotion (Zani et al. 2005; Zani and Kram 2008), slow-moving terrestrial animals, especially armoured species, have been neglected.

Although running speed offers a straightforward index for locomotor performances in many free-ranging animals, it may well not be a suitable measure in slow-moving and heavily protected terrestrial vertebrates such as tortoises. Hard rigid shell offers protection, while at the same time limits movement, imposes relatively short stout limbs, represents a burden and thus affects speed performances. In tortoises, the primary antipredator response involves hiding soft parts of the body into the shell, whereas foraging and other activities essentially depend on their ability to select and reach microhabitats in their natural environment. Traits that reflect the ability of organisms like tortoises to optimise displacements in their complex habitats might not necessarily involve speed. Instead, traits associated with body shape (Ireland and Gans 1972; Bonnet et al. 2001), with decisions to move versus to remain sheltered (Moulherat et al. 2014) or with risk assessment in landscape with uneven topography (Golubović et al. 2013a), may better account for the gross locomotor performances of these slow-moving animals.

In addition, locomotor performances may show some degree of sexual dimorphism (SD) because they influence reproductive success differently in females and males (Kelly et al. 2008; Kaliontzopoulou et al. 2012; Makiguchi et al. 2016). Compared to females, males tend to exhibit higher locomotor performances and more developed associated morphological attributes (Miles et al. 2007). Overall, morpho-functional and behavioural characteristics that determine locomotor performances are expected to vary among individuals, between sexes and among populations. Differences among individuals and between sexes have been documented in many species (Le Galliard et al. 2004; Oufiero and Garland 2007), but inter-population studies are relatively scarce (Huey et al. 1990; Sinervo and Huey 1990; Miles 1994).

In this paper, we compared the locomotor performances in adult female and male Hermann's tortoises from six populations spread across distant areas and contrasted habitats. We measured three traits which are not restricted by running speed—muscular strength, time needed for overturning and time for jumping from a high step—which are important for tortoises to cope with different substrates and navigate in their natural habitat (Golubović et al. 2013a, b, 2014). We examined three main questions: do locomotor performances and antipredator behaviour differ between the sexes? Do they vary with habitat characteristics such as ruggedness of landscape, habitat type and presence of predators? Are there seasonal changes in measured performances?

Material and methods

Studied animals

The Hermann's tortoise (*Testudo hermanni*) is a medium-sized tortoise; females are typically larger sex, and they have relatively narrower shell openings compared to males (Đorđević et al. 2011). Hermann's tortoises occupy various habitats including cultivated plains, open Mediterranean scrublands, closed forests and hilly areas (Longepierre et al. 2001). In adults, mean distances travelled per day range from 31 to 80 m (Hailey 1989; Rozylowicz and Popescu 2012; Sibeaux et al. 2016). During displacements, tortoises must cross various obstacles such as shrubs, logs, boulders and steep slopes. However, hindrances to movement vary greatly among habitats and thus among populations (Golubović et al. 2013a, b, 2014). For example, thick bushes in dense shrub areas slow down progression and pose specific locomotor challenges to tortoises compared to steep, open areas with rocks, where individuals must climb or jump from steps with a risk to be flipped back on their dorsum (Golubović et al. 2013b, 2014).

Fieldwork was conducted in 2012 in five natural populations from Mediterranean and sub-Mediterranean habitats across the central part of the Balkan Peninsula and at one tortoise farm (details in Table 1).The farm population actually mixed up unknown numbers of individuals from different populations, while the specific constraints of habitat to find feeding resources, freshwater or buffered shelters are minimised. Tortoises were searched visually, captured, sexed, permanently marked, measured by calliper for straight carapace length (SCL) and weighted (BM) on a digital balance (OHAUS Scout Pro Balance, 4000 g × 0.1 g). In total, 236 tortoises were tested in spring (May–June) and another 216 individuals were tested in summer (August–September) (Table 1).

