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4 **TURNING TURTLE: SCALING RELATIONSHIPS AND SELF-RIGHTING ABILITY IN CHELYDRA SERPENTINA**  
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33 **ABSTRACT**

34 Testudines are susceptible to inversion and self-right using their necks, limbs, or both, to generate enough  
35 mechanical force to flip over. We investigated how shell morphology, neck length, and self-righting biomechanics  
36 scale with body mass during ontogeny in *Chelydra serpentina*, which uses neck-powered self-righting. We found  
37 that younger turtles flipped over twice as fast as older individuals. A simple geometric model predicted the  
38 relationships of shell shape and self-righting time with body mass. Conversely, neck force, power output, and  
39 kinetic energy increase with body mass at rates greater than predicted. These findings were correlated with  
40 relatively longer necks in younger turtles than would be predicted by geometric similarity. Therefore, younger  
41 turtles self-right with lower biomechanical costs than predicted by simple scaling theory. Considering younger  
42 turtles are more prone to inverting and their shells offer less protection, faster and less costly self-righting would  
43 be advantageous in overcoming the detriments of inversion.

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45 **1. INTRODUCTION**

46 Predator-prey dynamics drive adaptations in animals, including the evolution of protective armour. Body armour  
47 takes many forms and is widespread in extant reptiles, where spines, spikes, and osteoderms are commonplace  
48 [1]. Arguably, one of the most recognizable forms of body armour is the shell of turtles and tortoises, which is  
49 comprised of a dorsal carapace and a ventral plastron, features that distinguish them from all other vertebrates.  
50 Despite similarities in general appearance among Testudines, shell morphology varies substantially. For example,  
51 generally species that frequently swim [2] or burrow [3] have flatter shells that can be flexible, whereas those  
52 requiring better protection from predation [4], desiccation [5], and fluctuating body temperature [5] have taller,  
53 more rigid shells [6, 7]. Testudine shells are dynamic structures and can also have important physiological roles,  
54 which include acting as blood-pH buffers and as reservoirs for water, fat, or wastes [8]. While shells impact all  
55 aspects of Testudine biology, it is locomotor performance that is perhaps the most profoundly affected [9].

56

57 In almost all tetrapods, a flexible vertebral column is an important contributor to locomotion. However, in  
58 Testudines, only the neck and tail are flexible, because the spine is fused with the underside of the shell [10]. The  
59 pectoral and pelvic girdles are also located inside the shell, which restrict movement of the limbs. As a result of  
60 having an inflexible body, Testudines traversing uneven surfaces, encountering predators, or engaging in  
61 reproductive combat are prone to inverting. Turning upside-down can have serious life-and-death consequences.  
62 Once flipped onto their backs, Testudines are susceptible to thermal stress, starvation, stranding, and predation,  
63 if they cannot effectively self-right [11, 12]. Indeed, improved self-righting performance is associated with higher  
64 survival [13] and can have a substantial impact on an individual's fitness [14]. Accordingly, understanding the  
65 underlying mechanisms and constraints on self-righting has strong ecological relevance. Self-righting is also an  
66 intriguing biomechanical behaviour and Testudines themselves are especially interesting, as they are long-lived

67 and continue to grow throughout their lives [15]. For example, the common snapping turtle (*Chelydra serpentina*)  
68 grows from a carapace length of ~30 mm and body mass of 10 g, as a hatchling [16], to a carapace length of over  
69 50 cm and weighing over 40 kg, as an adult. Snapping turtles retain a high degree of carapace rotation as they  
70 walk [17] and the neck remains the primary driver in self-righting [18], throughout their lives.

