Atriplex, whereas other gerbils are more typically seed eaters (*16*). *Psammomys obesus* differs from *D. microps* in that it apparently consumes leaves in toto and that it produces a much more concentrated urine, about 5000 milliosmol/liter (*17*). Thus, the diets of *D. microps* and *P. obesus* are similar, but the adaptive means of meeting the physiological challenge of high salinity were different, being primarily behavioral in *D. microps* and more physiological in *P. obesus*. It is, nonetheless, notable that in similar ecological settings, natural selection has produced a similar adaptive pattern of divergence—leaf eating—in two species which are members of separate, but parallel, systems of typically granivorous rodents.

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12. For the feeding experiment with leaves, $N = 7$ for each species and ambient temperature was 12° to 15°C. For the experiment with a seed diet, $N = 8$ for each species and ambient temperature was 15°C. Mean survival for *D. microps* on a seed diet was 16 days.
13. For *D. microps*, $N = 8$, S.E. = 233; for *D. merriami*, $N = 7$, S.E. = 140.
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Running Up and Down Hills: Some Consequences of Size

Abstract. *Small mammals are able to run at about the same maximum speed vertically as horizontally, but larger mammals cannot do this. During level running a mouse weighing 30 grams uses about eight times as much energy per unit of body weight as does a chimpanzee weighing 17.5 kilograms (42.6 joules per kilogram meter versus 5.17 joules per kilogram meter). The additional energy required to lift 1 kilogram of body weight 1 meter while running uphill was similar for the two species (about 15.5 joules per kilogram meter). Therefore the increment in energy expenditure for mice to run uphill compared to running horizontally is about one-eighth that for a chimpanzee. Both mice and chimpanzees were able to recover about 90 percent of the energy stored running uphill on the way down.*

Some small animals appear to accomplish extraordinary energetic feats when they run vertically. Squirrels run up tree trunks at about the same speed that they run on level ground. Intuitively this seems unreasonable, for man must increase his metabolism markedly to maintain his speed upon encountering even a slight incline. How do small animals accomplish this feat of vertical running? Are they able to increase their metabolism by a relatively greater amount than man, or does it take them relatively less energy to run uphill?

Kleiber's familiar equation states that resting metabolism is proportional to the body weight to the ¾ power in mammals (*1*), and thus each gram of tissue from a 30-g mouse consumes oxygen at about 13 times the rate per gram of tissue from a 1000-kg horse. The mechanical work involved in lifting 1 kg 1 vertical meter, however, is the same for both the mouse and the horse (9.80 joules or 2.34 cal; 1 joule = 4.19 cal). If the mechanical efficiency of muscles of different sized mammals is also the same (*2*), then the same amount of energy should be expended in lifting 1 kg 1 vertical meter by both the mouse and the horse. Thus the relative increase in metabolic rate for the vertical component of running uphill in the mouse should be about 1/13th that for the horse.

Table 1. The values of various parameters of oxygen consumption as determined from the data in Fig. 1. S is the slope, determined by the method of least squares, of the relationship between oxygen consumption and running velocity and is given in milliliters of O_2 per kilogram meter. The y intercept of the oxygen consumption line is given in liters of O_2 per kilogram hour, n is the number of trials, and r is the correlation coefficient. The predicted values are the slopes for level running calculated on the basis of body weight (*4*).

Type of running	S	y intercept	n	r
		Mice		
Uphill	2.28	2.66	26	0.94
Downhill	1.96	2.68	22	0.87
Level	2.07	2.57	22	0.90
Predicted	2.17			
		Chimpanzees		
Uphill	0.44	0.85	23	0.90
Downhill	0.13	0.79	25	0.94
Level	0.25	0.79	69	0.92
Predicted	0.17			

Can small animals indeed run up inclines with relatively small increases in metabolism above that for level running, and how does the energetic cost of running up and down hills depend on an animal's size? To answer these questions we used three white mice (*Mus musculus*; average weight, 30.2 g) and two chimpanzees (*Pan troglodytes*; average weight, 17.5 kg). We trained the animals to run on treadmills while we measured oxygen consumption and carbon dioxide production. The animals ran at various speeds, on the level, on a +15° incline, and on a −15° incline. Wind velocity was approximately matched to tread speed. Air temperature was 22°C and relative humidity was less than 30 percent. We used only steady-state values for oxygen consumption (*3*).

