



Inferring cost of transport from whole-body kinematics in three sympatric turtle species with different locomotor habits

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1 **Inferring cost of transport from whole-body kinematics in three sympatric turtle**
2 **species with different locomotor habits**

3

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11

12 **Keywords**

13

14 Kinematics; Energy Recovery; Walking; Biomechanics

15

16 **Abstract**

17

18 Chelonians are mechanically unusual vertebrates as an exoskeleton limits their body
19 wall mobility. They generally move slowly on land and have aquatic or semi-aquatic
20 lifestyles. Somewhat surprisingly, the limited experimental work that has been done
21 suggests that their energetic costs of transport (CoT) are relatively low. This study
22 examines the mechanical evidence for CoT in three turtle species that have differing
23 degrees of terrestrial activity. Our results show that *Apolone* travels faster than the
24 other two species, and that *Chelydra* has higher levels of yaw. All the species show
25 poor mean levels of energy recovery, and, whilst there is considerable variation, never
26 show the high levels of energy recovery seen in cursorial quadrupeds. The mean
27 mechanical CoT is 2 to 4 times higher than is generally seen in terrestrial animals. We
28 therefore find no mechanical support for a low CoT in these species. This study
29 illustrates the need for research on a wider range of chelonians to discover whether
30 there are indeed general trends in mechanical and metabolic energy costs.

31

32 **Introduction**

33

34 Chelonians have very limited body wall mobility due to their rigid or semi-rigid
35 carapace and plastron. This unique body morphology has been studied in the context
36 of swimming (Mayerl and Blob, 2017; Pace et al., 2001; Rivera and Blob, 2013; Rivera
37 et al., 2006); bone loading (Butcher and Blob, 2008; Young and Blob, 2015; Young et
38 al., 2017), pelvic morphology (Mayerl et al., 2016), shoulder girdle mobility (Schmidt
39 et al., 2016), and self-righting behaviour (Várkonyi and Domokos, 2007), but terrestrial
40 kinematic analyses are rare (Blob et al., 2007; Rivera and Blob, 2010; Schoenfuss et
41 al., 2010). The metabolic CoT has been investigated during walking in only two
42 species: *Emydura macquarii*, and *Terrapene ornata* (Zani and Kram, 2008). Both
43 species showed CoT half of that expected but the data are noisy, with low R^2 , and are
44 curious given the likely influence of the mass and rigidity of the carapace-plastron
45 structure of the body wall.

46

47 There are several possible explanations for this low metabolic CoT in chelonians. Their
48 specialized articulation between the scapula and carapace (Nagashima et al., 2013),
49 which eliminates the need for the 'muscular sling' present in other quadrupeds (Carrier
50 et al., 2006), may save energy. In addition, some turtles possess mobile pectoral
51 girdles which could also help with locomotor efficiency (Mayerl et al., 2019).
52 Chelonians also possess slower, more efficient muscles (*in vitro*) relative to other
53 vertebrates (Woledge, 1968) and move slowly, thus increasing the duration of foot-
54 ground contact which may reduce energy cost (Kram and Taylor, 1990). However,
55 fluctuations in the kinetic energy (KE) and gravitational potential energy (PE) of the
56 centre of mass (COM) that are 180° out of phase and of equal amplitude are optimal
57 for maximizing energy recovery and this may be impaired by slow speed (Cavagna et
58 al., 1977). In giant Galápagos tortoises (*Geochelone elephantopus*), KE amplitude is
59 only one third of that of PE during walking (Zani et al., 2005) and the fluctuation is
60 random demonstrating little mechanical energy recovery (~30%, compared to values
61 up to 65-70% in dogs (Griffin et al., 2004)). Even so, the mechanical CoT in
62 *Geochelone* (~0.41 J kg⁻¹ m⁻¹) was similar to other limbed animals (Zani et al., 2005).
63 Unfortunately, the metabolic CoT has not been measured in *Geochelone* and the
64 mechanical CoT has not been investigated in other chelonians.

