Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods

Stephen M. Reillya,c,* Eric J. McElroya,c, Audrone R. Bikneviciusb,c

aDepartment of Biological Sciences, Ohio University, Athens, OH 45701, USA
bDepartment of Biomedical Sciences, Ohio University College of Osteopathic Medicine, Grosvenor Hall, Athens, OH 45701, USA
cOhio Center for Ecology and Evolutionary Studies, Ohio University, Athens, OH 45701, USA

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Abstract

A reanalysis of locomotor data from functional, energetic, mechanical and ecological perspectives reveals that limb posture has major effects on limb biomechanics, energy-saving mechanisms and the costs of locomotion. Regressions of data coded by posture (crouched vs. erect) reveal nonlinear patterns in metabolic cost, limb muscle mass, effective mechanical advantage, and stride characteristics. In small crouched animals energy savings from spring and pendular mechanisms are inconsequential and thus the metabolic cost of locomotion is driven by muscle activation costs. Stride frequency appears to be the principal functional parameter related to the decreasing cost of locomotion in crouched animals. By contrast, the shift to erect limb postures invoked a series of correlated effects on the metabolic cost of locomotion: effective mechanical advantage increases, relative muscle masses decrease, metapodial limb segments elongate dramatically (as limbs shift from digitigrade to unguligrade designs) and biological springs increase in size and effectiveness. Each of these factors leads to decreases in the metabolic cost of locomotion in erect forms resulting from real and increasing contributions of pendular savings and spring savings. Comparisons of the relative costs and ecological relevance of different gaits reveal that running is cheaper than walking in smaller animals up to the size of dogs but running is more expensive than walking in horses. Animals do not necessarily use their cheapest gaits for their predominant locomotor activity. Therefore, locomotor costs are driven more by ecological relevance than by the need to optimize locomotor economy.

Keywords: Locomotor energetics; Limb posture; Mammal locomotion; Biomechanics; Behavioral repertoire

Introduction

In recent decades the study of terrestrial locomotion has seen a welcome and varied array of perspectives from muscle to organismal levels. Studies of terrestrial locomotion can be divided roughly into three groups: functional studies, looking at limb movements and musculoskeletal function (e.g., Fischer et al., 2002; Roberts, 2002); energetic studies, relating oxygen consumption to the work, power and cost of movement (e.g., Cavagna et al., 1977; Donelan et al., 2002); and mechanical studies, using data on locomotor forces to examine movements of the center of mass (COM) of the whole body (or its components) as well as energy-saving effects of posture on locomotion.
mechanisms (e.g., Griffin et al., 2004a; Biewener, 2005). Each of these approaches has its body of work and general concepts, with a modest amount of overlap, but there are few examples of full integration (e.g., Minetti et al., 1999; Rubenson et al., 2004). In this paper, we review and attempt to integrate some of the emerging conceptual patterns from functional, energetic and mechanical approaches to the study of locomotion. We offer new interpretations and insights on the costs of locomotion and actual cost savings in terrestrial vertebrates when effects of limb posture (sprawling or crouched limbs versus erect limbs), gait and the ecological relevance of locomotor costs are considered.

A conceptual framework for understanding the relationship between animal function and the cost of locomotion is presented in Fig. 1. Legged animals are literally crawling all over this planet but they share three common goals regarding locomotion: food resource acquisition, predator avoidance and participation in social interactions critical for survival and reproduction. Although the importance of locomotion in animal fitness philosophically overlies all studies of locomotion, it is generally only mentioned in passing, if at all, in most of our atomized studies of locomotion. Animals move through a decision-making process (Fig. 1) linking the ecological relevance of locomotion (why they are moving) to the kind of locomotor behavior needed (how they will need to move) in order to instruct the body how to move. Issues of speed, substrate and stability inherently influence how animals need to move and how much it will cost, yet we have only begun to understand how these needs affect locomotor output and metabolic costs (Dickinson et al., 2000). Organismal function and metabolic cost of locomotion have been seen considerable study independently but little effort has been made to link aspects of locomotor output to factors influencing metabolic costs. Ultimately, we want to know how metabolic economy relates to the ecological relevance of locomotion.

Understanding the metabolic cost of locomotion

Body movements are produced via a locomotor output axis (Fig. 1): the nervous system controls motor output of the musculoskeletal system and coordinates footfalls (gaits) that deliver forces to the substrate in order to move the COM. The energetic cost of locomotion is directly related to overall muscular effort, yet the level of muscular activity itself is modulated by limb design, gait and several energy-saving mechanisms.

Primary metabolic cost of locomotion

The metabolic cost of locomotion is most commonly determined using steady-state oxygen consumption \( (V_{O_2}) \) per unit distance or time during constant-speed treadmill exercises. Most of the metabolic energy expended for locomotion powers the contraction of locomotor muscles used to support body weight and to control and move body segments (Taylor, 1985; Kram and Taylor, 1990); comparatively little work is done against the environment in order to move the COM over
a flat and level terrain (Pugh, 1971). Initial concepts on metabolic expenditure during locomotion focused on concentric muscle contractions that generated positive external mechanical work to lift and accelerate the COM (Cavagna et al., 1977). However, it was soon realized that positive external mechanical work was not tightly coupled with metabolic expenditure (Alexander et al., 1980; Heglund et al., 1982a; Taylor and Heglund, 1982; Full, 1989). Complicating factors for this include the cyclical storage and release of elastic strain energy in tendons and ligaments, isometric contractions (increased energy consumption without affecting mechanical work) and low muscle efficiencies (20–25%; Hill, 1938; Cavagna and Kaneko, 1977). A better predictor of metabolic cost is overall muscle force (Kram and Taylor, 1990) because muscle force output is the sum of all types of muscular contractions (incorporating isometric contractions; Roberts et al., 1997) and metabolic expenditure is directly related to the speed and magnitude of muscular force generation (Barany, 1967; Margaria, 1976; Rome, 1992). It then follows that the metabolic cost of locomotion can be reduced if animals can take advantage of limb designs and energy-saving mechanisms that lessen muscular effort or the rate of muscle contraction.

Energy-saving mechanisms in locomotion

One strategy for reducing energy expenditure during locomotion is postural (Biewener, 1989). In mammals a more upright posture increases the effective mechanical advantage (EMA) of anti-gravity muscles (e.g., gastrocnemius muscles about the ankle). In general, smaller mammals move with more abducted and flexed limbs than do larger mammals. Consequently, energetic demands for muscular activity to counter the flexing moment of the ground reaction force are relatively greater in smaller mammals. There is a restricted capacity of smaller mammals to counter this cost because crouched mammals do not increase postural erectness with size (Fischer et al., 2002). Postural effects on energy expenditure are little studied in non-mammalian quadrupeds. Contrary to mammals, the semi-erect postures of iguanas and alligators exhibit decreased EMA (at the ankle) with more upright posture (Blob and Biewener, 1999, 2001), but this seems to be related to their relatively larger feet (Reilly and Blob, 2003) and their unique torsional hindlimb rotation behavior (Reilly et al., 2005). It remains to be seen whether postural effects on EMA in reptilian and amphibian sprawlers parallel these species or mammals.

