

Giant Galápagos tortoises walk without inverted pendulum mechanical-energy exchange

Peter A. Zani*, Jinger S. Gottschall[†] and Rodger Kram

Department of Integrative Physiology, University of Colorado, Boulder, Colorado 80309-0354, USA

*Author for correspondence (e-mail: zani@colorado.edu)

[†]Present address: Department of Physiology, Emory University School of Medicine, Atlanta, GA 30322, USA

Accepted 23 February 2005

Summary

Animals must perform mechanical work during walking, but most conserve substantial mechanical energy via an inverted-pendulum-like mechanism of energy recovery in which fluctuations of kinetic energy (KE) and gravitational potential energy (GPE) are of similar magnitude and 180° out of phase. The greatest energy recovery typically occurs at intermediate speeds. Tortoises are known for their slow speeds, which we anticipated would lead to small fluctuations in KE. To have an effective exchange of mechanical energy using the inverted-pendulum mechanism, tortoises would need to walk with only small changes in GPE corresponding to vertical center-of-mass (COM) fluctuations of <0.5 mm. Thus, we hypothesized that giant Galápagos tortoises would not conserve substantial mechanical energy using the inverted-pendulum mechanism.

We studied five adult giant Galápagos tortoises *Geochelone elephantopus* (mean mass=142 kg; range=103–196 kg). Walking speed was extremely slow ($0.16 \pm 0.052 \text{ m s}^{-1}$; mean ± 1 s.d.). The fluctuations in kinetic energy ($8.1 \pm 3.98 \text{ J stride}^{-1}$) were only one-third as large as the fluctuations in gravitational potential

energy ($22.7 \pm 8.04 \text{ J stride}^{-1}$). In addition, these energies fluctuated nearly randomly and were only sporadically out of phase. Because of the dissimilar amplitudes and inconsistent phase relationships of these energies, tortoises conserved little mechanical energy during steady walking, recovering only $29.8 \pm 3.77\%$ of the mechanical energy (range=13–52%). Thus, giant Galápagos tortoises do not utilize effectively an inverted-pendulum mechanism of energy conservation. Nonetheless, the mass-specific external mechanical work required per distance ($0.41 \pm 0.092 \text{ J kg}^{-1} \text{ m}^{-1}$) was not different from most other legged animals. Other turtle species use less than half as much metabolic energy to walk as other terrestrial animals of similar mass. It is not yet known if Galápagos tortoises are economical walkers. Nevertheless, contrary to biomechanical convention, poor inverted-pendulum mechanics during walking do not necessarily correspond to high mechanical work and may not result in a high metabolic cost.

Key words: biomechanics, locomotion, ground-reaction forces, mechanical-energy recovery, *Geochelone elephantopus*.

Introduction

Walking animals must perform some mechanical work, but a large portion of the mechanical energy can be conserved by using a mechanism similar to an inverted pendulum (Cavagna et al., 1977). During walking, kinetic energy (KE) and gravitational potential energy (GPE) of the center of mass of the body (COM) are alternately exchanged. The exchange of mechanical energy is maximized when KE and GPE of the COM are of equal magnitude, regularly fluctuate 180° out of phase, and have similar shaped curves. Diverse taxa, from bipeds to eight-legged invertebrates, effectively utilize the inverted-pendulum mechanism (e.g. Cavagna et al., 1977; Full, 1989). Among vertebrates, the maximum energy recovered while walking using this mechanism ranges from 80% in penguins (Griffin and Kram, 2000), 70% in dogs (Griffin et al., 2004), 65% in humans (Cavagna et al., 1976), 44% in frogs (Ahn et al., 2004), 38% in lizards (Farley and Ko, 1997), 35%

in rams (Cavagna et al., 1977), to just 32% in alligators (Willey et al., 2004).

