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Divergence in Morphology, Clinging Ability and Self-Righting Ability of Two Sympatric Box Turtles (*Cuora*)

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ABSTRACT

Elucidating the relationships between morphology, performance and ecology is central to understand how morphology influences fitness. Previous work has already shown that two sympatric turtles, the Keeled box turtle *Cuora mouhotii* and the Flowerback box turtle *C. galbinifrons*, have divergent morphologies and occupy different microhabitats (steep, rocky hillslopes vs gentle, less rocky hillslopes). However, it is unclear how these differences are related to performance. In this study, we test the relationship between morphology and functional performance in these two species. The Keeled box turtle has a flatter shell, larger head, longer toes, better clinging ability, and better self-righting ability, whereas the Flowerback box turtle has a more domed shell, smaller head, shorter toes, decreased clinging ability, and decreased self-righting ability. Together, these results provide evidence that these two species are specialized to use different microhabitats. These differences likely allow the two species to exist in sympatry by reducing interspecific competition.

INTRODUCTION

Elucidating the relationships between morphology, performance, and ecology is critical to understand how morphology influences fitness (Arnold, 1983; Vanhooydonck *et al*., 2000; Rivera, 2008; Rivera *et al*., 2014). Therefore, measuring locomotor performance can reveal how morphology is related to an animal's behavior and ecology. This is because natural selection can favor individuals with enhanced performance in ecological relevant tasks (e.g. faster swimming is associated with increased fitness) (Irshick and Garland, 2001; Delmas *et al*., 2007). As for sympatric species, differences in locomotor performance can reveal how they have adapted to exist in different parts of the habitat. Two ecologically relevant tasks in terrestrial reptiles include clinging ability and self-righting ability. These tasks can show how animals are adapted to use different slopes or substrates (Claussen *et al*., 2002). Clinging ability is closely linked to climbing ability in rocky habitats (Goodman *et al*., 2007, 2008), because terrestrial reptiles must support their weight through clinging while climbing inclined or vertical substrates (Irschick *et al*., 1996). The short legs and flat body of arboreal lizard species lowers their center of gravity. A lower center of gravity and longer toes enhances stability and reduces the risk of being overturned or falling down (Pounds, 1988; Losos, 1990; Sinervo and Losos, 1991; Miles, 1994). Thus, a lower center of gravity and longer toes can enhance clinging ability (Cartmill, 1985). This trade-off between morphologies and clinging ability has not been investigated in chelonians.

Armored animals such as chelonians can easily lose their stability and overturn while walking across uneven surfaces, during encounters with predators, or during combat with other individuals (Finkler, 1999; Steyermark and Spotila, 2001). When overturned, chelonians are exposed to predation or desiccation; therefore, self-righting has a vital importance (Golubović *et al*., 2015). Chelonians are enclosed in a stiff shell which prevents torsion of their body. Therefore, the geometry of the carapace and morphology of limbs and head can have a great impact on self-righting efficiency (Domokos and Varkonyi, 2008). Despite the importance of morphology on self-righting ability, most studies only focus on a single measure (but see Chiari *et al*., 2017) like shell height (Bonnet *et al*., 2001; Zuffi and Plaitano, 2007; Golubović *et al*., 2015). Even less empirical data exists on clinging ability in turtles.

The keeled box turtle *Cuora mouhotii* (Gray, 1862; formerly *Pyxidea mouhotii*) and the flowerback box turtle *C. galbinifrons* (Bourret, 1939) exist sympatrically throughout Hainan Province, China (Zhao and Adler, 1993;

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Wang *et al*., 2011a, b). Their morphology and behavior are markedly different. The keeled box turtle has a relatively flat shell and prefers microhabitats with rock crevices and steep slopes, whereas the flowerback box turtle has a more domed shell and is restricted to microhabitats with high amounts of leaf litter on gentle slopes (Fig. 1; Xiao *et al*., 2017). These differences could represent a trade-off that allows these species to coexist in their perspective habitats. For example, since the keeled box turtle lives on steep rocky hill slopes where they are more susceptible to slipping or overturning, one would expect the morphology of this species to result in enhance clinging and self-righting ability. In contrast, the more domed shell of the flowerback box turtle might restrict this species from clinging onto steeper slopes and self-righting. Yet, a more domed shell has been show to tolerate stronger mechanical forces, such as those from terrestrial predators (Greene, 1988; Stayton, 2011). Therefore, the more domed shell of the flowerback box turtle might represent an adaptation to withstand predation rather than ability to walk on steep-rocky hill slopes. If these differences in morphology represent a trade-off in locomotor performance, one would expect the keeled box turtle to be better at clinging and self-righting. To date, no empirical evidence has linked morphology and microhabitat differences to locomotor performance in the keeled box turtle and flowerback box turtle. Therefore, in the present study, we compare morphology, clinging ability, and self-righting ability in these two species. We predict that morphological and microhabitat differences are associated with the ability to cling and self-right.