Another energy-saving mechanism occurs when walking animals vault over largely stiff limbs in a manner that resembles an inverted pendulum (Cavagna et al., 1977; but see Geyer et al., 2006). As the COM is alternately raised and lowered, animals can take advantage of out-of-phase fluctuations in gravitational potential (PE) and kinetic (KE) energies. The pendulum-like conversion of KE to PE and back into KE with each step reduces the positive external mechanical energy needed to move the COM upward and forward. This results in reductions in concentric muscle contractions and a lower metabolic effort needed to move the COM (Cavagna et al., 1977; Donelan et al., 2002; Srinivasan and Ruina, 2006). In general, animals of all sizes are able to realize at least some external mechanical energy savings by using this pendulum-like exchange of KE and PE (Cavagna et al., 1977; Dickinson et al., 2000; Reilly et al., 2006), although the capacity varies with locomotor mode, being greatest in walks, intermediate in gallops and least in trots (Cavagna et al., 1977; Minetti et al., 1999). The traditional parameter for assessing the efficacy of pendulum-like mechanics to recover external mechanical energy is percent recovery (%R; Cavagna et al., 1977). This parameter represents the most optimistic recovery since it tends to overlook the substantial loss of energy caused by collisions of the foot with the ground (Donelan et al., 2002; Ruina et al., 2005). Surprisingly few studies have addressed the actual metabolic savings realized by using pendulum-like movements of the COM (e.g., Ortega and Farley, 2005).

The third way animals can save energy during locomotion typically occur at faster speeds. The limbs of running animals are less rigid, so that they compress and then extend during the stance phase, allowing spring-like elements of the musculoskeletal system to passively store and return elastic strain energy during each step (Cavagna et al., 1977; Heglund et al., 1982a; Alexander, 1988; Blickhan, 1989; Biewener, 2003; Roberts et al., 1997). In this spring-mass model of running, the KE and PE that are stored in the spring elements of the limbs and spinal column during the first half of stance are recovered in the second half to increase the height and speed of the COM. While less positive work is required from concentric muscular contractions when animals take advantage of stored elastic strain energy to move the COM (Cavagna et al., 1977), some metabolic energy must still be used to perform isometric contractions to stiffen and control these springs (Roberts, 2002). However, because isometric muscle contractions are more economical at generating force than concentric contraction (due to the force–velocity relationship of muscle; Hill, 1938), metabolic energy is ultimately saved by replacing active work-producing concentric contractions with the passive biological springs controlled by isometric contractions (Roberts, 2002). Whereas some intramuscular components are clearly acting as springs (titin: Lindstedt et al., 2002; myosin, actin and crossbridges: Linari et al., 1998), tendons and ligaments of the limbs and vertebral
column have been shown to be the primary tissues involved in elastic strain energy cycling (Alexander, 1988; Bennett et al., 1986; Roberts et al., 1997; Roberts, 2002; Biewener, 2003). Elastic energy recovery has been estimated by direct measures of tendon stresses (Biewener, 1998; Roberts et al., 1997), by inference through measures of limb stiffness (Farley et al., 1993), by subtracting the sum of internal and external mechanical energies from the net cost of locomotion (Minetti et al., 1999) and by calculating the ratio of external mechanical power to metabolic power (Cavagna et al., 1977; Taylor and Hegnul, 1982). It is widely believed that large animals benefit from elastic energy savings more fully than smaller animals (Biewener et al., 1981; Alexander, 1988), although recent work theorizes that, within quadrupeds, spring savings may be important for small animals as well (Bullimore and Burn, 2005). Also, the relative contribution of springs to metabolic savings may be different for bipeds and quadrupeds (Bennett, 2000). Clearly, more data are needed to address the role of biological springs in affecting the metabolic cost of locomotion particularly in smaller quadrupedal animals.

In sum, the metabolic cost of locomotion largely reflects the cost of force production by muscles. Muscular activity levels can be moderated by moving with a more erect posture and using pendulum-like and spring-mass mechanics. The goals of this review are to focus on the output of the locomotor axis (Fig. 1) in a size range of model species in order to (1) examine the influences of limb design and posture on costs, (2) estimate how much pendular and spring savings contribute to reducing the actual metabolic cost of locomotion and (3) address the biological relevance of these energy-saving mechanisms by contrasting the costs of different gaits to the actual locomotor repertoires used by these animals in nature.

**Pure size effects on locomotor costs**

Although animals exhibit a variety of limbed locomotor systems spanning a million-fold increase in body mass, they appear to follow several "rules" concerning the metabolic cost of locomotion. Oxygen consumption within species increases linearly with speed but the rate of increase is greater in smaller species (Schmidt-Nielsen, 1972; Full, 1989). Furthermore, the metabolic cost of locomotion (computed as the mass-specific rate of oxygen consumption over resting levels regressed on speed; in ml O$_2$ kg$^{-1}$ m$^{-1}$ or, as applied here, J kg$^{-1}$ m$^{-1}$) is also greater in small species (solid line in Fig. 2), so that small animals use more energy to move 1 kg of mass over 1 m distance than do larger animals (Schmidt-Nielsen, 1972; Full, 1989). In marked contrast, total external mechanical energy scales as 1.07 mass$^{-0.01}$ (dotted line in Fig. 2; Full, 1989, 1991). Thus, the relative amount of external mechanical energy used to move the COM does not appreciably change with size ($\sim$1.1 J kg$^{-1}$ m$^{-1}$ regardless of size). [Values for external mechanical energy may actually be lower than found using the traditional (COM fluctuation) approach (e.g., disregard of simultaneous positive and negative work during periods of multiple limb support; Donelan et al., 2002). While this may displace this scaling constant of external mechanical energy on speed somewhat,

![Image](https://example.com/fig2.png)

**Fig. 2.** Logarithmic plot of the metabolic cost of locomotion used to move 1 kg of body mass 1 m in distance (squares) and the mass-specific external mechanical energy imparted to the center of mass by motion of the body during locomotion (dashed line at 1.1 J kg$^{-1}$ m$^{-1}$; Full, 1991). Mass-specific locomotor cost gets cheaper with size but the relative amount of energy imparted to the center of mass is constant ($\sim$1.1 J kg$^{-1}$ m$^{-1}$; Full, 1989). Data are for a range of mammals from Taylor et al. (1982).
there is no a priori reason to expect that the scaling coefficient will change appreciably relative to the cost of locomotion.] The linear relationships through these mouse-to-elephant energetic patterns have been used to suggest that there are similarities in the dynamics of locomotion (Alexander and Jayes, 1983; Farley et al., 1993) and general design constraints in jointed musculoskeletal systems (Full, 1989) across a wide range of tetrapods and that metabolic energetics are independent of animal shape and posture (Roberts, 1998).

While the metabolic cost of locomotion appears linear on a log/log plot (Fig. 2), a distinctly non-linear pattern occurs when the actual (unlogged) metabolic cost is plotted (Fig. 3a). Indeed, the rate of decrease in the cost of locomotion occurs when the actual (unlogged) metabolic cost is saving components.

To try to explain the differences in locomotor energetic patterns for crouched animals (shrew to coypu) versus more erect animals (genet to buffalo; Fig. 3b; Table 1). Only the ankle extensor data are presented here; however, the same patterns are found in the five other muscle groups studied by Alexander et al. (1981). The smaller, crouched animals exhibit an increase in relative muscle mass with size (slope = 12.7) while the larger, more erect animals are losing relative muscle mass with size (slope = −1.56). As with the metabolic cost plot (Fig. 3a), the inflection point in the muscle mass plot occurs near 1 kg. The increasing muscle mass in crouched animals appears to be related to size-dependent increases in cross-sectional area (Perry et al., 1988).

Why do crouched animals increase relative muscle mass with body size while erect animals lose it? One of the energy-saving mechanisms introduced earlier provides insight. As limb posture becomes more erect the effective mechanical advantage (EMA) of muscles controlling the joints increases, thereby reducing the mass-specific muscle force needed to support body weight during locomotion (Biewener, 1989, 2003).