It is well known that mechanical-energy conservation is influenced by walking speed. Cavagna et al. (1977) found that among species, the greatest energy recovery occurs over a narrow range of intermediate walking speeds for that species. At slow speeds, KE is insufficient to lift substantially the COM. Previous studies of the mechanics of relatively slow animals include geckos (Farley and Ko, 1997), penguins (Griffin and Kram, 2000), and alligators (Willey et al., 2004). While lizards and alligators exhibited fairly low values of mechanical-energy conservation, penguins have the highest recovery values. Willey et al. (2004) suggested that alligators conserve little mechanical energy due to frequent dragging of their feet, tail dragging and imprecise coordination of their feet. However, it also seems likely that

their inherently slow speed precludes substantial energy conservation.

We chose to study the mechanical-energy recovery during walking by giant Galápagos tortoises *Geochelone elephantopus* because of their extremely slow speeds, especially when expressed relative to body size (up to 200 kg). As Darwin (1839, p. 464) noted, “one large tortoise...walked...sixty yards in ten minutes”, or about 0.09 m s^{-1} . Unlike lizards and alligators, the tails of turtles do not play an important role in locomotion, except possibly on inclines (see Finkler and Claussen, 1997). Therefore, tortoises are an ideal group to test the importance of absolute speed on mechanical-energy recovery without being confounded by the presence of a substantial tail as in other non-avian reptiles.

Due to their slow walking speed, we anticipated that these tortoises would have small fluctuations in KE. If this prediction is correct, to have an effective exchange of mechanical energy using the inverted-pendulum mechanism tortoises would need to walk with unreasonably small changes in GPE corresponding to vertical COM fluctuations of $<0.5 \text{ mm}$. Thus, we hypothesized that giant Galápagos tortoises would not conserve substantial mechanical energy using the inverted-pendulum mechanism.

Materials and methods

We studied five adult giant Galápagos tortoises *Geochelone elephantopus* Harlan at the Oklahoma City Zoo (mean mass=142 kg; range=103–196 kg; measured using a force platform). The tortoises were about 100 years old, though all animals were in good health and remained reproductive (K. Hovey, personal communication). The University of Colorado Animal Care and Use Committee and the Oklahoma City Zoo approved the procedures.

We calculated the COM mechanical-energy fluctuations of these tortoises from ground-reaction force (GRF) data. We sampled GRFs (Fig. 1) at 1000 Hz from an AMTI model ZBP7124 force platform (1.83 m \times 0.61 m). To accommodate the width of the tortoises, we attached a rigid metal frame to the top of the force platform, covered it with a 0.04 m thick plywood surface (1.83 m \times 1.22 m), and glued non-compressible rubber matting to this surface to provide traction. This rigid top had a mass of approximately 100 kg. The force platform is designed for loads up to 2000 N. We calibrated the force platform with known loads.

We conducted all trials between 09:00 and 17:00 h at room temperatures, which fluctuated between 28 and 36°C. Tortoises were fed only hay for a week prior to our experiments. We used fresh fruits and vegetables to entice the animals to walk steadily across the platform for 20 trials each. Although walking speeds were self-selected by tortoises, they appeared highly motivated by the fruits/vegetables. We excluded trials with obvious pauses or stumbles. To verify that the relatively long trials needed to collect data did not incur drift in the force signals, we conducted calibration trials in which a person of known weight stood motionless on the force platform and then

did a series of squats for $\sim 10 \text{ s}$. We integrated GRF values (see below) to determine changes in the COM position. No drift was observed.

Video recordings (60 fields s^{-1}) allowed for determination of limb phases and duty factors. We calculated limb phases as the proportion of the total stride time elapsed between the limb contact times. We calculated duty factors as the proportion of the total stride time that each limb was in contact with the ground. Paint marks on the shell enabled determination of average velocity for each step from video. We calibrated the video field from markers placed on the tortoise’s shell a known distance apart. In addition, we used video to determine hip height during walking from a marker on the shell, placed with aid of hip palpation. Hip height (l) was then used to calculate Froude numbers (dimensionless velocity) as $v^2 g^{-1} l^{-1}$, where v is velocity (m s^{-1}) and g is gravitational force, 9.81 m s^{-2} .

