

# Scaling of energetic cost of running to body size in mammals

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TAYLOR, C. RICHARD, KNUT SCHMIDT-NIELSEN, AND JACOB L. RAAB. *Scaling of energetic cost of running to body size in mammals.* Am. J. Physiol. 219(4): 1104–1107. 1970.—The purpose of this study was to see if a convenient relationship could be found between the energetic cost of running and the body weight of mammals. We found that steady-state oxygen consumption of seven groups of mammals (21 g–18 kg) increased almost linearly with running speed. Oxygen consumption ( $M$ , ml  $O_2$   $g^{-1}$   $hr^{-1}$ ) relative to running velocity ( $V$ , km  $hr^{-1}$ ) could be expressed by linear equations:

white mouse ( <i>Mus musculus</i> , 21 g)	$M = 2.83V + 3.34$
kangaroo rat ( <i>Dipodomys merriami</i> , 41 g)	$M = 2.01V + 1.75$
kangaroo rat ( <i>Dipodomys spectabilis</i> , 100 g)	$M = 1.13V + 1.81$
ground squirrel ( <i>Citellus tereticaudus</i> , 236 g)	$M = 0.66V + 1.27$
white rat ( <i>Rattus norvegicus</i> , 384 g)	$M = 1.09V + 1.48$
dog ( <i>Canis familiaris</i> , 2.6 kg)	$M = 0.34V + 0.75$
dog ( <i>Canis familiaris</i> , 18.0 kg)	$M = 0.17V + 0.65$

The  $y$ -intercepts (extrapolated zero running velocity) were above the resting oxygen consumptions. Cost of running 1 km (ml  $O_2$   $g^{-1}$   $km^{-1}$ ) decreased with increasing speed and approached a minimum value which is a constant for each animal. This minimum value is the slope of the curve for oxygen consumption vs. velocity. On logarithmic coordinates the minimum cost of running ( $M_{run}$ , ml  $O_2$   $g^{-1}$   $km^{-1}$ ) vs. body weight ( $W$ , g) yields a nearly straight line which can be expressed by the equation:  $M_{run} = 8.46W^{-0.40}$ . Previously published data from horse and dog (but not man) fit this curve.

exercise; oxygen consumption; locomotion; treadmill; metabolic rate; cost of transportation

A MAMMAL'S RESTING METABOLISM can be predicted reasonably well from its body weight. In 1883, Rubner (9) published his classic paper showing that the standard metabolism of dogs was related to their body weight. Small dogs had a higher metabolic rate per kilogram than large ones, metabolic rate being approximately proportional to surface area (or the  $\frac{2}{3}$  power of body weight). In 1932, Kleiber (5) extended the analysis of the relationship between metabolic rate and weight to mammals and birds ranging in size from the ring dove and rat to the steer. He found that standard metabolic rate was more closely related to the  $\frac{3}{4}$  power of body weight than to the  $\frac{2}{3}$  power (coefficient of correlation for  $\frac{3}{4}$  power was +0.98 while that of  $\frac{2}{3}$  power was +0.71). Kleiber's (6) simple relationship,  $M = 3 W^{0.75}$  ( $M$ , standard metabolism in kcal  $hr^{-1}$ ;  $W$ , body weight in kg) has been invaluable in comparing a

multitude of metabolism-dependent parameters of mammals of different weights and has served as a model for many anatomical and physiological comparisons.

When animals move, their metabolic rates increase, but no convenient relationship has been established for predicting the energy expended by mammals in moving from one place to another. In this investigation we set out to see if such a convenient relationship could be found which would allow us to calculate the energetic cost of running from the body weight of a mammal. We used mammals from 21 g to 18 kg, trained them to run on a treadmill, and measured their oxygen consumption.

Soon after the publication of Rubner's work, Zuntz (16) built a treadmill and measured the energy required to move a horizontal meter and to climb a meter on an inclined treadmill for humans, horses, and dogs. Slowtzo (10), working in the same laboratory, made measurements on dogs ranging in weight from 5 to 37 kg. Both investigators concluded that the cost of moving a horizontal meter was only approximately proportional to the  $\frac{2}{3}$  power of body weight, while the cost of climbing 1 m was nearly the same per kilogram, regardless of weight. From Slowtzo's time until very recently more attention has been given to the relationship between maximum sustained metabolism during work and body weight than to the cost to travel a kilometer. Brody (2), Wilkie (15), and Hemmingsen (4) all concluded that maximum sustained metabolism was proportional to  $W^{0.75}$ . Tucker (13, 14) reconsidered the energetic cost of traveling 1 km in birds and mammals. Using his own and other authors' data, he concluded that the minimum cost of flying a kilometer for birds was proportional to  $W^{0.77}$ . He concluded from data in the literature on running mammals that the cost of running 1 km was not a straight line when plotted on logarithmic coordinates but was a more complex relationship. Cost of running 1 km decreases with increasing speed (12) and this complicates the comparison of the cost of running of different species. A minimum cost is approached, however, and this is a constant for each animal. Using this asymptotic minimum cost, we have found a simple relationship between weight and cost of running in mammals (11).