71

72 A Testudine's ability to self-right is dependent on body size, body shape, and flexibility of the limbs, neck, or tail  
73 [19-21]. There are two distinct mechanisms by which Testudines self-right: (i) rotating the limbs, to generate  
74 rocking movements to ultimately induce body rolling, or (ii) extending the neck, to directly push against the  
75 ground and flip the animal over [20, 22]. Investigations of self-righting in Testudines are often limited to  
76 theoretical models of the impact of shell shape [20, 23, 24], the time to self-right (e.g., [25]), and biotic or abiotic  
77 influences (e.g., [11]). And, to our knowledge, just one study has looked at the biomechanics of self-righting [19].  
78 The challenge of self-righting is that the inverted animal is in a stable and low-gravitational potential-energy  
79 state. To self-right, Testudines must add gravitational potential energy to the system, by rotating the shell, until  
80 it reaches a tipping point, from which it will then roll to the non-inverted stable state and, thereby, overcoming  
81 the so-called 'potential hill' [20, 24]. Theoretically, shells that are very high and domed should be the easiest to  
82 self-right, because the required change in height of the centre of mass is relatively small. Conversely, species  
83 with flatter shells will need to raise the centre of mass by a greater extent [20]. Testudines that self-right by limb  
84 movements often have more domed shells [20], whereas those with flatter shells, such as mud (kinosternids),  
85 pond (emydids), snapping (chelydrids), and soft-shelled (trionychids) turtles, create thrust with their necks to  
86 self-right [20, 22]. For geometrically similar animals, the minimum energy required to self-right should increase  
87 with  $\text{mass}^{4/3}$ , since the height change will scale with  $\text{mass}^{1/3}$  and the potential-energy change is proportional to  
88 the change in mass  $\times$  height. In neck-based self-righting, this energy comes from a single work loop, and, since  
89 the work available in a work loop scales approximately isometrically with mass, we would expect neck-based  
90 self-righting to become progressively more difficult as body size increases.

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92 Self-righting speed and energetics might be particularly important in smaller juveniles, which are more prone to  
93 inversion and possess shells that offer little anti-predator defence. To self-right more quickly, selection could act  
94 on shell morphology; individuals with more domed-shaped shells should self-right more quickly and with less  
95 effort [23, 24], which might predict that shell shape changes during ontogeny. Alternatively, selection could act  
96 on the neck, since it is the primary structure these turtles use to self-right [22]. The aim of this study, therefore,  
97 was to examine the influence of body mass, shell shape, and neck length on neck-powered self-righting ability  
98 and the accompanying biomechanical costs, in a freshwater turtle species, *C. serpentina*. We used animals of  
99 different ages to provide the required variation in body size. We measured the self-righting neck force (which  
100 we used to estimate kinetic energy and power output) to investigate the scaling relationships between the

101 physical effort to self-right and body mass. Although we would expect scaling of mass<sup>4/3</sup> for the self-righting effort  
102 of geometrically similar shell shapes, we predicted that, due to selection against the possible increase in risks  
103 associated with being inverted, self-righting should be easier in younger/smaller turtles, which would be  
104 reflected in the speed and biomechanical cost.

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## 106 **2. MATERIALS AND METHODS**

### 107 **(A) ANIMALS**

108 Nongravid female common snapping turtles (*Chelydra serpentina*), ranging in body mass [254.3 g to 4515 g; n =  
109 33; **Electronic Supplementary Materials (ESM)**] and age (<1-1.5-, 4.5-, and 5.5-year-olds, n = 26, 4, and 3 turtles,  
110 respectively), were selected for the present study. Turtles were housed at 26°C, in small groups, within large  
111 plastic tubs (1.5-m wide, 1-m tall), with access to shallow water. All experimental trials took place at 26°C. Turtle  
112 husbandry and experimental procedures were carried out in accordance with an animal-care protocol (no. 11-  
113 007), approved by the University of North Texas Institutional Animal Care and Use Committee.

114

### 115 **(B) EXPERIMENTAL SETUP & DATA COLLECTION**

116 Before the commencement of any self-righting trials, morphological measurements of carapace width, carapace  
117 length, and shell height were taken, with digital calipers (Duratool, model D02264, Premier Farnell Ltd, Leeds,  
118 UK). Neck length was determined by encouraging the turtle to bite a piece of leather, then grasping the turtle's  
119 head (while wearing protective gloves) and gently extending it out from the shell to its full length. Using the  
120 calipers, the distance from the shell at the base of the neck to the tip of the snout was then measured and used  
121 as a proxy for neck length.

