THE ENERGETICS AND BIOMECHANICS OF TURTLE LOCOMOTION

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INTRODUCTION

Tortoise muscle has been shown to be very efficient *in vitro*[1]. Likewise, a semi-aquatic turtle has been shown to walk with remarkable metabolic economy[2]. Yet, Galápagos tortoises do not conserve substantial mechanical energy during walking[3] calling into question the link between locomotor energetics and mechanics. We gave begun to investigate if turtles in general are economical walkers and if so why.

METHODS

We measured the metabolic cost of locomotion in 18 terrestrial box turtles, *Terrapene ornata*. We trained turtles to walk steadily on a treadmill for 10-20 minutes while wearing a mask (Figure 1). We then measured steady-state oxygen consumption for 5-10 trials of level walking as well as walking up a 24° incline. In addition, we collected ground-reaction forces for individuals walking across a force platform to determine whether economical walking in box turtles is due to the inverted-pendulum mechanism of energy conservation[4].

RESULTS AND DISCUSSION

Minimum cost of transport for level walking (8.0 ± 2.97 J/kg/m) was roughly one-half the expected value (15.9 ± 1.50 J/kg/m) for animals of similar size (Figure 2). When walking up an incline turtles walked much slower (0.04 ± 0.016 m/s) and with a much higher cost of transport (15.0 ± 7.10 J/kg/m). By matching level and incline trials of similar speed we were able to calculate uphill efficiency (20.2 ± 9.16 %). This value is comparable to terrestrial mammals and birds of similar size. Thus, the low cost of transport during level walking does not appear to be due to high efficiency of turtle muscle.

Examination of turtle mechanics indicates that the magnitude of kinetic-energy fluctuations (0.01 ± 0.004 J/stride) were only one-quarter of fluctuations in gravitational potential energy (0.04 ± 0.017 J/stride). These energies were only sporadically out of phase and thus, turtles recovered only 25.2 ± 3.83 % of their mechanical energy per stride. Hence, it appears that economical level walking in turtles is not due to mechanical-energy conservation. We suggest that the low metabolic cost of turtle walking is related to their extremely slow muscles, consistent with the cost-of-generating-force hypothesis[5].

CONCLUSIONS

We studied the energetics and mechanics of turtle locomotion. Despite having poor mechanical-energy conservation (~25% energy recovery), turtles are very economical at level walking (half the expected metabolic cost). Yet, this does not appear to be due to extraordinary muscular efficiency (~21%). Thus, we suggest that economical walking in turtles in general is not dependent upon effective mechanical-energy recovery. Rather, the extremely slow muscles of turtles may account for their low metabolic expenditure during walking.

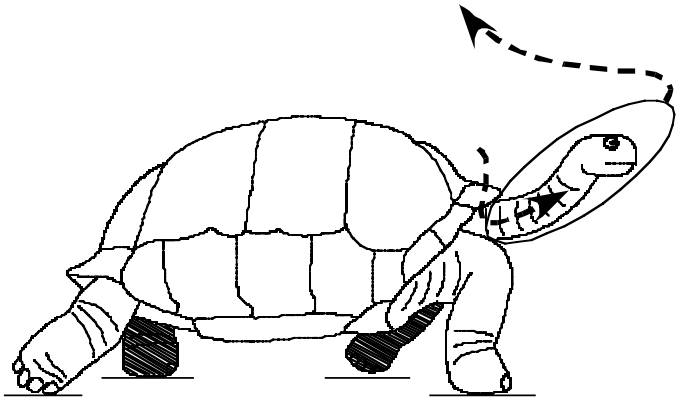

Figure 1: A walking turtle wearing an open-flow mask to collect respired air (flow direction indicated by arrows).

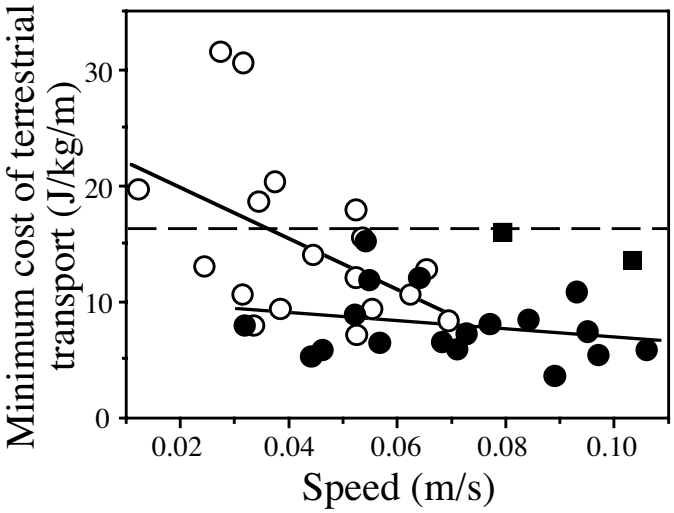

Figure 2: Minimum cost of transport vs. speed for level (filled symbols) and 24° incline (open symbols) walking in turtles. Dashed line is average expected level cost based on size.

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