

*Walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fish—and bicyclists*

Many of us have ridden bicycles at some time in our lives, and in fact this mode of transportation has become markedly more popular recently as a result of the energy shortage. Each morning at my own university, Duke, people can be seen riding machines with masses of 10 to 20 kilograms and struggling to reach one of the campus entrances at the top of a long, steep hill. As in many other aspects of animal locomotion, there is a paradox here. Why should people encumber themselves with such heavy apparatus, particularly while going uphill? Ask a rider this question, and the response is usually: "It's easier than walking" or "It's faster than walking." But why should it be?

A number of incorrect explanations are offered: "A bicycle has gears." Shifting gears allows the rider to vary the speed at which the feet move; but even if the foot speeds of a cyclist and a pedestrian are matched, the cyclist still goes farther and in less time on a given

amount of energy than the pedestrian. "Your weight is supported by the seat." But if you pedal standing up, biking still is faster and less costly of energy than going on foot. "Your center of gravity doesn't go up and down." But it does if you pedal standing up. Why, then, is bicycling easier than walking or running?

A comparable problem involves the speed of motion of different animals. A sparrow and a mouse have the same mass and, when moving at appropriate speeds, they have the same metabolic rate. Yet the sparrow moves ten times faster than the mouse. How can this be?

A related third problem involves animal migration. Let us define migration as movement from one point to another, achieving a displacement through a medium of at least 20 kilometers per day for at least 20 days, with a new starting point each day. Few if any terrestrial animals with masses less than one kilogram migrate by this definition—only the movements of lemmings come to mind. Several larger species with masses between 10 and 100 kilograms migrate: for example, hunting dogs, humans, mountain lions, cheetahs, and small antelopes. But migration is common among the largest terrestrial mammals, such as caribou, bison, and large antelopes. On the other hand, many flying birds migrate, and most flying birds have masses below one kilogram. Even some flying insects with masses of approximately one gram migrate, as do small swimming animals with masses of one kilogram and up. Why is it only among the terrestrial animals that migration is rare in

animals with masses less than one kilogram?

The answers to these questions depend on the energetic cost of moving about. Only the total amount of energy used by the muscles of locomotion need be considered—a complete description of the specific muscles involved and their motions is excluded from this analysis. Mechanical work and the forces and displacements upon which it depends are the subject matter of engineering; the viewpoint and terminology in this paper owe much to that field.

## Energy expenditure

Let us first define a quantity with which to measure the energetic cost of moving about. A living animal continually expends energy ( $e$ ) in the sense that it oxidizes a substrate, and the energy released is either lost as heat or used to do some form of work. The rate of energy release is commonly called the *metabolic rate*, although I will refer to it as the *power input* ( $P_i$ ), a term more consistent with engineering usage. Power input is determined by measuring rates of exchange of oxygen and carbon dioxide and applying standard energy conversion factors. If an animal with power input  $P_i = de/dt$  is moving along some level path  $x$  at the speed  $V = dx/dt$ , then the ratio  $P_i/V$  is  $de/dx$ , or approximately the energy expenditure to achieve a displacement of unit distance.

The energy expenditure is given exactly by the ratio  $P_i/V$  in these conditions if the ratio is independent of the animal's weight, or if the animal eats frequently enough

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to replace the weight of fuel it uses up in moving a unit distance. For a vertebrate, when the unit distance traveled is a kilometer or less, the body weight change even without eating is so small that the ratio  $P_i/V$  is virtually constant. Some migrating birds may use up to 25 percent of their body weight as fuel between feeding periods; in these cases, the relation between  $P_i/V$  and body weight must be taken into account.

The reciprocal of the ratio  $P_i/V$  is familiar to us as a measure of automobile fuel economy. "Miles per gallon" is simply proportional to the quantity  $V/P_i$ , the proportionality constant being necessary to convert power input from units of energy per time to volume per time. Transportation engineers commonly measure the fuel economy of a vehicle in ton-miles/gallon, which is simply the miles per gallon multiplied by the weight of the vehicle. Thus, the greater the ton-miles/gallon, the more weight a vehicle transports over a given distance on a given quantity of gasoline.

