Running on Two or on Four Legs: Which Consumes More Energy?

Abstract. *Disagreement exists over whether man's bipedal form of locomotion evolved as an economical means for covering long distances. There is also some disagreement about the energetic price man had to pay to free his hands. In an investigation of the relative energetic cost of bipedal and quadrupedal locomotion in primates, chimpanzees* (Pan troglodytes) *and capuchin monkeys* (Cebus capucinus) *were trained to run on a treadmill either on two or on four legs while their oxygen consumption was being measured. Both primates expend the same amount of energy whether running on two or on four legs. The relative energy cost of bipedal versus quadrupedal running should not be used in arguments about the evolution of bipedal locomotion in man.*

One of the features which distinguishes man from other primates is his bipedal form of walking and running. Anthropologists and biologists have speculated at length on the advantage of this type of locomotion, and a consensus seems to exist that freeing hands for other functions (the manipulation of tools or weapons, the carrying of infants and food) is an important advantage of bipedal locomotion (*1*, *2*). Some disagreement exists, however, about the energetic price man had to pay to free his hands. Many anthropologists have maintained that man's bipedal form of walking allows him to cover long distances economically (*2*, *3*), whereas some biologists (*1*) have argued that the uniqueness of man's bipedal form of locomotion suggests that it is inefficient.

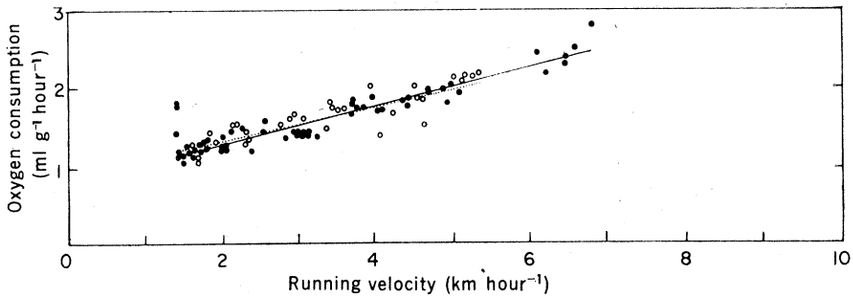

Fig. 1. Steady-state oxygen consumption (*7*) of chimpanzees running on four legs (solid circles and solid line) and on two legs (open circles and dotted line) at different running velocities. Slopes of the relationship between the oxygen consumption and the running velocity were determined by the method of least squares. The slope of the curve for running on four legs was 0.25 ml of oxygen per gram per kilometer; y intercept = 0.79 ml of oxygen per gram per hour; number of measurements (n) = 69; correlation coefficient (r) = 0.92. The slope of the curve for running on two legs was 0.23 ml of oxygen per gram per kilometer; y intercept = 0.90 ml of oxygen per gram per hour; $n = 32$; $r = 0.84$. The slope predicted for running along a level surface on the basis of body weight (*4*) was 0.17 ml of oxygen per gram per kilometer.

Recent measurements of the energy cost of quadrupedal locomotion suggest that the energetic cost of man's bipedal locomotion might be very high in comparison (*4*). Man uses about twice as much energy to move 1 g of body weight 1 km as would be predicted for a quadrupedal animal of the same weight. Does this reflect the high energetic cost of moving bipedally? A recent study on the ostrich-like *Rhea*, another large bipedal animal, supports the hypothesis that moving on two legs requires about twice as much energy as moving on four (*5*). Much of the physical work involved in man's running is consumed in the alternate acceleration and deceleration of the body with each stride (*6*). It seems possible that a quadrupedal animal might run more evenly and thereby minimize the expenditure of this kinetic energy.

We decided to investigate the relative cost of bipedal versus quadrupedal locomotion in primates by comparing the energetic cost of both forms of locomotion in a single animal that normally moves in both ways. We trained two chimpanzees (*Pan troglodytes*; average weight, 17.5 kg) and two capuchin monkeys (*Cebus capucinus*; average weight, 3.34 kg) to run on a treadmill either on two or on four legs. We also utilized a spider monkey (*Ateles geoffroyi*; average weight, 3.54 kg) which normally moves on two legs when running on the ground. The animals were fitted with ventilated masks, and we measured the steady-state oxygen consumption while they ran at various speeds (*7*).

