Running in cheetahs, gazelles, and goats: energy cost and limb configuration

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The energetic cost of running in mammals has recently been found to vary in a predictable manner with body weight (8). The reason for this useful empirical relationship is far from clear. Running, unlike flying or swimming, involves little external work on the environment once an animal reaches a constant speed (7). However, kinetic energy is expended in accelerating and decelerating the limbs, even when an animal runs at a constant speed. This has led both physiologists (5) and anatomists (3, 4) to assume that a good part, if not most, of the energy expended during running in animals of approximately the same mass was nearly identical over a wide range of speeds. Also, the observed energetic cost of running was almost the same as that predicted on the basis of body weight for all three species: cheetah, 0.14 ml O₂ (g *km)-¹ observed vs. 0.15 ml O₂ (g *km)-¹ predicted; gazelle, 0.16 ml O₂ (g *km)-¹ observed vs. 0.15 ml O₂ (g *km)-¹ predicted; and goat, 0.18 ml O₂ (g *km)-¹ observed vs. 0.14 ml O₂ (g *km)-¹ predicted. Thus the relationship between body weight and energetic cost of running apparently applies to animals with very different limb configurations and is more general than anticipated. This suggests that most of the energy expended in running at a constant speed is not used to accelerate and decelerate the limbs.

C. RICHARD, AMIRAM SHKOLNIK, RAZI DMI'EL, DAN BAHARAV, AND ARIEH BORUT. Running in cheetahs, gazelles, and goats: energy cost and limb configuration. Am. J. Physiol. 227(4): 848-850. 1974.—Functional anatomists have argued that an animal can be built to run cheaply by lightening the distal parts of the limbs and/or by concentrating the muscle mass of the limbs around their pivot points. These arguments assume that much of the energy expended as animals run at a constant speed goes into alternately accelerating and decelerating the limbs. Gazelles, goats, and cheetahs offer a nice gradient of limb configurations in animals of similar total mass and limb length and, therefore, provide the opportunity to quantify the effect of limb design on the energy cost of running. We found that, despite large differences in limb configuration, the energetic cost of running in cheetahs, gazelles, and goats of about the same total mass was nearly identical over a wide range of speeds. Also, the observed energetic cost of running was almost the same as that predicted on the basis of body weight for all three species: cheetah, 0.14 ml O₂ (g *km)-¹ observed vs. 0.15 ml O₂ (g *km)-¹ predicted; gazelle, 0.16 ml O₂ (g *km)-¹ observed vs. 0.15 ml O₂ (g *km)-¹ predicted; and goat, 0.18 ml O₂ (g *km)-¹ observed vs. 0.14 ml O₂ (g *km)-¹ predicted. Thus the relationship between body weight and energetic cost of running apparently applies to animals with very different limb configurations and is more general than anticipated. This suggests that most of the energy expended in running at a constant speed is not used to accelerate and decelerate the limbs.

THE ENERGETIC COST OF RUNNING IN MAMMALS HAS RECENTLY BEEN FOUND TO VARY IN A PREDICTABLE MANNER WITH BODY WEIGHT (8). THE REASON FOR THIS USEFUL EMPIRICAL RELATIONSHIP IS FAR FROM CLEAR. RUNNING, UNLIKE FLYING OR SWIMMING, INVOLVES LITTLE EXTERNAL WORK ON THE ENVIRONMENT ONCE AN ANIMAL REACHES A CONSTANT SPEED (7). HOWEVER, KINETIC ENERGY IS EXPENDED IN ACCELERATING AND DECELERATING THE LIMBS, EVEN WHEN AN ANIMAL RUNS AT A CONSTANT SPEED. THIS HAS LED BOTH PHYSIOLOGISTS (5) AND ANATOMISTS (3, 4) TO ASSUME THAT A GOOD PART, IF NOT MOST, OF THE ENERGY EXPENDED WHEN AN ANIMAL RUNS IS USED IN THIS MANNER. IF THIS IS THE CASE, THEN IT IS POSSIBLE TO DESIGN THE LIMBS TO MINIMIZE THIS ENERGY EXPENDITURE AND TO ENABLE THE ANIMAL TO MOVE CHEAPLY. THE KINETIC ENERGY NECESSARY TO ROTATE A LIMB IS EQUAL TO ITS MOMENT OF INERTIA TIMES THE SQUARE OF ITS ANGULAR VELOCITY. THE