The oxygen consumption of mice running on the level increased nearly linearly with running speed (Fig. 1), and the slope of this line was approximately the same as that predicted by the equation of Taylor, Schmidt-Nielsen, and Raab (*4*) (observed 2.07 ml of O_2 per kilogram meter versus predicted 2.17 ml of O_2 per kilogram meter). There was no statistically significant difference between running uphill on an incline of $+15°$, running on the level, or running downhill on an incline of $-15°$ (Fig. 1 and Table 1). The chimpanzee also increased its oxygen consumption linearly with increasing running speed, and the observed slope was close to the predicted slope (Fig. 1 and Table 1). Running uphill on an incline of $+15°$ nearly doubled the slope, and running downhill on an incline of $-15°$ approximately halved the slope (Fig. 1 and Table 1). The difference between the three slopes (uphill versus level and downhill versus level) was significant ($P < .01$).

One can calculate the net energy expended by mice and chimpanzees in lifting 1 kg of body weight vertically 1 meter while running uphill. Let S (measured in milliliters of O_2 per kilogram meter) be the slope of the line that relates oxygen consumption to running velocity on an uphill incline of angle θ, and let S_0 indicate the value of S for level running. The net energy cost (in joules) of lifting 1 kg of body weight 1 meter is

$$\frac{S - S_0}{\sin \theta} \times 20.1 \ \frac{\text{joules}}{\text{milliliter of } O_2}$$

where $\sin \theta$ indicates the fraction of a meter climbed per meter run. To calculate the energy recovered running downhill we use the difference between the slopes for level running and for downhill running. Table 2 shows the results of these calculations and compares the energy expended in climbing with the mechanical work done by the mice and chimpanzees. We do not have a good enough separation between the level, uphill, and downhill slopes of the mice to allow definitive conclusions about the amount of energy required to lift 1 kg 1 meter. We can conclude, however, that the value is similar for mice and chimpanzees and is relatively independent of the size of an animal. We tried running mice on steeper inclines to get a better separation of the three slopes. The inclines that yield a good separation are so steep (about 50°) that the mice slip and the observed separation may be more the result of the slipping than the incline.

Both the mouse and the chimpanzee recover most of the mechanical energy "stored" during uphill running on their way down (Table 2). Thus gravity is used very efficiently to accelerate the limbs during downhill running.

We conclude that running uphill involves a relatively smaller increase in energy expenditure over horizontal running for small animals than for large animals. This follows from the observations that small animals have a relatively higher energy cost for level running and about the same energy cost for lifting 1 kg 1 meter as large animals. For example, if the net cost of lifting 1 kg 1 meter vertically remained the same on the vertical as on the 15° incline, then to run vertically at a speed of 2 km per hour would require an increase in oxygen consumption over that for level running of 23.5 percent for a 30-g mouse; 189 percent for a 17.5-kg chimpanzee; and 630 percent for a 1000-kg horse.

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Table 2. Energy required and mechanical efficiency for the vertical component of running up a 15° incline, and energy recovered and mechanical efficiency of recovery of stored energy during downhill running. The energy given (1 joule = 4.19 cal) is that expended in raising 1 kg of body weight 1 meter or that recovered upon lowering 1 kg of body weight 1 meter. The mechanical efficiency is calculated as (mechanical work)/(energy expended) for uphill running and as (energy recovered)/(mechanical energy stored) for downhill running. See text for calculations. Values for sheep (*5*) and man (*6*) are from the literature.

Animal	Weight (kg)	Uphill: Energy expended joule/kg · m	Uphill: Efficiency (%)	Downhill: Energy recovered joule/kg · m	Downhill: Efficiency (%)
Mice	0.030	16.3*	60	8.53*	87
Chimpanzee	17.5	14.8	66	9.32	95
Sheep	29.0	26.9	36		
Man†	70.0	28.7	34	3.35	34

* These values were obtained by using the numerical values for slopes for uphill, downhill, and level running. They are only approximations because these slopes were not significantly different for mice. † Efficiency of recovering energy for man running downhill varies with the steepness of the incline, from nearly 100 percent on an incline of −3° to 0 on an incline of −18°. On inclines steeper than − 18° more energy is required to run downhill than to run on a level surface.

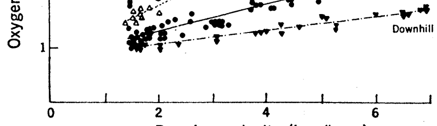

Fig. 1. Steady state oxygen consumption (*3*) at various running velocities for 30-g mice and 17.5-kg chimpanzees during running on the level, running uphill at a +15° incline, and running downhill at a −15° incline.

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