Since biologists traditionally have been more interested in how much energy an animal uses than in how far it travels on a given amount of energy, let us stick with our quantity  $P_i/V$  with energy in the numerator and modify it to correspond with the reciprocal of the engineer's ton-miles/gallon. This is accomplished by dividing  $P_i/V$  by body weight ( $W$ , the product of body mass and the acceleration of gravity). If power, velocity, and weight (a force) are all expressed in a consistent system of units, the quantity  $P_i/(WV)$  is dimensionless and has the same value in any system of units. Let us call the dimensionless quantity  $P_i/(WV)$  the cost of transport.

The cost of transport as I have defined it expresses approximately the energy expenditure per unit weight of an animal moving at a given speed on a level path for a unit distance. Clearly, the cost of transport varies markedly with speed, since it is infinite when the animal stands still, but becomes finite when speed is greater than zero. In fact, cost of transport will have a minimum value at some speed, and this speed will be that

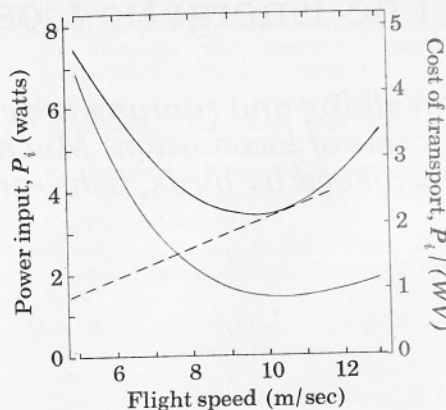


Figure 1. The curves show the relation between power input and speed (black) and cost of transport and speed (color) for a small parrot, with a mass of 0.35 kg, in level flight. The bird uses fuel at a high rate at both high and low speeds but has a minimum power input at an intermediate speed. The cost of transport has its minimum value at a higher speed, which can be determined graphically from the point where a line drawn through the origin of the axes for power input and flight speed is tangent to the corresponding curve.

at which the animal can cover distance on the level with the least energy expenditure. For example, a human with a mass of 70 kg achieves the minimum cost of transport at a fast walk—1.75 m/sec (3.85 mph). The metabolic rate at this speed is 452 watts, and the cost of transport is 0.376. When jogging briskly (at a speed of 3.5 m/sec, or 7.7 miles per hour, or 1 mile in 7.8 minutes) the metabolic rate is 1,122 watts and the cost of transport rises to 0.467.

The relation between power input and speed, and cost of transport and speed, can be illustrated with data from a small parrot in level flight (Fig. 1). The budgerigar or common pet-store parakeet can be trained to fly freely in a wind tunnel while wearing a mask, and thus its power input can be measured during flight at various speeds (Tucker 1968). As with all heavier-than-air flying machines, the budgerigar uses fuel at a high rate (has a high power input) at both high and low speeds but has a minimum power input at some intermediate speed. The speed for minimum cost of transport may coincide with this speed but usually is higher. It can be determined graphically as the speed at which a line through the origin of a graph for  $P_i$  and  $V$  is tangent to the curve for  $P_i$ .

In Figure 2, I have plotted the minimum costs of transport for a variety of swimmers, fliers, and runners, as well as some of those for man-made devices and various forms of human locomotion. Since the range of masses on the abscissa of the figure covers 12 orders of magnitude from a fruit fly to a freight train, it is not surprising that the minimum costs of transport vary widely. What is surprising is that swimming, flying, and pedestrian animals fall roughly into separate groups, irrespective of their taxonomic status. Thus if the mice are excluded from the pedestrians, a single line describes the minimum costs of transport for runners varying in size from small lizards and running birds to a horse. Likewise, a single line fits the data for swimming fishes, and another line fits that for fliers ranging in size from a fruit fly to the largest of all muscle-powered fliers—man, flying, of course, with the aid of machinery that provides wings and a bicyclelike transmission through which the legs can drive a propeller.