Fig. 1. External morphology of *Cuora mouhotii* (left) and *C. galbinifrons* (right). Taken by H. Shi.

MATERIALS AND METHODS

Animal ethics

This study was approved by the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (HNECEE-2014-002) and was carried out in strict accordance with the institutional guidelines. Fieldwork was carried out with permission from the Diaoluoshan Forest Bureau. No turtles incurred injury or died in this study.

Sample size

We analyzed 14 keeled box turtles (8 females and 6 males) and 10 flowerback box turtles (6 females and 4 males). We only tested adult keeled box turtles larger than 130 mm carapace length and flowerback box turtles larger than 160 mm (Shi *et al*., 2011). All turtles were from the Diaoluoshan Mountain in Hainan province, China and experiments were carried out at the field station in Diaoluoshan Mountain.

Performance

Clinging ability was quantified by placing individual turtles on the middle of a 2 m long level board that had a rough surface, lifting the board at a constant speed, and then recording the slope of the board when the turtle slipped down. Each turtle was tested with two measurements. The highest slope recorded for each turtle was used as the individual's maximum clinging ability.

Self-righting ability was assessed by measuring the success rate and time required of each turtle to right itself after being placed on its carapace on a smooth sand surface. If a turtle failed to right itself within 2 min, it was allowed to rest (right-side up) for 1 min, after which it was turned back on its carapace. The procedure was repeated six times for each turtle. The minimum time required for successful self-righting was used as the self-righting time of each individual, and the percentage of successes among the six attempts was used as the righting success rate. Turtles that failed to right themselves were excluded from the analyses of self-righting time.

Both performance experiments were conducted in a laboratory at about 23 °C, which has been reported as an optimal performance temperature for the two species (Wang, 2010). Clinging ability and self-righting ability were measured on different days.

Morphological measurements

The following morphological measurements were taken from all experimental individuals using a digital calipers (accuracy 0.02 mm; Tricle Brand, Shanghai, China): carapace length (CL, straight distance from the front of the cervical scute to the rear of the supracaudal scute), carapace width (CW, the maximal width at the level of the sixth marginal scute), carapace height (CH, the maximum vertical height from carapace to plastron, usually at the sixth marginal scute), forelimb length (FLL, measured from elbow to palm), hindlimb length (HLL, measured from knee to foot), and toe length (TL, measured the longitudinal length of the proximal phalanx of the third toe). Because some turtles rely on their head and neck as fulcrum to right (Delmas *et al*., 2007; Domokos and Várkonyi, 2008), we also measured head characteristics: head length (HL, measured from the tip of the snout to the rear edge of jaw), head width (HW, measured at the widest part of the skull), and head height (HH, measured at the highest part of the skull just posterior to the orbital). In addition, we calculated the ratio of carapace height to width (R) as a measure of shell contour (or the relative positions of the carapace and the plastron), since it is reportedly correlated with righting ability (Domokos and Várkonyi, 2008).

Statistical analyses

All statistical procedures were performed in SPSS 16.0 (SPSS,Inc., Chicago, IL), Prior to statistical analysis, we examined the normality (Kolmogorov-Smirnow test) and homogeneity of variance (Levene test) for all performance data and morphological measurements. Two-sample Student's *t*-tests were used to test whether the two species differed in maximum clinging ability, self-righting time, and self-righting success rate. One-way ANOVA was used to test whether the two species differ in carapace length, and in order to remove the effect of body size, one-way ANCOVA (carapace length as the covariate) was performed to test whether the two species differed in all the other morphological variables. Moreover, to check for the effect of sex, we also tested whether females and males differ in performance and morphology for each species by using two-sample Student's *t*-tests, and one-way ANOVA and ANCOVA (carapace length as the covariate), respectively. For all statistical analyses, an alpha level of $\alpha = 0.05$ was selected as criterion for statistical significance.