To calculate the mechanical energies of the COM, we integrated the GRF values as per Cavagna (1975), modified for three dimensions (Griffin and Kram, 2000; Donelan et al., 2002). Force integration was conducted over an integral number of steps, during which all stance limbs were on the force platform. One step = half a stride or the time between one foot contact and its following contralateral pair (e.g. left front to right front). We calculated the % mechanical energy

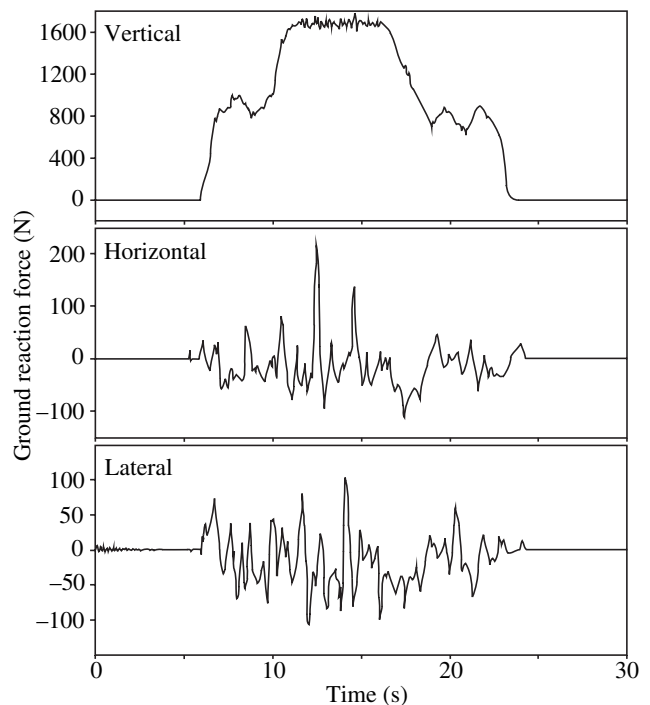


Fig. 1. Vertical, horizontal, and lateral force tracings from a typical walking trial (corresponding to Fig. 3A). Tortoise mass=171 kg. Data were filtered using a fourth order low-pass filter at 20 Hz. At 5.73 s, the animal placed its left front foot on the force platform, followed by the right front at 7.43 s. Full support on the force platform occurred with the lifting of the right hind foot at $\sim 11 \text{ s}$. The step analyzed in Fig. 3A occurred with right front contact at 13.33 s to left front contact at 15.28 s. Only the hind feet remained on the platform by $\sim 19 \text{ s}$ and the last hind foot lifted from the platform at $\sim 24.5 \text{ s}$.

recovered during a step following Cavagna et al. (1977). This traditional method of calculating mechanical-energy recovery is not perfect and overlooks the substantial loss of energy at each foot-ground contact as the COM is redirected and accelerated (Donelan et al., 2002). However, it was not feasible to obtain the individual leg-force measurements needed for calculating mechanical work with the individual-limbs method. We determined the mechanical work per distance by calculating the external work of the COM per step, multiplying by step frequency, and dividing by speed and mass.

Statistical analyses were performed in SuperANOVA 1.11 (Abacus Concepts Inc., 1991) for Macintosh.

Results

The tortoises walked using a semi-erect posture, holding their plastron (ventral shell) a considerable distance above the ground (approximately 10–20 cm) with no tail-ground contact during walking. We obtained an average of 10 good trials per individual tortoise. Tortoises' limb-phase relationships (Fig. 2) were very similar to those reported previously for smaller turtles (Jays and Alexander, 1980) and the relative timing of each footfall did not change with speed ($F < 0.56$, $P > 0.46$). Their gait was a lateral sequence diagonal couplet (Fig. 3; Hildebrand, 1985) in which the contralateral hind-foot always followed the movement of the fore foot. This gait pattern is typical of other reptiles (Farley and Ko, 1997; Willey et al., 2004). On average, each foot was on the ground for $80.5 \pm 0.58\%$ (hereafter, mean \pm 1 S.D.) of the stride with the hind feet having slightly, but statistically significantly greater, duty factors than the fore feet (duty factors = 81.9 ± 0.71 vs 79.1 ± 0.69 , respectively; $F_{1,18} = 7.9$, $P = 0.012$).

