

# Energy cost of bipedal running

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FEDAK, MICHAEL A., BERRY PINSHOW, AND KNUT SCHMIDT-NIELSEN. *Energy cost of bipedal running*. Am. J. Physiol. 227(5): 1038-1044. 1974.—This study compares the energy cost of running in two- and four-legged animals. In seven species of birds (0.04–22 kg) steady-state oxygen consumption during running at various speeds increased linearly with running speed. The slope ( $E_{run}$ ) of the regression line was a constant for each species, but smaller birds had a steeper slope than larger birds (as previously reported for mammals).  $E_{run}$  values for two-legged and four-legged runners plotted on logarithmic coordinates against body weight fall along two different straight lines.  $E_{run}$  decreases more rapidly with body weight in four-legged than in two-legged runners. The lines cross at about 1 kg body wt. Thus, for small body size (<100 g) the predicted cost of transport is significantly less for two-legged than for four-legged runners. For large body size (>5 kg) the opposite is true. For an animal the size of man, two-legged running is energetically over twice as expensive as four-legged running.

birds; body size; exercise; oxygen consumption; treadmill running

MANY KINDS OF TERRESTRIAL ANIMALS move about on jointed legs. Species vary widely in size and shape. How do the energetic requirements of locomotion in these animals compare with each other? How do they compare with the energy requirements of other forms of locomotion? Answers to these questions will come from mechanical and energetic analyses of moving animals.

The mechanics of walking and running has received more attention for humans than for other animals. Detailed analyses of whole-body movements during walking and running were made by Fenn (8, 9) and Elftman (7), and many other workers have analyzed the mechanics of single joints or parts of the human body. An extensive bibliography is found in ref. 20.

Few mechanical analyses of the locomotion of other animals have been carried out. Muybridge (21) made photographic analyses of complete step cycles for a variety of animals. Howell (13) discussed the variety of gaits (taken to mean the pattern of limb movements) in mammals as well as speed and endurance records. These works are descriptive and involve little mechanical analysis. Manter (16) presented information on limb positions and force application in cats and Barclay (1) did the same for dog, goat, and sheep. Hildebrand (11) made an interesting comparison of gait, stride length, speed, and endurance in the horse and cheetah. Gray has summarized the information on terrestrial locomotion in vertebrates as well as invertebrates (10). We have found no mechanical analyses of terrestrial locomotion in birds.

From this diverse literature we can make three points that will have some bearing on the data presented in this paper: *a*) Animals exhibit a great variety of gaits (21); *b*) most of the work done by locomotory muscles in level running at constant velocity on a firm substrate acts to accelerate the animal's body upward and forward and to return limbs to the proper position to do this work (1, 3, 5, 16); *c*) in all the gaits studied, during some phase of the locomotory cycle, muscles are stretched while they maintain tension and thus consume metabolic energy while work is done on them (1, 7, 16).

The information on the energetics of animal locomotion has recently been reviewed by Schmidt-Nielsen (22) and Tucker (29), who also included some information on humans (for further discussion of humans, see refs. 2, 19, and 27). Taylor et al. (23) studied the energetics of small and large animals running up and down inclines, and Chodrow and Taylor (6) presented data on limbless locomotion in snakes.

Taylor et al. (26) studied a variety of four-legged runners and concluded that there is a simple relationship between the body size of an animal and the minimum metabolic cost of traveling a unit distance. They gave an equation that could predict from the body weight the energetic cost of running for a quadrupedal mammal.

The only data available at that time on any two-legged runner were those for man. The measured cost in man was approximately twice that predicted by Taylor's equation. Subsequent data for a large running bird, the rhea (*Rhea americana*), also fell far above the value predicted for its body size from the quadruped equation (24).

These deviations from the quadruped pattern suggested a comparison over a wider size range of the energetics of running in two- and four-legged animals. In this paper we present data from a variety of running birds and compare all the data now available.

## METHODS

Seven species of birds ranging in size from 0.04 to 22 kg were trained to run on treadmills. All birds were obtained from animal dealers and, with the exception of the painted quail, were maintained in an outdoor enclosure 20 by 30 feet. The painted quail were kept indoors in pairs in small cages with exercise wheels. All birds were fed Purina game bird chow supplemented with fresh vegetables and mealworms.