Table 1 Number of females and males tested (respectively) in spring and summer season

Locality	*N* spring	*N* summer	Rugg. M (Q1; Q3)	T spring	T summer	Type of habitat
Farm	20; 20	20; 20	0.97 (/)	18	19.6	Anthropogenic flat ground without obstacles
Pčinja	19; 19	11; 20	5.56 (4.14; 6.98)	16.45	18.7	Sub-Mediterranean oak forest with meadows
Golem Grad	15; 16	10; 20	4.53 (2.59; 7.53)	15.55	17.8	Sub-Mediterranean forest of *Juniperus excelsa*
Konjsko	22; 20	20; 20	2.89 (1.84; 3.82)	15.45	17.85	Sub-Mediterranean oak forest with meadows
Danilovgrad	23; 20	16; 22	2.06 (1.62; 2.44)	19.95	23.2	Degraded Mediterranean macchia
Vranjina	24; 18	16; 21	9.09 (7.34; 10.08)	20.05	23.2	Degraded Mediterranean macchia

Habitat characteristics are represented by terrain ruggedness given as median (M), first and third quartiles (Q1; Q3), average temperatures for spring (May and June) and summer (August and September) and description of habitat type for each locality included in the study

Habitat characteristics

Polygons of the studied areas were hand drawn using Google Earth, and the obtained surfaces were used to characterise habitats in GIS. Raster calculation and extraction of values were done using the raster package in R. The terrain ruggedness index (Wilson et al. 2007) was calculated from a digital elevation raster in resolution of 30 m^2 (EEA 2013). Since a set of values were extracted from each polygon, terrain ruggedness was presented as median value and quartiles (Table 1). Based on terrain ruggedness, we grouped the habitats in four classes: (1) farm (median below 1), (2) Konjsko and Danilovgrad (median between 2 and 3), (3) Pčinja and Golem Grad (median between 4 and 6) and (4) Vranjina (median above 9). The average temperatures per month were extracted from the WorldClim dataset in resolution of 1 km^2, covering the period from 1960 to 1990 (Hijmans et al. 2005). We used only the temperatures for months in which the study was performed: May, June, August and September. Based on habitat types and on average temperatures per season (Table 1), we grouped the habitats in three classes: (1) farm, with anthropogenic habitat; (2) sub-Mediterranean habitats with average temperatures around 16 °C in spring and 18 °C in summer, which include Pčinja, Golem Grad and Konjsko and (3) degraded Mediterranean macchia with average temperatures around 20 °C in spring and 23 °C in summer, which include Vranjina and Danilovgrad.

Locomotor performances

Each tortoise completed a three-stage test in order to measure (1) muscular strength, (2) willingness to jump from a relatively high step and (3) self-righting when overturned on its back. Muscular strength was measured first to limit possible effect of exhaustion. Afterwards, in random order, tortoises performed jumping and righting tests, which seem to rely on the inclination and agility rather than on absolute muscular force. Willingness to jump from a step and righting ability are used here as a measure of adaptation for living in steep terrains with abundant rocks. Each individual was tested only once and released promptly at the place of capture. It was not possible to record blind data because our study involved focal animals in the field.

Muscular strength (MS) was measured using a digital dynamometer (force gauge LUTRON FG-20KG) attached to the tortoise with a rope (Golubović et al. 2014). Each tortoise was then placed on a flat hard substrate without rocks or vegetation. The test started when the tortoise attempted to escape and lasted for 3 min. Maximal value was retained for analyses.

Willingness to jump was assessed by placing the tortoise on a horizontal board (95 × 45 cm) set 80 cm above the ground, representing a step to cross comparable to large boulders or logs, which are present in the natural habitats of Hermann's tortoises (Golubović et al. 2013a). Ground surrounding the board was covered by a 5-cm-thick sponge material to prevent injury. Individuals first tended to remain motionless with limbs and head retracted. We recorded the time elapsed until the first movements (reaction time, RTj) and until the tortoise jumped (net time, NTj). This test was restricted to 8 min maximum, since not all the individuals jumped.

Righting test started by placing each tortoise on its back on flat hard soil, without rocks or vegetation on which it could cling, thus affecting righting performance. Individuals first remained motionless with the head and legs retracted. We recorded time elapsed until the first visible movement (RTr) and until the tortoise self-righted (NTr). The test lasted 8 min maximum, since several tortoises failed to flip back on their legs.

Reaction times (RTj and RTr) provide information about the antipredator response of tortoises (Martín et al. 2005; Polo-Cavia et al. 2008; Ibáñez et al. 2014; Golubović 2015). However, when retracted into the shell, tortoises' position seems to affect reaction times. Those placed on their backs remain motionless for longer periods compared to those in a prone position (Martín et al. 2005; Ibáñez et al. 2014). It has been suggested that this difference (i.e. the position-sensitive antipredator response) increases with predation risk, possibly because individuals lying on their back are more vulnerable and wait longer to ensure that the predator has gone (Martín et al. 2005).