The data in Figure 2 quantify the paradoxes described at the beginning of this paper: Bicyclists are willing to carry along the extra masses of their machines, because the minimum cost of transport for a cyclist is about one-fourth that for a walker. In fact, a cyclist has the lowest cost of transport ever measured for an animal, although the line for swimmers suggests that large fishes and whales can do better. A sparrow, which is identical in mass and metabolic rate to a mouse but flies an order of magnitude faster than a mouse runs, has a minimum cost of transport an order of magnitude lower than a mouse. And the size distribution for migratory animals suggests that migration occurs most frequently in animals with minimum costs of transport less than 2. Presumably, higher costs of transport require more energy for migration than an animal can afford.

## An analysis of power

Why should cost of transport differ so markedly for animals of comparable sizes but different forms of locomotion? An answer to this question may be obtained by turning to



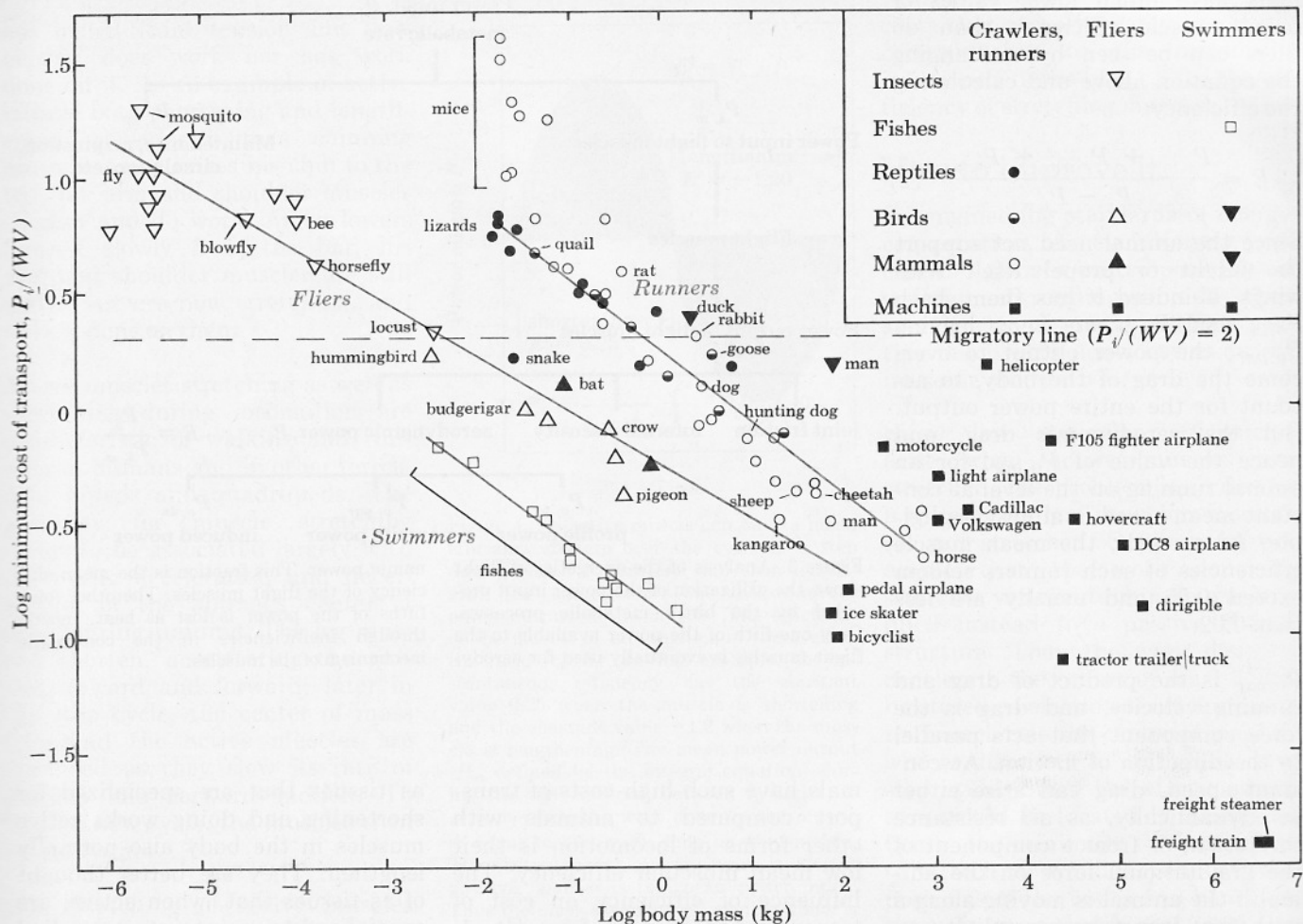


Figure 2. Minimum costs of transport are plotted for a variety of swimmers, fliers, runners, and some man-made machines. Representative species are identified at random.

Although the costs of transport vary widely, animals tend to fall into groups based on their type of locomotion, regardless of their taxonomic status. Sources used in the com-

pilation of this figure are marked with an asterisk in the References list at the end of the article.

an analysis of the energetic cost of flight in birds, which has been pursued so thoroughly that the line for flying birds in Figure 2 can be predicted (Tucker 1973a). The analysis can then be applied to walkers and runners.

First the power released from the oxidation of fuel is divided into that diverted to the flight muscles ( $P_{i,w}$ ) and that diverted to other purposes ( $P_{i,m}$ ), such as maintenance, circulation, and respiration (Fig. 3). The power diverted to the flight muscles is the larger portion, but only a fraction of it appears as the rate at which work is done on the air ( $P_{o,pr}$ , power output) by the wings. Since a negligible part of the mechanical work rate is used to overcome the internal friction of the joints and moving tissues, the aerodynamic work rate is essentially the rate at which the muscles do mechanical work.

