Bipedal Form and Locomotor Function: Understanding the Effects of Size and Shape on Velocity and Energetics

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ABSTRACT

Volumes have been written to address the locomotor anatomy of hominids, yet despite this intense scrutiny, we still do not fully understand the relationship between bipedal form and locomotor function. Energetic expenditure (as a measure of locomotor function) can be modeled using techniques that exploit empirical or theoretical methods, but none of these approaches fully captures how energetic expenditure varies within or among species at a particular, or through evolutionary, time. Form, too, is imperfectly understood. That form in the most general sense strongly affects energetic expenditure seems clear, but exactly how size should be represented (which combination of lengths and masses) and what effect shape has is not understood. Further complicating these issues is the pragmatic problem that extinct animals are often represented by incomplete fossils that only provide a hint of potential form differences.

Despite these problems, we believe some trends can be discerned. Size, especially leg length, is associated with velocity and, therefore, correlated with daily range. In the absence of confirmed differences in shape, size does not drive energetic efficiency. Consequently, differences in size among extinct bipeds should be interpreted as indicating differences in environmental context, not in levels of efficiency. We believe that small non-modern hominid species, i.e., *Homo floresiensis* and *Australopithecus (Paranthropus)* sp., are small because they did not need to be big in order to walk fast and go far.

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INTRODUCTION

Habitual terrestrial bipedalism, an adaptation with profound morphological consequences, is the defining characteristic of *Hominidae*. This locomotor adaptation set in motion the evolution of a suite of uniquely human adaptations including our current dependence on material culture and our conspicuously large brain. In contrast to the complexities of the many consequent adaptations, bipedal locomotion is very simply a method of transporting the body (in particular, digestive and reproductive organs) through the environment in order to obtain those spatially distributed resources necessary for survival and reproduction (i.e., food, water, and mates). Volumes have been written to address the locomotor anatomy of hominids, yet despite this intense scrutiny, we still do not fully understand the relationship between bipedal form and locomotor function.

Effective bipedalism requires certain morphological characteristics (e.g., two limbs capable of supporting the body mass), but it does not dictate one morphological form. Much like quadrupedalism, particular forms of bipedalism may have adapted to specific selective environments. The idea of multiple bipedal forms, first proposed by Jungers (Jungers 1982) and Rak (Rak 1991), resonates with recent ecological work that indicates that the environment and ecological pressures in which bipedalism arose may be very different from those in which the genus *Homo* evolved (Bramble and Lieberman 2004; Collard and Wood 1999; Wood and Strait 2004). The inter-relatedness of form, function, and environmental context is the cornerstone of Darwinian evolution, but it has not received a thorough review in the context of post-origin hominid bipedalism (although see Ward (Ward 2002) for such a review on bipedal origins). Our goals for this review follow below, but note that we limit our discussion to the time period after the transition from quadrupedalism (or whatever was the locomotor form of the last common ancestor). We begin by identifying features of bipedalism that are likely targets of natural

TABLE 1. ASPECTS OF LOCOMOTOR PERFORMANCE.

Aspects of locomotor performance	Definition	Units
Velocity	distance moved divided by time taken	m/s
Energetic economy	amount of energy used in completion of a task	mlO_2 or J
Energetic efficiency	ratio of work done to energy required	---
Cost of Transport	energy used to travel a meter; proxy of energetic efficiency	mlO_2/kgm or J/kgm
Home area	territory or area that is frequently used by an individual or its group	m^2
Day journey	distance traveled in a typical day	m

selection, that is, those functional characteristics that could have been optimized (e.g., energetic efficiency, aerobically sustainable velocity). Then, we examine morphological characters that are known to affect specific target characteristics and assess the current state of knowledge concerning the relationship between locomotor form and function. We also explore a potentially important caveat to locomotor research which is the dangers of applying relationships that appear to hold at one scale of inquiry (e.g., among individuals within a species) to other levels of investigation (e.g., between species). Finally, we use this information to evaluate several forms of hominid bipedalism.

ASPECTS OF LOCOMOTOR PERFORMANCE
Natural selection acts to drive a population to the top of its local adaptive peak, resulting in a morphology with higher fitness. A form is more effective (i.e., fitter), if it is better at 'getting the job done,' whatever that job might be. Efficacy, however, can be broadly interpreted for locomotion generally and for bipedalism specifically: What does it mean to be an *effective* biped? Since the function of locomotion is to move the body through the environment, there are several potential aspects of locomotor performance that selection may act to optimize, including (but not limited to) comfortable or normal velocity, maximum velocity, energetic economy, energetic efficiency, home area and day journey (Table 1). Therefore, the total adaptive landscape may have several adaptive peaks, each one of which optimizes a particular combination of aspects of locomotor performance for a specific niche. For instance, one population may track an adaptive peak for specialization in exploiting large day journey while another is selected for economy. The result would be several forms of bipedalism, each one specialized to make use of a different portion of the environment.

Several authors have argued persuasively that energy is a (or perhaps *the*) primary aspect of locomotor performance that selection acted upon to alter hominid locomotor anatomy (Hunt 1994; Rodman and McHenry 1980; Stanford 2006; Wrangham 1980). Foley's (1992) statement that "…the principle cost of any locomotor system is energy" emphasizes the point and is well-taken because energetic costs and savings have patent implications for reproductive success. Natural selection should act to increase the amount of energy that can be dedicated to reproduction, and thus locomotor costs should be minimized to the greatest extent possible. Such reduction can take two forms—increased energetic efficiency and/or greater economy. Efficiency is the ratio of work performed to energy used, while economy is the amount of energy used in absolute terms (Steudel 1994). Thus, greater efficiency allows an organism to do more with less, while greater economy means a lower overall energy budget and, hence, that relatively more energy for tasks other than locomotion is available from a given environment. In another way of looking at this difference, imagine two primates: primate A has a body mass of 50kg and requires 5 J/kgm to move while primate B has a body mass of 1kg and requires 10 J/kgm to move. If the energy required to move a kilogram of body mass a meter is assumed to be a proxy of efficiency (as is frequently done), then primate A is more efficient than primate B. Primate A is, however, less economical than B, because A uses 250 J/m (=50kg * 5 J/kgm) while B uses 10 J/m (=1kg * 10 J/kgm). If efficiency is the only constraint, then primate A has the "better" adaptation. If the environment is economically limited to a return of 20 J/m, then primate A starves, despite its efficiency.

Although energy is clearly important, it is becoming apparent that selection may act preferentially to optimize other aspects of locomotor performance, with the potential effect of increasing energy requirements. For instance, Pontzer and Wrangham (2004) argue that chimpanzees sacrifice quadrupedal energetic efficiency in support of arboreal capabilities, suggesting that energy is not always the most important factor dictating locomotor anatomy. Energetic savings (either via economy or efficiency) would be of little adaptive value if such savings sacrifices the safe completion of a particular required task. For example, a specific walking velocity may be the least costly for a primate, but if the primate fails to cover the distance to the next fruit tree before dark, the potential energy savings is irrelevant.

Thus, a strong argument can be made for the primacy of accomplishing a specific task, with energetics only as a secondary concern. For a biped, a locomotor task could be conceived in terms of distance (e.g., between the watering

hole and the grove of fruiting trees) and/or time (e.g., 12 hours of available daylight), but, in fact, it seems as if both are important. Primates are almost universally diurnal, and thus time presents a fixed constraint on primate activity because all nutritional and reproductive requirements must be met in that timeframe. The environment, however, dictates the spatial density of resources (food and others) and hence securing adequate resources mandates that a specific distance be traversed daily in a particular environment. As a result, distance represents a requirement for evolutionary success. This distance/time duality suggests that velocity may be a significant selective pressure on locomotor anatomy, even if evolving to optimize velocity may incur increased energetic costs. Collectively, we propose that selection should act to make a biped as fast as it needs to be to travel the distance that it needs to travel, but no faster, while simultaneously reducing the energy requirements (via either greater economy or efficiency) to the greatest extent possible.

QUANTIFYING TARGETS FOR RESEARCH PURPOSES: WHAT DO WE WANT TO MEASURE AND HOW DO WE MEASURE IT?