The fluctuations in COM KE (8.1 ± 3.98 J stride $^{-1}$; Fig. 3) were only a third as large as the fluctuations in COM GPE (22.7 ± 8.04 J stride $^{-1}$). Much of this difference was due to the fact that tortoises walked extremely slowly (0.16 ± 0.052 m s $^{-1}$; within-stride $\Delta v_{\text{fore-aft}} = 0.03 \pm 0.054$ m s $^{-1}$), with KE

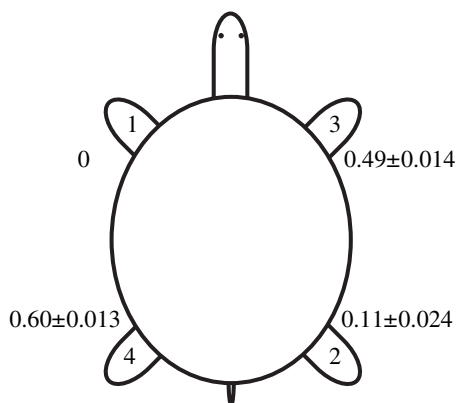


Fig. 2. Limb-phase relationships for giant Galápagos tortoises during walking. Numbers within each limb indicate order of footfalls (i.e., diagonal couplet). Numbers outside each limb indicate limb phase, that is, proportion (mean for all trials \pm 1 S.D.) of the total stride time elapsed between the limb contact times.

occasionally reaching zero during normal steady locomotion. This slow speed in tortoises equates to a Froude number (dimensionless velocity) of 0.008 ± 0.0040 (Table 1).