The oxygen consumption of these birds was calculated from measurements taken while they ran steadily at known

speeds. Treads were driven by variable-speed motors that could maintain any desired constant speed ( $\pm 1\%$ ).<sup>1</sup>

The expired gas from running birds was captured in an airstream pulled through a loosely fitting mask that the birds were trained to wear or through a glass or Plexiglas chamber surrounding the running bird. Masks were tested for loss of expiratory gas under each experimental condition by measuring oxygen consumption at lower and lower flow rates until an apparent reduction in oxygen consumption occurred, whereupon the airflow rate was increased by at least one-third. Chambers were tested for leaks by bleeding in known amounts of  $\text{CO}_2$  or  $\text{N}_2$  and checking that the appropriate dilution of the oxygen concentration was recorded. No measurable leaks were observed at the flow rates used.

Gas flow rates greater than  $100 \text{ ml min}^{-1}$  were measured with rotameters calibrated with Brooks Vol-U-Meters under pressures identical to those found in the experimental system. Flows could be measured with negligible systematic error and with imprecision estimated to be less than 2%.

Low gas flow rates ( $< 100 \text{ ml min}^{-1}$ ) were metered (*i. i.*) directly by a Brooks Vol-U-Meter. Water-filled manometers were used to monitor pressure differences across flowmeters and to measure differences between analysis cells and ambient pressures in the gas analyzers. All volumes are given in STPD.

Oxygen fractional concentrations ( $\text{FO}_2$ ) were recorded continuously with a modified Beckman G-2 paramagnetic oxygen analyzer, which at maximum sensitivity produced a full-scale response to a change from 20.94 to 20.84%  $\text{O}_2$ . The oxygen analyzer was calibrated by changing the analyzer cell pressure.  $\text{FO}_2$  could be measured to an absolute concentration difference of  $\pm 0.002\%$ .  $\text{CO}_2$  concentrations were measured with a Beckman model 215A infrared gas analyzer. Its span was adjusted to produce deflections of similar magnitude to those on the oxygen analyzer.

Oxygen consumption ( $\dot{V}\text{O}_2$ ) was calculated by formula number 2 given by Tucker (28).  $\text{CO}_2$  production, which is needed for this calculation, was found using a nulling method described by Tucker (30).  $\dot{V}\text{O}_2$  could be measured with a systematic error of less than 3.5% (7% for the bobwhite). Imprecision was estimated to be 4% or less.

Oxygen consumption of each bird was measured over the full range of speeds the bird would maintain for 20 min or more. Data were used only when the bird was running freely and steadily and when the measured  $\text{FE}_{\text{O}_2}$  was steady. No attempt was made to match airspeed past the bird to tread speed. All birds ran at ambient temperatures of  $25 \pm 1^\circ\text{C}$ .

The data obtained from the rhea have been published previously (24). The methods applied to the rhea differed from those described above in that a fan was used to match airspeed to tread speed. However, turning the fan on and

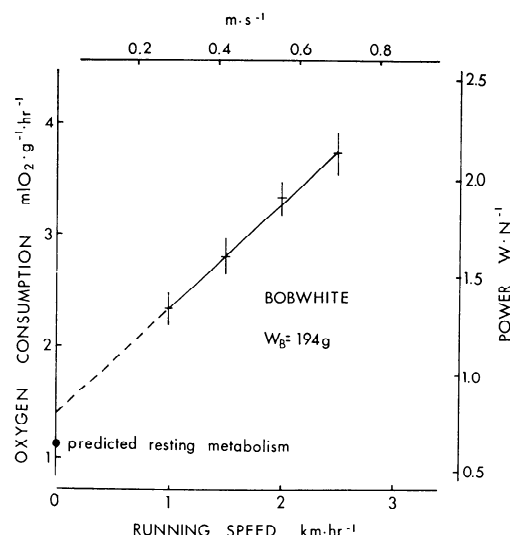


FIG. 1. Oxygen consumption plotted against speed for bobwhite quail. Five individuals, mean weight 194 g (range 165–208 g). Oxygen consumption rate, converted to power input, is plotted on right ordinate (assuming that 1 ml  $\text{O}_2$  yields 20.1 J). Vertical bars represent 2 SE on each side of mean. Predicted resting metabolism is calculated from Lasiewski and Dawson's equation for nonpasserine birds (15). Regression equations and statistical parameters are given in Tables 1 and 2.

off produced no measurable changes in the  $\dot{V}\text{O}_2$  of the rhea at any speed.

