



The energetic cost of locomotion: humans and primates compared to generalized endotherms

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Abstract

A wide range of selective pressures have been advanced as possible causes for the adoption of bipedalism in the hominin lineage. One suggestion has been that because modern human walking is relatively efficient compared to that of a typical quadruped, the ancestral quadruped may have reaped an energetic advantage when it walked on two legs. While it has become clear that human walking is relatively efficient and human running inefficient compared to “generalized endotherms”, workers differ in their opinion of how the cost of human bipedal locomotion compares to that of a generalized primate walking quadrupedally. One view is that human walking is particularly efficient in comparison to other primates. The present study addresses this by comparing the cost of human walking and running to that of the eight primate species for which data are available and by comparing cost in primates to that of a “generalized endotherm”. There is no evidence that primate locomotion is more costly than that of a generalized endotherm, although more data on adult Old World monkeys and apes would be useful. Further, human locomotion does not appear to be particularly efficient relative to that of other primates.

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Introduction

The earliest recognizable human traits to appear in the hominin lineage were the stigmata of erect bipedal posture and locomotion. While the exact form of locomotion that characterized the common ancestor of our lineage and that of the African apes is unknown, it is universally accepted as being some form of quadrupedalism

(see Richmond et al., 2001 for a recent review). Identifying the selective pressures that led to this shift in locomotor mode from the quadrupedalism characteristic of prehomnins would elucidate the origin of the human adaptation. What selective influences might have led our early ancestors to adopt this unique form of locomotion?

A wide range of possible scenarios have been posited and discussed in the literature, but none has emerged as compelling (Hunt, 2001). These include bipedal displays (e.g. Jablonski and Chaplin, 1993), thermoregulatory advantages, (e.g.

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Wheeler, 1991, 1992), food carriage (e.g. Lovejoy, 1981), tool carriage (e.g. Washburn, 1967), small object feeding (e.g. Jolly, 1970; Hunt, 1996), vigilance (e.g. Dart, 1959; Day, 1977), and energetic efficiency (e.g. Rodman and McHenry, 1980). (See Rose, 1991, for an excellent review.) The present study contributes to the discussion of whether selection for energetic efficiency was an important factor in the origin of bipedality.

It has become clear that human walking is inexpensive and human running is usually expensive compared to that of a typical quadruped (Steudel, 1994, 1996). There is, however, no consensus on the efficiency of human locomotion compared to that of other primates. Rodman and McHenry (1980) compared the cost of human walking to that of chimpanzees and concluded that human walking is considerably cheaper. Jablonski and Chaplin (1993), on the other hand, looked at the cost of human locomotion compared to that of the patas monkey and concluded that “no special advantage can be identified for human bipedalism over primate quadrupedalism.” Leonard and Robertson (1997, 2001) have argued that human bipedalism is efficient relative to the quadrupedalism of primates generally based on the primate cost equation developed by Taylor et al. (1982). The present study addresses the energetics of human locomotion based on a variety of studies and puts it in the context of a broad sample of primates and of birds and mammals to attempt to clarify this discussion. The cost of locomotion in primates is also compared to that of “generalized endotherms”.

The data

The data on which these discussions are based are measurements of the energetic cost of locomotion in a variety of mammals. Because ongoing submaximal locomotion is usually powered almost entirely by ATP generated by aerobic pathways, experimenters measure the rate of oxygen consumed by a subject under a variety of locomotor conditions, usually on a treadmill. Often the cost of a given locomotor activity is simply reported in milliliters of oxygen, or converted to Joules

or kilocalories. The cost of an activity can be expressed as a rate, called the “cost of locomotion”—the cost to engage in the activity for a particular amount of time. Other authors focus instead on 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 (e.g. Taylor et al., 1982). While larger animals expend a greater total number of calories because they are doing more work (moving a greater mass), 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.