The fraction of the power input to the muscles that appears as power output is the mean muscle efficiency ( $E$ ). Muscle efficiency has been measured in a variety of animals and usually has a maximum value between 0.2 and 0.3 (Hill 1939; Margaria 1968; Stainsby and Barclay 1972; Woledge 1968)—about the same as that of an internal combustion engine. I will assume that the mean efficiency of the muscles of a flying bird is 0.2.

The power output of the flight muscles can be quantified. It is made up of three parts: One part is used to support the bird's weight ( $P_{o,in}$ , induced power); a second part is used to overcome the drag of the bird's body exclusive of the wings ( $P_{o,par}$ , parasite power); and the third part is used to move the wings through the air ( $P_{o,pr}$ , profile power). The method of estimating these power output terms is de-

scribed in Pennycuik (1968, 1969) and Tucker (1973a).

The verbal description above is summarized in the equation

$$P_i = (P_{o,in} + P_{o,par} + P_{o,pr})/E + P_{i,m} \quad (1)$$

Of the three power output terms, the estimate of profile power has the greatest uncertainty, for it has been neither measured directly nor estimated accurately from theory. The mean efficiency might be somewhat higher or lower than 0.2, but it is unlikely to be as low as 0.13. To account for the latter value, profile power would have to have the impossibly low value of zero.

Using the power output of the leg muscles rather than the wing muscles, we can apply this analysis to running animals. That these ani-

mals have much lower values of mean muscle efficiency than do fliers can be seen by rearranging the equation above and calculating the efficiency:

$$E = \frac{P_{o, in} + P_{o, par} + P_{o, pr}}{P_i - P_{i, m}} \quad (2)$$

Since the animal need not support its weight or propel itself with wings, if indeed it has them, both  $P_{o, in}$  and  $P_{o, pr}$  are zero, leaving  $P_{o, par}$ , the power output to overcome the drag of the body, to account for the entire power output. But the aerodynamic drag, and hence the value of  $P_{o, par}$ , for an animal running on the level at constant mean speed is almost negligible. As a result, the mean muscle efficiencies of such runners seldom exceed 0.05 and usually are less than 0.02.

