

Role of Locomotor Economy in the Origin of Bipedal Posture and Gait

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It was recently argued (Leonard and Robertson, 1995, 1997) that there are significant differences between human males and females in the energetic cost of locomotion (or transport), and that human females in particular reap a great energetic savings as compared to a typical quadruped. This purported difference is used to bolster the idea that the energetic advantages of human, particularly female, locomotion might have been important in the origin of bipedality. Discussions of this topic rely heavily on measurements of the energetic cost of locomotion in a variety of mammals compiled by a number of authors. Work on this subject is based on the fact that ongoing submaximal locomotion is usually powered almost entirely by ATP generated by aerobic pathways. Experimenters consequently measure the rate of oxygen consumed by a subject under a variety of locomotor conditions, often on a treadmill. Protocols usually contain elements that ensure that locomotion will be fueled aerobically (e.g., Taylor et al., 1982). Often the cost of a given locomotor activity is simply reported in ml O₂, or, alternately, converted to Joules or Kcal. The cost of an activity can be expressed as a rate, called the "cost of locomotion," i.e., the cost to engage in the activity for a particular amount of time. It is also common to report instead the cost to travel a particular distance, called the "cost of transport." It has been demonstrated that the amount of energy that an animal consumes in traveling is highly dependent on its mass (for a summary, see Taylor et al., 1982). Larger animals typically expend a greater total number of calories because they are doing more work (moving a greater mass). On the other hand, the cost per kilogram of body mass is typically smaller in a larger animal, and this reduction has been well-documented (e.g., Taylor et al., 1982). Because body mass is rarely a constant in most interesting comparisons of locomotor energetics, nearly all studies involving comparisons of locomotor costs have reported the cost per kilogram.

Leonard and Robertson (1995, 1997) cite data that they believe have been "recently synthesized by the World Health Organization" (FAO/WHO/UNU, 1985). In fact, the findings on locomotor energetics in that publication are based exclusively on a much

earlier synthesis (McDonald, 1961, see footnote on p. 184). That early work had the benefit of a very large sample size. Its disadvantage, however, is that the sample was drawn from a wide variety of still earlier works in which a number of methodologies were used. Some studies used Douglas bags for collecting all expired gases (closed circuit), while others used open circuit techniques. Some protocols involving Douglas bags required subjects to carry equipment while their cost of locomotion was determined; in other protocols, the equipment was carried in some other manner (McDonald, 1961). Thus the data from the many previous studies were not always comparable. As McDonald (1961) points out, it was not always clear whether the weights given for subjects were for the subject alone or whether it included the weight of the equipment carried by some subjects in some of the protocols. Thus the potential for error was substantially greater than in a study conducted under a single experimental protocol in a single laboratory. Leonard and Robertson (1995, 1997) appear to be unaware that there has been considerable discussion in the 40 years since the work by McDonald (1961) on the question of gender differences in locomotor energetics. Numerous studies have been done using experimental designs very much more carefully controlled than that of McDonald (1961), in that male and female subjects in each study had their costs measured using the same experimental protocol. These have resulted in other conclusions.

The vast majority of recent studies on gender differences in the cost of human walking have reported that there is no difference between the sexes in the cost/kg (Bhambhani and Singh, 1985, 12 males, 12 females; Miller and Stamford, 1987, 4 males, 3 females; Waters et al., 1988, 39 adult males, 34 adult females; Pivarnik and Sherman, 1990, 12 males, 12 females; Zamparo et al., 1992, 6 males, 3 females; Sherman, 1998, 22 males, 22 females). These studies

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TABLE 1. Cost for a 60-kg animal to walk 1 km ($ml O_2$) and the percentage difference between the cost for humans and that of an average quadruped (%)

