

Bioenergetics and the Origin of Hominid Bipedalism

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ABSTRACT Compared to most quadrupedal mammals, humans are energetically inefficient when running at high speeds. This fact can be taken to mean that human bipedalism evolved for reasons other than to reduce relative energy cost during locomotion. Recalculation of the energy expended during human walking at normal speeds shows that 1) human bipedalism is at least as efficient as typical mammalian quadrupedalism and 2) human gait is much more efficient than bipedal or quadrupedal locomotion in the chimpanzee. We conclude that bipedalism bestowed an energetic advantage on the Miocene hominoid ancestors of the Hominidae.

Habitual bipedalism is rare among mammals, and its rarity can be interpreted as meaning that it is inefficient, therefore unlikely to evolve (Bartholomew and Birdsell, '53). Consequently, special factors are usually advanced to explain the origin of bipedalism in Hominidae, including tools (Washburn, '60, '63), new feeding adaptations (DuBrul, '62; Jolly, '70), carrying (Hewes, '61, '64), display (Livingstone, '62; Wescott, '67), or a combination of several of these (Sigmon, '71). Some have posited that human bipedalism may be efficient for moving long distances (Campbell, '66; Napier, '63, '67; Pilbeam, '70; Washburn, '60, '63), but empirical studies have shown that at maximum speed human bipedalism costs twice as much energy per kg per km as is predicted for a true mammalian quadruped of the same size (Taylor, et al., '70). In addition, Taylor and Rowntree ('73) found that for chimpanzees and capuchin monkeys, energetic costs of traveling quadrupedally and bipedally are about the same, and they conclude that efficiency of bipedal versus quadrupedal locomotion should therefore not be used in arguments on the advantages and disadvantages of human bipedalism.

Recent discoveries in East Africa suggest that bipedalism was the primary hominid adaptation. Pelvic remains of Pliocene hominids show that bipedalism was well established by 3 M years ago (Johanson and White, '79; McHenry, '75; Robinson, '72). Hominid footprints at Laetoli attest to an even earlier date for the origin of bipedalism (Leakey and Hay, '79). The modern hominid dental complex had

not fully evolved by 3 M years as indicated by the *Australopithecus afarensis* gnathic remains (Johanson and White, '79). Stone tool manufacture appeared even later, possibly at 2.5 M years (Johanson, et al., '78) but certainly by 1.8 (Isaac, '78). Encephalization above average hominoid levels may have started early, but did not begin its enormous increase until after 2 M years (McHenry, '75). Bipedalism, therefore, may have been the first change in human evolution, an idea championed by Lamarck (1809), Haeckel (1868), Darwin (1872), and other early evolutionists.

Given this new evidence, it is particularly important to evaluate selective factors that may have favored human bipedalism since such factors may have precipitated later human adaptation. We propose that existing empirical studies support the hypothesis that bipedalism increased the energetic efficiency of hominid travel and that this increase was an important factor in the origin of bipedalism. Two premises are necessary to arrive at this proposal: first, that relevant comparisons should be made at normal speeds of travel; and second, that since bipedal hominids are probably descended from quadrupedal hominoids, the relevant comparisons are of bipedalism and quadrupedalism of hominoids rather than of hominids with true quadrupeds such as rodents, dogs, and ungulates.

Observations of chimpanzees in the wild provide data for calculation of approximate normal travel speed of a quadrupedal, terrestrial hominoid. Wrangham ('77) found that adult male chimpanzees traveled a median of 3.8, 4.2,

and 6.4 km each day in three different seasons, and took 59 minutes, 105 minutes, and 148 minutes, respectively, to travel those distances. From these data we calculate that average travel speed for a male chimpanzee is 2.9 km/hr. The living human walks at a normal speed of approximately 4.5 km/hr (Ralston, '76).

Taylor et al. ('70) calculated the minimum cost of running one km, M_{run} (ml O_2 /g/km), for a variety of quadrupedal mammals¹; M_{run} is the slope of the regression of oxygen consumption on velocity. They show that M_{run} for humans falls well above that predicted from the regression for true quadrupeds of similar body size, but they also point out that, "the usefulness of this relationship is limited by the fact that the minimum cost to run is approached only when a mammal runs near its highest speed" (Taylor et al., '70, p. 1106). In fact, the theoretical value of M_{run} is achieved only at infinite speed as a consequence of the way in which it is derived. Since few mammals travel at such high speeds, it is useful to compare costs of running at normal speeds, and Taylor et al. ('70, p. 1107) also provide an equation predicting the cost to travel 1 km at any speed, M'_{run} (ml O_2 /g/km).

Taylor and Rowntree ('73) measured costs of travel at various speeds for two young chimpanzees, and various authors have published energetic costs of human walking and running. We present the comparison of human and chimpanzee in Table 1. The actual costs of travel for walking humans are slightly less than those predicted for a quadrupedal mam-

mal of the same size, but the costs of travel for the chimpanzee are approximately 150% of those predicted for a true quadruped of similar size.

Part of this result has been produced elsewhere. For example, Fedak et al. ('74) show that human running is 75% less efficient than human walking, so that it is not surprising that comparisons of humans with quadrupedal mammals at walking speed demonstrate greater relative efficiency for the human than comparisons at running speed; and Tucker ('75, Fig. 2) shows that human walking is not energetically expensive relative to true quadrupedalism. The important new point made here is that *bipedalism of living hominids is considerably more efficient than quadrupedalism of living hominoids*. It is likely that the Miocene hominids were not as efficient bipeds as are modern humans; it might be expected, without examination of observations presented here, that there was a period of awkward, inefficient transition through an adaptive trough separating quadrupedal from bipedal walking by the ancestral hominoid. If

¹ The use of the term "run" (vs. the term "walk") by Taylor et al. ('70) and by Taylor and Rowntree ('73) appears not to refer to a true gait. Although the gaits of the subjects of their experiments are not specified, the speeds at which measurements were made include slow speeds, at which the subjects presumably were walking, as well as high speeds, at which the subjects probably were truly running. It is interesting that for all the nonhumans costs of running/walking fall on a straight line with respect to speed, although it might be expected that efficiencies would change with change in gait. On the other hand, human efficiencies clearly change with change in gait (Margaria et al., '63; Ralston, '76; Zarrugh, et al., '74).