For conciseness, we referred to the term agility to integrate the three different metrics of locomotor performances we recorded in Hermann's tortoises. Supposedly, in a tortoise perspective, stronger individuals that were more prone to jump from a steep step and faster to right themselves were more agile.

Statistical analyses

We modelled the variation in RTr, RTj, NTr and NTj as a response to the additive and interactive effects of sex, season, population (pop), habitat type (hab), terrain ruggedness (rug), muscular strength (MS), straight carapace length (SCL) and body mass (BM). Furthermore, in the models describing reaction times to jump and right (RTj and RTr), we added as predictors the eventual success or failure to right and jump, respectively, in order to see whether response time can in any way be a predictor of success. All continuous variables (RTr, RTj, NTr, NTj, MS, SCL and BM) were log-transformed due to non-normality. BM, SCL and MS are not independent, thus we only looked for their separate and additive effects; on the other hand, we allowed for all possible additive and interactive effects of sex, season and population. In order to account for pseudo-replication from repeated measurements on several individuals, as well as between habitat types and ruggedness of terrains, we included these variables as separate random factors during the model selection procedure. The amount of between-group variance of the random factor and the Akaike information criterion (AIC) were used as indicators on whether to keep the random factor or not. Finally, since the variables 'hab' and 'rug' proved to be better predictors than the populations themselves, and since they are categorical variables accordingly clumping populations together, they were moved from random to fixed factors in place of the population variable 'pop'. After trying all additive and interactive combinations and successively dropping variables from the model, we used AIC to compare all possible models and, along with AIC weights, chose the best fit model for each response variable (Burnham and Anderson 2002). The models are presented in Supplementary Table 1.

Influences of discrete variables (sex, season and locality) on jumping and righting success were examined using χ^2 tests and χ^2 contingency tables. Yates' correction was applied when at least one cell of the table had small sample size. Wilcoxon matched pair tests were used to assess differences between reaction times (RTr and RTj) for each locality separately. Since no farm tortoises succeeded to jump from the step board, they were excluded from several analyses. Spearman's rank-order correlation tests were used to examine the relationship between the proportions (%, arsine transformed) of tortoises which successfully finished jumping and righting tests.

Statistical analyses were performed in software package Statistica 7.0 (StatSoft Inc.) and the software R (R Core Team 2014) using the packages 'nlme' (Pinheiro et al. 2014) and 'AICcmodavg' (Mazerolle 2013).

Results

Generalised linear models

In the lack of notable variance between groups of the proposed random factors, along with lesser model fit suggested by the AIC, we dropped the random factors and used generalised least squares to describe tortoise reaction and net times to right and jump (Supplementary Table 1).

Each response variable used a different set of predictors to best describe its variation; SCL was the only explanatory variable whose additive effect consistently explained part of the variation of each response variable. Besides SCL, NTr was well described by the interactive effects of season, habitat type and sex, with tortoises from habitat type 3 (degraded Mediterranean macchia) being consistently significantly faster ($R^2 = 0.880$, $t = -2.016$, $p = 0.04$) within sexes, seasons and size categories. Habitat type was also a good predictor of the reaction time to jump, along with the additive effects of muscular strength and SCL. NTr alike, RTj was shortest in habitat type 3 (degraded Mediterranean macchia, $R^2 = 1.513$, $t = -3.749$, $p < 0.001$), followed by type 2 (sub-Mediterranean habitats, $R^2 = 1.513$, $t = 3.614$, $p < 0.001$), leaving tortoises from habitat type 1 (anthropogenic habitat) as the slowest to react. Along with body size, terrain ruggedness was a good descriptor of NTj: tortoises from terrain type 4 were significantly faster in their decision to take the plunge (Vranjina, $R^2 = 1.316$, $t = -3.753$, $p < 0.001$). Finally, RTr was modelled to comply with the additive effects of body size, muscular strength, sex and locality. Sexes differed significantly in their response time ($R^2 = 1.240$, $t = -2.891$, $p = 0.004$), with females taking longer, whereas a general larger size led to a faster response time ($R^2 = 1.240$, $t = -2.162$, $p = 0.031$). Tortoises from Golem Grad ($R^2 = 1.240$, $t = 4.609$, $p < 0.001$), Konjsko ($R^2 = 1.240$, $t = 5.767$, $p < 0.001$) and Pčinja ($R^2 = 1.240$, $t = 8.730$, $p < 0.001$) were significantly slower in their response times compared to other localities. Pčinja tortoises took the longest to react and Golem Grad tortoises the shortest within this group.