## MATERIALS AND METHODS

*Animals.* Six white mice (19–23 g, *Mus musculus*), five Merriam's kangaroo rats (37–45 g, *Dipodomys merriami*), six bannertailed kangaroo rats (88–121 g, *Dipodomys spectabilis*), three ground squirrels (185–310 g, *Citellus tereticaudus*), six

white rats (335–430 g, *Rattus norvegicus*), two small adult mongrel dogs (2.3–2.9 kg, *Canis familiaris*) and two Walker foxhounds (18.0–18.1 kg) were trained to run on treadmills. The rodents were housed in activity wheels between experiments and the dogs were exercised regularly.

**Procedures.** Oxygen consumption and rectal temperature were measured while animals rested quietly and while they ran on a treadmill at various speeds. All animals, including the kangaroo rats, used all four legs during running. Air temperature was between 22 and 27 C and relative humidity less than 50%. Measurements were recorded continuously, but we used only values obtained after the animals had attained a steady-state oxygen consumption. We considered a steady state to have been reached when there was less than a 5% variation in oxygen consumption during a 30-min period.

The treadmill for rodents was enclosed in a sealed Lucite chamber. Room air was pulled through the chamber at flow rates between 335 and 1,040 liters hr<sup>-1</sup> (STP). Dogs wore a mask while they ran and room air was pulled past their faces at rates between  $2.76 \times 10^3$  and  $1.2 \times 10^4$  liters hr<sup>-1</sup> (STP). Flowmeters were calibrated to better than 1% accuracy using a Brooks Vol-u-meter under pressure gradients indential to those existing in our experimental system. The difference in oxygen concentration between inflow and outflow air was measured with a Beckman model G-2 paramagnetic oxygen analyzer. On maximum sensitivity this analyzer registered full scale deflection for a difference of 0.1% O<sub>2</sub> between standard gas and air sample. It was calibrated by varying the gas pressure within its cell, and the calibration was checked regularly with gases of known concentrations. Rectal temperature of the rodents was measured with thermocouples connected to a recording potentiometer (accuracy  $\pm 0.1$  C). Rectal temperature of the dogs was measured with calibrated thermistor probes (accuracy  $\pm 0.2$  C).

## RESULTS

Steady-state oxygen consumption of each animal increased nearly linearly with increasing speed (Fig. 1). Oxygen consumption ( $M$ , ml O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>) relative to running velocity ( $V$ , km hr<sup>-1</sup>) could be expressed by the following linear equations (method of least squares):

white mouse (21 g)	$M = 2.83V + 3.34$
kangaroo rat (41 g)	$M = 2.01V + 1.75$
kangaroo rat (100 g)	$M = 1.13V + 1.81$
ground squirrel (236 g)	$M = 0.66V + 1.27$
white rat (384 g)	$M = 1.09V + 1.48$
dog (2.6 kg)	$M = 0.34V + 0.75$
dog (18.0 kg)	$M = 0.17V + 0.65$

The  $y$ -intercepts (extrapolated zero running velocity) were higher than both the observed resting oxygen consumptions and the metabolic rates predicted by Kleiber's equation (Table 1).

It might be argued that the difference between the  $y$ -intercept and resting oxygen consumption could be a temperature effect, for the rectal temperature of all running animals increased with increasing speed. This argument, however, cannot be substantiated. If the resting metabolism is corrected for the rectal temperatures observed in animals

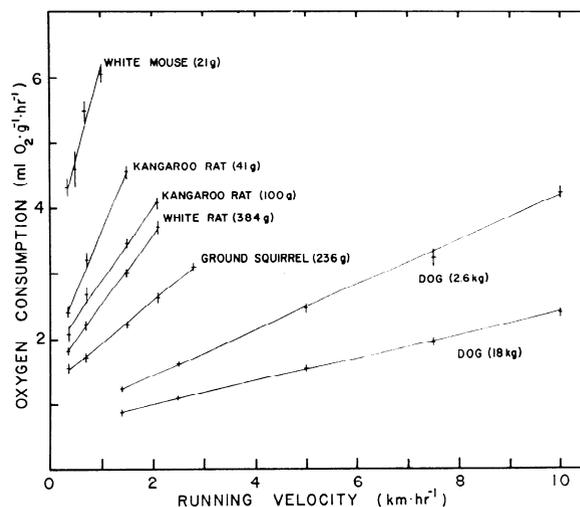


FIG. 1. Oxygen consumption at various running speeds for 7 groups of mammals. Horizontal bars indicate mean oxygen consumption, vertical bars represent  $\pm 2$  SE. Straight lines are fitted by method of least squares and their equations are given in text.