Exercise; energetics; metabolism

The angular velocity can be ignored, since at a given ground speed it will be identical for limbs of the same length, as long as the animal moves them in a similar manner.

The optimal design of limbs will depend on how an animal uses them. Functional anatomists have argued convincingly that animals that cover long distances have limbs designed to enable them to move cheaply (3, 4, 5), and the gazelle is usually given as one of the best examples of an animal built under design constraints imposed by economy of locomotion. The cheetah is a good example of an equally good runner (at least in terms of speed) that has been built under different design constraints. The cheetah accelerates rapidly and uses its front legs to knock down its prey. Moving cheaply certainly is not as important to the cheetah as having limb bones able to withstand the stresses involved in both rapid acceleration and clubbing down prey. As one might expect, the limbs of the cheetah appear massive when compared to those of a gazelle of similar length (which are light and so fragile that great care must be taken when handling these animals so as not to break their legs). Also, the muscle mass of the cheetah's legs extends a considerable distance down the limb and is not concentrated around the pivot point.

This is in marked contrast to the leg of the gazelle, where the center of mass of the leg is almost superimposed on the pivot point.

Animals, however, never run at a constant speed. The center of mass of an animal accelerates and decelerates during each stride, both in a horizontal and a vertical plane. The energy expended in these velocity changes accounts for a large part of the total energy expended during running in man, where they have been quantified (1, 2). Energy expended in this manner can be independent of limb configuration.

The purpose of this study was to compare the energy expended during running in animals of approximately the same body mass and with limbs approximately the same
length, but with different limb mass and distribution of this mass along the limb. We hoped to determine how generally the relationship between energetic cost of running and body mass might be applied and to gain some insight into how an animal expends energy as it runs. We selected cheetahs, goats, and gazelles as experimental animals for this study.

**Materials and Methods**

*Animals.* Two cheetahs (*Acinonyx jubatus*), three goats (*Capra hircus*), and three gazelles (*Gazella gazella*) were used. The cheetahs (1 male, avg wt 44 kg; 1 female, avg wt 34 kg) were purchased from a farmer in Southwest Africa. The animals were hand reared from birth and were sent by air freight to our laboratory when adults. The three gazelles (all males, avg wt 23.15 kg) were hand reared in the Zoological Garden of Tel-Aviv University. The goats (all females, avg wt 28 kg) were purchased from local Massachusetts farmers.

*Procedures.* Steady-state oxygen consumption was measured while animals ran on a treadmill at various speeds. We considered the animals to be in a steady state when: 1) oxygen consumption varied less than ±3% over a 10-min interval and 2) the oxygen debt incurred was so small that including the payoff of oxygen debt over a 30-min period following the run did not add more than 2% to the steady-state values. Air temperature was 22°C and wind speed was approximately matched to treadmill speed.

The animals wore a ventilated mask through which room air was metered at a rate between 36 and 1,000 liters·min⁻¹ (STP). An aliquot of air leaving the mask was dried, carbon dioxide was absorbed, and then the aliquot was passed through a paramagnetic oxygen analyzer to determine the concentration of oxygen (Beckman model F-3 or Beckman model G-2, sensitivity 20-21% or 19-21% oxygen for full-scale deflection). Oxygen concentration was corrected for changes in volume due to the absorption of carbon dioxide from the air stream. Flowmeters were calibrated to better than 1% accuracy using gas flow calibrators (Brooks Instrument Company Vol-U-Meters). The accuracy of the oxygen determination was measured by flowing nitrogen at known rates into the mask (diluting the oxygen in room air much the way an animal does) and determining the change in oxygen concentration of the air flowing through the mask. The accuracy was found to be better than ±2%.

