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Effects of body temperature on righting performance of native and invasive freshwater turtles: Consequences for competition

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HIGHLIGHTS

- Righting behavior is critical to survival of turtles.
- Righting response of *M. leprosa* and *T. scripta* turtles is enhanced at the preferred basking temperature of each species.
- Righting behavior might be coadapted to preferred basking temperature in freshwater turtles.
- A higher efficiency of introduced *T. scripta* at righting might favor its expansion in new environments.

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ABSTRACT

Righting behavior of aquatic turtles might be subject to coadaptation pressures between preferred basking temperature and locomotion, given that it is mainly performed on land and may critically determine the survival of turtles. We analyzed the effect of body temperature (T_b) on righting performance of two species of freshwater turtles, the endangered native Spanish terrapin (*Mauremys leprosa*), and the red-eared slider (*Trachemys scripta elegans*), an introduced invasive species that is displacing native turtles in the Iberian Peninsula. Interspecific differences in morphology, basking requirements and behavioral responses have been found between Spanish terrapins and introduced sliders. Therefore, we hypothesized that T_b might differentially affect righting behavior of these two turtle species. We found a clear effect of T_b on righting response of both *M. leprosa* and *T. scripta*, with the performance enhanced at the preferred basking temperature of each turtle species. These results suggest that righting might be coadapted to preferred basking temperature in freshwater turtles. Also, *M. leprosa* required longer times to right on average than *T. scripta*, which denotes a higher efficiency of introduced sliders at righting performance. These interspecific behavioral asymmetries in righting performance between native and exotic turtles might contribute to the greater competitive ability of introduced *T. scripta*, favoring the expansion of exotic sliders in the new environments in which they are introduced, in detriment to native Spanish terrapins.

1. Introduction

According to the thermal coadaptation hypothesis, the preferred temperature (T_{set}) of a species should match the thermal optimum (T_o) of thermally sensitive processes that influence fitness [1,2]. In ectotherms such as reptiles, temperature is a major limiting factor affecting locomotor performance, which is determinant in critical activities such as foraging, mating, or predator avoidance [3,4]. Thus, coadaptation between T_{set} and T_o for locomotion is present in many reptile species, including lizards [5,6] and snakes [7,8]. However, it has been claimed recently that T_{set} and T_o might not be coadapted for locomotor performance in turtles with pronounced aerial basking behavior, since individuals usually lose the heat gained from basking very rapidly when entering the water [9].

A locomotor activity of special interest in turtles is the ability of righting. The capacity of turtles to turn themselves over when they result overturned accidentally is critical to survival, since turtles in an upside-down position are particularly exposed to predators, changes in body temperature (T_b) and dehydration, and may experience difficulty breathing [10–13]. Many freshwater turtles have developed specific skills to right [14] and righting response is considered a good indicator of fitness in aquatic turtles [12,15]. However, righting performance has been shown to be uncorrelated with swimming and other locomotor performances of aquatic turtles [16], which suggests that righting might be subject to different coadaptation pressures. Because most critical righting behavior occurs mainly on land, where turtles can maintain substantially higher T_b, it might be possible that selective pressures favor the convergence between preferred basking temperature and T_o for

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righting performance in aquatic turtles. By regulating T_b to approach T_o, turtles may benefit from a positive effect on their lifetime fitness. Thus, a strong thermal dependence of righting has been observed in a variety of turtle species [12,16,17]. More recently, Ben-Ezra et al. [9] found that T_{set} encompasses T_o for righting in the northern map turtle (*Graptemys geographica*), an active aerial basker. However, enough evidence for co-adaptation between T_{set} and T_o for righting in aquatic turtles is not yet provided, and the relationship between behavioral thermoregulation and locomotor performance in turtles with striking aerial basking remains unclear.

In this study, we analyzed the effect of body temperature on righting behavior of two species of freshwater turtles which actively bask aerially: the Spanish terrapin (*Mauremys leprosa*) and the red-eared slider (*Trachemys scripta elegans*). The Spanish terrapin is widespread in the south and central Iberian Peninsula and northwestern Africa [18]. However, this species has suffered a considerable recession during the last few decades, being currently considered as an endangered species [19]. Besides habitat destruction and human pressure, the remaining populations must endure competition with exotic introduced turtles, mainly American sliders [20–22]. Although the nature of the interspecific interactions between native and introduced turtles is not completely clear, recent studies have highlighted diverse competitive advantages of sliders over Spanish terrapins, such as a more accurate assessment of predatory risk in altered habitats, displacement of native turtles mediated by chemical cues avoidance, a greater thermal inertia that favors heat retention and digestive processes or more competitive basking and feeding abilities [23–28]. Both *M. leprosa* and *T. scripta* turtles are predominantly aquatic, but they come onto land for activities such as basking or egg-laying [29,30]. In such vulnerable situations, turtles are extremely alert and vigilant, since they are potential prey of birds and mammals [31,32]. Thus, overturning accidentally while walking or climbing solaria, or during predatory attacks, may have serious or even lethal consequences for turtles, if they are not efficient at self-righting.