Postural effects on the costs of locomotion

Muscle mass and mechanical advantage

Given that the cost of locomotion is primarily driven by the metabolic cost of muscle activation, we first consider how postural effects on relative limb muscle size and joint mechanical advantage influence metabolic and mechanical energy costs (Figs. 3b, c). Here, again, the broad-scale approach appears to mask clear differences between the posture groups. For example, leg muscle mass (relative to body mass) scales linearly and nearly isometrically with body size in shrew-to-buffalo regressions (Alexander et al., 1981), whereas coding these data by posture reveals contrasting patterns for crouched animals (shrew to coypu) versus more erect animals (genet to buffalo; Fig. 3b; Table 1).
locomotion would be expected to increase with size because relatively larger muscles are necessary to support more body mass with the same flexed limb posture. Clearly, some other contrasting factors are driving the 12-fold difference in the decline of the cost of locomotion in crouched vs. erect animals.

**Stride characteristics**

Allometric studies show that stride frequency decreases and stride length increases over a large range of body sizes (Heglund and Taylor, 1988; Biewener, 2003). Because speed effects are substantial, these stride
characteristics are commonly reported as the slope of each parameter regressed against speed (inset plots in Fig. 3d; Strang and Steudel, 1990). No significant differences in relative stride lengths (slope of stride length on speed) are noted when animals are split into the two postural groups (stride length inset plot and Table 1. Least-squares regression statistics for locomotor characteristics of crouched (plantigrade) vs. erect (digitigrade, unguligrade) postured mammals as a function of size

<table>
<thead>
<tr>
<th>Variable</th>
<th>Posture</th>
<th>n</th>
<th>Slope (±95% CI)</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cost of locomotion</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log/Log</td>
<td>Crouched</td>
<td>10</td>
<td>−0.383 (±0.103)</td>
<td>&lt;0.0001</td>
<td>0.950</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>24</td>
<td>−0.164 (±0.050)</td>
<td>&lt;0.0001</td>
<td>0.823</td>
</tr>
<tr>
<td></td>
<td>w/o springs(^b)</td>
<td>7</td>
<td>0.116 (±0.120)</td>
<td>0.0550</td>
<td>0.243</td>
</tr>
<tr>
<td>Raw/Log</td>
<td>Crouched</td>
<td>10</td>
<td>−24.783 (±8.203)</td>
<td>0.0001</td>
<td>0.927</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>24</td>
<td>−1.950 (±0.730)</td>
<td>&lt;0.0001</td>
<td>0.790</td>
</tr>
<tr>
<td></td>
<td>w/o springs(^b)</td>
<td>11</td>
<td>1.547 (±1.658)</td>
<td>0.0617</td>
<td>0.249</td>
</tr>
<tr>
<td><strong>Relative ankle extensor mass</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log/Log</td>
<td>Crouched</td>
<td>6</td>
<td>0.310 (±0.121)</td>
<td>0.0016</td>
<td>0.962</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>26</td>
<td>−0.110 (±0.064)</td>
<td>0.0020</td>
<td>0.568</td>
</tr>
<tr>
<td>Raw/Log</td>
<td>Crouched</td>
<td>6</td>
<td>12.697 (±3.330)</td>
<td>0.0005</td>
<td>0.982</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>26</td>
<td>−1.560 (±0.712)</td>
<td>0.0001</td>
<td>0.700</td>
</tr>
<tr>
<td><strong>Hindlimb effective mechanical advantage</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log/Log</td>
<td>Crouched</td>
<td>7</td>
<td>0.014 (±0.213)</td>
<td>0.8725</td>
<td>0.075</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>6</td>
<td>0.232 (±0.278)</td>
<td>0.0806</td>
<td>0.758</td>
</tr>
<tr>
<td>Raw/Log</td>
<td>Crouched</td>
<td>7</td>
<td>0.006 (±0.071)</td>
<td>0.8224</td>
<td>0.105</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>6</td>
<td>0.371 (±0.448)</td>
<td>0.0826</td>
<td>0.755</td>
</tr>
<tr>
<td><strong>Stride frequency (strides m(^{-1}))</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log/Log</td>
<td>Crouched</td>
<td>8</td>
<td>−0.456 (±0.123)</td>
<td>&lt;0.0001</td>
<td>0.919</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>14</td>
<td>−0.244 (±0.209)</td>
<td>0.0202</td>
<td>0.788</td>
</tr>
<tr>
<td>Raw/Log</td>
<td>Crouched</td>
<td>8</td>
<td>−2.992 (±1.880)</td>
<td>0.0081</td>
<td>0.846</td>
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<tr>
<td></td>
<td>Erect</td>
<td>14</td>
<td>−0.460 (±0.133)</td>
<td>&lt;0.0001</td>
<td>0.908</td>
</tr>
<tr>
<td><strong>Stride length (s stride(^{-1}))</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log/Log</td>
<td>Crouched</td>
<td>8</td>
<td>−0.376 (±0.205)</td>
<td>0.0042</td>
<td>0.877</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>14</td>
<td>−0.422 (±0.092)</td>
<td>&lt;0.0001</td>
<td>0.945</td>
</tr>
<tr>
<td>Raw/Log</td>
<td>Crouched</td>
<td>8</td>
<td>0.056 (±0.052)</td>
<td>0.0053</td>
<td>0.867</td>
</tr>
<tr>
<td></td>
<td>Erect</td>
<td>14</td>
<td>0.143 (±0.051)</td>
<td>&lt;0.0001</td>
<td>0.869</td>
</tr>
</tbody>
</table>

*Variables with significant differences (p<0.05) between crouched and erect mammal slopes (for both log/log and raw/log regressions) (hindlimb effective mechanical advantage is marginally significant at the 0.08 alpha level).

\(^a\)Data sources: cost of locomotion: Taylor et al. (1982); relative ankle extensor mass: Alexander et al. (1981); hindlimb effective mechanical advantage: Biewener (1989, 2005); stride frequency and length: Strang and Steudel (1990), Van de Graff et al. (1982).

\(^b\)Erect w/o springs data are costs of locomotion+% elastic energy recovery from Biewener (1998, Table 3): kangaroos, wallabies, dogs, humans, and small horses; Minetti et al. (1999): large horses.

Fig. 3. Postural effects on the costs (a), limb biomechanics (b, c) and stride characteristics (d) in mammals plotted against log body size. Regression coefficients are listed in Table 1. Animals are categorized as having crouched (▲, △) or erect (■, □) limb postures illustrated by the limb diagrams drawn to the same scale in (a). Terminal taxa for each linear data set are labeled on each graph. Note that limb postures change little in the crouched (plantigrade) forms while the erect forms transition from digitigrade to unguligrade limb designs. (a) Same data as in Fig. 1 except the cost is presented in actual (non-logged) units. (b) Ankle extensor muscle masses for Insectivora, Rodentia, Fissipedia and Artiodactyla from Alexander et al. (1981, Fig. 1). (c) Hindlimb effective mechanical advantage from Biewener (1989, 2005). (d) Effect of speed (insets) and size (main graph) on stride characteristics. In order to compare stride characteristics across species one has to account for speed effects within species; this is done by calculating the regression slopes of stride frequency and length against speed for each species (Strang and Steudel, 1990). The inset graphs show the range of slopes that describe how stride length (filled symbols) and stride frequency (open symbols) change with speed in crouched (triangles) and erect-postured (squares) mammals. The main graph illustrates stride frequency and length vs. speed slopes over a wide range of body masses (data are from Strang and Steudel, 1990; skunk calculated from Van de Graff et al., 1982).
solid symbols in Fig. 3d; Table 1). In other words, animals of all sizes increase stride length similarly as they move faster. By contrast, relative stride frequency (slope of frequency on speed) is much greater in crouched animals compared to erect species (2–8-fold greater; stride frequency inset plot in Fig. 3d). As a result, speed increases are matched with substantially more rapid limb movements in crouched animals (6-fold difference between crouched and erect slopes; open symbols in Fig. 3d; Table 1).