Speed (km/hr)	Humans						"Average quadruped," Taylor et al., 1982, Cost
	Cotes and Meade (1960)		Margaria et al. (1963)		McDonald (1961)		
	Cost	%	Cost	%	Male and female average cost	%	
5.0	10,175.2	81.2	10,378.7	82.9	10,179.5	81.3	12,524.9
6.0	10,052.4	84	10,808.0	90.7	10,643.4	89.4	11,910.7
6.5	11,113.0	95	10,107.7	86.6	11,064.5	94.7	11,677.7

were much more carefully controlled than McDonald (1961), in that males and females were subjected to the same experimental protocols. Though McDonald (1961) pooled data from more than 30 studies resulting in a total sample of 333 males and 58 females, only five studies included both male and female subjects. One of these had a very small sample size (3 males and 2 females). Only one of the remaining four articles (Booyens and Keatinge, 1957) concluded that there was any difference between males and females in the mass-specific cost of locomotion. The others concluded that cost was the same in males and females. Ralston (1958) attributed this difference to inadequacies in the Douglas bag system used in Booyens and Keatinge (1957). Similarly, studies on adolescent humans have revealed no significant gender differences in their locomotor costs/kg (Ariens et al., 1997, 84 males, 98 female; Walker et al., 1999, 47 males, 35 females). Two studies (Howley and Glover, 1974; Falls and Humphrey, 1976) actually reported higher costs per kilogram for walking in human females than in human males (the opposite of the pattern reported by McDonald, 1961), although Falls and Humphrey (1976) doubted that their small observed difference was real. Thus the suggestion by Leonard and Robertson (1995, 1997) that there would have been gender differences in the locomotor economy of early hominids is contradicted by a wide range of recent work.

Studies of human running have produced very different results from those on walking. Although one early study reported no difference in the cost/kg of running in human males and females (Mayhew et al., 1979), later work has shown human females to have higher costs/kg to run than their male counterparts (Helgerud et al., 1990; Daniels and Daniels, 1992).

Just how energetically favorable is human walking compared to that of the average quadruped? Table 1 presents values for the energetic cost for a 60-kg human to walk 1 km at a variety of walking speeds, using data from three different studies. Table 1 also includes the cost for an average quadruped to walk at the same speeds and distance, based on the equation in Taylor et al. (1982), and the percentage difference of each human estimate from the generalized quadrupedal estimate. The choice of speeds was guided by two studies that allowed human subjects to select their own preferred walking speeds.

Bhambhani and Singh (1985) asked subjects (12 males and 12 females) walking on a treadmill to choose the "most comfortable" speed. The average values for females was 4.6 km/hr, and 4.89 km/hr for males. Booyens and Keatinge (1957) asked free walking human subjects (10 males and 10 females) to select the speeds at which they would choose to walk a) "leisurely" and b) "to catch a bus." The average values for females were a) 5.44 km/hr and b) 6.48 km/hr. Average values for males were a) 5.52 km/hr and b) 6.52 km/hr. As can be seen from Table 1, human walking costs only between 81.2–94.7% (average, 87.3%) that of an generalized quadruped of the same size moving at the same speed. That modern human walking is relatively economical is well-established (see also Alexander, 1991; Steudel, 1996).

All the above comparisons are between various estimates of the cost of human walking and estimates for a "generalized" or "average" quadruped. This convention ignores the fact that quadrupedal species vary considerably in their locomotor costs and economy. Many species of quadrupedal mammals have energetic costs of locomotion that are also very substantially below the average. To put the economy of human walking into a broad mammalian context, I took the average percentage savings for human locomotion given above and asked how many of the quadrupedal eutherian species that have been studied (Taylor et al., 1982) show the same or greater energetic savings. Sixteen (30%) of the 53 eutherians reported by Taylor et al. (1982) had locomotor costs as low as or lower than humans. Seen in this broad mammalian context, the economy of modern human walking is not particularly remarkable. Modern humans can move with considerable efficiency, but so can a great many quadrupeds. Selection for more economical locomotion does not have to involve bipedality, and usually does not. This suggests that some other factor(s) must have been important in leading our ancestors to adopt bipedality.

Finally, it is important to bear in mind in discussions of the origin of bipedalism, that the animal becoming erect was a quadruped with adaptations for quadrupedal locomotion. To suppose that a quadrupedally adapted primate would suddenly reap all the energetic advantages present in a species that has been bipedal for millions of years seems highly improbable. The bipedality of modern *H. sapiens* is

simply not equivalent to the bipedality of the ancestral quadrupedally adapted hominoid.

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