RESULTS

Performance

The mean maximum clinging ability of the two species differed significantly (Fig. 2) Student's *t*-test, $t = 4.043$, $P = 0.001$). The clinging ability of the keeled box turtle (42.57°) was greater than that of the flowerback box turtle (33.90°). The mean maximum clinging ability was similar between sexes for each species (keeled box turtle: female = 43.63°, male = 41.17°; Student's t-test, $t = 0.796$, $P = 0.442$; flowerback box turtle: female = 31.33°, male = 37.75°; Student's t-test, $t = -2.655$, $P = 0.065$).

The mean minimum self-righting time of the keeled box turtle (11.75s) was less than of the flowerback box turtle (31.71s) (Fig. 3; Student's t-test, $t = -3.705$, $P = 0.001$), and the mean success rate of the keeled box turtle (78.57%) was greater than of the flowerback box turtle (31.66%) (Fig. 3; Student's t-test, $t = 6.104$, $P < 0.0001$). These results indicate that the keeled box turtle has better ability to self-right when compared to the flowerback box turtle. The mean minimum self-righting time was similar between sexes for each species (keeled box turtle: female = 6.18s, male = 19.17s; Student's t-test, $t = -1.764$, $P = 0.135$; flowerback box turtle: female = 33.25s, male = 29.40s; Student's t-test, $t = 0.442$, $P = 0.67$). Also, the mean success rate was similar between sexes for each species (keeled box turtle: female = 87.50%, male = 66.67%; Student's t-test, $t = 1.371$, $P = 0.217$; flowerback box turtle: female = 30.55%, male = 33.32%; Student's t-test, $t = -0.432$, $P = 0.677$).

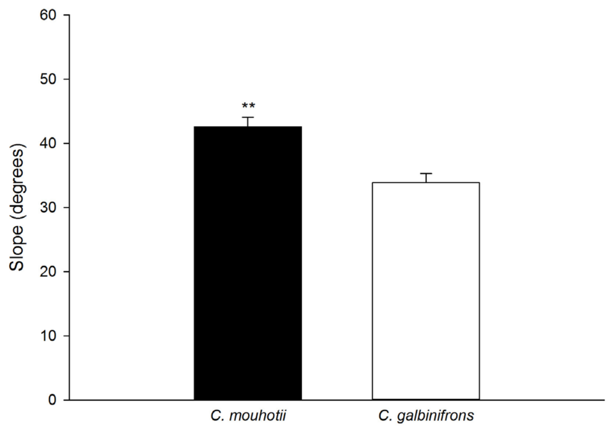

Fig. 2. Clinging ability of two *Cuora* spp. Values indicate the mean ± SD maximum clinging ability, which was measured as the maximum slope at which turtles slid off a rough wood board. Asterisks indicate significant differences (**$P < 0.001$), according to a two-sample Student's t-test.

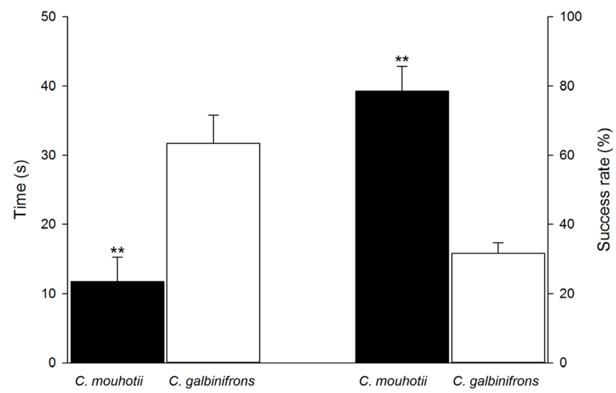

Fig. 3. Self-righting ability of two *Cuora* spp. Values and error bars indicate the mean±SD minimum righting time and self-righting success rate. Asterisks indicate significant differences (**$P < 0.001$), according to two-sampled Student's t-test.

Morphological measurements

The carapace length of the two species did not differ significantly (one-way ANOVA, Table I). One-way ANCOVA, with carapace length as the covariate, indicated that the carapace height, ratio of carapace height to width, head length, head width, head height, and toe length of the two species all differed significantly, whereas the limb dimensions (i.e., forelimb length and hindlimb length) of the two species were similar (Table I). The keeled box turtle had a flatter carapace, larger and longer head, and longer toes, whereas the flowerback box turtle had a more domed carapace, smaller head, and shorter toes. There are no sexual differences in morphology in either species (Table II).

Table I. Morphological measurements (mean ± SD) of two *Cuora* spp and results of one-way ANOVA for carapace length and one-way ANCOVA for the remaining parameters by carapace length as covariate.