65

66 We investigated body kinematics and energy recovery in three sympatric, fresh-water
67 turtles: spiny soft-shell turtle, *Apalone spinifera*; common snapping turtle, *Chelydra*

68 *serpentina*; and red-eared slider, *Trachemys scripta*. These species are ecologically
69 distinct: *Apalone* is a free-swimming aquatic form (Plummer et al., 1997) with reduced
70 carapace structure; *Chelydra* is a bottom-dwelling aquatic form with a pronounced
71 carapace and limited plastron but capable of extended terrestrial locomotion
72 (Steyermark et al., 2008); *Trachemys* is semi-aquatic (Cagle, 1950) with a robust
73 carapace and plastron. Based on findings in other species we would predict a low
74 mechanical cost of locomotion in these taxa, but that costs might not depend on
75 pendular energy recovery. We would also expect higher costs of locomotion in the
76 more aquatic species since these are more likely to have anatomical specialisations
77 for swimming.

78

79 **Materials and Methods**

80

81 6 *Apalone spinifera* and 13 *Trachemys scripta* were wild-collected near lake Lewisville
82 TX and 21 *Chelydra serpentina* were sourced from captive stock held at the University
83 of North Texas (UNT). All experiments were approved by the UNT. Turtles were
84 maintained at 24°C in 50-500 L tanks. All species were fed Mazuri® food (Mazuri®,
85 PMI Nutrition International, Brentwood, MO) 2-4 times per week and maintained on a
86 12:12 h light-dark cycle. On the day of study, five infrared markers were attached to
87 the shell using non-toxic cyanoacrylate (four on the perimeter and one to the apex).
88 An Optitrack system (www.optitrack.com) with six 0.3 megapixel, 100 fps FLEX:V100
89 cameras was used for motion capture. The animals were placed on a 3x5 m floor mat
90 to prevent slipping and recorded continuously for 5-10 minutes. Each animal was
91 tested at least 5 times on separate days.

92

93 Bouts were identified from the kinematic data by finding periods where the animal
94 followed an approximately straight course with constant speed over several gait cycles.
95 139 bouts were analysed using a variant of Procrustes shape analysis that used the
96 visible markers to calculate a mean shape by overlaying each set of markers and
97 finding the translation and rotation that minimises the sum of square distances
98 between the matched markers. We then calculated the translation and rotation that
99 mapped the mean shape to the markers in an individual frame. The coordinate system
100 for this mapping was chosen so that the origin was the centroid of the markers in the
101 first frame, the Z axis was vertical and the X axis was oriented to the mean direction

102 of travel. A 10 Hz two-pole Butterworth low-pass filter was applied using Matlab filtfilt
103 function (www.mathworks.com) to reduce the high frequency noise in the kinematic
104 data (Winter, 1990). The translation represents the linear motion of the centroid of the
105 marker system, approximating the centre of mass of the animal. The rotation
106 represents the rotation of the animal's carapace during locomotion.

107

108 Energy recovery was calculated from the interchange between the gravitational and
109 kinetic energy using the formulation shown in Equation 1 (Dipaola et al., 2016) where
110 ER is energy recovery (%), W_p is the difference between the maximum and minimum
111 gravitational potential energy in a single stride, W_k is the difference between the
112 maximum and minimum kinetic energy of the centre of mass, and W_{totCM} is the
113 difference between the maximum and minimum values of the sum of kinetic and
114 gravitational potential energy over the stride.

115

116 Equation 1

$$117 \quad ER = \frac{(W_p + W_k) - W_{totCM}}{(W_p + W_k)} \times 100$$

118

119 **Results**

120

121 During recorded locomotor trials *Apalone* starts to move immediately and rapidly in a
122 straight line. The animal can repeat this action but tires, with each repeat slowing and,
123 eventually, remaining motionless with head and limbs retracted. Both *Chelydra* and
124 *Trachemys* tend to remain immobile with their heads and limbs retracted when first
125 placed on the substrate. After a few minutes they begin to walk slowly, often in a
126 circular fashion. However, this can transition into a more directed, faster, straight line
127 movement. Both *Chelydra* and *Trachemys* tend to pause when walking and do not
128 appear to tire rapidly.

129

130 The speeds chosen by turtles suggest that there are no characteristic, preferred
131 speeds for these species, and little obvious effect of body size (Figure 1A-D). Both
132 *Apalone* and *Chelydra* are larger than *Trachemys* in our sample but only *Apalone* is
133 noticeably faster than the others, both in absolute terms and when geometrically

134 corrected for body mass. However, the fastest animal recorded was one of the smaller
135 *Trachemys* specimens. Rotations of the carapace were variable (Figure 1E) and there
136 is no obvious effect of body mass but there are species level differences, with
137 *Trachemys* having less rotation than the others. Yaw was very pronounced in *Chelydra*
138 whereas in the other species roll is the largest component.