122

123 The experimental setup consisted of a force plate, with a pressure pad on top, covered by a thin rubber mat. The  
124 force plate (3D Force Plate Type 9286B, Kistler® Instruments Ltd, Hook, Hampshire, UK) was used to measure the  
125 vertical reaction force exerted by a turtle during self-righting. Force data were recorded (at 420 Hz), using the  
126 BioWare® data-acquisition software (type 2812A, Kistler®). To measure the relative contributions of the neck  
127 and body to the vertical force, a pressure pad (Pressure Mapping Sensor 7101, Tekscan, Inc, South Boston, MA,  
128 USA) was placed on top of the force plate. The pressure pad data were recorded (at 100 Hz) using the FootMat®  
129 Research software (v 7.1, Tekscan). A camera (Sony® Cyber-shot RX10 III) was used to record videos (at 100 fps)  
130 of the self-righting movements. The self-righting times were calculated from videos, using Tracker  
131 (<https://physlets.org/tracker>; The Open Source Physics Project). The self-righting time is defined as the duration  
132 from the moment a turtle's head first contacted the pressure pad/force plate until the head was no longer in  
133 contact with the setup (see Fig. 1A-D).

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135 **(c) DATA ANALYSIS**

136 Vertical force distributions (see Fig. 1E) were obtained from the pressure-pad data and used to calculate the  
137 relative magnitude of neck force production to the total ground reaction force for the turtle, as shown by the  
138 representative curves in Fig. 1F. This relative value was then multiplied by the absolute vertical force that was  
139 recorded by the force plate (Fig. 1F), which allowed us to determine absolute neck force in Newtons. All force-  
140 plate and pressure-pad data were filtered with a 10-Hz, two-pole Butterworth low-pass filter, using the `filtfilt`  
141 function on Matlab (v R2020a, MathWorks, Natick, MA, USA), which reduced high-frequency noise present in  
142 the data.

143  
144 Previous reports have shown that shell morphology affects self-righting time [20, 23, 25]. Therefore, we  
145 calculated two indices of shell shape: Sphericity Index (SI) and Flatness Index (FI) [23], as defined in equations  
146 2.1 and 2.2.

147

148 2.1

149 
$$SI = \left( \frac{W \times H}{L^2} \right)^{\frac{1}{3}}$$

150 2.2

151 
$$FI = \frac{L + W}{2H}$$

152 Where  $W$  and  $L$  are maximum carapace width and length, respectively, and  $H$  is shell height. Larger sphericity  
153 and flatness values indicate greater and flatter shell curvature, respectively.

154

155 Impulse ( $J$ ) was calculated as the area under the force-time curve (Fig. 4F), using equation 2.3:

156

157 2.3

158 
$$J = \sum F_t \Delta t$$

159 Where  $F_t$  is the instantaneous vertical force and  $\Delta t$  is time increment.

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161 From the impulse, kinetic-energy equivalent (KEE) was calculated (assuming a start from rest, so that the initial  
162 momentum is zero), using equation 2.4:

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164 2.4

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$$KEE = \frac{J^2}{2M_b}$$

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Where  $M_b$  is body mass.

From KEE, mean power-output equivalent ( $PE$ ) was calculated, using equation 2.5:

2.5

$$PE = \frac{\Delta KEE}{t_{Flip}}$$

Where  $t_{Flip}$  is self-righting time.

Finally, from KEE, height-change equivalent ( $\Delta HE$ ) was calculated and normalized to carapace width, using equation 2.6:

2.6

$$\Delta HE = \frac{\Delta KEE}{M_b \cdot g \cdot W}$$

Where  $g$  is gravity ( $9.81 \text{ m s}^{-2}$ ).

$\Delta HE$  was calculated as a measure of self-righting efficiency, given that we would expect the minimum  $\Delta HE$  to be half the shell width with a flat shell, and less than half for more rounded shells. It can be higher too if the turtle does not choose the most efficient trajectory, and if the KEE at maximum height is still substantial. Lower  $\Delta HE$  values thus indicate higher self-righting energetic efficiency.