Because we have identified velocity and energetic cost as two important aspects of bipedal performance, it is absolutely imperative that these two terms be defined precisely. Velocity is distance traveled divided by time taken and is generally expressed in meters per second. Energetics is more complicated, and we have made a basic distinction (as have others (e.g., Steudel 1994)) between 'energetic economy' and 'energetic efficiency.' Energetic economy is the absolute amount of energy required for an individual to complete a specific task, whether this task be walking from one group of trees to another or sustaining life throughout a day. The total amount of energy needed to perform all tasks during the course of the day is the animal's total daily energy budget (Leonard and Robertson 1997). Economy is generally expressed in units of mechanical (J) or physiological energy (ml O_2).

Energetic efficiency is conceptually the most difficult of the aspects of locomotor performance to understand for two reasons. First, we may speak about two different kinds of efficiency, only one of which we are concerned with here. The kind we are not concerned with could be termed 'physiological efficiency.' The physiological system which transforms nutritional energy (food) into chemical energy, and then into motion, is a complex one and there are many pathways which can be more or less efficient. The lungs can absorb more oxygen in a breath, the blood can carry more oxygen per stroke of the heart, or the muscle fibers can be aligned to produce stronger contractions, to name three possibilities, in one individual than in another. Individuals can also improve their efficiency at a task through practice of it. While physiological efficiency is interesting, important, and certainly a source of variation in locomotor research (especially for humans), here we are concerned with efficiency *sensu strictu*—the ratio of 'energy out' and 'energy in.'

In physics and engineering, mechanical efficiency is defined specifically as the ratio of the work performed divided by the energy input (Meriam 1978). Real-world machines, biological or inanimate, obtain efficiencies of <100%. For instance, muscle fibers can operate with efficiencies of 50% (Heglund and Cavagna 1985). Because the 'energy in' (food) and 'work out' (motion) of biological organisms exist in vastly different forms, the animal's locomotor anatomy and physiology must carry out a complex conversion.

The energy input for locomotion is metabolic energy. Animals consume nutritional energy (food) and convert it to chemical energy (adenosine triphosphate, ATP) which directly powers most biological functions, including muscle contractions. Currently, there is no non-invasive method to determine empirically the energy used by muscles to produce movement. The chemical energy that is used to create motion is, however, generated through a complex molecular process that is most efficient (and sustainable only) in the presence of oxygen. The rate of using metabolic energy is, therefore, often assessed through a proxy of respiration, the volumetric rate of oxygen consumption ($\dot{V}O_2$). Greater oxygen consumption indicates more conversion of nutritional energy to ATP and more use of ATP in muscular action. An important caveat is that movement is not, however, the only muscular activity that uses oxygen. For instance, isometric muscular contractions use oxygen, but do not produce motion.

While metabolic energy is the currency of life and powers locomotion, the purpose of locomotion is to move the body through the environment – a task which can be quantified in terms of mechanical energy. The change in the mechanical energy of a system between time periods is the quantity work. Normally defined as the application of a force through a distance ($W = \int_c F ds$ where W=work, F=ground reaction force in the direction of travel, s=the displacement in the direction of travel: Meriam 1978), work quantifies how much energy must be added to (or taken from) a system to produce the change in position. Mechanical work can be calculated during locomotion using equations of motion, but this is not frequently done because the motion, the masses in motion, and/or the forces acting must be well-defined in time and space and they seldom are.

Due to this lacuna, the displacement in the work integral is assumed to be the distance moved through the environment, while the force is taken to be proportional to the individual's body mass (Steudel 1994). Neither of these assumptions is unreasonable, but they are questionable. One potential problem is that the work integral is dependent upon the path taken. Another is that the (assumed) isometric influence of body mass on ground reaction force may be inaccurate.

By convention in locomotor research, efficiency is expressed as the energy consumed per kilogram per unit distance – which is better known as the cost of transport (CoT). Thus, for the purposes here, we will equate CoT with true efficiency, although we acknowledge that this is speculative. CoT is calculated by dividing the rate of energy consumption (J/s or ml O_2/s) by velocity (m/s) by body mass
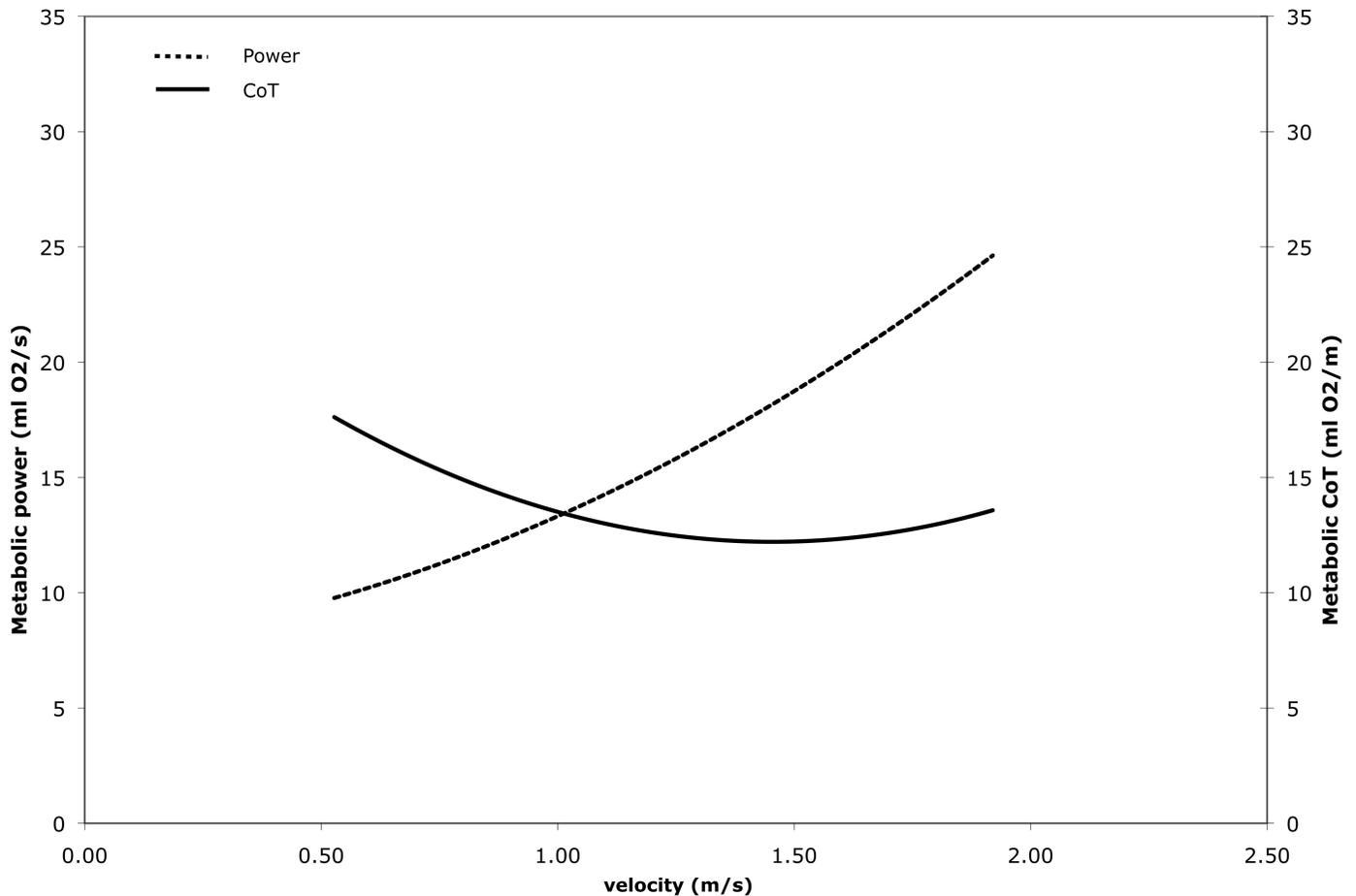
Figure 1. Relationship between velocity and two measures of energetic consumption, power and cost of transport (CoT). Curves represent idealized adult values and were developed from the adult data detailed in Kramer and Sarton-Miller (2008).

(kg). The minimum CoT is the minimum amount of energy that is used to traverse the environment.

VELOCITY, EFFICIENCY, AND ECONOMY: HOW ARE THEY RELATED?