139

140 The calculated energy recovery is low (Figure 2ABC) as predicted from the variations
141 in both the linear and angular kinematics. We also calculated the external work directly
142 by summing the positive components of total energy (PE + KE) which provides a useful
143 measure of the mechanical CoT (external work/distance). The mass-specific power
144 (external work/duration) for the individual species at their different self-selected
145 speeds (Figure 2D) shows the characteristic increase in power with speed that would
146 be expected but there is a great deal of scatter, and the effect for *Apalone* is very weak.
147 Figure 2E shows the effect of speed on the mass-specific mechanical CoT. Only
148 *Chelydra* and *Trachemys* show a positive relationship between mechanical CoT and
149 speed. Figures 2FG show the between-species mean values for power and
150 mechanical CoT which are appreciably higher on average for *Apalone*.

151

152 **Discussion**

153

154 Our mechanical CoT data provide no evidence for the low metabolic CoT previously
155 reported (Zani and Kram, 2008). The mean mechanical CoT was higher in each of
156 these species compared to other legged animals (Full reports values around 1 J kg^{-1}
157 m^{-1} for mammals, birds, crustacea and insects with no appreciable effect of body size
158 (Full and Tu, 1991) but there is considerable variation from $0.47 \text{ J kg}^{-1} \text{ m}^{-1}$ in
159 *Spermophilus tereticaudus* to $1.85 \text{ J kg}^{-1} \text{ m}^{-1}$ in *Macaca speciosa* (Nudds et al., 2009)).
160 Being aquatic or semi-aquatic potentially represents a trade-off in locomotor efficiency
161 between locomotor modes. Indeed *Apalone*, the most aquatic, has the highest mass-
162 specific mechanical CoT. These data also suggest that *Trachemys*, being semi-
163 aquatic, can employ more energy efficient gaits. The higher values may therefore
164 represent the gaits chosen for reasons other than energy efficiency such as escape,
165 exploration, and crypsis. There was a great deal of between bout variation in the
166 measured CoT (range $0.65\text{-}10.9 \text{ J kg}^{-1} \text{ m}^{-1}$) which would suggest that the study
167 animals were not choosing to minimise CoT. The only other experimental values for

168 chelonians show similar between bout variation (range 0.1-1.0 J kg⁻¹ m⁻¹) (Zani et al.,
169 2005) also suggesting a great deal of flexibility in CoT values used.

170

171 Pendular energy recovery for these animals seems unlikely. They showed no obvious
172 preferred speeds, carapace rotations were variable, and the KE and PE of the body
173 COM did not fluctuate relative to one another in a predictable fashion. Clearly, more
174 studies are needed to understand how the various mechanisms that might lead to
175 reduced energy costs are interacting within chelonians. Indeed measurements of
176 external work are a very limited proxy for the actual mechanical cost of locomotion and
177 ideally, full inverse dynamic studies should be performed (Winter, 1990), coupled with
178 specific models of muscle energy conversion (Sellers et al., 2003).

179

180 The results illustrate the kinematic features that may underlie the differences in
181 locomotor efficiency between the three species. *Apalone* is much faster than the other
182 two species suggesting that out of an aquatic setting this species employs an escape
183 gait. The other two species show an increase in cost of locomotion with speed, but for
184 *Apalone*, all speeds are energetically expensive. The trunk rotation data are interesting
185 since these represent the movements of a rigid or semi-rigid box that may impede
186 some of the compensatory movements of the limb girdles and the vertebral column
187 that may reduce CoT in other tetrapods, even though recent work has shown that in
188 some turtle species, girdle movement can be surprisingly large (Mayerl et al., 2019).
189 There are few comparative studies of body rotation and the values reported are
190 typically between 4° to 10° (Byström et al., 2009; Dunbar, 2004; Dunbar et al., 2008;
191 Jayes and Alexander, 1980; Stokes et al., 1989). The mean values shown are not
192 therefore especially extreme, however this hides the fact that for some normal walk
193 sequences we see much higher values (~25°) particularly in roll and yaw suggesting
194 that carapace rotation is an important component of CoT.