TABLE 1. Comparative energetic costs of walking for quadrupedal chimpanzee and bipedal human at normal travel speeds

Speed	Subject	Body weight	Predicted cost ¹ (ml O_2 /g/km)	observed cost (ml O_2 /g/km)	Observed/ predicted cost ($\times 100$)
2.9 km/hr ²	Chimpanzee	17.5 kg	0.351	0.522	149%
	Human	70.0 kg	0.225	0.193 ³	86%
4.5 km/hr ⁴	Chimpanzee	17.5 kg	0.287	0.426 ⁵	148%
	Human	70.0 kg	0.180	0.170 ³	94%

¹ Cost for a true quadruped of the same weight, predicted from equation 4 of Taylor et al. ('70): $M'_{run} = 8.5 W^{-0.40} + \frac{6.0}{V} W^{-0.025}$, W = weight (g); V = speed (km/hr).

² Average speed of male chimpanzees in the wild; see text for explanation.

³ Value estimated from the fitted relationship of E_m , the energy expenditure per meter walked, to walking speed of Zarrugh et al. ('74): $E_m = \frac{32}{V} + 0.0050 V$; V = speed (m/min), units converted to ml O_2 /g/km. Similar results are given by Margaria et al. ('63).

⁴ Normal, and optimal, human walking speed (Ralston, '76; Zarrugh et al., '74).

⁵ Value estimated from the fitted relationship of oxygen consumption to velocity for quadrupedal chimpanzees of Taylor and Rowntree ('73): $M'_{run} = 0.25 + \frac{0.79}{V}$; V = speed of walking (km/hr).

so, some special advantage would have to exist for evolution of bipedalism to occur. But Taylor and Rowntree found that for chimpanzees, *the costs of quadrupedal and bipedal travel are the same.*² We interpret their result to show that there was no energetic rubicon separating hominoid quadrupedal adaptation from hominid bipedalism. Under a selective regime favoring energetic efficiency, structural variations in the direction of improved bipedal walking (which must have existed for bipedalism to evolve for any reason) could have been favored quickly without the problem of crossing an intuitively likely, but manifestly nonexistent, adaptive trough in the transition.

Why are chimpanzees such inefficient quadrupeds? We note that morphology of locomotion is often a compromise with other dimensions of existence. So, for example, Pinshow et al. ('77) found that geese and particularly penguins are inefficient bipedal birds, and they suggest their inefficiency is due to the fact that, "the morphology of penguins and geese may in part represent a compromise between aquatic and terrestrial locomotion." Similarly, morphology of chimpanzees may be viewed as a compromise between demands of arboreal feeding and terrestrial travel with consequent inefficiency of walking.

The most widely accepted scenario for the origin of bipedalism follows Haeckel (1868) and Darwin (1872): bipedalism arose when our primate ancestor came to live somewhat less in trees and more on the ground "... owing to a change in its manner of procuring subsistence, or to a change in the conditions of its native country" (Darwin, 1872:135). Subsistence change may have been involved (Jolly, '70), but a more conservative view is to propose that the initial hominoid-hominid divergence did not involve a dietary change, but merely a change in the distribution of typical hominoid food sources. According to this hypothesis, ancestral hominids were faced with a foraging regime that demanded more travel for the same food intake, thus selecting for improved energetic efficiency of terrestrial travel between food sources. It is well known that climatic fluctuations in the Miocene led to changing distributions of forests and open country (Campbell and Bernor, '76; Bernor, '78). In areas of receding forests the ancestral populations faced a foraging regime in which food was more dispersed and demanded more travel to harvest, assuming diet was not modified at first. Although structural modification in the direction of improved *quadrupedal* efficiency might have oc-

curred, this route would have conflicted with ability to harvest food at food sources. Bipedalism provided the possibility of improved efficiency of travel with modification only of hindlimbs while leaving the hominoid structure of forelimbs free for arboreal feeding. We therefore concur with Romer, as have others (Hockett and Ascher, '64), that the hominid ancestor "... may have evolved potentialities as a ground walker so that he could live successfully in the trees ..." (Romer, '59; p. 327). The energetic advantage offered by bipedalism must have been an important factor in the emergence of bipedalism in one group of hominoids. It is not necessary to posit special reasons such as tools or carrying to explain the emergence of human bipedalism, although forelimbs free from locomotor function surely bestowed additional advantages to human walking.

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² Taylor and Rowntree ('73) measured costs of travel for a capuchin monkey (*Cebus capucinus*) walking bipedally and quadrupedally, and found that for these monkeys the costs of travel were also the same for each mode. In addition it was found that energetic costs of travel for the capuchin were essentially the same as predicted for a quadruped of the same size, and it was found that energetic costs for a bipedal spider monkey (*Ateles geoffroyi*, which only travels bipedally on the ground) were essentially the same as expected for a same-size quadruped. These results suggest that 1) relative efficiency of quadrupedal and bipedal locomotion may be general within the Primates and 2) hominoid morphological specializations may have had a detrimental effect on energetic efficiency of terrestrial locomotion compared to other primates.

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