The relationship between velocity and $\dot{V}O_2$ has received a considerable amount of attention for many years (e.g., Booyens and Keatinge 1957; Minetti, et al. 1994; Steudel-Numbers and Tilkens 2004; Taylor et al. 1982; Taylor et al. 1970; Workman and Armstrong 1963; Zuntz and Geppert 1886). Cost of transport can be calculated from $\dot{V}O_2$ as can economy, both of which are useful for comparing among individuals and groups. In most animals (although kangaroos are an exception [Dawson and Taylor 1973]), as an individual increases its velocity, its rate of energy consumption also increases (Figure 1). The relationship between velocity and CoT does not, however, follow this pattern. Within an individual, for a given gait (e.g., walking or running), there exists a velocity with the lowest CoT, or alternatively, the greatest efficiency (Saibene and Minetti 2003).

The relationship between energy and velocity is elucidated more clearly when velocity is portioned into distance and time. As the distance moved during an interval of time increases, the energy consumed increases. The relationship between energy, distance, and time is idealized for an av-

erage person in Figure 2, using data described in Kramer and Sarton-Miller (2008). For example, if this average person has only 2 hours in which to travel 13km, they will do so using ~2750 ml O_2, but if they have 4 hours to make the same journey, they will only use ~2400 ml O_2 (see Figure 2a). A similar comparison can be made for a given distance. For instance, if the individual needs to travel 3.6km, the minimum energetic expenditure (~650 ml O_2) occurs at a time of 3600 sec (see Figure 2b). If the travel distance doubles to 7.2km, energetic expenditure doubles to ~1300 ml O_2 as does the time, to 7200 s. If distance is held constant, an energetically optimal time and, hence, velocity exists (the velocity of minimum CoT), but if time is fixed, there is no optimal distance or velocity.

SIZE AND SHAPE: HOW DO THEY INFLUENCE VELOCITY, EFFICIENCY, AND ECONOMY?

Natural selection can act on velocity and decrease energetic costs by changing the morphological characteristics of the organism, two of the most important of which are **size** and **shape** (Figure 3). Size impacts the life of an organism and the life history of a species through a myriad of characteristics, including such disparate ones as age at maturity and the velocity, economy, and efficiency of locomotion. If the domains of size and shape were orthogonal, their effects
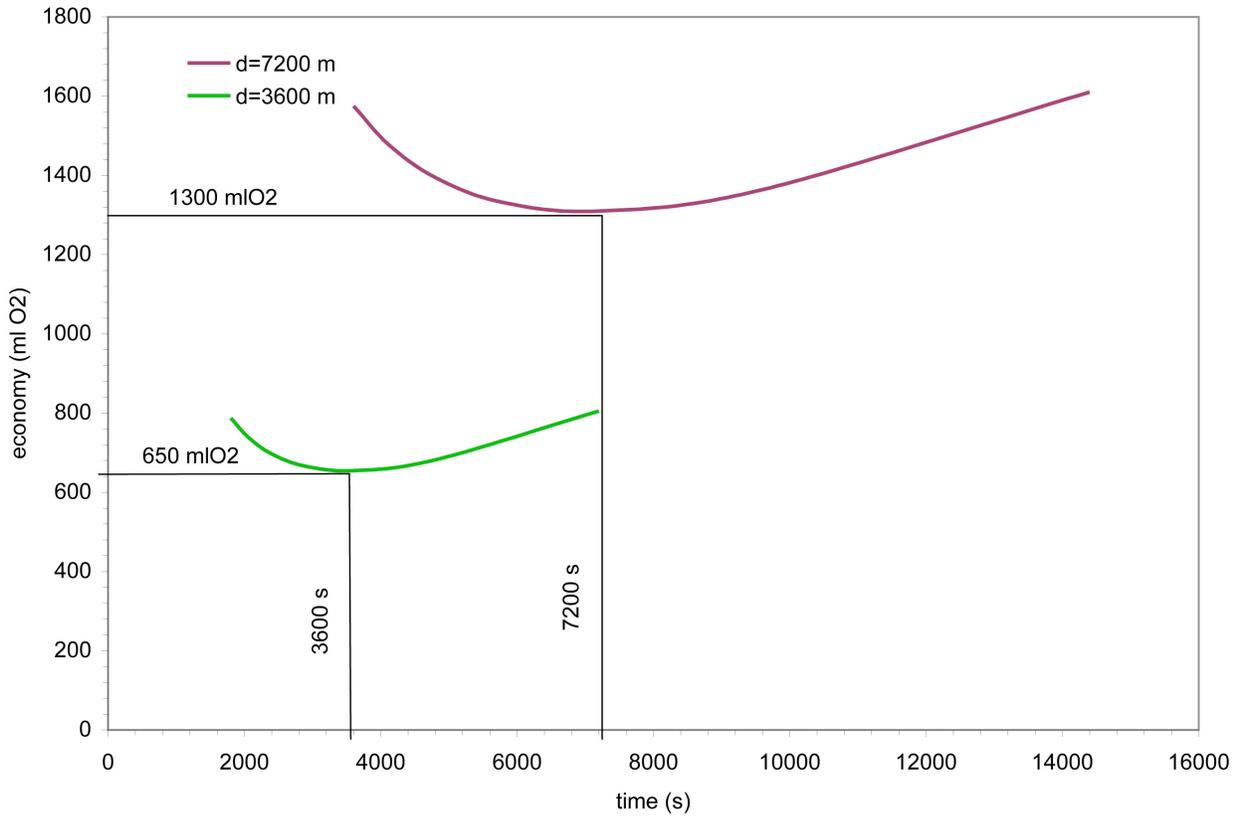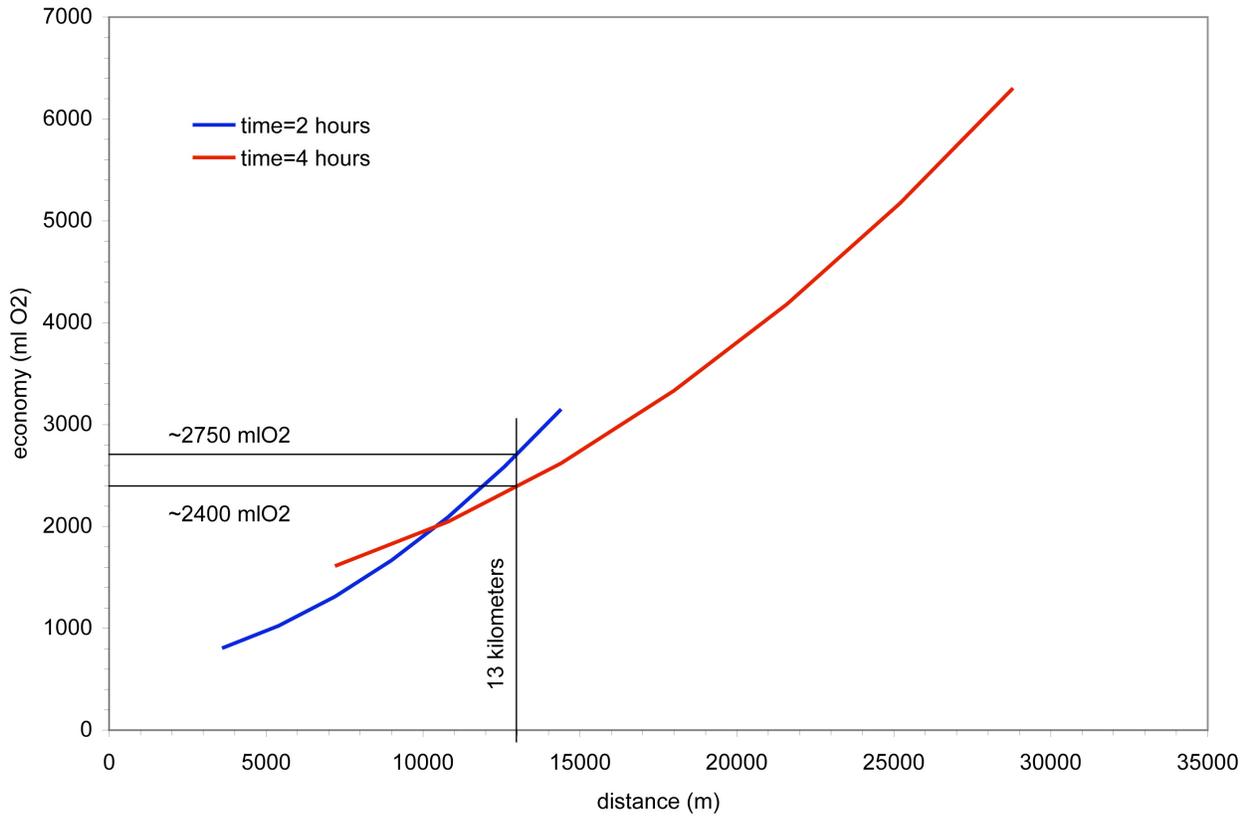
Figure 2. Relationship between energy consumption, time, and distance: top) distance vs. energy; bottom) time vs. energy. Examples given in the text are indicated on the graph. Data for an idealized person that matches the group regression of mass and velocity on metabolic rate from Kramer and Sarton-Miller (2008).
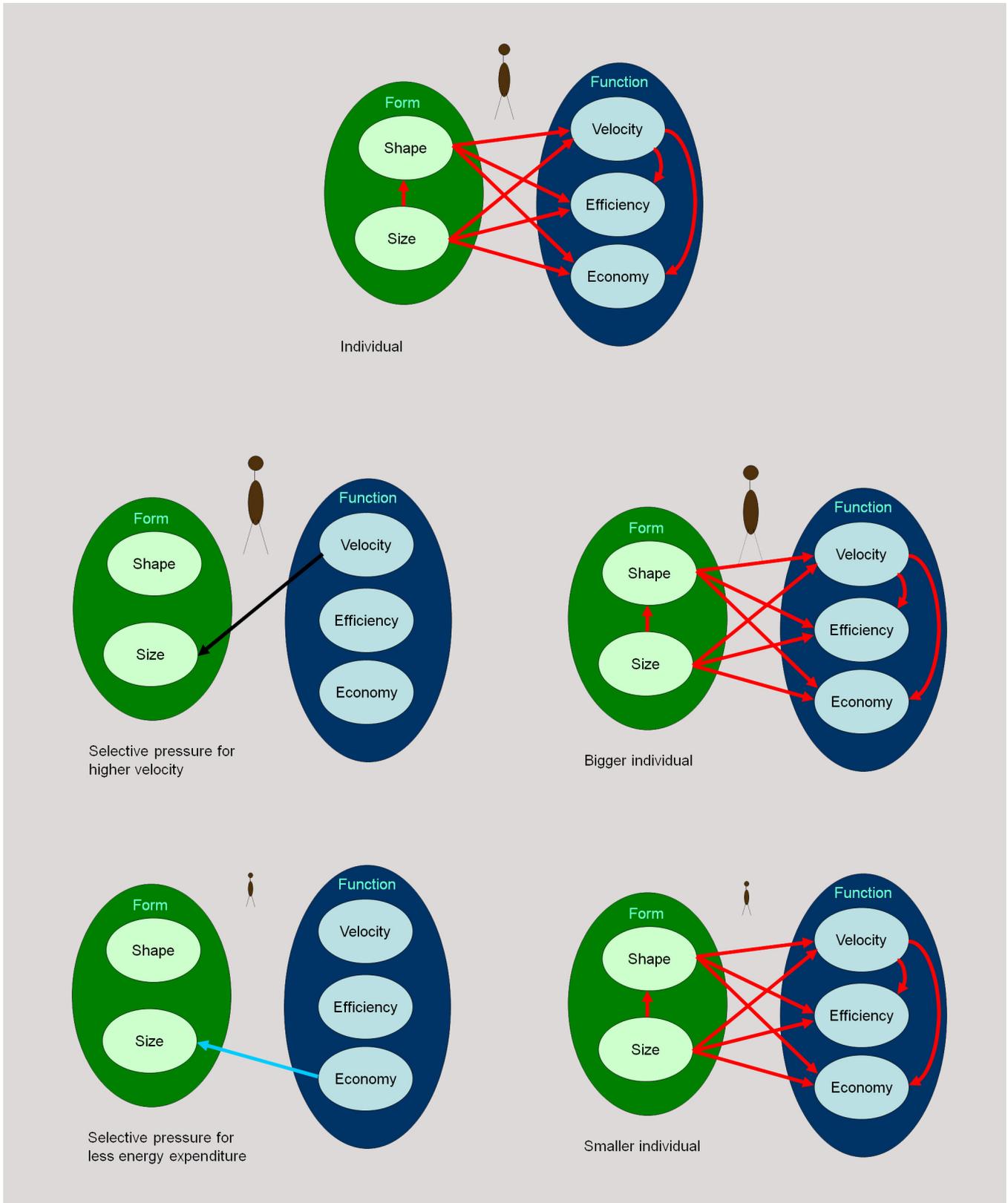
Figure 3. Morphology (size and shape) affects function (velocity, economy, and efficiency) in an individual (red arrows), although the exact nature of the interactions is currently obscure. Through evolutionary time, however, function may dictate morphology. For instance, in a particular environmental context, velocity (black arrow) or economy (blue arrow) may dictate size.