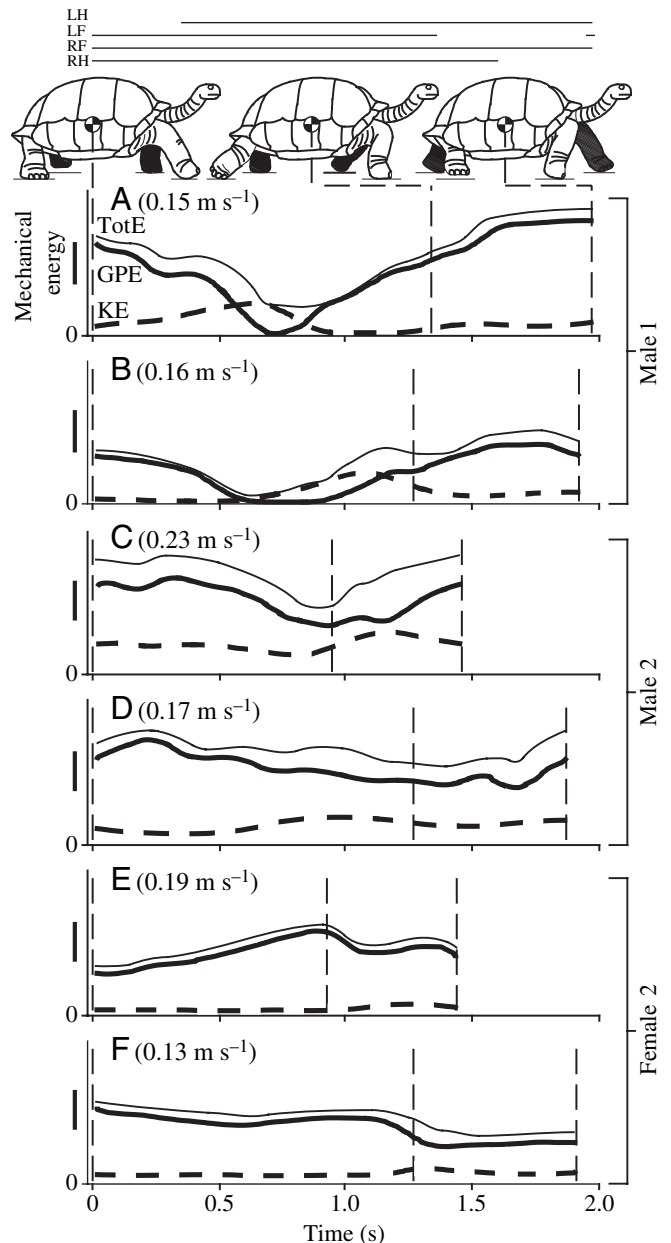


Fig. 3. Fluctuations in kinetic energy (KE; broken line), gravitational potential energy (GPE; thick solid line), and total energy (TotE; thin solid line) of COM (hatched circles in drawings) during one walking step (right-front (RF) to left-front (LF) footfalls as in drawings) for three tortoises. Note absence of similar amplitude or out-of-phase relationship for fluctuations in KE and GPE. (A,B) Two trials from Male 1; (C,D) two trials from Male 2; (E,F) two trials from Female 2. Scale bars (10 J) reference both KE and GPE; y-axis zeros reference KE only. Thin horizontal lines above drawings indicate each foot's contact during step in A; data in B-F from a similar RF-LF step (foot contacts not shown). Vertical broken lines link tortoise cartoon footfalls (RF contact, LF lift, and LF contact) to that point in each step.

Table 1. Individual morphology and locomotor data from five giant Galápagos tortoises

ID	Mass (kg)	Velocity (m s ⁻¹)	Froude number	Stride time (s)	Stride length (m)	Duty factor (%)	
						Fore	Hind
Male 1	171.3	0.15±0.021	0.008±0.0017	4.3±0.46	0.62±0.044	79.8±3.50	79.6±3.93
Male 2	195.7	0.22±0.028	0.013±0.0030	3.5±0.33	0.72±0.032	76.9±5.55	79.1±5.58
Female 1	103.3	0.08±0.009	0.002±0.0004	5.0±0.46	0.43±0.028	80.5±5.63	83.5±3.13
Female 2	116.6	0.18±0.030	0.010±0.0030	3.1±0.31	0.57±0.071	80.7±2.83	83.0±3.41
Female 3	125.4	0.15±0.032	0.008±0.0028	3.4±0.36	0.46±0.066	77.8±3.38	84.3±2.35

Values are means ± 1 s.d.

Surprisingly, the medio-lateral movements accounted for about two-thirds of the total KE fluctuations. This percentage of total KE fluctuation is even greater than the 30% reported for waddling penguins (Griffin and Kram, 2000). However, in mass-specific terms the medio-lateral KE fluctuations for tortoises (0.07 ± 0.019 J kg⁻¹ m) are slightly less than those of penguins (0.10 ± 0.059 J kg⁻¹ m; T. M. Griffin, personal communication).

The average COM vertical amplitude was 1.6 ± 0.37 cm within a stride. Considering that the leg length of these tortoises (0.33 m) was approximately one-third that of humans (0.9 m), these COM fluctuations (and hence GPE fluctuations) are proportionally similar to the fluctuations of humans (typically ~5 cm; Inman et al., 1994).

Tortoises did not systematically utilize an inverted-pendulum mechanism of energy recovery while walking (Fig. 3). When we calculated the mechanical-energy recovery (*sensu* Cavagna et al., 1977) we found that tortoises recovered

just $29.8\pm 3.77\%$ of the total mechanical energy (range=13–52%; Fig. 4). This value of mechanical-energy recovery is very near the lowest average reported for any legged terrestrial animal during walking (frogs: mean=32%, range=20–44%, Ahn et al., 2004; alligators: mean=20%, range=6–32%, Willey et al., 2004; see also Cavagna et al., 1977). The low values of mechanical-energy recovery were due to dissimilar amplitudes and inconsistent phase fluctuations of KE and GPE. In addition, we calculated the amount of energy converted from GPE to KE as well as from KE to GPE. We found essentially no difference in the direction of energy exchange: GPE to KE was 48.5% of total energy exchange; KE to GPE was 51.5%. Because we were unable to identify a consistent pattern of peaks or troughs in mechanical energies in many cases (Fig. 3), we felt it unwarranted to calculate the relative phase fluctuations of KE and GPE. Unlike other species (Cavagna et al., 1977; Willey et al., 2004), tortoises did not recover more mechanical energy with increasing speed (Fig. 4A) and even had a slight negative trend to this relationship. External mechanical work per distance (*sensu* Cavagna et al., 1977) averaged 0.41 ± 0.092 J kg⁻¹ m⁻¹ (Fig. 4B) and also had a slight negative trend.