	C. mouhotii	*C. galbinifrons*	F	P
n	14	10		
CL	165.18 ± 18.68	172.12 ± 11.39	1.084	0.309
CW	115.88 ± 7.84	116.36 ± 7.40	1.192	0.287
CH	66.68 ± 4.15	82.02 ± 5.85	67.149	< 0.0001
R	0.58 ± 0.03	0.71 ± 0.04	75.553	< 0.0001
HL	47.01 ± 6.69	36.91 ± 1.56	45.503	< 0.0001
HW	30.02 ± 2.90	26.39 ± 2.02	36.507	< 0.0001
HH	25.33 ± 2.27	18.49 ± 1.68	111.048	< 0.0001
FLL	35.83 ± 4.90	37.98 ± 4.89	2.01	0.14
HLL	38.82 ± 4.95	39.01 ± 5.08	0.539	0.472
TL	22.84 ± 2.71	19.79 ± 3.12	8.466	0.009

CL: carapace length; CW: carapace width; CH: carapace height; R: carapace height / carapace width; HL: head length; HW: head width; HH: head height; FLL: forelimb length; HLL: Hindlimb length; TL: toe length.

DISCUSSION

In this study, we found that two sympatric turtle species, the keeled box turtle and flowerback box turtle, differed significantly in clinging ability, self-righting ability, and morphology. Compared to the flowerback box turtle, the keeled box turtle has better clinging ability, better ability to self-right, a flatter carapace, a bigger head, and longer toes.

Despite the lack of study on clinging ability in chelonians in the field, this ability is common in some species. For instance, we have observed that the big-headed turtle (*Platysternon megacephalum*) clinging on to the surface of a steep streamside cliff (personal observation). Similarly, Xiao *et al*. (2017) observed the keeled box turtle clinging on the inclined rocks in the field on more than one occasion. The flatter carapace of the keeled box turtle likely aids in clinging ability on inclined substrates, providing a lower center of gravity and increasing a turtle's stability on steeper surfaces (Domokos and Várkonyi, 2008; Chiari *et al*., 2017). Similar patterns are seen in lizards, where long toes increase clinging ability (Cartmill, 1985). Although clinging ability is related to limb lengths in lizards (Goodman *et al*., 2008), this study indicates that limb lengths between the two-turtle species were similar, whereas the maximum slope achieved without falling was greater in the keeled box turtle than the flowerback box turtle. Therefore, the flattened carapace and long toes of the keeled box turtle is likely responsible for this species ability to cling steeper surface than the flowerback box turtle. However, it is possible that differences in friction on the plastrons of the two species are partly responsible for the enhanced performance in the keeled box turtle. We should test the hypothesis in future studies.

We found that the keeled box turtle can cling to surfaces approximately 10° steeper than the flowerback box turtle (average slope: 42.57° vs. 33.90°). This difference in clinging ability is dramatic because no turtle can cling to anything greater than 90°, and 60° is an extremely steep slope for turtles (e.g. keeled box turtle, Xiao *et al*., 2017). Also, the maximum slope that a juvenile of *Chelydra serpentina* can climb is 45° (Finkler and Claussen, 1997), that of *Terrapene ornate* 40° (Claussen *et al*., 2002), and *T. carolina* 50° (Muegel and Claussen,1994). For these chelonians, climbing speed was significantly reduced as slope increased. These clinging and climbing abilities might limit the turtles' special distribution (Muegel and Claussen, 1994; Finkler and Claussen, 1997; Claussen *et al*., 2002). Therefore, differences in clinging ability observed in this study may permit the keeled box turtle to occupy steeper slopes and limit the flowerback box turtle to more gentle slopes in the field (average slope: 30.3° vs. 22.3°; Xiao *et al*., 2017).

The superior self-righting ability of the keeled box turtle is likely related to its microhabitat use and morphology. The keeled box turtle live on steep-rocky hill slopes where the risk of stumbling and being overturned is greater (Xiao *et al*., 2017), they overcome this challenge with a flatter shell (average carapace height / width ratio=0.58) and larger head that facilitate self-righting. Generally, the self-righting strategy of turtles with a flatter shell (carapace height / width < 0.6) is accomplished by a strong vertical push with the head against the substrate with the hyperextension of the neck, which sufficiently lifts the turtles over the primary energy barrier

Table II. Morphological measurements (mean±SD) of female and male for the two *Cuora* spp and results of one-way ANOVA for carapace length and one-way ANCOVA for the remaining parameters by carapace length as covariate.