on locomotion would be easier to tease apart. Size, however, frequently impacts shape (i.e., non-isometry) and can, thus, have a secondary influence mediated by shape. The relationship between size and shape (form), on the one hand, and velocity, efficiency, and economy (function), on the other, is further complicated by the fact that velocity impacts efficiency and economy, as is depicted graphically (see Figure 3). These relationships also have a temporal component. For instance, within a given environment and for an individual, form variables are assumed to determine function, but in an evolutionary context, the requirements of function may select for particular forms. Our goal is to examine how size and shape influence velocity, efficiency, and economy in a specific form so that inferences can be made about function among forms.

FUNCTIONAL VARIABLES

SIZE

Size, although an elusive attribute to capture, is generally quantified by volumetric measures (e.g., body mass) or linear ones (e.g., leg length and stature for bipeds). Body mass and linear measures are highly correlated (i.e., heavier animals are often taller), making them difficult to understand independently. Despite their correlation, volumetric and linear aspects of size may exert different influences on function. For instance, body mass appears to affect efficiency (Taylor et al. 1982), while leg length appears to affect stride length and velocity (Alexander and Maloiy 1989).

A method commonly used to circumvent this issue is to compare individuals on a per kilogram of body mass basis. This works for models that are based on mechanical energy calculations (Crompton et al. 1998; Kramer 1999; Willems et al. 1995), because mechanical energy is directly proportional to mass, but may not be valid for metabolic models because it assumes an isometric relationship (mass raised to the exponent 1) between mass and metabolic energy *a priori*. Abundant evidence (e.g., Taylor, et al. 1982) indicates that the exponent is not 1. Rather, heavier animals appear to have lower rates of energy expenditure than would be expected (negative allometry or a mass exponent of <1), but exactly how much lower remains to be determined. In other words, if the exponent for mass-compensated CoT is not 1, what is it?

Researchers have used exponents that range from 0.33–1.0 when exploring the energy expenditure of walking, and no consensus position has yet emerged (e.g., Aull, et al. 2008; Markovic et al. 2007; Steudel-Numbers and Weaver 2006). This is a critical issue because the assumption of the exponent used to normalize for mass determines how volumetric and linear size variables interact statistically. For instance, if we were to use the extremes and the data of Kramer and Sarton-Miller (2008), the exponent on mass determines whether or not shorter-legged individuals use more, less, or the same energy as longer-legged forms when individuals of the same body mass are compared. The predictive equation for $\dot{V}O_2$ divided by body mass is:

$\dot{V}O_2/m = 0.165\text{Velocity} - 0.359\text{LegLength} + 0.357$ ($r^2=0.67$). When $\dot{V}O_2$ is divided by body mass raised to the 0.33 ex-

ponent (to transform a volume measure like body mass to a linear measure: Steudel-Numbers and Weaver 2006), the equation becomes:

$\dot{V}O_2/m^{0.33} = 2.17\text{Velocity} + 2.14\text{LegLength} + 0.279$ ($r^2=0.73$).

(Note that the sign on the coefficient for leg length changes.) This clearly needs further study.