Discussion

Giant Galápagos tortoises do not systematically utilize an inverted-pendulum mechanism of energy recovery during walking. While our findings are numerically similar to those reported for alligators in terms of energy recovery (Willey et al., 2004), tortoises do not show a clear and repeatable pattern of energy fluctuations as alligators do. Willey et al. (2004) postulated that the poor mechanical-energy recovery in alligators was due to a combination of factors, including tail and foot dragging, imprecise coordination of feet, and slow speed. Giant Galápagos tortoises do not have a massive tail that drags while walking. In addition, tortoises have excellent coordination of the feet. While tortoises use a limb-phase relationship (Fig. 2) and footfall pattern (Fig. 3) similar to alligators, variations in the pattern are rather small (for all strides, limb phase varies by a maximum of only 3–4% and is not dependent upon speed). This suggests that neither tail dragging nor foot coordination can explain the poor energy exchange in walking tortoises.

The extremely slow walking speed of these animals is a

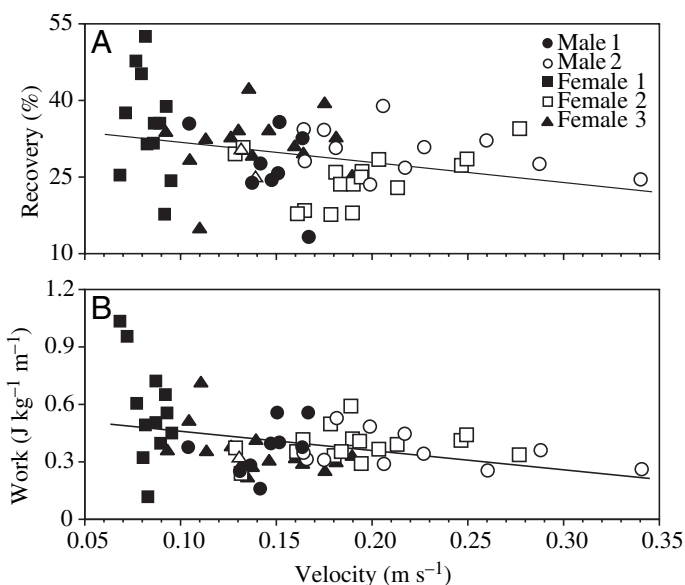


Fig. 4. Relationship between velocity and (A) mechanical-energy recovery using the inverted-pendulum mechanism, and (B) external work per unit mass per distance. Individuals (as in Table 1) are designated by symbol; all steady-state walking trials are included ($N=64$). Trend lines are for least-squares regressions including all trials.

major factor contributing to their poor mechanical-energy recovery. Previous studies have concluded that walking speed affects mechanical-energy recovery in general, with intermediate speeds resulting in the greatest percent recovery (Cavagna et al., 1977). Giant Galápagos tortoises are certainly slow, especially for their size, walking at an average of just 0.16 m s^{-1} . As a result, their KE fluctuations are much smaller than their GPE fluctuations (Fig. 3). In order to utilize the inverted-pendulum mechanism of energy recovery, tortoises would need to walk either with smaller fluctuations in GPE or larger fluctuations in KE. We estimate that their COM fluctuations would need to be $<0.5 \text{ mm}$ to match their KE fluctuations. In order to match their GPE fluctuations, tortoises would need velocity fluctuations roughly 2–3 times their current fluctuations. Tortoises simply do not have sufficient KE to lift their COM up and over the stance limbs during each step. In addition to the dissimilar magnitude of energies, their relative phase relationship appears to allow for only intermittent exchange of mechanical energy.

Despite the poor mechanical-energy exchange, the mass-specific total external mechanical work required to travel a given distance in these tortoises is similar to other legged animals. Previous studies of walking have found that the mass-specific mechanical work to travel a given distance ranges from about $0.2\text{--}0.5 \text{ J kg}^{-1} \text{ m}^{-1}$ (Cavagna et al., 1977; Willems et al., 1995; Griffin and Kram, 2000; Griffin et al., 2004). Our data show that tortoises require $0.42 \pm 0.083 \text{ J kg}^{-1} \text{ m}^{-1}$, which is not exceptional.