The baseline expectation for the cost of locomotion or cost of transport are based on data on 62 mammalian and avian species, including eight primate species, summarized by Taylor et al. (1982). The equations describing the relationship between cost and speed for each species are presented in their Table 1. They also developed a general equation (their Eq. (9)) summarizing the relationship of energetic cost of locomotion in relation to speed and body mass across their entire sample that I use here. I will refer to predictions from this equation as being for the generalized endotherm. The available primate data are from a variety of sources (Taylor and Rowntree, 1973; Parsons and Taylor, 1977; Mahoney, 1980; Taylor et al., 1982). Values for human locomotion were obtained from a variety of studies and graphed individually to allow an evaluation of consistency. Only estimates of cost from studies whose designs produced steady-state values at a variety of speeds and where subject mass was taken into account were chosen. Publications combining results from a variety of previously published works were excluded. I included some of the older classic publications, particularly those cited in earlier works on this subject (Margaria, 1938; Ralston, 1958; Margaria et al., 1963; Dill, 1965; Van der Walt and Wyndham, 1973; Mayhew et al., 1979) as well as some recent work (Conley and

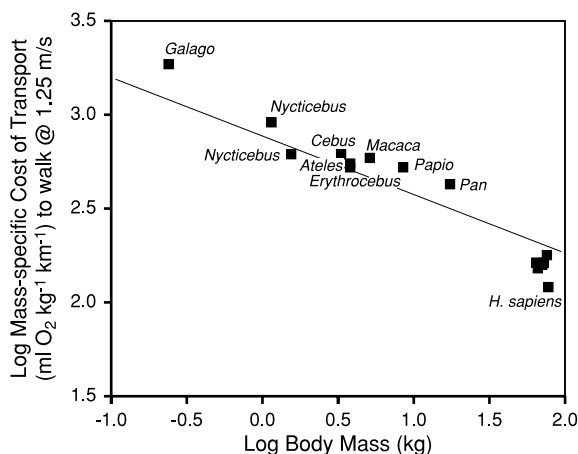


Fig. 1. The relationship between the energetic cost to walk a kilometer at 1.25 m s^{-1} and body size, plotted with both variables converted to \log_{10} . The solid line represents values from the general equation developed by Taylor et al. (1982). The values for individual primate species are indicated, including six independent estimates of the cost of human walking.

Krahenbuhl, 1980; Waters et al., 1988; Daniels and Daniels, 1992; Sherman, 1998). I calculated the cost to walk at 1.25 m s^{-1} and to run at 2.5 m s^{-1} for each species and, for humans. These speeds were chosen as appropriate walking or running speeds for the various species included. For humans 2.5 m s^{-1} is a slow jog and is a reasonable running speed for the smaller species as well. A comfortable walking speed for all but one of the species included here is 1.25 m s^{-1} was selected for primates of the sizes included here. This would be slightly above the speed at which an animal of *Galago* size would be expected to switch from a walk to a trot (1.08 m s^{-1} , Heglund and Taylor, 1974), but appropriate for all other species.

Cost of walking in humans and other primates compared to generalized endotherms

Fig. 1 shows the cost of walking 1 km at 1.25 m s^{-1} for a generalized endotherm at a range of body masses based on Taylor et al. (1982) (solid line). Individual data points based on the nine reported equations for nonhuman primates, and six estimates of the cost of human walking from

the sources listed earlier are also shown. Most primate species fall near the line based on the general equation. Values for some primate species fall above the line based on the generalized model; values for human walking fall below. The cost of transport at 1.25 m s^{-1} in primates does not appear to differ markedly from the equation based on the generalized model. While some primate species show deviations from the general line, so do individual species of birds and mammals (Steudel-Numbers, 2001).

At this (walking) speed, the values for two of the three Old World monkeys (*Macaca* and *Papio*) and for *Pan*, all show positive deviations from the general line. Should we conclude that Old World monkeys and apes as a group have higher than expected costs? Given the small sample size, such a conclusion is far from compelling. Further, the masses reported for the Old World monkeys and *Pan* indicate that the test animals were below usual adult size, suggesting that they may have been juveniles (see below). Data on the species for which we have the most information (*Homo sapiens*) show that juveniles of that species exhibit less efficient patterns of locomotion than do adults (Sutherland et al., 1980; Waters et al., 1988). Nakatsukasa et al. (2002) report a similar result in macaques. If this pattern is general, this may account for some positive deviation, though the extent of this will be dependent on how immature the animal was.