All data were graphed with GraphPad Prism 8 (GraphPad Software, San Jose, CA, USA). To determine scaling relationships, data were log-transformed and regression lines plotted, with the equation  $\log(y) = \log(a) + b \cdot \log(x)$ , using the ordinary least-squares (OLS) method on GraphPad and coefficients of determination ( $R^2$ ) were calculated. Isometric and allometric scaling relationships were determined by comparing the predicted slope with the allometric slope ( $b$ ), using the 95% confidence intervals (CIs). Assuming geometric similarity (i.e., isometry) across body mass ( $M_b$ ), all linear dimensions were expected to scale to  $M_b^{1/3}$ ; force was expected to scale to  $M_b^{2/3}$ ; KEE should scale as  $M_b^{4/3}$ ; self-righting time should scale as  $M_b^{1/2}$ ; and mean PE as  $M_b^{5/6}$ . Formal derivations of these predicted relationships are in the supplementary information. Scaling relationships were considered to show isometry when the predicted slope fell within the 95% CIs ( $0.95 \leq b < 1.05$ ), positive allometry when predicted  $b > 1.05$ , and negative allometry when predicted  $b \leq 0.95$ . For the derivation of these scaling relationships, see Derivation of Scaling Predictions in the Electronic Supplementary Materials.

198 **3. RESULTS**

199 **(A) MORPHOMETRICS**

200 The log-log models fit the data extremely well for linear shell dimensions, with  $R^2$  values ranging from 0.979 to  
201 0.988 and the 95% CIs of the slopes overlapping the  $\frac{1}{3}$  value that would be predicted from geometric similarity,  
202 thereby, providing no evidence for shell-shape change (as defined in the current study) with increasing body  
203 mass during ontogeny (Fig. 2A, Tables 1, and Table S1). Furthermore, derived measures of sphericity and flatness  
204 were calculated and, unsurprisingly, given the likely geometric scaling of the shell shape, had no dependency on  
205 body mass, although individual values did show moderate variability (Fig. 2B and Fig. S1). Neck length also fit the  
206 log-log model well ( $R^2 = 0.895$ ); however, the 95% CI range (0.246 to 0.316) suggests that scaling is anisometric,  
207 with larger animals having shorter necks than would be predicted by geometric scaling (Fig. 2C, Table 1, and  
208 Table S1). The scatter might reflect greater ontogenetic variability or simply greater measurement uncertainty  
209 for this parameter.

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211 **(B) SELF-RIGHTING DYNAMICS**

212 To analyse self-righting performance, we plotted the log of self-righting time (defined as the duration of time in  
213 which the neck is applying force via the head) against the log of body mass (Fig. 2D). The OLS regression was  
214 significant (slope = 0.357, 95% CIs = 0.173 to 0.54; Table 1) and the 95% CIs overlap the 0.5 value for the exponent  
215 predicted by our model based on geometric similarity. Smaller turtles self-righted proportionally faster (Table 1  
216 and Table S1), but the duration of time it took for a turtle to place its head on the ground to initiate the self-  
217 righting maneuver (the pre-neck latency time) and the duration of time to complete the self-righting maneuver  
218 when the turtle no longer used the neck to flip over (the post-neck latency time) did not differ between the age  
219 groups (Fig. S2).

220 We also plotted the log of kinetic-energy equivalent against the log of body mass (Fig. 3A) and found a  
221 modest effect, since the OLS slope is 1.548 (95% CIs = 1.341 to 1.755; Table 1 and Table S1), which does not  
222 overlap the 1.333 predicted by geometric similarity, suggesting the energy expended by a larger turtle is  
223 increasing more rapidly than our model would predict. To investigate the interaction between self-righting time  
224 and energetics, we plotted the log of mean of power-output equivalent against the log of body mass (Fig. 3B).  
225 We found an OLS slope of 1.191 (95% CIs = 0.961 to 1.422; Table 1 and S1), which is higher than the 0.833  
226 predicted by our model, indicating that the larger turtles are using higher power output to self-right than would  
227 be predicted by geometric scaling. To further illustrate how much more energetically expensive it is, for larger  
228 turtles, we calculated the shell width normalised height-change equivalent as a fraction of carapace width (Fig.  
229 3C). This value should be unchanged with body mass, but, in fact, increases as the animals get larger.