Much to our surprise, there was no measurable difference in the amount of oxygen consumed by the chimpanzee (Fig. 1) or the capuchin monkey (Fig. 2) when running on two or on four legs (at any speed). There was no sta-

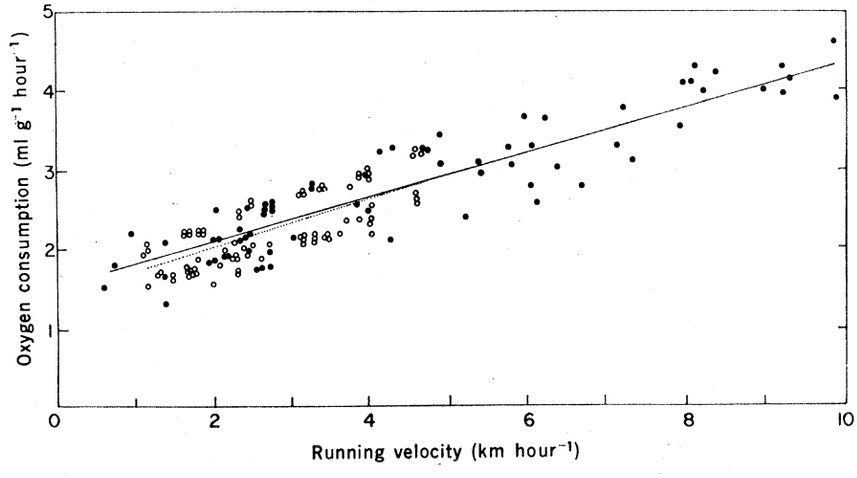

Fig. 2. Steady-state oxygen consumption (*7*) of capuchin monkeys running on four legs (solid circles and solid line) and on two legs (open circles and dotted line). The slopes of the relationships between the oxygen consumption and the running velocity were determined by the method of least squares. The slope of the curve for running on four legs was 0.28 ml of oxygen per gram per kilometer; y intercept = 1.50 ml of oxygen per gram per hour; $n = 73$; $r = 0.90$. The slope of the curve for running on two legs was 0.32 ml of oxygen per gram per kilometer; y intercept = 1.42 ml of oxygen per hour; $n = 79$; $r = 0.89$. The slope predicted for running along a level surface on the basis of body weight (*4*) was 0.33 ml of oxygen per gram per kilometer.

tistical difference between the slope of the curve for the relationship between oxygen consumption and running velocity for quadrupedal locomotion in the chimpanzee and the slope of the corresponding curve for bipedal locomotion. There was likewise no statistical difference between the slopes of the corresponding curves for the capuchin monkey.

The observed cost of locomotion in the chimpanzee was about 50 percent higher than would be predicted from the relationship between the cost of running and body size for quadrupedal animals. The observed and predicted costs of running in the capuchin monkey were nearly identical. The energy cost of bipedal locomotion in the spider monkey was also close to the predicted value for quadrupedal running (0.41 versus 0.38 ml of oxygen per gram per kilometer).

It is clear, although somewhat unexpected, that a number of primates expend the same amount of energy whether they move on two or on four legs. Thus the cost or efficiency of bipedal versus quadrupedal locomotion probably should not be used in arguments weighing the relative advantages and disadvantages that bipedal locomotion conferred on man.

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References and Notes

1. G. A. Bartholomew and J. B. Birdsell, in *Ideas on Human Evolution, Selected Essays, 1949–1961*, W. Howells, Ed. (Atheneum, New York, 1967), pp. 378–395.
2. J. Napier, *Sci. Amer.* **216**, 56 (April 1967); ———, in *Classification and Human Evolution*, S. L. Washburn, Ed. (Aldine, Chicago, 1963), p. 186; D. Pilbeam, *The Evolution of Man* (Funk & Wagnalls, New York, 1970), p. 95; S. L. Washburn, *Sci. Amer.* **203**, 3 (September 1960).
3. S. L. Washburn, in *Classification and Human Evolution*, S. L. Washburn, Ed. (Aldine, Chicago, 1963), pp. 190–203; B. Campbell, *Human Evolution* (Aldine, Chicago, 1966), p. 203.
4. C. R. Taylor, K. Schmidt-Nielsen, J. L. Raab, *Amer. J. Physiol.* **219**, 1104 (1970).
5. C. R. Taylor, R. Dmi'el, M. Fedak, K. Schmidt-Nielsen, *ibid.* **221**, 597 (1971).
6. G. A. Cavagna, F. P. Saibene, R. Margaria, *J. Appl. Physiol.* **19** (No. 2), 249 (1964).
7. Wind velocity was matched to tread speed. The air temperature was 22°C, and the relative humidity was less than 30 percent. Room air was pulled past the faces of the animals at between 50 and 150 liters per minute (at standard temperature and pressure). The difference in oxygen concentration between air flowing into and out of their masks was measured with a Beckman model G-2 paramagnetic oxygen analyzer. We used only steady-state oxygen consumption values. We considered a steady state to have been reached when there was less than a 5 percent variation in the oxygen consumption during a 30-minute period. At speeds exceeding 4 km/hour the animals tired, and we used 15- instead of 30-minute periods. We calibrated flowmeters to an accuracy of better than 1 percent, using a Brooks "Vol-u-meter" under pressure gradients identical to those used in our experimental system. The accuracy of the entire system was determined by bleeding known amounts of nitrogen into the face mask at air flows identical to those used in the experiments and determining the dilution of oxygen in the room air. The accuracy was better than ± 2 percent.
8. This work was supported by National Science Foundation grant GB 27539 and a John Milton Fund grant from Harvard University. We thank the Boston Zoological Society and R. G. Naegeli, director of Zoological Parks for the Metropolitan District Commission of Boston, for the loan of the chimpanzees.