These stride characteristics appear to have different effects on the metabolic cost of locomotion in the two postural groups. The swinging limb may be modeled as a conventional pendulum (Ahlborn, 2004) and, as such, has an intrinsic frequency (at which the pendulum swings without energy input) that is inversely proportional to limb length. This implies that the short limbs of small, crouched animals have the potential to operate with a higher intrinsic frequency at the same cost as the slower frequencies of long limbs of larger, erect animals. However, two factors argue otherwise. First, each support phase is associated with some muscular effort to support the body weight and this effort is proportionally greater when the limbs are flexed. Second, additional muscle activity is needed to swing limbs faster than the limbs’ intrinsic frequency and faster rates of muscle force generation cost more (Taylor, 1985; Heglund and Cavagna, 1987; Kram and Taylor, 1990). Across crouched animals, the smallest species move with the highest stride frequencies and, correspondingly, have the highest metabolic costs of locomotion (Figs. 3a, d). As size increases and stride frequency decreases, so too drops locomotor cost in crouched animals. Therefore, the greater metabolic cost of locomotion in crouched animals can be primarily explained by the fact that they take more steps with their shorter legs than larger erect animals to cover the same distance (Heglund and Cavagna, 1987). In erect species the low slopes for both relative stride frequency and length against speed make it difficult to assess how stride characteristics will affect the metabolic cost of locomotion.

**Contributions of dynamic energy-saving mechanisms**

Why is the metabolic cost of locomotion so much lower in erect animals? While decreasing muscle mass accompanied by increasing EMA partially explains this lower cost, another part of the answer may also be related to the actual capacity of dynamic energy-saving mechanisms (pendular and spring savings; Fig. 1) to effectively contribute to reducing muscular effort and thus metabolic cost.

**Calculating the “gross cost of locomotion”**

Measured values for the net metabolic cost of locomotion (Table 2: variable 1) inherently incorporate savings due to pendulum-like and spring-mass mechanics. In the following analysis, we generated a hypothetical variable (“gross cost of locomotion”) that estimates the total metabolic energy expenditure assuming that the positive work contributed by pendular and spring mechanics was instead generated by muscular work.

First, the metabolic energy savings resulting from pendulum-like and spring-mass mechanics must be approximated. The metabolic energy savings via pendular mechanics are estimated as the product of the percent recovery via pendular mechanics (%R) and positive external mechanical energy. As noted previously, positive external mechanical energy is fairly invariant at ~1.1 J kg⁻¹ m⁻¹ (Full, 1989, 1991; dashed line in Fig. 3a). Assuming that muscles achieve a maximal efficiency of 25% when performing positive work (Hill, 1938; Cavagna and Kaneko, 1977), muscles need to consume 4 times the energy in order to provide the same amount of positive work that pendular exchange provides. Thus, the term for metabolic energy savings by pendular exchange [Table 2: variable 3] simplifies to:

\[
\text{Metabolic energy savings by pendular exchange} = \frac{R}{100} \times 1.1 \text{ J kg}^{-1} \text{ m}^{-1} \times 4.
\]

The metabolic energy savings via spring-mass mechanics [Table 2: variable 5] can be computed as:

\[
\text{Metabolic energy savings by springs} = \text{% elastic energy recovery} \times \text{net cost of locomotion} \times 4.
\]

Elastic energy recovery is reported in the literature as a percentage of net cost of locomotion (e.g. Biewener, 1998), thus the product of % elastic energy recovery and net metabolic cost of locomotion estimates the amount of mechanical work done by springs in terms of metabolic cost. Once again, multiplication by 4 takes into account the upper limits of muscle efficiency when converting work from elastic strain energy into work performed by muscles.

Finally, the gross metabolic cost of locomotion [Table 2: variable 6] is estimated as:

\[
\text{Gross metabolic cost of locomotion} = \text{net cost of locomotion} + \text{metabolic energy savings by pendular exchange} + \text{metabolic energy savings by springs}.
\]
Table 2. Components of the costs of locomotion by gait in a size range of tetrapods for which data are availablea

<table>
<thead>
<tr>
<th>Cost variables</th>
<th>Lizards (21 g)</th>
<th>Ground squirrel (238 g)</th>
<th>Dog (20 kg)</th>
<th>Horse (140–280 kg)</th>
<th>Horse (515 kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Net metabolic cost of locomotion (J kg(^{-1}) m(^{-1}))</td>
<td>127.84</td>
<td>88.04</td>
<td>50.25</td>
<td>17.01</td>
<td>7.74</td>
</tr>
<tr>
<td>(oxygen consumption in Joules)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. % Pendular recovery of total external mechanical energy</td>
<td>42</td>
<td>10</td>
<td>17</td>
<td>6</td>
<td>60</td>
</tr>
<tr>
<td>3. Metabolic energy saved by pendular exchange (J kg(^{-1}) m(^{-1})) (</td>
<td>=(\text{var. 2/100} \times 1.1 \text{ J kg}^{-1} \text{ m}^{-1} \times 4)</td>
<td>)</td>
<td>1.85</td>
<td>0.44</td>
<td>0.75</td>
</tr>
<tr>
<td>4. % Elastic energy recovery (% net metabolic cost)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5. Metabolic energy saved by springs (J kg(^{-1}) m(^{-1})) (</td>
<td>=(\text{var. 4/100} \times \text{var. 1} \times 4)</td>
<td>)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6. Gross metabolic cost of locomotion (J kg(^{-1}) m(^{-1}))</td>
<td>129.69</td>
<td>88.48</td>
<td>51.00</td>
<td>17.27</td>
<td>10.38</td>
</tr>
<tr>
<td>(</td>
<td>=(\text{var. 1+var. 3+var. 5})</td>
<td>)</td>
<td>98.6</td>
<td>99.5</td>
<td>98.5</td>
</tr>
<tr>
<td>7. % Muscle activity (var. 1/\text{var. 6}) \times 100</td>
<td>1.4</td>
<td>0.5</td>
<td>1.5</td>
<td>1.5</td>
<td>25.4</td>
</tr>
<tr>
<td>8. % Pendular savings (var. 3/\text{var. 6}) \times 100</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>9. % Spring savings (var. 5/\text{var. 6}) \times 100</td>
<td>1.4</td>
<td>0.5</td>
<td>1.5</td>
<td>1.5</td>
<td>25.4</td>
</tr>
<tr>
<td>10. % Mechanical savings (var. 8+var. 9)</td>
<td>1.85</td>
<td>0.44</td>
<td>0.75</td>
<td>0.26</td>
<td>2.64</td>
</tr>
</tbody>
</table>

Literature values for the metabolic cost of locomotion (calculated for the most efficient speed for each gait), % mechanical energy recovered by pendulum-like mechanics and % elastic energy recovery were used to calculate contributions of spring and pendular savings (variables highlighted bold) to realized costs of locomotion for different gaits (in actual J kg\(^{-1}\) m\(^{-1}\) and % of cost). Cost variables 1, 8 and 9 are illustrated in Fig. 4.

aData sources and notes for Variables 1, 2, and 4:


Ground squirrel (Spermophilus saturatus) costs from Hoyt and Kenagy (1988) and Kenagy and Hoyt (1989).