## RESULTS

The relation between oxygen consumption and running speed for the bobwhite quail is plotted in Fig. 1.<sup>2</sup> Metabolic rate increased linearly with increasing speed. Bobwhites would not run for 20 min or more at speeds higher than  $2.5 \text{ km h}^{-1}$ , although they could run at much higher speeds for shorter periods. The treadmill on which the bobwhite ran was capable of  $7 \text{ km h}^{-1}$  and the birds could maintain this speed for about 30 s. They may be able to run still faster.

The dotted line in Fig. 1 is the extrapolation of the regression line to the Y axis (zero speed). The intercept is above the observed resting metabolic rate as well as the predicted resting rate for the quail (see Table 1). The other birds studied also had Y intercept values that were about 1.5 times the predicted resting rate (SE 0.15). The observed resting metabolic rates for all the birds were always somewhat higher (38% on the average) than the predicted rates. However, the birds had not been fasting and were in a brightly lit room. Thus birds may not have been resting in all cases.

Figure 1 permits us to obtain two important quantities, the cost of transport and the change in power with a change in speed (= slope of regression line). The cost of transport ( $E_T$ ) is the oxygen consumed per unit body weight while traveling a given distance. It can be calculated by dividing the oxygen consumption (per unit body weight) at a given speed by that speed. Thus, for bobwhite quail weighing 194

<sup>1</sup> Inaccuracy statements follow references to particular measurements and take the form ( $\pm S, \pm P$ ), where S is systematic error and P is imprecision. Unless otherwise stated, S is computed from the manufacturer's specification or our estimate of the maximum error. S is an absolute value in the units of measurement or a percent. Imprecision is the computed standard error of a measurement. The error-propagation formulas used are from ref. 14, chapter 5.3, using guide lines in chapter 1.6. Errors indicated by the letter i are considered insignificant ( $< 1\%$ ).

<sup>2</sup> Conversion factors used: 1 g (force) = 0.00981 N; 1 ml  $\text{O}_2 \text{ g}^{-1} \text{ km}^{-1}$  = 0.569  $\text{W N}^{-1}$ ; 1 ml  $\text{O}_2 \text{ g}^{-1} \text{ km}^{-1}$  = 2.05  $\text{J N}^{-1} \text{ m}^{-1}$ ; 1  $\text{km h}^{-1}$  = 0.278  $\text{m s}^{-1}$ ; J = joules, W = watts, N = newtons.

TABLE 1. Comparison of resting metabolic rates and oxygen consumption extrapolated to zero running speed

Species	No. of Animals	Mean Body Wt, g*	Resting Metabolism, ml O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup>		
			Observed†	Pre-dicted‡	Y intercept
Painted quail ( <i>Excalfactoria chinensis</i> )	5	42 (36-58)	2.08 (±0.12)	1.62	2.33
Bobwhite quail ( <i>Colinus virginianus</i> )	5	194 (165-208)	1.34 (±0.05)	1.07	1.40
Chukar partridge ( <i>Alectoris graeca</i> )	3	489 (467-542)	1.35 (±0.05)	0.83	1.48
Guinea fowl ( <i>Numida meleagris</i> )	3	1,207 (1,086-1,356)	1.05 (±0.04)	0.65	1.36
Greylag goose ( <i>Anser anser</i> )	4	3,813 (3,750-4,700)	0.63 (±0.03)	0.47	0.47
Wild turkey ( <i>Meleagris gallopavo</i> )	2	4,306 (3,650-5,180)	0.56 (±0.04)	0.45	0.65
Rhea ( <i>Rhea americana</i> )	2	22,000 (18,000-25,000)	0.38	0.29	0.39

\* Range in parentheses. † ±1 SE in parentheses. ‡ From Lasiewski and Dawson equation for nonpasserine birds (15).

g running at 2.5 km h<sup>-1</sup> the cost of transport will be 3.7 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> divided by 2.5 km h<sup>-1</sup>, or 1.5 ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup>.