Righting and jumping success: differences between sexes, between seasons and among localities

Both sexes were equally successful during jumping and righting tests (localities per season separately, χ^2 test, $p > 0.05$ in all cases); only in Pčinja during summer did males right themselves more frequently than females (Yates corrected $\chi^2 = 7.74$, df = 1, $p = 0.005$). Sexes were also equally efficient when only animals which completed both

tests were analysed for each locality per season. When seasons were pooled, only at Pčinja was sexual dimorphism found, with males being more efficient (χ^2 = 8.51, df = 1, p = 0.003). At each locality, tortoises (sexes pooled) had similar righting success in both seasons (χ^2 test, $p > 0.05$ in all cases). Jumping success generally did not differ between the seasons, except for Macedonian populations which were more successful in summer (Golem Grad, χ^2 = 6.34, df = 1, p = 0.012; Konjsko, Yates corrected χ^2 = 12.82, df = 1, $p < 0.001$). Tortoises from contrasted habitats (Table 1) differed in righting (χ^2 = 164.0, df = 5, $p < 0.001$) and jumping success (χ^2 = 54.3, df = 4, $p < 0.001$; Fig. 1). Spearman's rank-order correlation tests, by sex per locality, showed a significant positive correlation between percentage of tortoises which successfully performed jumping and righting tests (r_s = 0.7579, $p < 0.01$; Fig. 1). When sexes were analysed separately, correlations were significant for males (r_s = 0.8407, $p < 0.04$) but not for females (r_s = 0.6571, $p > 0.05$).

Comparison between reaction times (RTj and RTr)

RTj was longer compared to RTr at most localities (Wilcoxon matched pair test: $p < 0.001$), except for the farm and Golem Grad where tortoises needed similar time to move when placed in an upright position and when flipped over (Table 2).

Discussion

The three metrics of locomotor performances we recorded in Hermann's tortoises varied markedly among populations living in different habitats. Tortoises from Mediterranean habitats exhibited the fastest and the most efficient response when confronted to an obstacle or when overturned. On the other hand, we found limited effects of seasons and sex.

Prominent inter-population differences in agility suggest considerable effects of biotic and abiotic characteristics of the habitat, such as presence of predators, landscape topography or quantity and shape of obstacles (Miles 1994; Melville and Swain 2000; Goodman et al. 2008). Differences among Hermann's tortoise populations were reported for self-righting, jumping and manoeuvrability to cope with thick vegetation (Golubović et al. 2013a, b, 2014; Supplementary Table 2). The current results compare different habitats and include three different metrics, thus offering a more integrative view. They suggest that the agility of tortoises is associated with the ruggedness of the terrain and habitat type (Figs. 2 and 3, Table 2, Supplementary Table 1). In this study, tortoises from Mediterranean habitats swiftly and efficiently responded to all tests. In Mediterranean macchia, where sparse shrubs offer limited protection from over-heating in the course of daily displacements during hot dry summers, individuals must

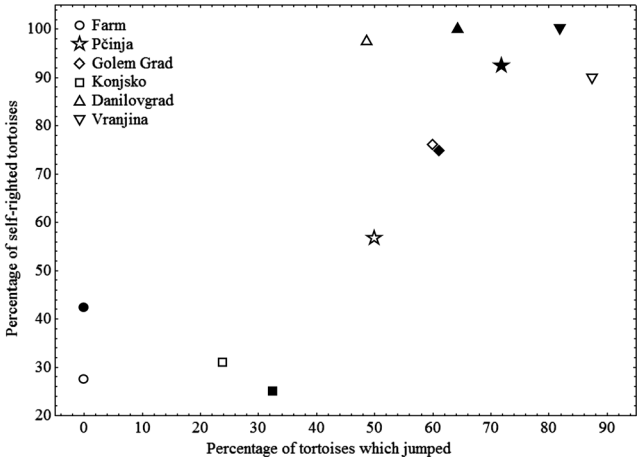

Fig. 1 Proportion (%) of tortoises that achieved the tests. Females and males are respectively indicated with *white* and *black symbols*

be efficient to reach thermally buffered refuges. Indeed, remaining stuck (e.g. blocked by an obstacle) or motionless (e.g. overturned and retracted into the shell) in the open might be rapidly lethal in such habitats due to over-heating (Lagarde et al. 2012; Moulherat et al. 2014). Precisely, numerous physical obstacles such as large rocky steps and boulders characterise the topography of Danilovgrad and Vranjina localities (Tables 1 and 2, Fig. 2). This result mirrors finding from studies in lizards where rocky habitats strongly influence morpho-functional and locomotor performances (Vitt et al. 1997; Revell et al. 2007; Goodman et al. 2008).