195

196 **Conclusion**

197

198 These three species of aquatic and semi-aquatic turtles have high mechanical CoT
199 and little or no opportunity for pendular energy recovery. Observed gaits were highly
200 variable with qualitative differences. This work illustrates the relatively poor level of
201 understanding that we currently have for low speed locomotion where traditional

202 energy recovery models are not applicable, and there is a need for more detailed
203 analysis across more species.

204

205 **Acknowledgements**

206

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208

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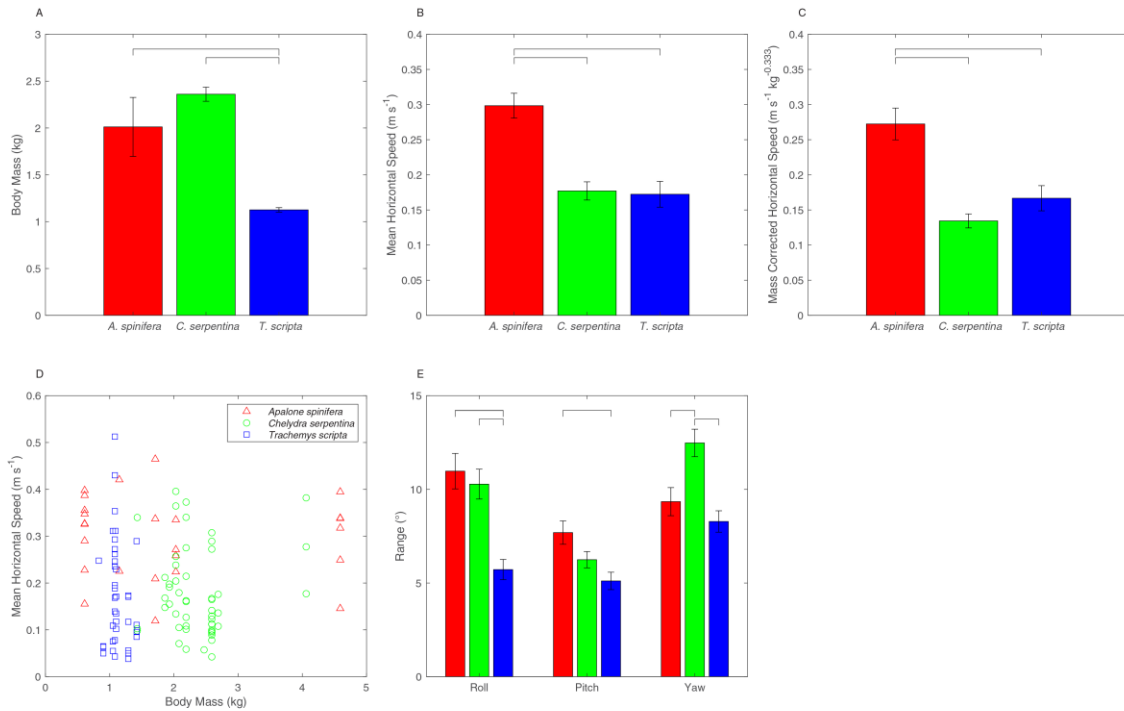
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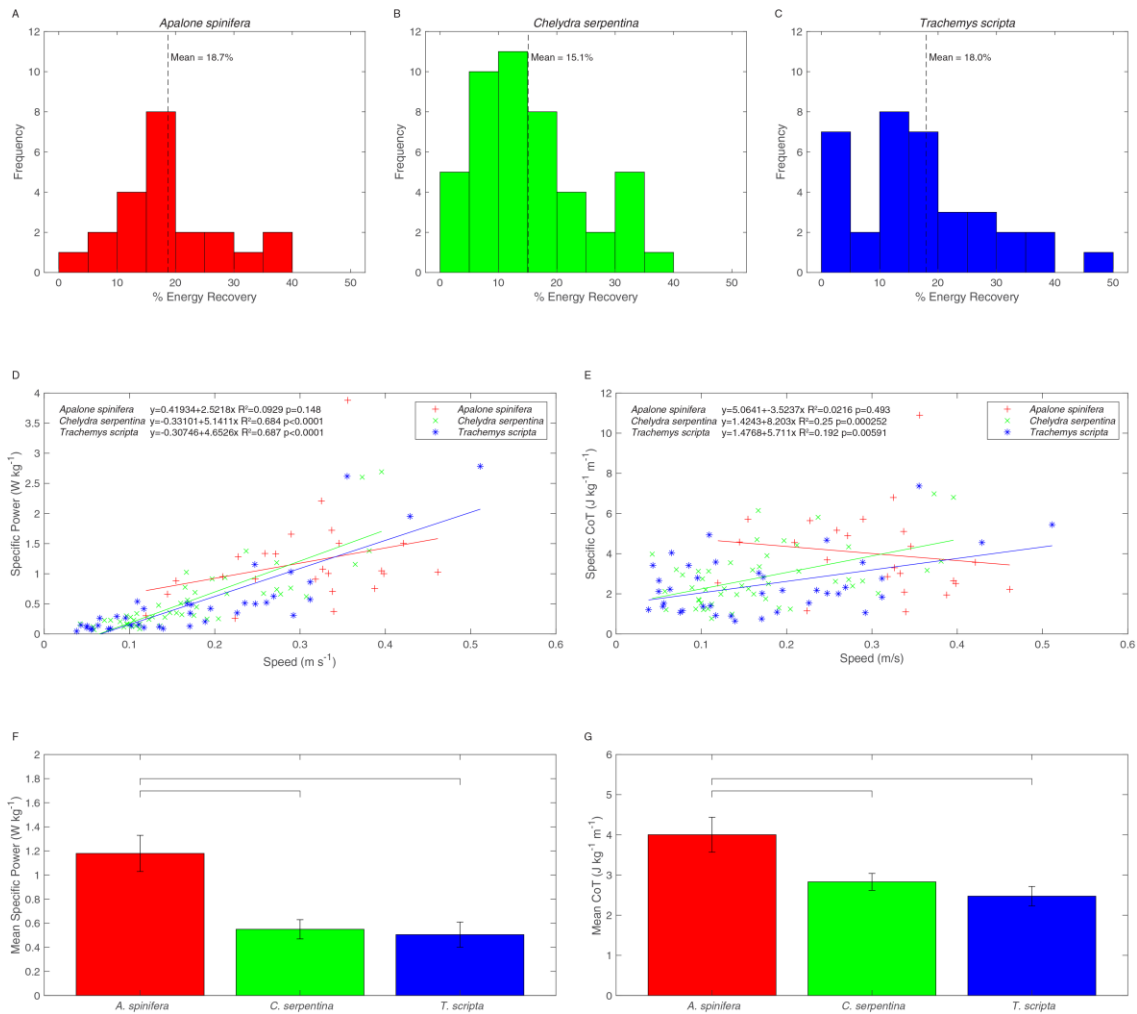
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306