Since oxygen consumption is used as an indirect measure of metabolic energy input, the cost of transport will have units of energy divided by a force (weight) times distance. In a consistent system of units it will be dimensionless.

The cost of transport ( $E_T$ ) expresses a cost effectiveness and would be of interest when considering whole-animal energy budgets such as the energetic cost of a migration. Below, cost of transport is used as a basis of comparison between different types of locomotion. In all cases, when such data are presented for running animals, the values are minimum costs and are therefore calculated at highest sustained running speeds. Minimum costs for other forms of locomotion may occur at intermediate speeds (22).

The other quantity of interest is the slope of the line relating O<sub>2</sub> consumption to speed. This slope ( $E_{run}$ ) is an energy term that has the same units as cost of transport but not the same numerical value, since the calculation of slope involves subtraction of the Y-intercept value of metabolic rate. The cost of transport may, for reasons expressed below, approach the numerical value of the slope in large animals running at high speed.  $E_{run}$  should not be confused with a "net cost" of running (which is usually obtained by subtracting the resting metabolic rate), for the Y intercept does not coincide with resting metabolic rate.

The slope of the line ( $E_{run}$ ) has no time dimension and is constant for a given animal regardless of running speed. It is a useful quantity for comparing the energetics of running in animals differing in geometry, resting metabolism, size, or speed.

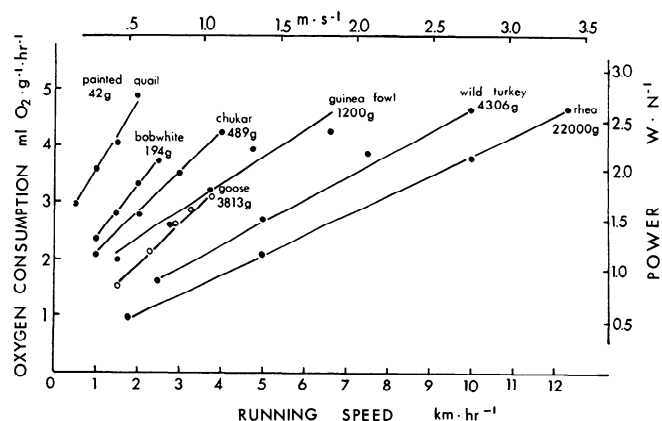


FIG. 2. Relation between oxygen consumption and speed for all birds studied. Points represent observed mean values. Open circles represent means from geese. See Table 2 for regression equations and statistical data.

Figure 2 gives data from all the species studied.<sup>3</sup> The axes in Fig. 2 are similar to those in Fig. 1. Statistical information for each regression line is found in Table 2.

Figure 2 shows that all birds studied have a linear increase of power input with speed. The Y-intercept value of metabolic rate is largest relative to total metabolic rate in small animals moving at low speeds. At any speed, the Y-intercept value is a larger fraction of the total metabolic rate in small animals than it is in large animals. For a particular animal the Y-intercept value is largest relative to total metabolic rate at low speeds and smallest at high speeds.

The smallest bird used, the Chinese painted quail, has the steepest slope. Data for progressively larger birds fall toward the right. The slopes of the regression lines tend to decrease with increasing body size. The slope for the painted quail is nearly 4 times that for the rhea. The only exception to this trend is the greylag goose, which weighs nearly 4 kg and has a slope nearly equal to that of the chukar partridge of one-eighth the weight. After observing geese running, however, this finding is not surprising. In contrast to the other birds studied, geese are awkward runners. It may well be that their body geometry represents a compromise between swimming and running and that their economy of terrestrial transport suffers.

## DISCUSSION

*Similarities between bipeds and quadrupeds.* The relation between metabolic rate and speed is similar in birds and quadrupedal mammals. For nearly all runners studied, the rate of oxygen consumption is linearly related to speed (over the range of speeds that they can maintain without going into substantial oxygen debt). The regression line does not extrapolate to resting rate at zero speed. Among

<sup>3</sup> Since completion of this manuscript we have obtained some data from one individual tinamou, *Nothoprocta pentlandi* (310 g). This bird would only run at speeds between 1 and 2 km/h. The  $E_{run}$  of this bird was almost 1.5 times that predicted on the basis of body weight. The equation relating metabolic rate to running speed for the tinamou is  $Y = 1.2x + 0.7$ , where  $Y$  = metabolic rate in ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> and  $x$  = running speed in km h<sup>-1</sup>.