The situation is further complicated because size also influences velocity which influences economy and efficiency. In general, smaller (Alexander and Maloiy 1989), or particularly, shorter–legged, animals move slower than do larger ones (Jungers 1982). For instance, relatively long-legged patas monkeys walk faster (and have commensurately larger day ranges) than do sympatric short-legged vervet monkeys (Isbell et al. 1998). The exact relationship between velocity and size is, however, not known. Larger animals move faster, but how much faster? Or to phrase it a different way: When are animals of different sizes moving at the same velocity *for their body size*. Alexander and Jayes (1983) proposed that, providing that the requirements of dynamic similarity were met, velocity could be made equivalent among animals by using the Froude number: $Fr=v_2/gL$ where v is velocity, g is the gravitational constant, and L is leg length. Comparison among animals from different species with large differences in leg length when traveling at the same Fr has shown that the animals use the same mass-specific energy (Alexander and Jayes 1983), but this result was not obtained when comparing among individuals within a species (*Homo sapiens*) (Kramer and Sarton-Miller 2008; Steudel-Numbers and Weaver 2006). Thus, while it is true that efficiency, economy, and velocity are affected by size parameters, the exact relationships remain unclear. Further, one manifestation of size (e.g., body mass) may affect economy while another affects velocity (e.g., leg length).

Finally, we acknowledge that although size is of fundamental importance to energetics, many other consequences of and selective pressures on body size exist. For instance, the strong positive relationship among daily range, body size (mass), and food requirements is consistent among diet types and most mammalian orders (Carbone et al. 2005) and large size may be protective in times of environmental variability by allowing for periods of fasting (Reynolds 2007). Nonetheless, whatever the causes of size differentials, these differences affect locomotion.

SHAPE

The other factor, shape, is an even more difficult concept to pin down than size, but shape can be conceptualized as the relative size of parts within a whole. Shape can include many characteristics, like the cross-sectional area of the limbs relative to their length, the distribution of fat and fat-free mass within the limb, or the length of the legs relative to that of the trunk. It can also include proportions of elements within limbs (like crural index). Shape affects energy expenditure in complex ways, specific to the particular situation. For instance, we know that changing the distri-

bution of mass such that more mass is positioned distally on a limb increases energy expenditure (Myers and Steudel 1985), but we do not know if changing the relative lengths of the thigh and calf affect locomotor energetics.

The potential importance of shape becomes apparent when we realize that many studies that were designed to study the effect of some measure of size, likely reflect differences in shape as well. Among people, energetic expenditure is predicted by velocity, body mass, and leg length (Kramer and Sarton-Miller 2008; Steudel-Numbers and Tilkens 2004). Longer-legged people use less energy (on a per second or a per meter basis) *if mass and velocity are held constant*. Holding mass and velocity constant, however, may yield skewed results for several reasons. First, comparing people of different leg lengths with the same mass requires a change in shape, potentially conflating the energetic effects of changes in size with those of shape. It is not clear, then, if the effect of "leg length" found by Steudel-Numbers, Kramer and their colleagues was due to length or shape (slender vs. stocky limbs).

Additionally, comparing people of different leg lengths at the same velocity is not equitable. Even though CoT may be virtually the same in people with leg lengths from 0.71–0.92m (Steudel-Numbers and Tilkens 2004), comfortable (and maximum) walking velocity of humans is associated with stature (Bohannon 1997) and, presumably, leg length (Vancata 1991; Webb 1996). The ability of the ankle plantarflexors (*gastrocnemius* and *soleus*) to provide propulsive force (push-off) diminishes near, and may be a trigger of, human gait transition (Neptune and Sasaki 2005). Near gait transition, the plantarflexors operate in an adverse contractile state (shorter lengths and faster shortening velocities leading to lower force production). With shorter tibial length, this adverse condition occurs at lower velocities (Hreljac 1995; Kramer 1998).

The only theoretical method to create equivalent velocities, the Froude number correction (Alexander and Jayes 1983) described above, does not detect individual differences among people (Kramer and Sarton-Miller 2008; Steudel-Numbers and Weaver 2006). Froude number has been reported to compensate for group differences in energy expenditure of humans (DeJaeger et al. 2001; Minetti et al. 2000; Saibene and Minetti 2003), but whether or not this effect was simply the effect of velocity remains unclear (Kramer and Sarton-Miller 2008).

These factors are complex and to our knowledge no empirical and/or modeling effort has attempted to methodically study all using the same techniques. This work would need to be done in an extant group that is amenable to use as research subjects because $\dot{V}O_2$ needs to be assessed. The situation becomes even more difficult when groups that are extinct are the topic of interest. Fossil remains only hint at the possible variation in the factors. Mass and shape can only be estimated using known variation in these parameters in representative extant groups. Only linear size (e.g., bone segment lengths) is readily discernible from the fossil record.

RELEVANCE TO FOSSIL HOMINIDS: WHAT CAN WE SAY ABOUT THE PAST, KNOWING WHAT WE KNOW?

Given all of these caveats, what do we really know and what can we reasonably project? First, of all the determinants of energy expenditure, the only one for which we have direct fossil evidence is size, but even this is only quantified by lengths. Complete bones from which lengths can be determined are (occasionally) found. Femora and tibiae are particularly important for studies of locomotor energetics, because they reflect leg length, but pectoral, pelvic, and rib bones also are important because, if associated with leg bones, their lengths may reflect truncal size.

Other attributes can be predicted from bone parameters using regression formulae developed from extant primate groups. For instance, body mass can be predicted, perhaps relatively well, from long bone metrics (McHenry 1991, 1992; McHenry and Berger 1998; Styne and McHenry 1993), as can stature (Hens et al. 2000). Predicted parameters are problematic, however, because they rely on accepting that the variation in extant groups is the same as that of extinct ones (Smith et al. 1996).

Given this issue, then, it seems most prudent to restrict analyses to parameters that can actually be measured on fossils. So, what about leg length? While fossil femora are rare, fossil tibiae are almost non-existent and few specimens of either are complete or even almost complete. Some trends, however, do emerge from the sparse evidence (Figure 4 and Table 2).

Long bone lengths for fossil specimens attributed to *Orrorin tugenensis* and *Australopithecus (Paranthropus)* sp. are shorter than those of fossil *Homo*, with a few exceptions. The femur of OH-62 falls outside the range of fossil *Homo* (see Figure 4a), but its status in *Homo* has been questioned (Richmond et al. 2002). The femur and tibia attributed to *Homo floresiensis* (see Figures 4a and b), both of which are complete or nearly so, are well outside the range of *Homo sapiens*, including groups with small stature like African Pygmies and Andaman Islanders (Sylvester et al. 2008), but the taxonomic status of *H. floresiensis* is much debated and many aspects of the morphology of *H. floresiensis* are primitive (Jungers et al. 2008).

The femora of AL 333-3, STW 443, and STW 99 fall inside the range of modern humans, while SK 82 and AL 333-4 are the length of the shortest femora of small-statured humans. McHenry (1991) regards the length estimations of AL 333-3, STW 99, and 82 as "…merely rough approximations…" because the length was reconstructed from femoral head diameter. The length attributed to STW 443 is derived from an acetabulum, while that of AL 333-4 is from a distal femoral fragment. Harmon (2005) recently reconstructed the length of AL 333-3, which resulted in a 2cm reduction in length from that produced by using femoral head diameter. Further, the recently described (Harmon 2005) australopithecine femur, AL 827, has a large femoral head, but a reconstructed length of 0.369m.