230

231 **4. DISCUSSION**

232 In most species, juveniles are more susceptible to mortality and often must avoid the same predators as adult  
233 conspecifics [26]. Natural selection tends to counteract this higher mortality, often by favouring improved  
234 locomotor performance through relatively longer limbs, faster muscle contractile velocities, and other physio-  
235 morphological changes that favour faster speeds and higher accelerations [26]. In the present study, we show  
236 that a simple geometric model, based on body mass, predicts shell shape and self-righting time when neck force  
237 is applied, in *C. serpentina*. However, we also show that energy and power outputs are greater during the self-  
238 righting process than would be predicted by our model (Fig. 3A, B, Table 1, and Table S1). The disproportionate  
239 increase in energetic cost is clearly shown by the height-change equivalent (Fig. 3C). Furthermore, younger  
240 turtles have disproportionately longer necks, which could be part of the reason they have lower-than-expected  
241 power outputs for their body size. Although our model does not predict the total time taken to self-right, smaller  
242 turtles complete the self-righting process faster than larger turtles in absolute terms and apply force via their  
243 neck for a shorter time (Fig. S1, Table S1). Considering that self-righting is a common locomotor behaviour  
244 exhibited by turtles [22], these scaling relationships and differences in self-righting might be widespread among  
245 other Testudine species, to assist younger individuals in avoiding a vulnerability that contributes to the high  
246 predation they face in nature [27].

247

#### 248 **(A) INTERACTION BETWEEN SHELL SHAPE AND SELF-RIGHTING EFFORT**

249 Our analyses demonstrated that shell shape in *C. serpentina* does not deviate from geometric scaling throughout  
250 ontogeny (Fig. 2C) and, therefore, cannot be associated with the changes seen in self-righting energy and power  
251 (Fig. 3A, B). In this respect *C. serpentina* appear to be different from some Testudine species, in which juveniles  
252 inhabit a different micro-environment, which can drive morphological and biomechanical adaptations between  
253 life stages [28, 29]. Accordingly, there are no morphological traits of the shell that would ameliorate the  
254 increased difficulty of self-righting as the turtles grow and age. Indeed, self-righting time increases with body  
255 mass, as predicted (Fig. 2D). Since the various risks of being inverted reduce with increased body size, this would  
256 support the idea that the evolutionary pressure is primarily on smaller turtles, considering there is no evidence  
257 of adaptations to reduce self-righting times in the larger animals. Our results parallel a study on Hermann's  
258 tortoises (*Testudo hermanni*), which shows that immature individuals self-right faster and with a higher  
259 probability of success than sexually mature adults [30]. Immature tortoises also display more anti-predatory  
260 behaviours, like boldness, and spend less time hiding in their shells during simulated predatory attacks, because  
261 their shells are weaker than adults [30]. Our data show that larger snapping turtles spend a longer time and  
262 disproportionately higher energy on self-righting when using the neck (even more than required by geometric  
263 similarity), suggesting that there might be an evolutionary pressure on juveniles for faster self-righting and to  
264 reduce its associated costs.

265



266 Although shell shape indices (sphericity and flatness) were not associated with changes in self-righting time in *C.*  
267 *serpentina* (Fig. 2B), they are good predictors of interspecific differences in self-righting in Testudines [20, 23-  
268 25]. When comparing snapping turtles with two freshwater turtle species (that also use their necks to self-right),  
269 higher sphericity indices (SIs) are associated with faster self-righting time. The snapping turtle has the most  
270 domed shell (average SI =  $0.758 \pm 0.003$ ) and self-rights fastest, followed by the red-eared slider (*Trachemys*  
271 *scripta elegans*; SI =  $0.7 \pm 0.01$ ) [25], and then the Spanish terrapin (*Mauremys leprosa*; SI =  $0.64 \pm 0.004$ ) [25].  
272 These intraspecies differences might persist throughout life, given that shell sphericity does not vary after the  
273 hatchling life-stage, as found in *C. serpentina* (this study and [31]) and in *T. scripta* [25, 32]. However, there are  
274 also instances of intraspecific differences in shell shape that are driven by habitat or sexual selection. For  
275 example, rainforest-dwelling scorpion mud turtles (*Kinosternon scorpioides*) have shorter shells than conspecifics  
276 living in dry forests [33], which are better for hiding, but would presumably hinder self-righting [20], and inverted  
277 male angulate tortoises (*Chersina angulata*), when battling other males for access to females, will self-right faster  
278 if they have a wider carapace [34]. Given the wide distribution of snapping turtles in North America [15], it would  
279 be interesting in further studies to determine whether there are geographical or sex differences in shell  
280 morphology that influence self-righting biomechanics.