TABLE 2. Equations relating observed oxygen consumption to speed in running birds

Species	No. of Observations	Estimation Regression Equation $Y = ax + b$	$s_a$	$s_b$	$s_y$	$s_x$	$s^2_{yx}$	F
Painted quail	45	$Y = 1.2x + 2.3$	0.10	0.11	0.64	0.46	0.10	142
Bobwhite	51	$Y = 0.9x + 1.4$	0.08	0.15	0.62	0.56	0.10	132
Chukar	45	$Y = 0.69x + 1.5$	0.05	0.14	0.89	1.16	0.17	161
Guinea fowl	64	$Y = 0.47x + 1.4$	0.03	0.15	0.92	1.70	0.21	188
Goose	84	$Y = 0.72x + 0.5$	0.04	0.10	0.63	0.81	0.07	420
Turkey	53	$Y = 0.41x + 0.6$	0.01	0.10	1.20	2.84	0.09	746
Rhea*		$Y = 0.34x + 0.4$						

$Y$  = metabolic rate in ml  $O_2$   $g^{-1}$   $h^{-1}$ ;  $a = E_{run}$  = slope in ml  $O_2$   $g^{-1}$   $km^{-1}$ ;  $b$  = zero speed intercept;  $s$  = standard deviation of subscripted variable;  $s^2_{yx}$  = residual mean square and  $F$  = the  $F$  statistic for the linear term (all  $P < 0.001$  that relations are nonlinear).

\* Quoted from Taylor et al. (24).

TABLE 3. Equations describing regression lines relating  $E_{run}$  to body size\*

Species	Regression Equation $Y = ax + b$	$s_a$	$s_b$	$s_y$	$s_x$	$s^2_{yx}$
Birds only	$Y = -0.20x + 0.39$	0.04	0.12	0.20	0.91	0.01
All						
2 Legs	$Y = -0.24x + 0.49$	0.03	0.12	0.25	0.94	0.01
4 Legs	$Y = -0.42x + 0.96$	0.02	0.08	0.64	1.51	0.01

$Y = \log E_{run}$ ;  $x = \log W_B$ ;  $a$  = slope;  $b$  = intercept at  $\log W_B = 0$ ;  $E_{run}$  is in units of ml  $O_2$   $g^{-1}$   $km^{-1}$ ;  $W_B$  = body weight in g;  $s$  = standard deviation of subscripted variable; and  $s^2_{yx}$  = residual mean square. \* See Fig. 3.

bipedal mammals this seems to be true of running humans (18) and of three other species of primates (25), but it is not true of walking in humans (4). Nonlinearities at low or even higher speeds might show up in other animals—for example, if a particular gait could be maintained beyond the usual switch points between the gaits.

**Differences associated with body size.** In both two- and four-legged runners the slopes of the regression lines relating  $\dot{V}O_2$  to speed ( $E_{run}$ ) decrease with increasing body size, but quantitatively this decrease is more gradual in bipeds than quadrupeds.

When the values for  $E_{run}$  from running birds are plotted against body weight on logarithmic coordinates, they fall near a straight line that has a slope of  $-0.20$  (Table 3). When  $E_{run}$  values from all bipeds are plotted together (Fig. 3), they all fall on a line not significantly different from birds alone. Slopes ( $E_{run}$ ) for quadrupedal mammals when plotted in this way also fall along a straight line, but this line has a slope of  $-0.42$  (26).

The lines for bipeds and quadrupeds cross at body weights of under 1 kg (see Fig. 3). In the range 100 g–5 kg the estimated slopes ( $E_{run}$ ) are separated by less than 2 SE of the estimate. The differences between bipeds and quadrupeds in this range are likely to be small.