Whether or not the apparent shift in the length of limb elements at the genesis of *Homo* represents a punctuated
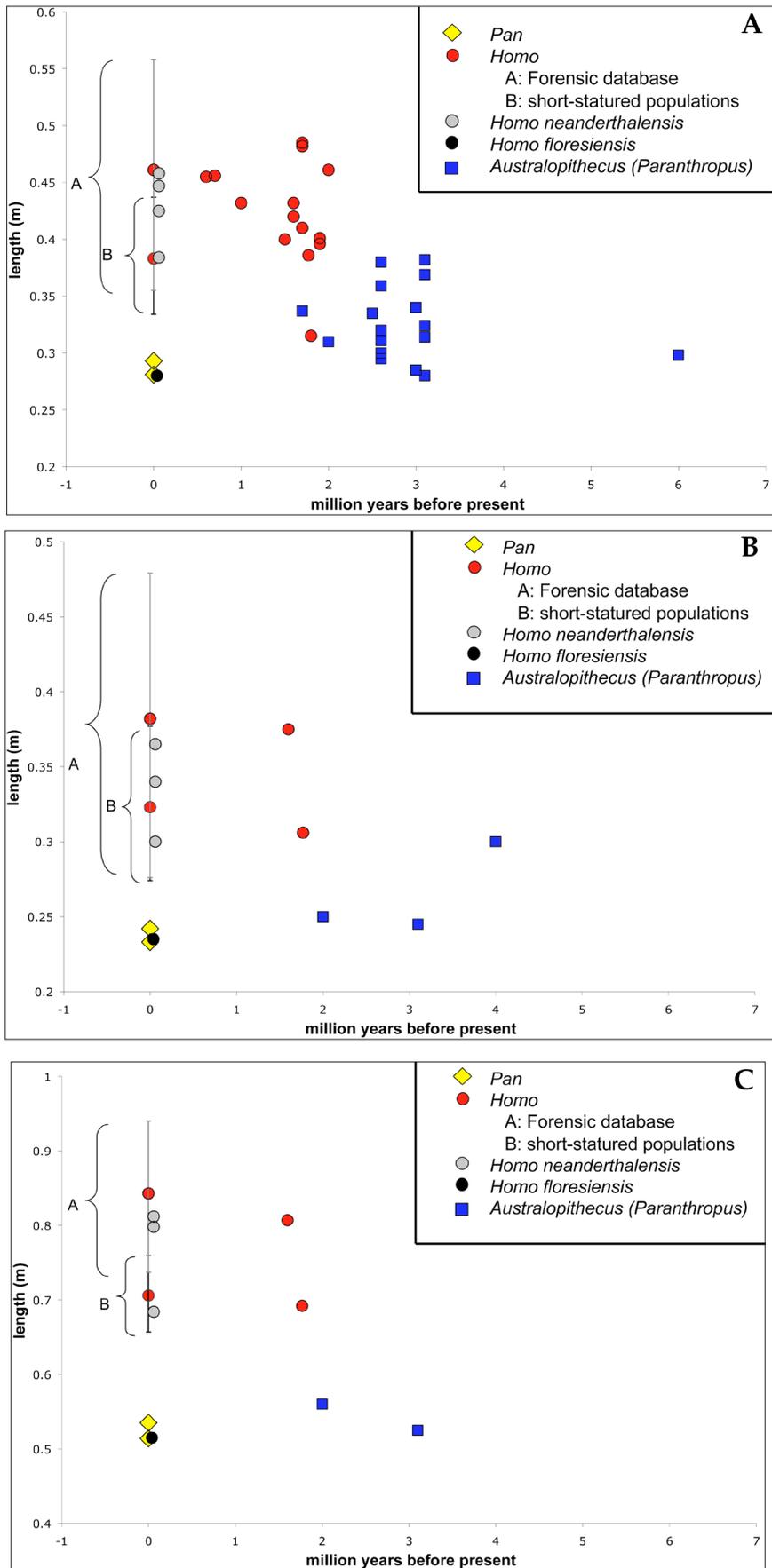
Figure 4. Change in lengths over time: a) femoral length; b) tibial length; c) leg length (=femur + tibia length). Details of fossil specimens are given in Table 1.

TABLE 2. LENGTH OF LOWER LIMB FOSSILS USED IN FIGURE 4.

Description	Date (million yrs before present)	Femoral length (m)	Tibial length (m)	Total length (m)	Source
BAR 1002'00	6	0.298			(Nakatsukasa et al. 2007)
KNM-KP 29283	4		0.3		(Leakey et al. 1995)
AL 288-1	3.1	0.28	0.245	0.525	(Vancata 1991; Webb 1996)
AL 333-4	3	0.34			(Vancata 1991; Webb 1996)
AL 129-1	3	0.285			(McHenry 1991)
STS 14	2.6	0.295			(McHenry 1991)
STW 25	2.6	0.32			(McHenry 1991)
STW 99	2.6	0.38			(McHenry 1991)
STS 392	2.6	0.311			(McHenry 1991)
STW 443	2.6	0.337			(McHenry 1991)
TM 1513	2.6	0.335			(McHenry 1991)
ER 1500	2	0.31	0.25	0.56	(McHenry 1991)
SK 82	1.7	0.337			(McHenry 1991)
BOU-VP-12/1	2.5	0.335			(Asfaw et al. 1999)
AL 333-3	3.1	0.382			(Harmon 2005)
AL 333-142/110/162	3.1	0.314			(Harmon 2005)
AL 827	3.1	0.369			(Harmon 2005)
AL 152-2	3.1	0.324			(Harmon 2005)
ER 3728	2	0.461			(McHenry 1991)
ER 1472	1.9	0.401			(McHenry 1991)
ER 1481	1.9	0.396			(McHenry 1991)
OH 62	1.8	0.315			(McHenry 1991)
D 4167	1.77	0.386	0.306	0.692	(Lordkipanidze et al. 2007)
ER 999	1.7	0.410			(Vancata 1991; Webb 1996)
ER 736	1.7	0.482			(McHenry 1991)
ER 1808	1.7	0.485			(McHenry 1991)
ER 737	1.6	0.42			(McHenry 1991)
WT 15000G	1.6	0.432	0.375	0.807	(McHenry 1991)
ER 803A	1.5	0.4			(McHenry 1991)
OH 34	1.0	0.432			(McHenry 1991)
OH 28	0.7	0.456			(McHenry 1991)
Trinil 3	0.6	0.455			(Day 1986; McHenry 1991)
Shanidar 1	0.06	0.458	0.34	0.798	(Porter 1999)
Shanidar 4	0.06	0.425			(Porter 1999)
Shanidar 5	0.06	0.447	0.365	0.812	(Porter 1999)
Shanidar 6	0.06	0.384	0.3	0.684	(Porter 1999)
LB1	0.038	0.28	0.235	0.515	(Brown, et al. 2004)
short-statured modern	0	0.383	0.323	0.706	(Sylvester et al. 2008)
forensic database	0	0.461	0.382	0.843	(Sylvester et al. 2008)
chimpanzee	0	0.281	0.233	0.514	(Zihlman 1984)
bonobo	0	0.293	0.242	0.535	(Zihlman 1984)

shift from short to long lengths or a gradual increase in leg length is not clear, but by 2mya longer-legged hominids were extant (see Figure 4c) (Jungers 1991). These longer-legged hominids were, presumably, absolutely bigger (heavier, taller) as well, but whether or not their shape was different from the shorter-legged hominids is not fully understood. It is important to note that differences in intermembral indices conflate the effect of arm and leg length, and hence tell little about either because arms and legs can belong to decoupled systems (Sylvester 2006). Arm length has not been shown to have an affect on the locomotor energetics of bipeds.

Also, the recently described pelvis from Gona, Ethiopia (BSN49/P27: Simpson et al. 2008) of *Homo* sp. and innomi-

nate from Jinniushan (Rosenberg et al. 2006) of *Homo erectus* seem to indicate that members of *Homo* could have had pelvic shapes more reminiscent of *Australopithecus* (e.g., laterally flaring ilia, broad bi-iliac breadth for body size) than *Homo sapiens*. The Kebara 2 pelvis (*Homo neanderthalensis*: Rak and Arensburg 1987) is also broad. These pelves stand in contrast to the reconstructed shape of WT-15000 with its more *sapiens*-like, narrower bi-iliac breadth (Brown et al. 1985), but this reconstruction has been questioned (Ruff 1995). Whether or not pre-*sapiens* forms exhibited modern pelvic shape in the presence of relatively long legs remains to be determined.

Given our ignorance of the effect of shape differences on locomotor parameters, size differences appear to be the

only variable of which much can be made. Three groups become apparent, each presumably adapted to particular environmental contexts—australopithecine, hominine, and *H. floresiensis*. If leg length (linear size) is indicative of velocity and, hence, daily journey, then these groupings may reveal environmental adaptation. Island habitats, like that of *H. floresiensis,* are likely dominated by smaller size and reduced mobility, i.e., small daily ranges. If small size in *H. floresiensis* is dictated by reduced reliance on far-flung resources, then this provides some support for the notion that the australopithecine group is associated with small daily ranges (Kramer and Eck 2000). The larger hominine group seems adapted to larger daily ranges.