TABLE 1. Oxygen consumption extrapolated to zero running velocity

Animal	Weight	$y$ -Intercept, ml O <sub>2</sub> g <sup>-1</sup> hr <sup>-1</sup>	Observed Resting Metabolism, ml O <sub>2</sub> g <sup>-1</sup> hr <sup>-1</sup>	Predicted Standard Metabolism ( $M_{std}$ ), ml O <sub>2</sub> g <sup>-1</sup> hr <sup>-1</sup>	$y$ -Intercept Predicted $M_{std}$
White mouse	21 g	3.34	$2.27 \pm .07$	1.64	2.0
Kangaroo rat	41 g	1.75	$1.51 \pm .06$	1.40	1.3
Kangaroo rat	100 g	1.81	$1.14 \pm .04$	1.11	1.6
Ground squirrel	236 g	1.27	$1.13 \pm .02$	0.90	1.4
White rat	384 g	1.48	$1.02 \pm .02$	0.80	1.8
Dog	2.6 kg	0.75	$0.61 \pm .06$	0.49	1.5
Dog	18 kg	0.65	$0.32 \pm .02$	0.31	2.1
Mean					1.7

Resting metabolism values are means  $\pm$  SE. Oxygen consumption extrapolated to zero running velocity ( $y$ -intercept) for seven groups of mammals, derived from the linear regression lines in Fig. 1. These values are compared to observed resting O<sub>2</sub> consumption and to predicted standard metabolism  $M_{std}$  (ml O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>) for the same animals ( $M_{std} = 3.5 W^{-0.25}$ ;  $W$  in g).

while running, assuming a  $Q_{10}$  of 3, the corrected resting metabolism increases nearly linearly with speed and extrapolates back to the actual resting metabolism at zero velocity. Figure 2 presents data from the white rat; these are typical of the situation in the other species.

## DISCUSSION

The energetic cost of running 1 km can be obtained by dividing oxygen consumption ( $M$ , ml O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>) by velocity ( $V$ , km hr<sup>-1</sup>). The cost of running 1 km decreases with increasing speed and approaches a minimum value for each of the examined animals (Fig. 3). This asymptotic value is identical to the slope of the curve for the relationship between oxygen consumption and velocity given in Fig. 1

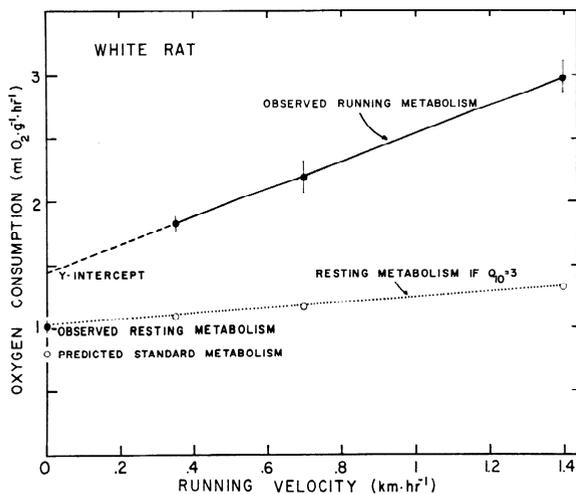


FIG. 2. Oxygen consumption of running rats (solid line). Extrapolated y-intercept (zero running velocity) is higher than observed resting  $O_2$  consumption. This difference cannot be explained by higher rectal temperature observed in running rats and a  $Q_{10}$  effect. Estimated effect on metabolic rate of increased temperature, assuming a  $Q_{10} = 3$ , is indicated as dotted line. Solid dots are mean oxygen consumption and vertical bars are  $\pm 2$  SE. Standard metabolism predicted by Kleiber's  $W^{0.75}$  relationship is also included.