**Possible reasons for differences.** The data presented in Fig. 3 suggest that the change with body size in the energetic requirement of running on two and on four legs is different. This finding is surprising. It suggests that, in spite of vast differences in gaits, limb moments, and muscle characteristics (12), there is some underlying similarity in energetic

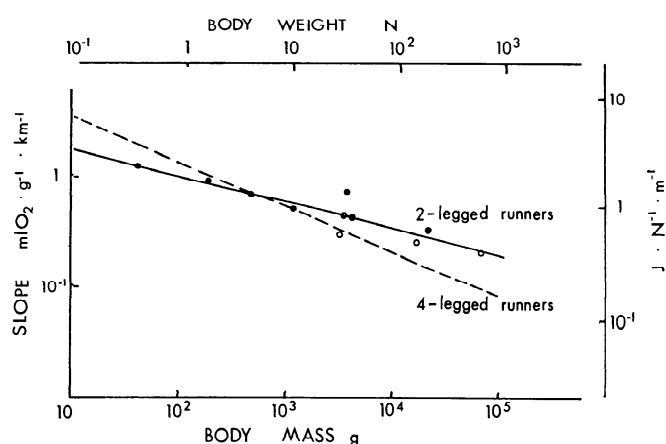


FIG. 3. Logarithmic plot of  $E_{run}$  against body size for all 2-legged runners for which data are available. Solid dots represent birds. Open circles represent primates, which, reading from left to right, are capuchin monkey (below line), spider monkey, chimpanzee (25), and man (18). Solid line is least-squares regression line through all points. Dotted line (4-legged runners) is from Taylor et al. (23). See Table 3 for equations and statistical data. The two lines have different slopes ( $P < 0.001$  that slopes are equal).

requirements between all the quadrupeds on one hand and all bipeds on the other. To attempt to explain the differences in scaling between two- and four-legged animals, let us consider how the power developed by running animals is used.

When an animal is running at constant velocity (i.e., constant step-to-step average velocity) on the level, the only external work it must do is to overcome the drag forces acting on it. The scalar product of this drag and the running velocity is the power output ( $P_o$ ) of the animal. The friction in running on a firm, nonslip surface is negligible, and even at the highest speeds observed, power used in overcoming air resistance probably accounts for less than 3% of the power input ( $P_i$ ) (see Tucker (31) and Table 4). If efficiency is defined as the ratio  $P_o/P_i$ , then efficiencies for running animals will range from nearly zero at low speed to a maximum of about 3%. (These low efficiencies may prevail only while running on firm, nonslip, level surfaces. Efficiencies developed while running up inclines certainly are greater, reaching values of over 20% (17, 23). Efficient-



TABLE 4. Estimated  $P_o$  used to overcome air drag of birds running at fastest speeds they would maintain for 20 min or more

Species	$v$ , m s <sup>-1</sup>	$A$ , m <sup>2</sup>	$P_o$ , W	$P_i$ , W	$\frac{P_o}{P_i}$
Painted quail	0.56	0.0065	0.0007	1.1	0.0006
Bobwhite	0.69	0.012	0.002	4	0.0006
Chukar	1.11	0.026	0.02	12	0.002
Guinea fowl	1.83	0.050	0.2	29	0.006
Goose	1.04	0.13	0.08	66	0.001
Turkey	2.78	0.12	2	111	0.01
Rhea	3.47	0.23	6	569	0.01

$P_o = 1/2 \rho C_D A v^3$ , where  $P_o$  is power output;  $\rho$  is density of air,  $C_D$  is drag coefficient (assumed to be 1),  $A$  = estimated frontal area, and  $v$  = velocity.  $P_i$  is metabolic rate.

cies developed on irregular, yielding, or sliding terrain may also be higher than 3%.) It can be expected that drag should be similar in two- and four-legged animals; even if it were not, power used in overcoming it is too small a fraction of the total power input to account for the observed differences in the relation between  $E_{run}$  and body size.

If only a small fraction of the power input is used to do external work, a large fraction must be used internally. External drag forces cannot account for the consistent change of power input with speed over a large size range. Therefore some aspect of the internal work must be responsible.