Although seasons may affect movement performance due to external conditions such as food availability and climate conditions, or internal causes such as reproductive status and body condition (Turchin 1998), our results have not shown this effect. In this study, seasons weakly (not significantly) influenced NTr (Fig. 3). Slightly faster self-righting response observed during summer months in Mediterranean habitats is in accordance with our hypothesis that swiftness could be a behavioural adaptation linked to very hot summers in degraded macchia (Table 2).

Generally, tortoises had shorter reaction time when placed in prone position compared to overturned position (also shown in *Mauremys leprosa*—Martín et al. 2005; Ibáñez et al. 2014). Tortoises in prone position are well protected, they can rapidly reach a refuge, and they can better survey their surroundings. In contrast, overturned ones are placed in a more vulnerable position; self-righting implies use of their head and neck as a lever, hampering their sight performance and exposing soft body parts. Our results support the hypothesis that reaction time increases with higher risk of predation (Martín et al. 2005). In localities where predators occur, tortoises postponed first visible movement when overturned (longer RTr). The farm and Golem Grad Island are free from predators for adult tortoises (e.g. badger, dog, fox and boar). Tortoises from these two sites displayed similar reaction time

Table 2 Mean ± standard deviation for reaction times and net times for self-righting (RTr, NTr) and jumping performances (RTj, NTj)

Locality	RTr	NTr	RTj	NTj	MS ♀	MS ♂	BM ♀	BM ♂
Farm	19.2 ± 22.57	207.3 ± 107.97	21.3 ± 28.20	/	24.7 ± 5.81	19.9 ± 6.27	1853.3 ± 171.35	1422.0 ± 171.69
Pčinja	129.6 ± 116.41	132.8 ± 87.80	49.5 ± 46.52	140.2 ± 98.74	22.0 ± 5.19	16.2 ± 3.20	1608.6 ± 439.42	1138.0 ± 218.59
Golem Grad	60.0 ± 62.35	154.1 ± 105.39	59.7 ± 62.77	165.5 ± 138.43	17.6 ± 5.30	15.4 ± 4.51	1057.5 ± 249.44	1072.1 ± 181.36
Konjsko	78.4 ± 81.73	175.3 ± 89.34	41.7 ± 41.03	230.6 ± 130.51	21.1 ± 6.25	14.2 ± 3.44	1488.4 ± 328.69	1087.0 ± 211.32
Danilovgrad	25.1 ± 34.12	80.3 ± 87.57	10.4 ± 28.45	174.8 ± 159.32	17.4 ± 4.00	10.2 ± 2.80	1100.8 ± 164.28	668.0 ± 126.00
Vranjina	36.7 ± 36.95	96.0 ± 107.70	12.1 ± 20.97	72.1 ± 94.73	9.9 ± 2.78	7.5 ± 1.52	663.1 ± 134.88	475.5 ± 82.34

Except in the case of muscular strength (MS) and body mass (BM), values are given for both sexes together

when set in a prone position and when overturned. Living under predator-free conditions may result in relaxing antipredator responses (Blumstein 2002), notably in reptiles living in well-isolated islands (Bonnet et al. 2005).

Female Hermann's tortoises, as in most *Testudo* species, are larger and heavier compared to males, with narrower shell openings that offer better protection but also limit limb movement (Bonnet et al. 2001; Willemsen and Hailey 2003; Zuffi and Plaitano 2007). Presumably, locomotor performances are also sexually dimorphic, with more mobile males (Bonnet et al. 2001; Golubović et al. 2013b; Stojadinović et al. 2013; Golubović 2015; Supplementary Table 2) intensively patrolling territories, fighting rivals, courting and mounting mates during the breeding seasons. Radio-tracking studies during the whole active season have confirmed this in *Testudo* species (Lagarde et al. 2003; Sibeaux et al. 2016). Yet, intensive multidirectional daily displacements of males do not necessarily translate into a larger home range; females often undertake long and relatively unidirectional daily displacements thereby covering larger surfaces than males (Lagarde et al. 2003; Moulherat et al. 2014; Sibeaux et al. 2016). However, locomotor performances cannot be easily summarised with few metrics; the mean distance travelled per day does not account for the complex challenges that tortoises must take up to navigate in their environment. The current study takes this into account and demonstrates that locomotor performances are affected by the sex only in the case of righting test, while having a significant effect only in reaction time (RTr). Nevertheless, focusing on those tortoises that were successful in both jumping and righting tests, an interesting trend emerged. Sexual dimorphism in agility was not observed in those populations that exhibited the lowest and the highest scores (farm and Konjsko versus Vranjina). In the populations with intermediate scores, males were more efficient compared to females, although this effect reached statistical significance only in Pčinja (Fig. 2). This trend suggests that the agility responses exhibited in habitats characterised by extreme constraints pose similar functional demands to both sexes.