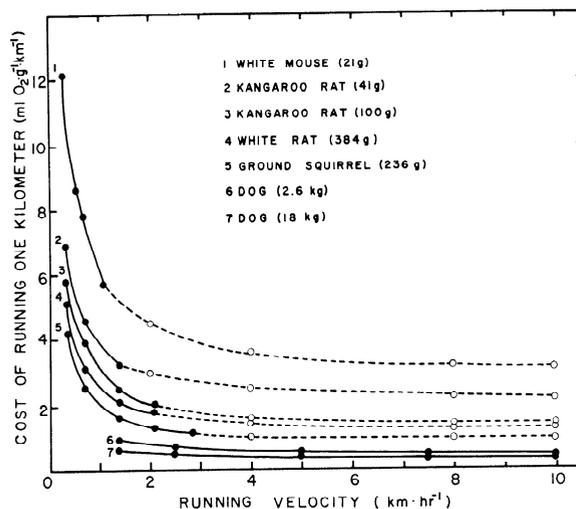


FIG. 3. Cost of running 1 km (oxygen consumption at a given velocity divided by that velocity) decreases as speed increases. Dashed portions of curves are extrapolated, based on assumption that oxygen consumption vs. running speed remains linear. At high speeds y-intercepts become numerically less important and curves approach minimum values. These minimum values equal slopes of curves relating oxygen consumption to speed of running (given in Fig. 1).

and, thus, is a constant which is characteristic of each animal.

The minimum cost to run 1 km is a convenient way to compare animals of different size, since it is a constant for each animal. Other authors have used other useful ways to express the energetic cost of exercise and work, for example, total metabolic cost, exercising less resting metabolism, and exercising metabolism less y-intercept. For our purposes the use of minimum cost avoids some difficulties. For example, both the total cost and the exercising less resting cost may vary severalfold with speed, and the choice of any one speed, or even the maximum speed

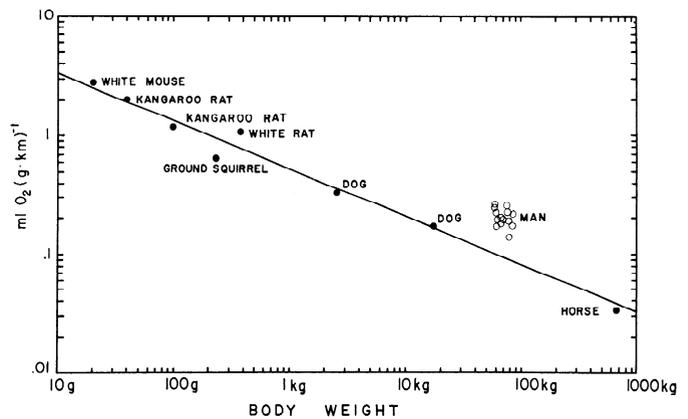


FIG. 4. Minimum cost of running (defined as slope of curve relating oxygen consumption to speed of an animal, see text) plotted against body weight on logarithmic coordinates yields a nearly straight line with a slope of  $-0.40$ . Previously published data from horse (2) fall on same line, but data from man (1, 3, 7, 8) fall above line.

reported for an animal, would be more arbitrary for a comparison of animals of different sizes.

On logarithmic coordinates, the minimum cost of running ( $M_{run}$ ,  $ml O_2 g^{-1} km^{-1}$ ) vs. body weight ( $W$ , g) yields a nearly straight line (Fig. 4) which can be expressed by the equation (method of least squares):

$$M_{run} = 8.46 W^{-0.40} \quad (1)$$

This simple equation allows the minimum cost of running to be calculated from body weight. 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. Data from man (1, 3, 7, 8) are well above the predicted  $M_{run}$  for other animals (Fig. 4). The high cost of running in man may reflect the fact that he uses two appendages for running, rather than four.

The cost of running at any speed could be calculated from an animal's weight if the y-intercept of the relationship between oxygen consumption and velocity could also be predicted. The y-intercepts in our study were, on the average, 1.7 times the standard metabolism predicted by Kleiber's  $W^{3/4}$  relationship (Table 1). Thus, an approximation of the actual cost of running at any speed ( $M'_{run}$ ) can be derived from an animal's weight ( $W$ ) by adding to its minimum cost of running ( $M_{run}$ ) 1.7 times the predicted standard metabolism ( $M_{std}$ ) divided by the velocity ( $V$ ) at which the animal travels. The equation for this relationship would be:

$$M'_{run} = M_{run} + \frac{1.7M_{std}}{V} \quad (2)$$

$M_{run}$  is given in equation 1, and  $M_{std}$  is derived from Kleiber's equation (units converted to  $ml O_2 g^{-1} hr^{-1}$ ):

$$M_{std} = 3.5W^{-0.25} \quad (3)$$

Insertion into equation 2 gives:

$$M'_{run} = 8.5W^{-0.40} + \frac{6.0}{V} W^{-0.25} \quad (4)$$

The cost for the entire animal to travel 1 km,  $M''_{\text{run}}$  (ml  $\text{O}_2 \text{ km}^{-1}$ ), is obtained by multiplying both sides of the equation by  $W$ :

$$M''_{\text{run}} = 8.5W^{0.60} + \frac{6.0}{V} W^{0.75} \quad (5)$$

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