Since external drag forces are small, animals running on hard, level surfaces need produce only a small forward thrust during each step to overcome them. Most of the work done is used to overcome the effects of decelerations due to the initial contact of the feet with ground, to raise the body (or part of the body) and to bring the legs into position to support the body as it falls, and to produce forward and upward thrust again. The legs must maintain muscle tension to keep the animal from landing in a heap. As the legs contact the ground the muscles therefore maintain tension while they are being stretched. We can imagine a most efficient animal such as an animated pogo stick that, having raised its body once, can land on passive elastic structures and with little further work bounce back up again. Such an animal would only have to do work to overcome drag forces. The running animals discussed here cannot do this. Some of the kinetic energy gained during the first part of the step cycle may be saved in elastic structures, but this cannot happen unless the muscles are tensed. Therefore this saving can only occur at the expense of metabolic work. That is, the efficiencies of muscles during some phases of a step cycle will be negative. The amount of energy stored during one phase of a step cycle and used in another and the net cost of this storage will depend on materials constants, muscle characteristics, and gait (3, 19).<sup>4</sup> There are, therefore,

<sup>4</sup> From Margaria et al. (18) we can calculate that the cost of transport for a walking man can be as little as 75% of that for the same man running at his most economical speed. Cavagna et al. (5) suggested that this economy may stem in part from the fact that in walking

possibilities for a great deal of variation in the amount of work done by muscles during the course of a particular step cycle.

Economy might be one important factor in determining the effects of natural selection on the mechanical characteristics of running animals. If so, we can rephrase our earlier question. What is it about the mechanics of two- and four-legged running that puts different constraints on the realized economy?

Tucker (31) has suggested that in walking and running humans (and presumably any other runners) efficiencies will be highest when the geometry of the animals is arranged so that the muscles will shorten and lengthen at rates where the absolute values of muscle efficiencies are highest. He points out that, during at least some part of the step cycle, the speeds of the feet (or toes) relative to the body ( $v_L$ ) must be as fast as the speed of the body relative to the ground ( $v_B$ ). Tucker further shows that high efficiencies and low costs of transport occur in human-powered transport devices (e.g., bicycles) where the  $v_L/v_B$  ratio is low, i.e., in situations where muscle contraction rates may be adjusted to maximize efficiency rather than be adjusted to ground speed.

It may be possible to extend this idea to two- and four-legged runners. Perhaps the extra pair of legs allows greater freedom to choose efficient speeds of muscle contraction. Just as the skilled bicyclist switches gear ratios to maintain high efficiencies, animals may switch gaits. Possessing four legs may increase the gait options.

The data needed to evaluate this suggestion have, to our knowledge, not been collected. However, running birds may be excellent systems for obtaining the necessary data. Since, when birds run, the vertebral column does not flex and head, body, and wing attitudes remain fixed relative to it, mechanical analysis will be much simplified. The reduced leg number may also ease analysis. These simplifications may facilitate modeling of the system in sufficient detail to provide explanation.

*Effects on cost of transport.* We cannot answer the question of why the energetic requirements of two- and four-legged running show a different body-size dependence, nor do we understand why the slopes should decrease as body size increases. We can, however, show what these differences mean to the animal in terms of cost of transport.

Cost of transport ( $E_T$ ) for bipeds may be calculated from the following equation:

$$E_T = E_{run} + \frac{1.5 M_{std}}{v} \quad (1)$$

The term  $1.5 M_{std}$  signifies the  $Y$  intercept, which averages about 1.5 times the predicted standard metabolic rate ( $M_{std}$ ).  $E_{run}$  is the previously defined slope, and  $v$  is running speed.

humans the kinetic energy of the moving body is converted into potential energy as the body pole-vaults up on the straightened leg and then back again to kinetic energy as the body falls forward on the still straight leg. The straight leg may act like a rigid column and less muscular work would then be required to support the body through a step cycle. They have likened the potential kinetic energy changes in walking to those in an egg rolling end over end.

$M_{std}$  calculated according to Taylor et al. (26) and converted into appropriate units is:

$$M_{std} = 4.6 W_B^{-0.28} \tag{2}$$

$E_{run}$  for two-legged runners (see Fig. 3 and Table 3) is:

$$E_{run} = \frac{dM}{dv} = 3 W_B^{-0.24} \tag{3}$$

$E_{run}$  and  $E_T$  are in ml  $O_2$  g<sup>-1</sup> km<sup>-1</sup>,  $M$  and  $M_{std}$  are in ml  $O_2$  g<sup>-1</sup> h<sup>-1</sup>,  $W_B$  is body weight in g, and  $v$  is running speed in km h<sup>-1</sup>.