281

## 282 **(B) ONTOGENY AND THE SCALING RELATIONSHIPS OF SELF-RIGHTING**

283 In agreement with our hypothesis that self-righting would be completed faster in smaller, compared to larger  
284 individuals, we demonstrated that the youngest turtles self-right about twice as fast as the older cohorts, when  
285 neck force is applied. This is in line with the predictions of our model. However, the energetic effort is  
286 considerably lower for smaller turtles and the only morphological measure that does not scale geometrically is  
287 neck length, which is disproportionally longer in smaller turtles. The neck, in this case, can be considered an extra  
288 limb and the disproportionally longer necks of younger snapping turtles agree with anisometric scaling  
289 trajectories seen for limbs in other tetrapods. For example, allometric growth of bird wings [35] and shark caudal  
290 fins [36] have been interpreted as enabling juveniles to move with greater speed or agility than adults. Moreover,  
291 like other turtle species, snapping turtles rapidly project their necks to hunt, and neck length is primarily driven  
292 by prey-capture dynamics [37]. Because younger turtles are predominantly carnivorous, rather than omnivorous  
293 (like older turtles) [38], their disproportionately longer necks, would also be more efficient for seizing moving  
294 prey [37]. Thus, in younger snapping turtles, a relatively longer neck can serve at least two important functions:  
295 capturing prey more effectively and facilitating more energetically efficient self-righting.

296

297 To examine how a disproportionately shorter neck in larger turtles' affects self-righting effort, given that shell  
298 shape does not change, would require an investigation of the ontogenetic changes in neck musculature. Indeed,  
299 our findings of negative allometric neck growth and mass-specific neck force being independent of body mass

300 (Table 1 and S1) also fit the general pattern of growth in snapping turtles. During ontogeny, head size changes  
301 with negative allometry, whereas bite force scales isometrically, relative to carapace length [38]. Such scaling  
302 patterns suggest that the size, strength, or physiology of the jaw muscles change throughout ontogeny, to  
303 preserve bite performance, despite a progressively smaller head [38]. Similar changes to the neck muscles might  
304 also occur during ontogeny, in snapping turtles. However, this remains to be determined.

305

## 306 5. PERSPECTIVES

307 In the present study, we have demonstrated that increasing body size during ontogeny increases self-righting  
308 times, as well as the accompanying biomechanical costs, and there is a reduction in the relative length of the  
309 neck, in snapping turtles. A young turtle's superior self-righting ability would be beneficial, as it would allow it to  
310 avoid the perils of being inverted as they traverse a landscape. Considering that *C. serpentina*, as well as other  
311 Testudine species, possess shells optimized for the environment that they inhabit [2, 3, 5, 33], intraspecific self-  
312 righting times and its biomechanical correlates could vary substantially, depending on geography. Therefore,  
313 future studies should investigate how the substrate from these different landscapes affects self-righting.  
314 Moreover, as interspecific differences in self-righting effort in Testudines is also influenced by shell shape, it is  
315 likely that it is also altered by shell rigidity. For example, common snapping turtles and spiny softshell turtles  
316 (*Apalone spinifera*) can live in the same environments, but the latter have more flexible and smoother shells, and  
317 prefer to stay in water than on land. Thus, it would be worthwhile to investigate the trade-offs in self-righting  
318 ability of species that have flexible shells or spend most of their time in water. Lastly, because larger turtles use  
319 disproportionately more energy during self-righting, it begs the question of where this extra energy goes. Since  
320 the turtles do not leave the ground and the shell does not alter in shape, it must mean that the extra energy is  
321 likely converted into unnecessary body movement, or lost due to increased rolling resistance. Given the diversity  
322 and abundance of Testudine species worldwide, as well as their vulnerability to anthropogenic and climate-  
323 change stressors, it is surprising how little we still know about some of their most basic biomechanical attributes  
324 that are associated with important survival behaviours, such as self-righting.