Compared to other terrestrial animals of similar mass (Full, 1989), some turtles use half as much metabolic energy to walk. However, the metabolic cost of walking is known for only two relatively small species of turtles (Baudinette et al., 2000; Zani et al., 2004). To test critically the causal link between mechanical-energy conservation and metabolic costs, we need metabolic data on Galápagos tortoises or mechanical and metabolic data on other turtle species. Tortoise walking may be metabolically inexpensive due to (1) extremely efficient muscles (Woledge, 1968; Nwoye and Goldspink, 1981; Rall, 1985), (2) extremely slow muscles that generate force economically (Kram and Taylor, 1990) or (3) the unique pectoral articulation between the scapula and carapace (top shell; Walker, 1986), which eliminates the ‘muscular sling’ (Goslow et al., 1981) used by mammals.

There are reasons to question the link between mechanical-energy recovery and metabolic cost of transport. For example, penguins recover up to 80% of their mechanical energy (Griffin and Kram, 2000), but have a metabolic cost of walking twice as expensive as other walking birds of the same mass (Pinshow et al., 1977). In contrast, lizards have relatively low mechanical-energy recovery during walking (~2–38%; Farley and Ko, 1997), but are remarkably economical (Autumn et al., 1997). Alligators have poor mechanical-energy recovery (~6–32%, mean=20%, Willey et al., 2004). However, based on data from Emshwiller and Gleeson (1997; T. T. Gleeson, personal communication) we have calculated the metabolic cost of transport to be $13.2 \text{ J kg}^{-1} \text{ m}^{-1}$, which is similar to other

300 g animals (Full, 1989). Because alligators rely on oxidative and non-oxidative metabolism to provide energy for walking, we combined rates of oxygen consumption during walking and subsequent recovery to estimate the cost of transport. This may overestimate the steady-state metabolic costs. Hence, contrary to biomechanical convention, there are clear examples where there is not a strong link between inverted-pendulum recovery and the metabolic cost of walking.

New approaches to understanding the mechanical determinants of the metabolic cost of walking are needed. Donelan et al. (2002) pointed out important flaws with measuring the mechanical work performed on the center of mass from the summed GRF values of all limbs. During the stance phase some limbs are performing negative work at the same time that other limbs are performing positive work. Donelan et al. (2002) proposed that it is important to measure the individual limb work performed to restore and redirect the COM velocity during step-to-step transitions. Alternatively, Griffin et al. (2003) provided evidence that in humans the metabolic cost of walking is more closely related to the cost of muscular force generation than the individual limb work that muscles must perform. Most recently, Grabowski et al. (2005) showed that supporting weight and performing work on the center of mass each have a distinct metabolic cost. Though developed for human bipedal walking, these new approaches may help to link the mechanics and energetics of locomotion in all animal species.

In summary, Galápagos tortoises walk extremely slowly, without systematic inverted-pendular mechanics, but with normal mechanical power outputs. Studies of the metabolic cost of locomotion in turtles are needed to determine how these unusual mechanics affect the energetics of walking.

We thank the Oklahoma City Zoo, particularly Ken Hovey and Brian Aucone, for their help facilitating this project; Aimee LaFave for assistance collecting data; Jim Usherwood and an anonymous reviewer for raising the issue of force-platform drift; Todd Gleeson for providing unpublished data on alligators; members of the Locomotion Laboratory at the University of Colorado for comments on previous drafts of this manuscript. This work was supported by National Institutes of Health (F32 AR08615 to P.A.Z.; AR44688 to R.K.) and the University of Colorado.