In SI units with dimensional constants converted, the above equations are:

$$E_T = E_{run} + \frac{1.5 M_{std}}{v} \tag{4}$$

$$M_{std} = 0.72 W_B^{-0.28} \tag{5}$$

$$E_{run} = \frac{dM}{dv} = 2 W_B^{-0.24} \tag{6}$$

$E_{run}$  and  $E_T$  are dimensionless;  $M$  and  $M_{std}$  are in W·N<sup>-1</sup>;  $W_B$  is body weight in N;  $v$  is running speed in m·s<sup>-1</sup>.

Similar equations for four-legged mammals are found in Taylor et al. (26).

Table 5 compares the cost of transport of two- and four-legged runners over a wide range of body sizes calculated from these equations. The differences are considerable. The cost for an animal the size of a small quail is about three-fourths that for a mouse of equal weight. For animals weighing about 1 kg the costs are about equal. For larger animals the cost for running on two legs is greater than on four. For bipedal animals the size of a man (or perhaps an ostrich) the predicted cost of running a kilometer is over twice that predicted for a quadruped of the same size.

*Comparison with flyers and swimmers.* Figure 4 compares the cost of transport in running birds to other forms of animal locomotion. The dotted line represents the plot of slopes ( $E_{run}$ ) for running birds in Fig. 3. The curved line above it represents cost of transport ( $E_T$ ) calculated from the equations given above at the highest (and therefore cheapest) speeds the birds would maintain.

The costs of two- and four-legged running have already been compared, and both are much higher than flying or

TABLE 5. Comparison of calculated cost of transport of 2- and 4-legged runners at maximum sustained speeds

Body Wt, g	Speed, km h <sup>-1</sup>	Cost		Cost Ratio, 2 Legs/4 Legs
		2 Legs	4 Legs	
40	2	2.34	3.14	.75
1,000	7	0.72	0.69	1.04
20,000	12.5	0.35	0.20	1.75
70,000	15	0.27	0.12	2.25

Costs ( $E_T$  in ml  $O_2$  g<sup>-1</sup> km<sup>-1</sup>) were calculated by equation 1 for bipeds and the equation:  $E_{T4} = 8.5 W_B^{-0.04.0} + 6 (W_B^{-0.25})/v$  for quadrupeds (26), where  $W_B$  is body weight in grams and  $v$  is speed in km h<sup>-1</sup>.

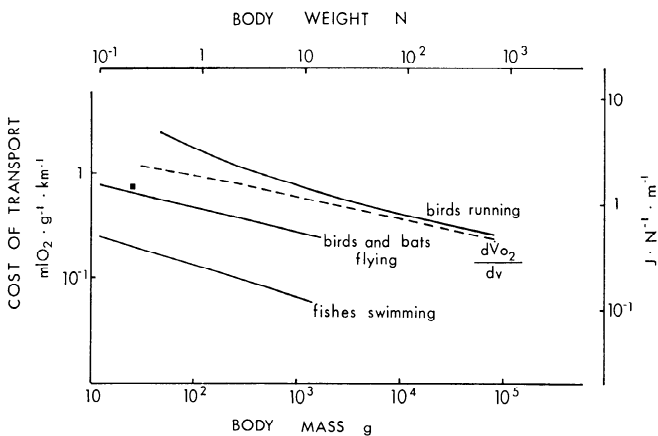


FIG. 4. Cost of transport ( $E_T$ ) of various forms of locomotion plotted on logarithmic coordinates against body weight. Dotted line represents regression line for birds in Fig. 3. It represents  $E_{run}$ , not  $E_T$ . Solid square is cost of transport of a 24-g snake (6).

fish swimming (data from Schmidt-Nielsen (22) and Tucker (29)). It is interesting that the cost of transport for a small snake (solid square) is much lower than for runners of the same size (6).

This work was supported by National Institutes of Health Research Grant HL-02228 and Research Career Award 1-K6-GM-21,522 to K. Schmidt-Nielsen.

Received for publication 24 October 1973.

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