In an attempt to evaluate whether locomotor costs had been measured on adult or immature specimens, I have compared the masses of the primates on which costs were measured to size estimates for their species available in the literature. Table 1 summarizes these results. All of the Old World monkeys on which locomotor costs were measured were substantially smaller than the smallest documented adult females in Delson et al. (2000), suggesting that they must have been juveniles. Similarly, the specimens representing *Pan troglodytes* were approximately half the size of the average adult female in the smallest subspecies reported by Smith and Jungers (1997). The probable juvenile status of these specimens was also remarked by Jablonski and Chaplin (1993). In confirmation of this, the Boston Zoo, from where

Table 1

A comparison of the size of primate subjects on which rate of oxygen consumption (V_{O_2}) was measured to that of average adults of those same species. Data on *P. troglodytes* are from the smallest subspecies (*P. t. schweinfurthii*) given in Smith and Jungers (1997). The last column expresses the mass of the subjects on which cost was measured as a percentage of the reported values for average adult females

Species	Mass (kg) on V_{O_2} subjects	Mass (kg) from Smith & Jungers (1997)		Mass (kg) from Delson et al. (2000)		Mass of cost subject as % average ♀
		\bar{X} ♀	\bar{X} ♂	\bar{X} ♀	\bar{X} ♂	
<i>G. senegalensis</i>	0.24	0.225	0.271			100.7
<i>N. coucang</i>	1.55	0.82	0.90			189.0
<i>N. coucang</i>	0.88	0.82	0.90			107.3
<i>C. albifrons</i>	3.34	2.29	3.18			146.9
<i>A. geoffroyi</i>	3.80	7.29	7.78			52.1
<i>M. speciosa</i>	5.10	8.4	12.2	7.8	12.24	60.7
<i>P. hamadryas</i>	8.5	10.65	18.95	11.5	21.1	79.8
<i>E. patas</i>	3.8	6.5	12.4	5.5	9.8	58.5
<i>P. troglodytes</i>	17.5	33.7	42.7			51.9

the specimens were on loan, estimated their probable birthdays as November, 1969 (Linda Rohr, Registrar, Boston Zoo, personal communication). The experiments were carried out in 1971 or 1972 (V.L. Rowntree, personal communication). Thus the chimpanzees must have been only 2 or 3 years old. In contrast, most of the smaller primate species are represented by individuals of approximately average adult masses. One exception to this is *Ateles geoffroyi*. While the two individuals on which the data are based were small, it appears that they were, in fact, adult. Parsons and Taylor (1977) report that the specimens were acquired as adults, both female, and that they spent more than 2 years training them, leaving little possibility of doubt. The two specimens of *Nycticebus coucang* provide an interesting comparison. Parsons and Taylor (1977) do not discuss the ages of their specimens, but state that the larger specimen was female, the smaller male. The larger specimen was substantially above average body mass, suggesting that she must have been adult. The smaller specimen (male) was somewhat below average adult mass, suggesting that he was less mature than the larger female specimen, providing an opportunity to evaluate the hypothesis that younger specimens give higher values. Interestingly, the value for the smaller, presumably (though not certainly) younger, male has an elevated cost value, while the

female's cost is typical for her size. Thus, the positive cost deviations of the specimens representing Old World monkeys and apes seem possibly attributable to their immature status. I conclude that these data do not support the idea that the cost of locomotion in primates generally, or in Old World higher primates, is higher than that of a generalized endotherm, although more data on adult Old World monkeys and apes would be useful. Human walking, however, uses less energy than that of either nonhuman primates or generalized endotherms.

Cost of running in humans and other primates compared to generalized endotherms

Fig. 2 shows the relationship of the cost to run 1 km at 2.5 m s^{-1} based on the general equation (Taylor et al., 1982, solid line) and individual data points for nonhuman primates based on the nine reported equations, and seven estimates of the cost of human running from the sources listed previously. Again, some species fall above the line based on the generalized model, but most primates have costs of locomotion similar to what would be predicted for a generalized endotherm. Four of the seven estimates of the cost of human running fall above the line, consistent with the widespread

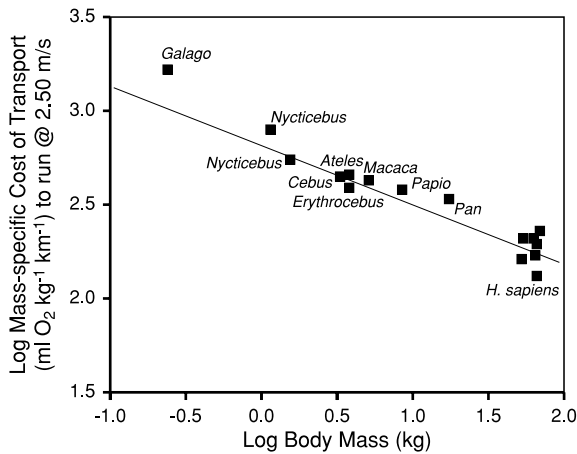


Fig. 2. The relationship between the energetic cost to run a kilometer at 2.50 m s^{-1} and body size, plotted with both variables converted to \log_{10} . The solid line represents values from the general equation developed by Taylor et al. (1982). The values for individual primate species are indicated, including seven independent estimates of the cost of human running.