Dogs (Canis domesticus) walk cost from Griffin et al. (2004b), trot, gallop costs from Biewener (1998).


Variable 2: Lizards % \(R\) from closely related species, Reilly et al. (unpublished data)

Ground squirrel % \(R\) from Heglund et al. (1982b).

Dog \(R\) from Cavagna et al. (1977) and Griffin et al. (2004b).

Horses \(R\) based on 515 kg horse data in Minetti et al. (1999).

Variable 4: Elastic energy recovery was considered to be negligible in small animals (Biewener, 2003) and all walking gaits (Biewener, 1989, Minetti et al., 1999).


280 kg horse: elastic energy storage from Biewener (1998) was used with metabolic costs from Hoyt and Taylor (1981), Farley and Taylor (1991) to calculate % elastic energy recovery as in Biewener (1998).

515 kg horse: % elastic energy recovery from Minetti et al. (1999) was calculated by dividing elastic energy storage per stride by metabolic cost per stride as in Biewener (1998).

\(1.1 \text{ J kg}^{-1} \text{ m}^{-1}\) is the mean value for total external mechanical energy across tetrapods (Fig. 1; Full, 1991). We converted the positive external mechanical work by pendular exchange and springs into metabolic costs of positive work that would have been performed if muscles replaced these energy-saving mechanisms. Following Biewener (1998), Biewener and Baudinette (1995) metabolic costs were estimated by multiplying the positive mechanical work done by 4 to account for muscle efficiency assumed to be 25% (Hill, 1938; Cavagna and Kaneko, 1977; Margaria, 1976).

This is what total metabolic cost would be if muscles had to perform the additional positive mechanical work necessary to replace the work done by pendular and spring mechanics.

Therefore, the gross metabolic cost of locomotion reflects the total cost of locomotion. It is from this value that we calculated the actual percent energetic savings of pendula and springs to reducing the gross cost of locomotion to the net cost of locomotion (Table 2: variables 6–9) and from which we then tease apart the relative contributions of muscle activation, pendula and springs to the total energy expenditure for locomotion. We now apply these variables as a means for addressing the question of why the net cost of locomotion is so much lower in large erect animals.

Only large erect animals reduce the metabolic cost of locomotion with pendular exchange

The different size-dependent trends of external mechanical energy and net metabolic cost of locomotion provide a clue for the relative importance of savings realized by pendulum-like mechanics (Fig. 3a). The lines for each parameter converge with increasing mass because external mechanical energy is constant with size (\(\sim 1.1 \text{ J kg}^{-1} \text{ m}^{-1}\), Full, 1989, 1991; dashed line in Fig. 3a). Consequently, external mechanical energy constitutes an increasingly greater portion of the
metabolic cost of locomotion in larger animals. This implies that pendular savings represent an increasingly important mechanism for reducing the metabolic cost of locomotion as erect animals get larger but are minor or insignificant in smaller crouched animals.

These predictions are borne out in the focal species for which we can compare the % contribution of metabolic energy saved by pendular exchange (grey bars in Fig. 4; Table 2: variable 8). Lizards, ground squirrels, dogs and horses have appreciable external mechanical energy recoveries via pendular mechanics (maximum %R; Table 2: variable 2) when walking (17–60%) and galloping (12–14%), yet the impact of actual pendulum-based energy savings varies with body size. The crouched species (lizard, ground squirrel) save trivial amounts of metabolic energy with pendular exchange (∼1.5%; Table 2: variable 8) because the magnitude of external mechanical energy is so small relative to the net metabolic cost of locomotion. By comparison, actual pendular savings in dogs and horses are much greater (25–47% in walking gaits and 7–14% in gallops; Table 2: variable 8). Another way to appreciate these differences is to compare walking in the smallest and largest animals: lizards and horses exhibit nearly the same mechanical energy savings by pendular exchange (∼40%R, Table 2: variable 3), but these equate to only 1.4% savings from the gross cost of locomotion in lizards versus ∼46% in horses (Table 2: variable 8). Clearly part of the decrease in net metabolic cost as erect animals get larger can be attributed to their increasing ability to realize greater metabolic cost savings from pendular exchange of KE and PE (Fig. 4).

Only large erect animals appear to reduce the metabolic cost of locomotion with springs

Because the capacity to store elastic energy increases as a function of cross-sectional area of the tendons involved (Biewener et al., 1981; Bennett et al., 1986; Biewener and Blickhan, 1988), energy savings from elastic storage are widely considered to be more important in large animals than in small animals (e.g. Biewener, 2003). The suggestion that elastic energy recovery may actually be more important in the locomotion of smaller mammals (Bullimore and Burn, 2005) is currently untested because, to date, the contribution of limb spring elements has not been well studied in small animals (with the exception of bipedal hopping animals that are over-designed as spring systems and enjoy 39–45% elastic energy returns; Alexander and Vernon, 1975; Baudinette et al., 1992; Biewener and Baudinette, 1995; Biewener, 1998). For the purposes of this analysis it is assumed that elastic energy storage in small unspecialized animals (lizards and ground squirrels) is zero.

Among erect quadrupeds, elastic energy recovery has been reported for 20 kg dogs, 280 kg horses and 515 kg horses (Biewener, 1998; Minetti et al., 1999). In the trot, elastic energy recoveries of 3%, 21% and 45% were reported for the trot, gallop (G) and bound (B). Black bars indicate the metabolic cost of locomotion (J kg⁻¹ m⁻¹) at the preferred speed within each gait (Table 2, variable 1). Percentages over the black bars indicate the change in cost incurred in changing gaits (magnitudes of differences are obscured by the log scale on the cost axis). Note that faster gaits are cheaper until the horses where running gets progressively more expensive. Hanging bars indicate the realized cost savings (% of gross metabolic cost) resulting from pendular and limb spring savings (Table 2, variables 8 and 9). Note that realized pendular and spring savings are insignificant to the cost of locomotion in small, crouched animals but become increasingly more important in erect animals as size increases.
estimated for dogs and small and large horses, respectively (Table 2: variable 4). Even greater potentials for elastic energy recovery were found for asymmetrical gaits (gallop): 5%, 18% and 64%, respectively. These levels of elastic energy recovery result in significant energy savings to the animals accounting for gross metabolic savings of 11%, 43% and 62% in the trot and 15%, 36% and 67% in the gallop (Table 2: variable 9). Both elastic energy recovery and its resulting energy savings exhibit a strong size dependency. These data show that springs function effectively in larger animals (those with more erect limbs) and, conversely, that the contribution of elastic energy recovery to metabolic cost of locomotion in quadrupeds (smaller than 20 kg) is likely to be increasingly inconsequential (Fig. 4, white bars on trot and gallop gaits).

Part of the increasing elastic energy recovery with mass in the more cursorial animals results from changes in the construction of tendons and muscles that control the springs, namely, the development of long and stout tendons and ligaments as well as super-pinnate muscles that function as spring dampeners (Wilson et al., 2000, 2001; Alexander, 2001; Hermanson, 1997). These limb design-based increases in elastic energy recovery are part of why costs continue to decrease in larger erect animals. In fact, metabolic cost of locomotion would increase, rather than decrease, with size if spring savings are removed from those animals in which it has been measured (Fig. 5, open squares; Table 1). The relative contribution of trunk elasticity and how it increases in larger animals is badly in need of study, as are springs and spring savings in small animals (<5 kg).