Righting response of turtles consists of two different stages, the lag phase (time elapsed to response) and the mechanical righting phase. Lag time represents the motivation to right, while mechanical righting time depends mainly on physical traits and physiological state of turtles [12,16]. Morphological comparisons indicate that factors such as neck-length to carapace-height ratio, tail length or shell height and width influence the tactic and efficiency of turtles at mechanical righting [14,33]. However, righting might also be influenced by environmental factors affecting physiological performance, especially temperature. Anatomical differences in carapace size and shape have been found between Spanish terrapins and introduced sliders [25], as well as interspecific differences in physiological and behavioral responses [23,24,26–28], which suggests that these two turtle species might also differ in efficiency of righting response. Also, preferred basking temperature and optimal righting performance might be differentially related in Spanish terrapins and sliders. We hypothesized that righting responses of *M. leprosa* and *T. scripta* might be determined by species specific behavior and/or morphological traits. But also, we hypothesized that there might be interspecific differences in the effects of T_b of turtles on righting performance, which might differentially affect the lag phase and mechanical aptitudes of turtles to perform righting. We compared behavioral and mechanical aspects of righting response of native *M. leprosa* and introduced *T. scripta* turtles, examining their relation with T_b of turtles. Our objectives were to determine 1) whether interspecific differences in righting response exist, 2) whether T_b of turtles affects the righting performance of native and invasive turtles, and 3) whether species are differentially affected by T_b. Finally, 4) we analyze whether possible differences between *M. leprosa* and *T. scripta* were due to dissimilarities in morphology that might affect mechanical righting.

2. Material and methods

2.1. Study animals

During May 2007, we captured with baited funnel traps 14 individuals of native Spanish terrapins (*M. leprosa*) (carapace length: mean ± SE = 14.9 ± 0.3 cm, range = 12.5–16.3 cm) in several ponds and creeks of the Guadiana River at Olivenza (Badajoz Province, southwestern Spain). These freshwater habitats, located inside dehesa woodlands with scattered holm oak (*Quercus ilex*) held an important population of Spanish terrapins. We also obtained 13 introduced red-eared sliders (*T. scripta*) (carapace length: mean ± SE = 14.3 ± 0.6 cm, range = 11.3–17.4 cm), from a large pond located in Madrid Province (central Spain), where they had been maintained under seminatural conditions by the conservationist private organization "EXOTARIUM" (Exotic Animal Rescue Center). These sliders had been recently extracted from introduced populations in central Spain to preserve the original ecosystem balance. None of the turtles presented shell imperfections that might hinder righting success.

Turtles were individually housed at "El Ventorrillo" Field Station (Navacerrada, Madrid Province), in outdoor aquaria (60 × 40 × 30 cm) that were filled with water and provided with stones that allowed turtles to bask. Turtles were maintained under natural temperatures and photoperiods and were fed small pieces of commercial compound feed three times per week. We held turtles in their home-aquaria for at least two weeks before testing, so that they became familiarized with captivity conditions. During this time, we minimized contact with animals to avoid habituation to the experimenter that could affect risk assessment during trials. At the end of experiments, all turtles had maintained or increased their body mass, and were returned to the EXOTARIUM's pond (sliders) or to their exact field capture sites (Spanish terrapins). The experiments enforced all current laws of Spain and of the Environmental Organisms of the "Junta de Extremadura" and "Comunidad de Madrid" where they were performed.

2.2. Morphological traits

We compared morphological traits of *M. leprosa* and *T. scripta*. Four parameters: *CL* (carapace straight length), *CW* (carapace straight width at the 6–7 marginal scutes joint), *CH* (maximum carapace height), and *TL* (tail length) were measured with a digital caliper (mitutoyo) to the nearest mm. Thus, we estimated carapace height-to-width ratio as *CH/CW* and tail-length-to-size ratio as *TL/CL*. Carapace height-to-width ratio approximates shell geometry and has been used to classify turtle species into equilibrium classes determining the strategy and efficiency of righting [33]. On the other hand, higher values of tail-length-to-size ratio favor mechanical righting of turtles such as chelydrids. Nevertheless, tail length seems unlikely to affect righting of sliders and Spanish terrapins, since the two turtle species possess much shorter tails in comparison [14].

We also estimated sphericity and flatness indices of both species of turtles, using Krumbein's Sphericity Index (*SI*) [34] and Cailleux's Flatness Index (*FI*) [35]:

$$SI = \left(\frac{qr}{p^2}\right)^{1/3} \quad FI = \frac{p+q}{2r}$$

where *p*, *q* and *r* were given by *CL*, *CW* and *CH*, respectively [25]. Higher values of sphericity index and lower values of flatness index mean a more domed shell, which entails lower energy barriers between stable and unstable equilibria [33].

Then, we compared carapace height-to-width ratios, sphericity and flatness indices, and tail-length-to-size ratios of the two turtle species, and analyzed within species the effects of sphericity and flatness indices and tail-length-to-size ratio on mechanical righting times of turtles.