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Isolation of Aleutian Mink Disease Virus by Affinity Chromatography

Abstract. *Affinity chromatography was used to isolate the Aleutian disease virus of mink. Dissociation of the immunoadsorbent-virus complex with 0.75 molar sodium chloride and then with a glycine-hydrochloride gradient released infective particles resembling picornaviruses. The elution profile suggests that two different types of virus-antibody complexes are formed, one dissociated by sodium chloride and another that requires glycine-hydrochloride in addition to sodium chloride for release of virus.*

Affinity chromatography has been widely used to isolate dilute antigens, enzymes, haptens, and ligands (*1*). However, viruses have not been isolated by this technique, presumably because of the difficulty in obtaining sufficient quantities of specific antibody. The virus causing Aleutian disease of mink (*2*) and ferrets (*3*) seemed suitable for isolation by this method, because large amounts of antibody (*4*) are produced during the disease, resulting in the excess of gamma globulin (hypergammaglobulinemia) characteristic of Aleutian disease.

Although Aleutian disease was described in 1958, the agent has remained unclassified, and the various strains used in research are uncharacterized. The virus that we passaged and used in this study had a target-size molecular weight of 1.5×10^6 (estimated from inactivation of virus by ionizing radiation) and produced typical infiltrates of lymphocytes and plasmacytes in all soft organs, with a doubling of serum gamma globulin concentration by 30 days after inoculation. The Aleutian disease antibody [found in the immunoglobulin G (IgG) fraction] from serum of chronically infected mink was separated free of virus by ion exchange

Table 1. Evidence of infectivity of eluates from experiments 1 and 2. Ornithine carbamoyltransferase (OCT) was assayed 7 days after inoculation. Lactate dehydrogenase (LDH) was assayed 10 to 21 days after inoculation. The quantitative phytohemagglutination (PHA) test, done weekly from 7 to 28 days after inoculation to evaluate cellular immunity, was scored as stimulation (S) or no response (NR). The IgG values were determined 64 days after inoculation. Plasmacytosis in kidney, liver, and spleen was graded from normal (0) to most severe (++++) when animals were necropsied 64 days after inoculation. A diagnosis of normal (N) or Aleutian disease (AD) was made for each animal. The eluate dilutions used for inoculation are given in parentheses.

Mink	Inoculation	OCT (units)	LDH (units)	IgG (%)	PHA	Lesions	Diagnosis
		Experiment 1					
23	NaCl eluate	125	10,000	22	NR	++	AD
20	NaCl eluate	90	8,000	30	NR	++	AD
29	NaCl eluate (10^{-3})	35	15,000	27	NR	++	AD
19	NaCl eluate (10^{-6})	50	5,000	40	NR	+++	AD
30	NaCl control	15	2,000	12	S	±	N
8	Acid eluate	14,000				+	AD*
9	Acid eluate	150	9,000	34	NR	++++	AD
10	Acid eluate (10^{-3})	1,400	12,000	27	NR	+	AD
7	Acid eluate (10^{-6})	50	6,000	31	NR	+++	AD
27	Acid control	10	1,500	9	S	0	N
24	Pronase eluate	15	1,200	11	NR	0	N
25	Pronase eluate (10^{-3})	1	1,700	8	S	0	N
		Experiment 2					
3	Acid eluate	960	18,000	19	NR	+	AD*
4	Acid eluate	185	14,000	26	NR	†	AD
5	Acid eluate	150	12,000	27	NR	†	AD

* Animal died. † Histologic material not examined.