Summarizing postural differences in the variables affecting the metabolic cost of locomotion

Differences in body construction and efficacy of energy-saving mechanisms between small crouched and large erect animals result in contrasting patterns of size-dependent changes in metabolic cost of locomotion (Fig. 6). Crouched animals essentially pay for locomotion with muscle activation alone because little relief is afforded by energy-saving mechanisms. Spring savings are expected to be little to none (at least for now, see Bullimore and Burn, 2005), and our analysis suggests that pendular savings are irrelevant as well. Indeed, potential metabolic savings via pendular and spring components constitute less than 2% of the gross metabolic cost of locomotion (Table 2: variable 8).

Limb posture does not appear to change much across the crouched animal size range and, thus, limb muscle masses enlarge in order to maintain low muscle stresses. Locomotion becomes metabolically cheaper with increasing body size in crouched animals primarily through reductions in stride frequency.

The shift to erect limb postures invoked a series of correlated effects on the metabolic cost of locomotion (Wilson et al., 2000, 2001). Increases in limb erectness are related to increases in effective mechanical advantage, decreases in relative muscle masses (and their relative cost), elongation of metapodial limb segments (as limbs go from digitigrade to unguligrade designs) and increasingly effective biological springs (Fig. 6). As a consequence of these changes, the metabolic cost of locomotion is lower in erect forms. In addition, the size-dependent decrease in cost within this group primarily reflects the increasing contribution of realized metabolic savings from pendula and springs and their increasing importance in unguligrade forms.

Gait effects on locomotor costs

Animals appear to fine-tune limb dynamics within gaits to move at certain preferred speeds at which metabolic cost is minimal (Hoyt and Taylor, 1981). More radical changes in limb dynamics are made between gaits. Gait transitions occur as changes in neuromotor output affecting inter-limb and intra-limb coordination (Fig. 1, locomotor output axis), yielding shifts in how the COM moves and thereby influencing fluctuations of kinetic, gravitational potential and elastic strain energies (Cavagna et al., 1977; Minetti, 1998; but see Ruina et al., 2005 for an alternative approach to modeling galloping). What happens to the mass-specific
metabolic cost of locomotion and the potential for reducing costs via pendular and spring mechanisms when animals increase speed by changing gaits? No universal answer is possible because, as our evaluation finds, it depends on the posture and size of the animal in question. To illustrate this, we compared the metabolic cost of locomotion and computed savings components (metabolic energy actually saved via pendular exchange and elastic energy recovery) for each gait in focal animals representing four orders of magnitude in mass (Table 2).

Small, crouched animals

Lizards (~10 g; \textit{Cnemidophorus, Callisaurus}) and squirrels (236 g; \textit{Spermophilus}) are crouched animals for which walking and running (trot, bound) data are available. In both groups, running is cheaper than walking: about a third cheaper for a trotting lizard and two-thirds cheaper for a bounding squirrel (bottom bars, Fig. 4). Realized pendular and spring savings are of little consequence in crouched animals (top bars, Fig. 4; Table 2). More likely, these animals realize metabolic cost reductions by decreasing muscle activation costs with changes in stride frequency and distance covered in the faster gaits (Fig. 3d). A predictor of the metabolic cost of locomotion is the reciprocal of stride length, or the number of strides per meter (Kram and Taylor, 1990). Stride length more than doubles while stride frequency only increases by about a third when lizards change from a walk to a trot (Avery et al., 1987). Thus, strides per meter decrease when lizards change from walking to trotting and, as predicted, cost of locomotion decreases (Fig. 4). Stride length data for squirrels are lacking but we can assume it increases with bounding, because minks, another animal with relatively long and thin body morphology that walks and bounds, double their stride length with no further increase in stride frequency when shifting from walks to bounds (Williams, 1983). Here, again, strides per meter decrease when squirrels change from walking to bounding and the cost of locomotion correspondingly decreases (Fig. 4). Thus, small crouched animals realize a decrease in metabolic cost of running over walking by primarily decreasing the number of strides they must take per meter traveled. Because metabolic energy saved by pendular exchange and elastic energy recovery in lizards and squirrels is no greater than 1.5% of the gross metabolic cost of locomotion, these animals benefit little from passive energy-saving mechanisms. In small crouched animals, faster gaits are cheaper but locomotion is generated and maintained by muscle contraction alone (98.5% or more of the gross cost of locomotion).
Larger, erect (digitigrade) animals

Dogs (20 kg) continue the speed- and gait-related changes in metabolic costs found in crouched animals (trots and gallops are 30% and 56% cheaper than walks, respectively; bottom bars, Fig. 4; Table 2). Stride frequency and length change as dogs move with faster gaits (frequencies rise from ~1 Hz in walks to ~2 Hz in trots and ~2.5 Hz in gallops as stride lengths increase from 1 to 1.5 to 2.4 m, respectively; Heglund and Taylor, 1988). Strides per meter decrease as dogs shift from walking (1 stride m$^{-1}$) to trotting (0.66 strides m$^{-1}$) to galloping (0.41 strides m$^{-1}$) and the cost of locomotion decreases as well (Fig. 4). Therefore, as in lizards and squirrels, gait-related changes in stride length in dogs parallel decreases in the cost of locomotion.

Yet the costs of locomotion in dogs are much lower relative to comparable gaits in the crouched species (Table 2, Fig. 4). This appears to be due to the fact that dogs realize metabolic benefits from pendulum-like mechanics and elastic energy recovery (top bars, Fig. 4). Across dog gaits the gross metabolic cost of walking is reduced by 25% via pendular savings, trotting cost is reduced by 11% spring savings and galloping cost is reduced by 10% pendular savings and 15% spring savings (Table 2: variables 8, 9). Hence, stride dynamics help decrease the cost of locomotion across gaits in dogs, as they do in crouched animals, but, unlike crouched species, dogs further decrease the overall cost of locomotion through effective energy-saving mechanisms (Table 2: variable 10).

Energy savings in unguligrade locomotion

Horses continue the general trend of decreasing the metabolic cost of locomotion with increasing size with costs across gaits falling to about half of those of dogs (Fig. 4, Table 2). Contributing to this trend is a further decrease in the number of strides per meter (Heglund and Taylor, 1988), enabled by the longer limbs of horses. Of greater significance to the lowered costs of horses compared to dogs, however, is the enhanced ability of horses to moderate muscular effort through energy-saving mechanisms. While dogs and horses have approximately the same ranges of gross metabolic costs of locomotion (3.5–10 J kg$^{-1}$ m$^{-1}$; Table 2: variable 6), horses generate two to three times more energy savings through pendular and spring–mass mechanics (Fig. 4). Mechanical mechanisms decrease the gross cost of locomotion by 11–25% in dogs and 45–74% in horses depending on the gait (Table 2: variable 10). Modifications in limb and axial designs coincident with the shift from digitigrady to unguligrady enable the limbs to better serve as both pendula and springs.

The limbs of horses are long, facilitated by especially elongate metapodials (Steudel and Beattie, 1993). Matched with these are musculotendinous and ligamentous units that enhance elastic energy recovery. Horse limbs contain long, thin tendons attached to muscles with short, pinnate fibers (Alexander, 1988; Biewener, 1998). Most noteworthy are the superficial and deep digital flexor tendons, which together with the suspensory ligaments, are stretched as the metapodial–phalangeal (fetlock) joints extend during weight-bearing. These tendons and ligaments have significant passive elastic properties, as indicated by peak strains as high as ~0.4 (Biewener, 1998). Further, the pinnate structure of the flexor muscles is consistent with energy conservation because muscle work is the product of force and length change (Roberts et al., 1997). Metabolic energy savings in horses can be further garnered through spring-like functions of ligaments along the vertebral column (Alexander, 1988).