observation that human running is relatively inefficient (Taylor et al., 1982; Carrier, 1984; Steudel, 1994, 1996). Three (of seven) estimates of the cost of human running, however, actually fall below the line based on the general equation. All these lower estimates are from studies on the running economy of highly trained distance athletes (Conley and Krahenbuhl, 1980; Daniels and Daniels, 1992). Apparently human runners specializing in long distance events are able to run at lower costs than the majority of their conspecifics. Daniels and Daniels (1992) suggest that economy may “determine the difference in performance between individuals with equal or near equal $\text{VO}_{2\text{max}}$.” These individuals are a highly select subset of the human population and, based on results on less highly trained individuals, atypical. While these elite athletes may differ more from the general human population than would commonly be the case in nature, it is interesting that several estimates of locomotor cost on a single species can produce results that vary so widely. Nonetheless, it is widely concluded that, with the exception of highly trained athletes, the cost of human running falls above the line based on the generalized model (Carrier, 1984; Alexander, 1991; Steudel, 1994, 1996).

An equation for the cost of locomotion in primates

In addition to providing a general equation for the cost of locomotion, Taylor et al. (1982) also calculated equations based on various subsets of their sample, including one for primates. Leonard and Robertson (1997, 2001) have used this primate equation to argue that human bipedal locomotion is particularly economical in comparison to what would be expected based on the primate equation. The Taylor et al. (1982) primate equation was never intended to focus on humans. They used the primate equation solely to conclude that the primate equation did not differ from that of the general equation at 95% confidence. Heglund (1985) subsequently discussed the same data with a focus on primates, once again pointing out the similarity to other mammals, but acknowledging some of the deviations that can be seen in Figs. 1 and 2. He downplayed the significance of the deviations, concluding that “large variations in this cost are necessary for any interspecific arguments about adaptive specializations based on the metabolic cost of terrestrial locomotion” (p. 324).

The data in Taylor et al. (1982) were not assembled to focus on human locomotor energetics. Most of the primate species in the sample were quite small (6 kg or less). *Papio* is represented at 8.5 kg, *Pan* at 17.5 kg, both probably juveniles (see above). The much larger *Homo* is represented at 68.8 kg (see their Table 1). No other primate species similar in size to *Homo* is included. Fig. 3 shows the cost to travel 1 km at 2.5 m s^{-1} for a generalized endotherm (solid curve) based on the equation in Taylor et al. (1982). The speed of 2.5 m s^{-1} was chosen because it is near the energetically optimal speed for humans to change gait (2.24 m s^{-1} , Hreljac, 1993) and one that could easily be used by animals of a wide range of sizes. The dotted curve is based on the cost to locomote at 2.5 m s^{-1} for each primate species given in Taylor et al. (1982). In this case, the value plotted is total cost of transport, rather than the logarithmically transformed, mass specific costs shown in Figs. 1 and 2. The omission of logarithmic transformation has two conspicuous and predictable effects: the linearity of the data is lost and the size differences between the large and small species