	C. mouhotii				*C. galbinifrons*			
	Female	**Male**	**F**	**P**	**Female**	**Male**	**F**	**P**
n	8	6			6	4		
CL	158.19 ±14.76	174.49±20.49	3.016	0.108	171.76 ±12.23	172.65±11.81	0.013	0.912
CW	114.94 ±6.22	117.15±10.12	2.836	0.120	114.88 ±7.52	118.57±7.68	1.091	0.331
CH	67.10±2.52	66.14±5.95	2.739	0.126	82.53±7.03	81.24±4.37	0.740	0.418
R	0.58 ± 0.03	0.57±0.03	0.245	0.631	0.71 ± 0.04	0.69±0.03	1.489	0.262
HL	44.93 ±5.20	49.99±7.80	0.181	0.679	36.21 ±2.16	37.96±3.41	1.388	0.277
HW	28.86 ± 1.90	31.57±3.43	0.780	0.396	26.16 ±1.55	26.75±1.72	0.634	0.452
HH	24.01 ±0.98	27.08±2.36	4.167	0.066	17.74 ±1.44	19.60±1.51	4.954	0.061
FLL	34.05 ±2.83	38.94±6.60	2.091	0.186	42.25 ±4.62	41.57±5.97	0.282	0.612
HLL	37.70 ±3.68	40.79±6.84	0.201	0.666	38.71 ±4.95	39.45±6.01	0.028	0.872
TL	23.29 ±3.22	22.07±1.54	1.412	0.269	19.44 ±3.79	20.31±2.15	0.141	0.718

CL: carapace length; CW: carapace width; CH: carapace height; R: carapace height / carapace width; HL: head length; HW: head width; HH: head height; FLL: forelimb length; HLL: Hindlimb length; TL: toe length.

(Domokos and Várkonyi, 2008). However, head morphology may be more important than neck length in regards to self-righting ability (Chiari *et al*., 2017), because head is the only mobile structure that comes into contact with the ground during righting attempts by many turtle species (Rubin *et al*., 2018). Moreover, since the neck of box turtle is difficult to fully extend when holding it, we did not take morphometric measurements to avoid injury to the neck in this study. Therefore, the greater clinging and self-righting ability of the keeled box turtle is likely an adaption to its steep and rocky microhabitats (Xiao *et al*., 2017).

In contrast, the more domed shell (average carapace height / width ratio = 0.7) of the flowerback box turtle, which limited its clinging and self-righting abilities, is likely a result of its tendency to live in microhabitats of deciduous leaves with relatively gentle slopes, where the ability to cling or self-right is less important (Xiao *et al*., 2017). The relatively high carapace of the flowerback box turtle lifts the species' center of gravity (Domokos and Várkonyi, 2008), which probably decreases its stability while clinging, resulting in a weaker clinging ability. Similar results are seen in lizards, where species from less rocky habitats have weaker clinging ability than their relatives from rocky habitats (Goodman *et al*., 2008). As tradeoffs, the shell of the flowerback box turtle can potentially tolerate much stronger mechanical forces from predators (Greene, 1988; Stayton, 2011; Polly *et al*., 2016). Moreover, the flowerback box turtle has a hinged plastron that allows it to close its shell completely and protection of its head and limbs from predators (Pritchard, 2008).

Moreover, the flowerback box turtle has an intermediate carapace shape (0.6 < carapace height / carapace width < 0.8) and exhibits a righting strategy that is intermediate between both flat shelled freshwater turtles and highly domed tortoises (Domokos and Várkonyi, 2008). When the flowerback box turtle overturns, it starts rolling spontaneously, assisted via limb and neck motion, to overcome shell irregularities (like a highly domed turtle), until it reaches a stable equilibrium. Then, the turtle rights itself using a vertical push with its head (like a flat turtle) and a simultaneous push with its legs. Therefore, the weaker self-righting ability of the flowerback box turtle is potentially because of its smaller head. However, although we found that the self-righting ability of the two species is related to their head morphology, we did not directly carry out a correlation analysis. Meanwhile, this has not yet been studied in previous studies. Thus, the relationship between head morphology and self-righting ability needs to be further studied on the basis of a large sample size in chelonian species.

CONCLUSION

This is the first study to show how morphology is linked to performance in ecologically relevant tasks of the two sympatric *Cuora* spp. The keeled box turtle's flat shell, large head, long toes, and enhanced locomotor performance allow this species to exist in steep-rocky microhabitats. In contrast, the flowerback box turtle's domed shell, small head, short toes, and weaker locomotor performance seem to be better suited for less rocky microhabitats with gentle slopes. These differences likely allow these two species to exist in sympatry by reducing interspecific competition.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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