Changes in unguligrade limbs may also contribute to lower net walking costs. Although unguligrady is commonly touted to be an adaptation for speed (Walker and Liem, 1994), a fully extended unguligrade limb contributes to longer stride lengths in walks and runs alike (Steudel and Beattie, 1993). Thus, longer, more erect limbs should perform better as pendula. Walking costs for horses estimated in Table 2 may be further reduced if some of the elastic strain energy stored in the tendons and ligaments during the walk (assumed here to be 0) can be recruited to reduce mechanical work. While the recovery of elastic strain energy is not conventionally associated with the pendulum-dominated walks, recent studies in humans (another highly cursorially adapted mammal) have theorized that ligaments and elastic tendons may contribute substantially to the COM work of walking (Kuo et al., 2005). Indeed, the stiff-legged paradigm of walking has been challenged and is being replaced by some degree of compliant leg behavior (Geyer et al., 2006). In horses, the fetlock joints extend during the stance phase of walks (Back et al., 1996) and measurable strains are developed in the deep digital flexor tendons and suspensory ligaments (Biewener, 1998), albeit to a lesser degree than during trots. Hence, two derived components of the limbs of ungulates traditionally associated with running (erect posture/limb lengthening and spring elements) may be effective in lowering the metabolic costs of walking as well. If limb posture and stride dynamics scale isometrically in generalized horses (Leach and Cymbaluk, 1986; Griffin et al., 2004b), then the larger horse will go farther with the same limb pendulum. Accordingly, the larger horses in our analysis have ~7% cheaper costs of walking compared to the smaller horses, even though gross pendular savings have only increased by 4.4% (Fig. 4; Table 2). While this is essentially a comparison of the walking cost data of 140 and 515 kg horses illustrated in Fig. 2 of Minetti et al. (1999), similar results were found.
by Griffin et al. (2004a, Fig. 2): there is a 35% decrease in costs for walking across horse breeds ranging from 90 to 720 kg. Thus, not only is the metabolic cost of moving 1 kg of body mass forward by one meter in horses about half or less than that for dogs, the cost of walking continues to decrease as horses get bigger.

Running is not cheaper in horses

Horses buck two trends in the cost of high-speed locomotion. First, the horse is the only animal in our study for which running gaits are not cheaper than walking gaits. Whereas other species display a 31–66% decrease between walking and running costs (Fig. 4), running gaits (trots, gallops) show essentially the same cost as walks in smaller horses (+3–6%) but appear to be more expensive in larger horses (+17%). The same pattern is evident in the horses studied by Griffin et al. (2004a, Fig. 2) where walking costs the same as trotting in smaller horses but trotting is ~19% more expensive in larger horses. Horses also buck the trend of decreasing costs of locomotion with size (Fig. 2, 3a). Small and large horses alike display similar costs of locomotion for trotting (Griffin et al., 2004a) and galloping (Fig. 2 in Minetti et al., 1999).

Why do the locomotor savings level off with size in running horses? Certainly, metabolic costs might be expected to be lower in the running gaits since both small and large horses take fewer strides per meter when shifting from walks to trots (140 kg: 1–0.5 strides m⁻¹; 515 kg: 0.52–0.32 strides m⁻¹; Minetti et al., 1999). Yet, consistent limb posture across horses precludes further shifts in EMA that might provide relief for the muscle work associated with supporting greater body weight in larger horses (Bertram and Biewener, 1990). Furthermore, if the muscular dimensions scale geometrically, then larger horses would require relatively more active muscle volume to support the same unit of body weight (Griffin et al., 2004b). Thus, savings level off with size in horses because the metabolic savings associated with increasing leg length and slower rates of generating force are offset by the relative greater volume of active muscle necessary in geometrically larger horses (Griffin et al., 2004a). In effect, it seems that domestic horse breeds are no longer changing posture, only size, and thus they are subjected to biomechanical changes that preclude the trend of decreasing costs in faster gaits. Consequently, the trends of postural changes driving decreases in both size- and gait-related costs of locomotion no longer apply in horses, and locomotor economy appears to have little to do with the evolution of size in horses (Griffin et al., 2004a). Perhaps unguligrady in larger horses should be considered as more of an adaptation to make walking a more cost-effective mode of slow transportation over long distances rather than making running gaits cheaper. This hypothesis is supported by the behavioral repertoire of horses (see next section) plus the fact that the shift to unguligrady in horse evolution occurred in concert with equine size reaching 100 kg, the attainment of monodactyly and an ecological change from forest to plains habitats, when a shift to longer distance walking presumably occurred (Thomason, 1991).

The relative costs of gaits versus the ecological relevance of locomotion

Legged animals have in common three main motivations for moving: acquiring food resources, avoiding predation and social interaction (Fig. 1). Although these critical selective factors drive the evolution of locomotion, very little understanding exists on how much animals move, how often they move fast or slow, what gaits they use in these behaviors or how locomotor behavior differs across the postural array of animals discussed in this study. In order to begin to consider the relevance of locomotion, we constructed daily locomotory patterns from focal studies of the actual species (or closely related representatives: coyote, Przewalski horses) for which we have been comparing costs and postures (Fig. 7). We assumed that locomotor repertoires provide a convincing proxy for the behavioral role of the locomotor adaptations and costs observed in these animals today. Do animals preferentially use their cheapest gaits for their dominant form of locomotion? Or does ecological relevance dictate what gaits are used the most?

The two focal lizard species represent examples of the two contrasting foraging modes observed in lizards in general. Sit-and-wait predation is primitive among lizards, and the basal taxa (Iguania, Gekkota) are almost universally ambush predators (exceptions are herbivores and ground geckos). Ambush lizards emerge in the morning, bask to preferred temperatures, and then take up ambush position and wait for prey to come by. Prey recognition and intraspecific communication are visual. There is a very small amount of slow locomotion involved in basking and getting to ambush stations but essentially all of their ambush, social and evasion locomotion involves bursts of fast locomotion using trotting gaits (Irschick and Jayne, 1998, 1999; Jayne and Irschick, 2000) and bounding mechanics (Farley and Ko, 1997; Biknevicius and Reilly, 2006). Focal studies of Callisaurus draconoides reveal that these “sit-and-wait” lizards only move 1.5% of their 10 h day on the surface (9 min covering 249 m) in attack, evasion, positioning and social movements (Fig. 7; Anderson and Karasov, 1981). Thus, they truly are sit-and-wait predators but when they move their predominant locomotor mode is fast locomotion, with a trot gait involving bounding mechanics.

In contrast, Chnemidophorus tigris is a wide-foraging lizard. Wide foraging has evolved independently several
times within lizards (ground geckos, Scincioidea, Lacertoidea, Anguimorpha) and is accompanied by a series of evolutionary shifts in the feeding system (transition from tongue feeding to tongue smelling) and chemosensory systems (increase in prey and intraspecific olfaction abilities). Wide-foraging lizards move slowly through the environment in search of prey via olfaction. *Cnemidophorus tigris* is active 5 h per day but spends 80% of this time (4 h covering 900 m) in more or less constant slow-walking foraging with 11% (19 h in 33 min per day) standing still in thermoregulatory or resting behaviors (Fig. 7; Anderson and Karasov, 1981; Anderson, 1993). Only 0.06% of the active day (<1 min) is spent in faster locomotion when they commute between bushes, avoid predation and chase conspecifics. We assume this faster locomotion involves trotting gaits and bouncing mechanics based on two closely related lizard species, *Ameiva ameiva* and *Tupinambis teguixin* (McElroy and Reilly, unpub. data).