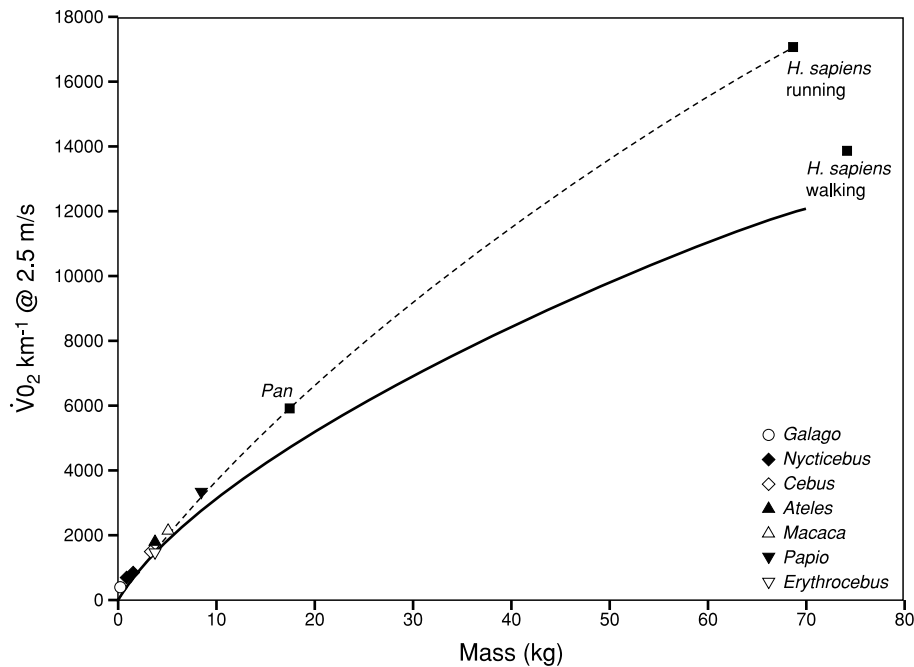


Fig. 3. The relationship between the cost to travel at 2.5 m s^{-1} for a “generalized endotherm” at a range of masses (solid line). The cost to travel at the same speed for a variety of primate species are also shown. The *Homo sapiens* running value is the only human data included in the primate equation calculated by Taylor et al. (1982). The dotted line shows the cost for primates to travel at this speed. The influence of the *H. sapiens* running data point is readily apparent. For comparison, I have plotted a value for the cost for a human to walk at this same speed, based on Margaria (1938). This value is noticeably lower and would be lower yet if the speed were closer to energetic optimality.

become much more apparent. Thus, it becomes evident that the human data have a very disproportionate effect on the curve used to describe the primate data.

The data on humans cited in Taylor et al. (1982), and used to generate the primate equation, are the classic Margaria et al. (1963) data on human *running*. Thus, Taylor et al. (1982) estimate the cost of human locomotion as 43.4% *above* that expected for a typical quadruped (see also Alexander, 1991). The effect of these data are particularly pronounced because, of the seven estimates of the cost of human running calculated from the articles cited previously and plotted in Fig. 2, the Margaria et al. (1963) data give the single highest estimate.

The data on *Pan* also suggest considerable inefficiency. As has been noted, the specimens of *Pan* on which cost data were obtained were quite clearly juvenile, which may well account for their

elevated cost. Thus, the two data points representing larger body weight primates both suggest inefficiency, while cost for the smaller primate species are similar to that of the generalized endotherm. Because 2.5 m s^{-1} is just above the energetically optimal speed to switch to a run, it is a reasonable speed at which to calculate both the cost of human running and of human walking. For comparison I include on Fig. 3 an estimate of the cost for human walking based on data in Margaria (1938). Although humans would normally run at this speed, the drop in estimated cost for human walking is conspicuous. The efficiency of human walking would be much more striking at a speed closer to energetic optimality. Thus, the Taylor et al. (1982) equation for the cost of locomotion in primates is heavily influenced by the inclusion of data on human running only and by the fact that *H. sapiens* is the only large body sized primate represented. Estimating the cost of locomotion for a

human sized primate based on the Taylor et al. (1982) primate equation would predict a cost characteristic of human running. As a consequence, the efficiency of human walking apparent in comparison to the predictions from the primate equation (Leonard and Robertson, 1997, 2001) reflects chiefly the great differences in efficiency between human walking and human running.

Summary

Arguments that bipedality originated in our lineage as a strategy to mitigate a high cost of locomotion that is a special characteristic of non-human primates, and thus our ancestor, are not supported by existing data. Estimates of the cost of locomotion in primates as a group are similar to that of generalized endotherms. Human walking is relatively efficient, either in comparison to other primates or to generalized endotherms. Human running tends to be less efficient than that of generalized endotherms except in the case of elite, highly trained distance athletes. The equation for the cost of primate locomotion developed by Taylor et al. (1982) was not designed for studies focusing on humans. *H. sapiens* was the only large body sized primate on which they had data and these data were for the relatively inefficient human running. Thus, comparing the cost of human walking to a prediction from the Taylor et al. (1982) primate equation is equivalent to comparing the cost of human walking to that of human running.

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