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

C. RICHARD TAYLOR, AMIRAM SHKOLNIK, RAZI DMI'EL, DAN BAHARAV, AND ARIEH BORUT
Museum of Comparative Zoology and Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138; and Department of Zoology, Tel-Aviv University, Tel-Aviv, and Department of Zoology, Hebrew University, Jerusalem, Israel

TAYLOR, 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 gradation 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 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 O\textsubscript{2} (g \cdot km\textsuperscript{-1}) observed vs. 0.13 ml O\textsubscript{2} (g \cdot km\textsuperscript{-1}) predicted; gazelle, 0.16 ml O\textsubscript{2} (g \cdot km\textsuperscript{-1}) observed vs. 0.15 ml O\textsubscript{2} (g \cdot km\textsuperscript{-1}) predicted; and goat, 0.18 ml O\textsubscript{2} (g \cdot km\textsuperscript{-1}) observed vs. 0.14 ml O\textsubscript{2} (g \cdot km\textsuperscript{-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.

eexercise; energetics; metabolism

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
ENERGY COST OF RUNNING AND LIMB DESIGN

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 that we purchased) and we made simple measurements of: 1) total mass of the animal, 2) total mass of the four limbs, 3) average length of the four limbs, and 4) average distance between the center of mass of the four limbs while extended and their pivot points.

The four limbs of each of the animals were separated from the body. Great care was taken to include all the tissue mass that moved during running and to identify the point of rotation of the front legs. Each limb was weighed and the center of mass was determined with the limb in the extended position by balancing it on a plexiglass sheet supported by a ball bearing. For the hindlimbs, the hip joint was considered to be the pivot point.

RESULTS

Both the mass of the limbs and the distance from the center of mass to the pivot point differed greatly between the cheetah, the gazelle, and the goat (Table 1). The mass of the four limbs of the gazelle was only 3/5 and that of the goat less than 2/3 the mass of the cheetah. The average distance from the center of mass of the limbs to their pivot points differed even more; for the gazelle it was 3/4 and for the goat 1/3 that observed for the cheetah. 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 h⁻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
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 $M_{\text{run}} = 8.46 W^{-0.43}$, 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.

We thank Prof. H. Mendelssohn for allowing us to use the three tame gazelles and Prof. Farish A. Jenkins, Jr., for helping us with the dissections.

This work was supported by grants from the National Science Foundation (GB-27539) and the National Geographic Society.

Received for publication 6 July 1973.

REFERENCES