Overall, by targeting environmental traits that were supposedly relevant during displacements, we found a marked habitat-related trend with a lack of effect of sex. Importantly, the three metrics recorded, muscular strength, willingness to jump from a step and self righting, along with lag time to move after a simulated predation attack, provided convergent

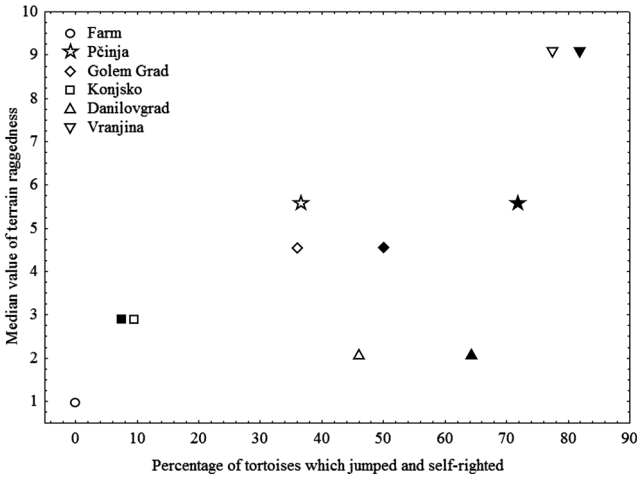

Fig. 2 Ruggedness of the landscape of each population studied and proportion (%) of tortoises that achieved two tests: jumping and righting. Females and males are respectively indicated with *white* and *black symbols*. Values for females and males from farm overlapped

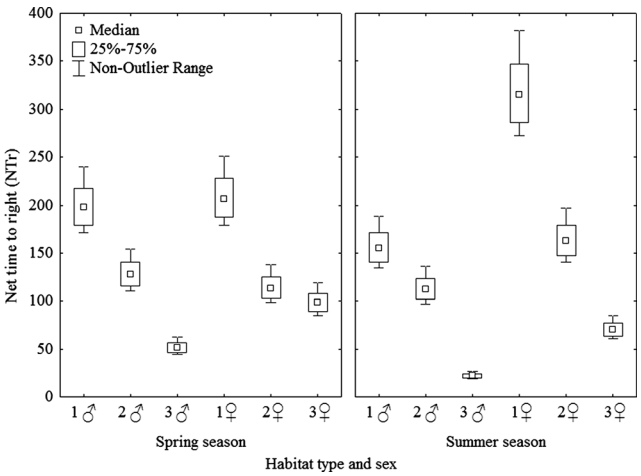

Fig. 3 *Box plots* for net time to right (NTr), categorised by habitat type: *1* anthropogenic, *2* sub-Mediterranean and *3* degraded Mediterranean macchia, sex and season

results. This suggests that the broad agility of tortoises during displacements was at least partly correctly described.

Conclusion

The three used metrics of locomotor performance provided convergent (hence coherent) information suggesting that measured locomotor performances were mostly influenced by habitat characteristics. Hot Mediterranean habitats with a rugged terrain promoted fast and efficient responses to overcome obstacle or to rapidly react after predation attempt. Farm tortoises provided an opportunity to gauge the situation where environmental constraints are relaxed, and expectedly showed low scores in the metrics measured. Yet, our study cannot tease apart the effect of phenotypic plasticity from local genetic adaptation. Future experimental studies should explore if, and to what extent, the observed differences among populations are plastic. This information might be useful for conservation managers, notably to optimise translocations, to reinforce threatened populations or to repopulate areas from where tortoises have been extirpated (Lepeigneul et al. 2014).

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Compliance with ethical standards

Data availability statement The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Experiments comply with the current laws of the countries in which they were performed. With the permissions of National Park "Galičica" (no. 11-4093/5), Agency for Environment Protection of Montenegro (no. UPI 2342/6) and Ministry of Environment, Mining and Spatial Planning of Serbia (no. 353-01-46/2012-03), animals were processed in the field. After non-invasive tests and measuring, which lasted up to 1 h, examinees were immediately released at the place of capture.

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