Trotting is clearly cheaper than walking in lizards (Fig. 4, Table 2). The generalized ambush feeders use the cheaper trotting gait (averaging 0.46 m s⁻¹) for both feeding, escape, and social behaviors and do not travel far (Anderson and Karasov, 1981). The slow active foragers use the more expensive walking gait (averaging 0.054 m s⁻¹) while foraging over longer distances but change to the less expensive trotting gait (averaging 1.17 m s⁻¹) for commuting, escape and social behaviors (Anderson and Karasov, 1981). What dictates the gait (and thus cost) used in locomotion in these two lizards is their foraging mode. Wide foraging is an emergent foraging strategy within lizards that invokes an increase in the metabolic cost of locomotion by using the more expensive slower gait needed for long-distance chemosensory-based foraging. The ecological benefit of the higher cost of slow foraging is the ability to consume greater amounts of higher-quality food resources (Nagy et al., 1984).

Ground squirrels (data from Hoyt and Kenagy, 1988; Kenagy and Hoyt, 1989) are also wide foragers and exhibit locomotory behaviors of slow foraging movements (walking gait) separated by fast commutes (bounding gait) between their distantly spaced food resources (fungi; Fig. 7). Slow movement (27% of the activity time is spent foraging at 0.07 m s⁻¹ covering 1.5 km) is necessary to locate and consume food while faster commuting (4% of the activity time at 2–6 m s⁻¹ covering 3.53 km) enables these animals to move between patches of resources and avoid predation (Hoyt and Kenagy, 1988; Kenagy and Hoyt, 1989). The faster gait saves squirrels time (0.27 vs. 4.67 h if walked) and energy (3.6-fold the cost if walked) compared to walking the same distance. Squirrels clearly spend less time foraging but cover 3.5 times more distance than do lizards; however, they appear to have the trade-off of needing to rest intermittently throughout the activity time on the surface. This may be related to the need for post-exercise oxygen consumption commonly incurred when small animals engage in short-duration locomotor behaviors (Gleeson and Hancock, 2001, 2002). However, in terms of ecological relevance, the slow locomotion used for wide foraging in both the *Cnemidophorus* and the ground squirrel necessitates the increased cost of muscle activation of the walking gait.

Horses are also slow foragers but, with their shifts in limb design and the relative costs of their gaits, walking appears to be their cheapest gait. Data on *Przewalski*
horses in Mongolia (comparable in size to the 515 kg horse) is used to illustrate the natural locomotor time budget for horses (Fig. 7; Boyd and Bandi, 2002; Boyd, unpublished data). Wild horses spend 7 h per day walking slowly while grazing, and another 1.76 h is spent in slow walking while commuting. Trotting and galloping are only employed 22 min per day (19 and 3 min, respectively) in fast commuting locomotion, primarily to get to and from shade or water. In addition, for every minute spent foraging, horses also spend a minute resting or standing. Thus, in terms of time budgets, an argument can be made that horses are primarily built to walk and stand. Although horses are generally considered to be supreme cursors (Walker and Liem, 1994), they only trot and gallop 2.3% of the time! Really, horses are “supreme walkers”. Horses (all unguligrades?) appear to have evolved more in the direction of efficient walking and have bottomed out (or even rebounded) from the pattern of decreasing metabolic cost of locomotion with increasing body mass.

Dogs, on the other hand, appear to be the supreme cursors. Faster gaits are cheaper in dogs (Fig. 4), and their predominant locomotor mode used during foraging is long-term fast locomotion (Fig. 7). For example, coyotes spend about 8 h per day foraging, of which 7 h are spent trotting and galloping in general search of food while only 1 h is spent in slower foraging as they focus in on a given prey item (Fig. 7; Switalski, 2003). Thus, the active long-distance foraging mode of dogs appears to be facilitated by its erect posture, medium size and improved springs that make its faster gaits an order of magnitude cheaper than the preferred gaits of the crouched animals and 30–56% cheaper than its own walking gait.

Conclusions and future directions

That small and large animals face different challenges is not new, and many studies have noted size-dependent differences in many aspects of locomotion. The reevaluation of anatomical and locomotor energetic data presented here further highlights that size does matter but primarily because of correlated changes in posture. Several clear patterns emerge from our reanalysis.

There are nonlinear patterns of change in metabolic cost, limb muscle mass, EMA and stride characteristics with body size in tetrapods. These patterns are related to the transition from crouched to erect limb postures. Therefore, posture and size together better explain locomotor patterns than size alone. In small crouched animals, stride frequency is the primary determinant of the cost of locomotion. In larger erect animals, the energetic savings from pendular and spring mechanics have major effects on the costs of locomotion. Comparisons of gaits show that running is cheaper than walking except in horses. However, animals do not necessarily use their cheapest gaits when moving during their predominant field activity. Rather, it appears that the output of organismal locomotor decision making (Fig. 1) is driven more by what the animal needs to do (e.g., foraging, escape, social interactions) and evolutionary constraints (tail dragging: Willey et al., 2004; limb rotation: Reilly et al., 2005; primitive abdominal functions: Reilly and White, 2003; shell: Zani et al., 2005) than the need to optimize locomotor economy.

These patterns reveal several issues to be explored further. First, vaulting and bouncing mechanics are primitive features of locomotion in tetrapods (Reilly et al., 2006). If pendular and spring savings are indeed inconsequential for small crouched animals, then they may be spandrels (Gould and Lewontin, 1979) of legged locomotion whose energy-saving potential was later exapted (Gould and Vrba, 1982) by the evolution of more erect posture and larger size. Second, the patterns observed in the largest and most erect group are tantalizing. While the shift to unguligrady enhances the efficiency of both walking and running compared with plantigrade and digitigrade animals, unguligrade running costs the same or more than walking in spite of enhanced limb spring efficiencies in horses. This suggests that unguligrady is negatively affecting cursoriality. Unguligrady (increased metapodial length, reduced autopodial elements), which is usually invoked as part of a suite of adaptations for cursoriality, may have been a key innovation for efficient slow grazing when equids moved onto the savannas (Thomason, 1991). However, a nagging question of whether equids are representative of all unguligrades remains and comprehensive studies of non-equid ungulates are needed.

Third, whereas the present study provides an ecological context for the use of different gaits by terrestrial tetrapods, the conclusions are based on a limited data set, namely, those few animals (which are mostly mammals) for which locomotor time budgets, gaits, limb posture, metabolic cost and mechanics are known. A crucial and largely untouched area of research remains in quantifying time and energy budgets from the perspective of locomotor behaviors and especially gaits from which mechanics can be inferred. Of particular interest are comprehensive studies on plantigrade and digitigrade species in the 1–20 kg size range where shifts in strategies for locomotor costs appear. This size/limb shape threshold may reveal the basis for the ability to shift from slow to fast foraging gaits that may have influenced the evolution of the optimal size of carnivores. In addition, comprehensive studies of semi-erect and sprawling tetrapods are badly needed because they may not necessarily follow the patterns of mammals.
Finally, future studies of biomechanics would benefit from an organismal perspective (Fig. 1) because we still know little of how axial and limb neuromuscular systems generate and change gaits, which in turn affect COM movements and stretch springs to take advantage of energy-saving mechanisms. The integration of data on gait, mechanics, energetics, limb kinematics and ecological relevance requires us to include as many common variables as possible in our work, especially actual data rather than scaling relationships, so that interdisciplinary studies of locomotion can overlap many levels of analysis.

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References


Lindstedt, S.L., Reich, T.E., Keim, P., LaStayo, P.C., 2002. Speed, stride frequency and body size and gait in Didelphis marsupialis and Virginia opossum (Didelphis marsupialis) and in other non-cursorial mammals. J. Zool. 165, 303–315.