307 Figure 1. (A) Mean body masses (one-way ANOVA $F=25.983$, $p<0.001$; Tukey HSD
 308 AS:TS $p<0.001$, CS:TS $p<0.001$). (B) Mean horizontal speeds (one-way ANOVA
 309 $F=14.945$, $p<0.001$; Tukey HSD AS:CS $p<0.001$, AS:TS $p<0.001$). (C) Mass corrected
 310 horizontal speeds (one-way ANOVA $F=17.609$, $p<0.001$; Tukey HSD AS:CS $p<0.001$,
 311 AS:TS $p<0.001$). (D) Self-selected speeds recorded in the different locomotor bouts.
 312 (E) Carapace rotation ranges (Roll: one-way ANOVA $F=12.782$ $p<0.001$; Tukey HSD
 313 AS:TS $p<0.001$, CS:TS $p<0.001$; Pitch: $F=5.453$ $p=0.005$; Tukey HSD AS:TS $p=0.004$;
 314 Yaw: $F=10.723$ $p<0.001$; Tukey HSD AS:CS $p=0.013$, CS:TS $p<0.001$). Error bars
 315 show the standard errors of the mean. *Apalone* $N=5$, *Chelydra* $N=10$, *Trachemys* $N=8$.

316

317



319

320

321 Figure 2. (A-C) Histograms showing the distributions of energy recovery measured for
 322 the locomotor bouts. The vertical lines show the arithmetic means for each species.

323 (D) Mechanical power; (E) Mechanical CoT; (F) Mean power (one-way ANOVA
 324 $F=10.063\ p<0.001$; Tukey HSD AS:CS $p<0.001$, AS:TS $p<0.001$); (G) Mechanical CoT
 325 (one-way ANOVA $F=6.648\ p=0.002$; Tukey HSD AS:CS $p=0.014$, AS:TS $p=0.002$).

326 Error bars show the standard errors of the mean.

327