Measuring the energy expended in moving the limbs as animals run at different speeds would require knowing the mass, the center of mass of the different segments of the limb, and the moment of inertia around each center of mass and doing kinematic analyses of high-speed films at a variety of speeds. The cheetahs and gazelles were too valuable and the equipment required too costly to make these important measurements. However, dead specimens of all three species became available (a cheetah that died in a zoo, a gazelle that was shot for an ecological study, and a goat of similar total mass and limb length between the cheetah, the gazelle, and the goat). Thus, according to the arguments made by anatomists, the gazelle certainly appears built to run cheaply, at least when compared to the cheetah.

Despite the large differences in limb configuration, there was little difference between the energy expended while running by the cheetah, the gazelle, or the goat at any speed. Steady-state oxygen consumption increased nearly linearly with increasing speed in all three species (Fig. 1) and the correlation coefficient for the linear regression between oxygen consumption and speed was extremely high (0.93 for cheetah, 0.94 for gazelle, and 0.95 for goat).

**Discussion**

It is surprising that there is so little difference between the amount of energy expended while running by the cheetah, the gazelle, and the goat, despite the large differences both in mass of the limbs and the way in which the mass is distributed along the limbs. Even though these measurements do not accurately reflect the moment of inertia of the limb of a running animal, the magnitude of the difference is so large that one would expect to observe a significant difference in the amount of energy expended during running by the three animals, at least when they are using similar strides. Cheetahs, goats, and gazelles do have similar strides at speeds up to about 10 km·hr⁻¹, and thus the gazelle and the goat should expend much less energy in accelerating and decelerating their limbs when moving at these speeds than the cheetah. Since total energy expenditure of the three animals is nearly identical as they run at the same speed, either the amount of energy expended in accelerating and decelerating the limbs is small compared to the amount of energy expended in other ways during running or the greater

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<th>TABLE 1. Differences in limb configuration of gazelle, cheetah, and goat of similar total mass and limb length</th>
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moment of inertia of the cheetah limb is compensated for by greater elastic storage of energy. It would appear that although the anatomist's arguments about how to build limbs to minimize the energy cost of running are intuitively appealing and correct, the magnitude of the effect is so small that we could not observe it by measuring the oxygen consumption of running animals.

Recently Taylor, Schmidt-Nielsen, and Raab (8) have found an empirical relationship between energy cost of running and body mass in a number of mammals. The slope of the relationship between oxygen consumption and body mass can be predicted by the simple equation $M_{\text{run}} = 8.46 W^{-0.48}$, where $M_{\text{run}}$ is the slope of the relationship between oxygen consumption and running speed (in ml O$_2$ (g-km)$^{-1}$) and $W$ is body mass (in g). The observed slopes of gazelles, cheetahs, and goats fell very close to the slopes predicted on the basis of body weight: the observed slope of the cheetah was 0.14 ml O$_2$ (g-km)$^{-1}$ vs. the predicted slope of 0.13; the observed slope of the gazelle was 0.16 ml O$_2$ (g-km)$^{-1}$ compared to the predicted slope of 0.15; and the observed slope of the goat was 0.18 ml O$_2$ (g-km)$^{-1}$ compared to the predicted value of 0.14. At higher running velocities the contribution of the intercept to the total oxygen consumption becomes small, and the slope times the velocity represents the major portion of the cost of running.

The equation of Taylor, Schmidt-Nielsen, and Raab for calculating the slope appears valid for a great number of quadrupedal animals even though they differ greatly in the structural arrangement of the limbs. The explanation of this empirical relationship, however, still remains unclear.

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