References

- Abacus Concepts Inc. (1991). *SuperANOVA*. Berkeley: Abacus Concepts Inc.
- Ahn, A. N., Furrow, E. and Biewener, A. A. (2004). Walking and running in the red-legged running frog, *Kassina maculata*. *J. Exp. Biol.* **207**, 399–410.
- Autumn, K., Farley, C. T., Emshwiller, M. and Full, R. J. (1997). Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. *Physiol. Zool.* **70**, 660–669.
- Baudinette, R. V., Miller, A. M. and Sarre, M. P. (2000). Aquatic and terrestrial locomotory energetics in a toad and a turtle: a search for generalisations among ectotherms. *Physiol. Biochem. Zool.* **73**, 672–682.
- Cavagna, G. A. (1975). Force platforms as ergometers. *J. Appl. Physiol.* **39**, 174–179.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work

- in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243-R261.
- Cavagna, G. A., Thys, H. and Zamboni, A.** (1976). The sources of external work in level walking and running. *J. Physiol.* **262**, 639-657.
- Darwin, C.** (1839). *Voyage of HMS Beagle*. London: H. Colburn.
- Donelan, J. M., Kram, R. and Kuo, A. D.** (2002). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**, 117-124.
- Emshwiller, M. G. and Gleeson, T. T.** (1997). Temperature effects on aerobic metabolism and terrestrial locomotion in American alligators. *J. Herpetol.* **31**, 142-147.
- Farley, C. T. and Ko, T. C.** (1997). Mechanics of locomotion in lizards. *J. Exp. Biol.* **200**, 2177-2188.
- Finkler, M. S. and Claussen, D. L.** (1997). Use of the tail in terrestrial locomotor activities of juvenile *Chelydra serpentina*. *Copeia* **1997**, 884-887.
- Full, R. J.** (1989). Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 175-182. Stuttgart: Georg Thieme Verlag.
- Goslow, G. E., Jr, Seeherman, H. J., Taylor, C. R., McCutchin, M. N. and Heglund, N. C.** (1981). Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. *J. Exp. Biol.* **94**, 15-42.
- Grabowski, A., Farley, C. T. and Kram, R.** (2005). Independent metabolic costs of supporting body weight and accelerating body mass during walking. *J. App. Physiol.* **98**, 579-583.
- Griffin, T. M. and Kram, R.** (2000). Penguin waddling is not wasteful. *Nature* **408**, 929.
- Griffin, T. M., Main, R. P. and Farley, C. T.** (2004). Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? *J. Exp. Biol.* **207**, 3545-3558.
- Griffin, T. M., Roberts, T. J. and Kram, R.** (2003). Metabolic cost of generating muscular force in human walking: insights from load-carrying and speed experiments. *J. Appl. Physiol.* **95**, 172-183.
- Hildebrand, M.** (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 38-57. Cambridge: Belknap Press of Harvard University Press.
- Inman, V. T., Ralston, H. J. and Todd, F.** (1994). Human locomotion. In *Human Walking* (ed. J. Rose and J. G. Gamble), pp. 1-22. Baltimore: Williams and Wilkins.
- Jayes, A. S. and Alexander, R. M.** (1980). The gaits of chelonians: walking techniques for very low speeds. *J. Zool., Lond.* **191**, 353-378.
- Kram, R. and Taylor, C. R.** (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.
- Nwoye, L. O. and Goldspink, G.** (1981). Biochemical efficiency and intrinsic shortening speed in selected fast and slow muscles. *Experientia* **37**, 856-857.
- Pinshow, B., Fedak, M. A. and Schmidt-Nielsen, K.** (1977). Terrestrial locomotion in penguins – it costs more to waddle. *Science* **195**, 592-594.
- Rall, J. A.** (1985). Energetic aspects of skeletal muscle contraction: Implications of fiber types. *Exerc. Sports Sci. Rev.* **13**, 33-74.
- Walker, W. F.** (1986). *Vertebrate Dissection*. Philadelphia: Saunders College Publishing.
- Willems, P. A., Cavagna, G. A. and Heglund, N. C.** (1995). External, internal and total work in human locomotion. *J. Exp. Biol.* **198**, 379-393.
- Willey, J. S., Biknevicius, A. R., Reilly, S. M. and Earls, K. D.** (2004). The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*. *J. Exp. Biol.* **207**, 553-563.
- Wolledge, R. C.** (1968). The energetics of tortoise muscle. *J. Physiol.* **197**, 685-707.
- Zani, P. A., Sidenblad, K., Van Dijck, A., Gleeson, T. T. and Kram, R.** (2004). Low metabolic cost of level locomotion in box turtles (*Terrapene ornata*): why so inexpensive? *Integr. Comp. Biol.* **44**, 670.