325

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### 425 **AUTHOR CONTRIBUTIONS**

426 Conceptualization: J.R.C.; Methodology: W.I.S. and J.R.C.; Formal analysis: I.M.R. and K.A.R.R.; Investigation:  
427 I.M.R., K.A.R.R., W.I.S., D.A.C., and J.R.C.; Writing – original draft: I.M.R.; writing – review and editing: I.M.R.,  
428 K.A.R.R., W.I.S., D.A.C., and J.R.C.; Supervision: J.R.C.; Project administration: J.R.C.; Funding acquisition: J.R.C.,  
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431 **COMPETING INTERESTS**

432 The authors declare no competing interests.

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434 **DATA ACCESSIBILITY**

435 The dataset associated with this study is available from the [Dryad Digital Repository](#).

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440 **TABLES**

441

**Table 1. Scaling relationships between morphometric/biomechanical variables and body mass or between morphometrics and maximum neck force.** The regression slope indicates proportional change in variable size with increasing body mass, and 95% confidence intervals (CIs) are shown (N = 33). Measured slopes in agreement (using 95% confidence intervals) with predicted slopes from our geometric model are indicated by a check mark (✓) and measured slopes lesser or greater than model predictions are indicated by negative signs (–) and positive signs (+), respectively.

| Dependent variable            | Independent variable | Slope predicted by geometric model | Measured slope | In agreement with model prediction? | Lower 95% CI | Upper 95% CI | R <sup>2</sup> | P-value |
|-------------------------------|----------------------|------------------------------------|----------------|-------------------------------------|--------------|--------------|----------------|---------|
| Carapace length (mm)          | Body mass (kg)       | 0.33                               | 0.323          | ✓                                   | 0.31         | 0.336        | 0.988          | ≤ 0.001 |
| Carapace width (mm)           | Body mass (kg)       | 0.33                               | 0.336          | ✓                                   | 0.318        | 0.354        | 0.979          | ≤ 0.001 |
| Carapace height (mm)          | Body mass (kg)       | 0.33                               | 0.31           | ✓                                   | 0.295        | 0.335        | 0.984          | ≤ 0.001 |
| Neck length (mm)              | Body mass (kg)       | 0.33                               | 0.281          | –                                   | 0.246        | 0.316        | 0.895          | ≤ 0.001 |
| Self-righting time (s)        | Body mass (kg)       | 0.5                                | 0.357          | ✓                                   | 0.173        | 0.54         | 0.337          | 0.004   |
| Neck force (N)                | Body mass (kg)       | 0.67                               | 0.901          | +                                   | 0.757        | 1.045        | 0.84           | ≤ 0.001 |
| Kinetic energy equivalent (J) | Body mass (kg)       | 1.33                               | 1.548          | +                                   | 1.341        | 1.755        | 0.882          | ≤ 0.001 |
| Power output (W)              | Body mass (kg)       | 0.83                               | 1.191          | +                                   | 0.961        | 1.422        | 0.782          | ≤ 0.001 |
| Neck force (N)                | Neck length (mm)     | 2                                  | 2.976          | ✓                                   | 2.447        | 3.505        | 0.809          | ≤ 0.001 |
|                               | Carapace length (mm) | 2                                  | 2.77           | ✓                                   | 2.325        | 3.215        | 0.839          | ≤ 0.001 |
|                               | Carapace width (mm)  | 2                                  | 2.607          | ✓                                   | 2.146        | 3.067        | 0.811          | ≤ 0.001 |
|                               | Shell height (mm)    | 2                                  | 2.837          | ✓                                   | 2.34         | 3.334        | 0.814          | ≤ 0.001 |

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