But what are the energetic consequences of the difference in size among the groups, of differences in leg length? Steudel-Numbers and Tilkens (2004) used empirical results from modern humans to conclude that the beneficial effect of longer legs apparent at a particular velocity could have compensated for the increase in energetic expenditure associated with the increased body mass for early *Homo* over australopithecines. Because average size differences among species of *Homo* are similar to those among individuals in *H. sapiens* (Steudel-Numbers and Tilkens 2004), their empirical equation may be reasonable for comparison among species in *Homo*. The Gona and Jinniushan pelves complicate this extrapolation, though, because they indicate that trunk shape in pre-*sapiens Homo* may have differed from that of modern people. Comparisons across genera are even more problematic than those within because more shape differences exist. An empirical equation that explains intraspecific size and shape variation may not be predictive of variation at higher taxonomic levels.

Of particular concern to the question of how size affects locomotor energetics is the question of how to address the effect of body mass on energetics. As discussed above, increasing body mass increases the energy used to move, but the relationship is not isometric. Creating mass-specific versions of $\dot{V}O_2$ has been popular because they allow for a 2-dimensional representation (velocity vs. mass-specific $\dot{V}O_2$) of a 3-dimensional problem (velocity vs. $\dot{V}O_2$ vs. mass), but their creation assumes a relationship between mass and $\dot{V}O_2$ that has not been established. Given that shape varies among individuals and that we do not yet know how to compensate for body mass, relationships between size and $\dot{V}O_2$ of humans are difficult to extrapolate to non-human species with any degree of certainty. If metabolic comparisons between extant and extinct species are not appropriate, then mechanically-based ones are the only option currently available to explore the consequences of size differences. We fully acknowledge that mechanically-based models are themselves fraught with difficulties if the goal is to determine absolute levels of energetic expenditure. Mechanical models are, however, well-suited to the task of comparing between configurations, to begin to understand the effect of changing size and shape parameters on economy, efficiency and velocity.

In mechanical calculations when shape is held constant and equivalent tasks are compared (i.e., when comparisons are made between dynamically similar animals moving are equal Fr), size as quantified by leg length does not have an effect on mass-specific CoT (Alexander and Jayes 1983). Obviously, larger individuals use more absolute energy to move a given distance because they move more mass, so they are less economical (Steudel 1994). Larger individuals with their longer legs can move faster than smaller ones, and when compared while moving *at the same velocity*, larger individuals have a lower mass-specific mechanical CoT (higher efficiency) than smaller ones. Nonetheless, larger animals use more energy in absolute terms (less economical) even when traveling at the same velocity.

To restate, size as measured by leg length and/or body mass does not affect CoT, which is generally accepted to be reflective of efficiency, when dynamically similar animals (i.e., shape is held constant) are compared using mechanical models. Individuals in larger species use more energy (are less economical) but can travel at higher velocities than those in smaller species. All other constraints being equal, size appears to be a trade-off between economy and velocity.

CONCLUSION

Function (economy, efficiency, and velocity) is inextricably linked to form, as expressed in terms of size and shape, but the relationship is labyrinthine. Energetic expenditure can be modeled using techniques that exploit empirical or theoretical methods, but none of these approaches fully captures how energetic expenditure varies within or among species at a particular, or through evolutionary, time. Empirical methods, such as measuring $\dot{V}O_2$, provide insights about differences that exist among extant species, but lack the refinements necessary to be extrapolated to extinct groups. Mechanical techniques, such as those that exploit motion or force production calculations, are useful in comparing among idealized morphologies, but cannot yet predict absolute levels of energetic expenditure.

Form, too, is imperfectly understood. That size in the most general sense strongly affects energetic expenditure seems clear, but exactly how size should be represented (which combination of lengths and masses) is not understood. Comprehending the relationship between shape and energetic expenditure is in its infancy. Further complicating these issues is the pragmatic problem that extinct animals are often represented by fossils that only give a measure of length.

 Given those caveats, comparisons between different, but evolutionary stable, forms of hominid bipedalism suggest that velocity, and its relationship to day journey, is an important factor shaping bipedal adaptation. We believe that small non-modern hominid species, i.e., *Homo floresiensis* and *Australopithecus (Paranthropus)* sp., are small because they did not need to be big in order to walk fast and go far. Their size makes them neither transitional nor compromised nor inefficient. Rather, it reflects adaptation to their environment.

REFERENCES

Alexander, R.M. and A.S. Jayes. 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *Journal of Zoology London* 201: 135–152.

Alexander, R.M. and G. Maloiy. 1989. Locomotion of African mammals. *Symposia of the Zoological Society of London* 61:163–180.

Asfaw, B., T. White, O. Lovejoy, B. Latimer, S. Simpson, and G. Suwa. 1999. *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* 284(5414): 629–635.

Aull, J.L., D.A. Rowe, R.C. Hickner, B.M. Malinauskas, and M.T. Mahar. 2008. Energy expenditure of obese, overweight, and normal weight females during lifestyle physical activities. *International Journal of Pediatric Obesity* 3(3): 177–185.

Bohannon, R. W. 1997. Comfortable and maximum walking speed of adults aged 20-79 years: reference values and determinants. *Age Ageing* 26(1): 15–19.

Booyens, J. and W.R. Keatinge. 1957. The expenditure of energy by men and women walking. *Journal of Physiology* 138(2): 165–171.

Bramble, D.M. and D.E. Lieberman. 2004. Endurance running and the evolution of *Homo*. *Nature* 432(7015): 345–352.

Brown, F., J. Harris, R. Leakey, and A. Walker. 1985. Early *Homo erectus* skeleton from west Lake Turkana, Kenya. *Nature* 316(6031): 788–792.

Brown, P., T. Sutikna, M.J. Morwood, R.P. Soejono, Jatmiko, E.W. Saptomo and R.A. Due. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431(7012): 1055–1061.

Carbone, C., G. Cowlishaw, N.J. Isaac and J.M. Rowcliffe. 2005. How far do animals go? Determinants of day range in mammals. *American Naturalist* 165(2): 290–297.

Collard, M. and B. Wood. 1999. Grades among the African early hominids. In *African Biogeography*, edited by T. Bromage and F. Schrenk, pp. 316–327. Oxford Press, New York.

Crompton, R.H., L. Yu, W. Weijie, M. Gunther, and R. Savage. 1998. The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in *Australopithecus afarensis*. *Journal of Human Evolution* 35(1): 55–74.

Dawson, T.J. and C.R. Taylor. 1973. Energetic cost of locomotion in kangaroos. *Nature* 246: 313–314.

Day, M. 1986. *Guide to Fossil Man*. 4th ed. University of Chicago Press, Chicago.

DeJaeger, D., P.A. Willems and N.C. Heglund. 2001. The energy cost of walking in children. *Pflugers Archive European Journal of Physiology* 441(4): 538–543.

Foley, R. 1992. Evolutionary ecology of fossil hominids. In *Evolutionary ecology and human behavior*, edited by E. Smith and B. Winterhalder, pp. 131–164. Aldine de Guyter, New York.

Harmon, E. 2005. *A comparative analysis of femoral morphology in Australopithecus afarensis: implications for the evolution of bipedal locomotion*, PhD dissertation, University of Arizona.

Heglund, N.C. and G.A. Cavagna. 1985. Efficiency of vertebrate locomotory muscles. *Journal of Experimental Biology* 115: 283–292.

Hens, S.M., L.W. Konigsberg, and W.L. Jungers. 2000. Estimating stature in fossil hominids: which regression model and reference sample to use? *Journal of Human Evolution* 38(6): 767–784.

Hreljac, A. 1995. Determinants of the gait transition speed during human locomotion: kinematic factors. *Journal of Biomechanics* 28(6): 669–677.

Hunt, K.D. 1994. The evolution of human bipedality: ecology and functional morphology. *Journal of Human Evolution* 26: 183–202.

Isbell, L. A., J.D. Pruetz, M. Lewis, and T.P. Young. 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. *American Journal of Physical Anthropology* 105(2): 199–207.

Jungers, W.L. 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297: 676–678.

Jungers, W.L. 1991. *A pygmy perspective on body size and shape in Australopithecus afarensis (AL 288-1, "Lucy")*. CNRS, Paris.

Jungers, W.L., S.G. Larson, W. Harcourt-Smith, M.J. Morwood, T. Sutikna, R. Awe Due, and T. Djubiantono. 2008. Descriptions of the lower limb skeleton of *Homo floresiensis*. *Journal of Human Evolution* 57: 538–554.

Kramer, P.A. 1998. *Locomotor energetics and leg length in hominid evolution*, PhD dissertation, University of Washington.

Kramer, P.A. 1999. Modelling the locomotor energetics of extinct hominids. *Journal of Experimental Biology* 202(Pt 20): 2807–2018.

Kramer, P.A. and G.G. Eck. 2000. Locomotor energetics and leg length in hominid bipedality. *Journal of Human Evolution* 38(5): 651–666.

Kramer, P.A. and I. Sarton-Miller. 2008. The energetics of human walking: Is Froude number (Fr) useful for metabolic comparisons? *Gait and Posture* 27: 209–215.

Leakey, M.G., C.S. Feibel, I. McDougall, and A. Walker. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376(6541): 565–571.

Leonard, W.R. and M.L. Robertson. 1997. Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology* 102(2): 265–281.

Lordkipanidze, D., T. Jashashvili, A. Vekua, M.S. Ponce de Leon, C.P. Zollikofer, G.P. Rightmire, H. Pontzer, R. Ferring, O. Oms, M. Tappen, M. Bukhsianidze, J. Agusti, R. Kahlke, G. Kiladze, B. Martinez-Navarro, A. Mouskhelishvili, M. Nioradze, and L. Rook. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449(7160): 305–310.

Markovic, G., V. Vucetic and A.M. Nevill. 2007. Scaling behaviour of VO2 in athletes and untrained individuals.

Annals of Human Biology 34(3): 315–328.

McHenry, H.M. 1991. Femoral lengths and stature in Plio-Pleistocene hominids. *American Journal of Physical Anthropology* 85(2): 149–158.

McHenry, H.M. 1992. Body size and proportions in early hominids. *American Journal of Physical Anthropology* 87(4): 407–431.

McHenry, H.M. and L.R. Berger. 1998. Body proportions of *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *Journal of Human Evolution* 35(1): 1–22.

Meriam, J. 1978. *Dynamics*. John Wiley and Sons, New York.

Minetti, A.E., L.P. Ardigo, F. Saibene, S. Ferrero, and A. Sartorio. 2000. Mechanical and metabolic profile of locomotion in adults with childhood-onset GH deficiency. *European Journal of Endocrinology* 142(1): 35–41.

Minetti, A.E., F. Saibene, L.P. Ardigo, G. Atchou, F. Schena and G. Ferretti. 1994. Pygmy locomotion. *European Journal of Applied Physiology and Occupational Physiology* 68(4): 285–290.

Myers, M.J. and K. Steudel. 1985. Effect of limb mass and its distribution on the energetic cost of running. *Journal of Experimental Biology* 116: 363–373.

Nakatsukasa, M., M. Pickford, N. Egi, and B. Senut. 2007. Femur length, body mass, and stature estimates of *Orrorin tugenensis*, a 6 Ma hominid from Kenya. *Primates* 48(3): 171–178.

Neptune, R. R. and K. Sasaki. 2005. Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *Journal of Experimental Biology* 208(Pt 5): 799–808.

Pontzer, H. and R.W. Wrangham. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *Journal of Human Evolution* 46(3): 317–335.

Porter, A. 1999. Modern Human, Early Modern Human and Neanderthal Limb Proportions. *International Journal of Osteoarchaeology* 9: 54–67.

Rak, Y. 1991. Lucy's pelvic anatomy: its role in bipedal gait. *Journal of Human Evolution* 20: 283–290.

Rak, Y. and B. Arensburg. 1987. Kebara 2 Neanderthal pelvis: first look at a complete inlet. *American Journal of Physical Anthropology* 73(2): 227–231.

Reynolds, S.C. 2007. Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa. *Journal of Human Evolution* 53(5): 528–548.

Richmond, B.G., L.C. Aiello and B.A. Wood. 2002. Early hominin limb proportions. *Journal of Human Evolution* 43(4): 529–548.

Rodman, P.S. and H.M. McHenry. 1980. Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology* 52(1): 103–106.

Rosenberg, K.R., L. Zune, and C.B. Ruff. 2006. Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proceedings of the National Academy of Sciences USA* 103(10):

3552–3556.

Ruff, C.B. 1995. Biomechanics of the hip and birth in early *Homo*. *American Journal of Physical Anthropology* 98(4): 527–574.

Saibene, F. and A.E. Minetti. 2003. Biomechanical and physiological aspects of legged locomotion in humans. *European Journal of Applied Physiology* 88(4–5): 297–316.

Simpson, S.W., J. Quade, N.E. Levin, R. Butler, G. Dupont-Nivet, M. Everett, and S. Semaw. 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322(5904): 1089–1092.

Smith, R., G. Albrecht, J. Damuth, M. Di Bacco, M. Fortelius, P. Gingerich, L. Godfrey, M. Sutherlund, W. Jungers, S. Leigh, and M. Leney. 1996. Biology and Body size in human evolution: statistical inference misapplied. *Current Anthropology* 37: 451–481.

Stanford, C.B. 2006. Arboreal bipedalism in wild chimpanzees: implications for the evolution of hominid posture and locomotion. *American Journal of Physical Anthropology* 129(2): 225–231.

Steudel, K. 1994. Locomotor energetics and hominid evolution. *Evolutionary Anthropology* 1: 42–48.

Steudel-Numbers, K.L. and M.J. Tilkens. 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *Journal of Human Evolution* 47(1–2): 95–109.

Steudel-Numbers, K.L. and T. Weaver. 2006. Froude Number Corrections in Anthropological Studies. *American Journal of Physical Anthropology* 131: 27–32.

Styne, D.M. and H. McHenry. 1993. The evolution of stature in humans. *Hormone Research* 39 (Supplement 3): 3–6.

Sylvester, A. 2006. *The Decoupling Hypothesis: a new theory for the origin of hominid bipedalism.* PhD, University of Tennessee.

Sylvester, A., P. Kramer, and W. Jungers. 2008. Modern humans are not (quite) isometric. *American Journal of Physical Anthropology* 137: 371–383.

Taylor, C.R., N.C. Heglund, and G.M. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* 97: 1–21.

Taylor, C.R., K. Schmidt-Nielsen, and J. Raab. 1970. Scaling of energetic cost of running to body size in mammals. *American Journal of Physiology* 219(4): 1104–1107.

Vancata, V. 1991. The roots of hominid bipedality. In *Origine(s) de la bipedie chez les hominides*, edited by Y. Coppens and B. Senut, pp. 143–158, Editions du CNRS, Paris.

Ward, C.V. 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *American Journal of Physical Anthropology* Supplement 35: 185–215.

Webb, D. 1996. Maximum walking speed and lower limb length in hominids. *American Journal of Physical Anthropology* 101(4): 515–525.

Willems, P.A., G.A. Cavagna, and N.C. Heglund. 1995. External, internal and total work in human locomotion.

Journal of Experimental Biology 198(Pt 2): 379–393.

Wood, B. and D. Strait. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* 46(2): 119–162.

Workman, J.M. and B.W. Armstrong. 1963. Oxygen cost of treadmill walking. *Journal of Applied Physiology* 18: 798–803.

Wrangham, R. 1980. Bipedal locomotion as a feeding adaptation in Gelada baboons, and its implications for hom-

inid evolution. *Journal of Human Evolution* 9: 329–331.

Zihlman, A. 1984. Body mass and tissue composition in *Pan paniscus* and *Pan troglodytes*, with comparisons to other hominoids. In *The Pygmy Chimpanzee Evolutionary Biology and Behavior*, edited by R. Susman. Plenum Press, New York.

Zuntz, N. and G. Geppert. 1886. Ueber die Natur der normalen Athemreize und den Ort ihrer Wirkung. *European Journal of Applied Physiolpgy* 38: 337–338.