$P_{o, par}$  is the product of drag and running velocity, and drag is the force component that acts parallel to the direction of motion. At constant speed, drag can arise either aerodynamically, as air resistance to motion, or from a component of the gravitational force on the animal if the animal is moving along a path that is not horizontal. It can also result if some other force is applied to the runner—for example, through the handles of a wheelbarrow pushed by a human or through a harness that is attached to a wagon pulled by a horse.

In the case of a man running free and in place on a horizontal, rigid treadmill belt, both aerodynamic drag and mean muscle efficiency are zero, even though the runner moves at an exhausting pace. No matter how quickly the treadmill runner exhausts himself, he can do no work. He is unable to turn an electrical generator or even to overcome the friction in the bearings of the treadmill, and an electric motor or some similar energy source must be supplied for the latter purpose. If a force parallel to the treadmill belt is applied to the runner, by tilting the treadmill, allowing him to push on a bar, or blowing air on him with a fan to generate aerodynamic drag, then parasite power and mean muscle efficiency are no longer zero and the runner can do work.

The main reason why running ani-

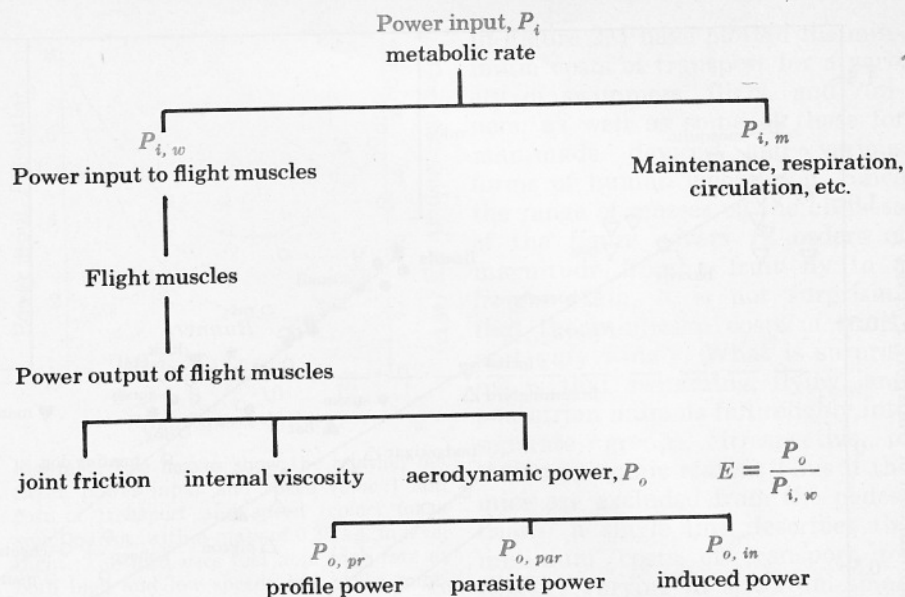


Figure 3. Analysis of the energetics of flight shows the utilization of the power input provided by the bird's metabolic processes. Only one-fifth of the power available to the flight muscles is eventually used for aerody-

namic power. This fraction is the mean efficiency of the flight muscles. The other four-fifths of the power is lost as heat, mostly through inefficiencies in the contractile mechanism of the muscles.

mals have such high costs of transport compared to animals with other forms of locomotion is their low mean muscular efficiency. The influence of efficiency on cost of transport can be seen from Eq. 1. At a given speed, the lower the efficiency, the higher the power input and the higher the cost of transport. The influence of efficiency on cost of transport can also be demonstrated experimentally. A person's muscles can attain an efficiency of 0.25 when they drive the machinery of a bicycle. A cyclist moves at a cost of transport less than half that of a runner, who has a mean muscular efficiency near zero. In addition, the cyclist far outstrips the runner in ability to maintain a high speed. A good cyclist can ride 40 kilometers (25 miles) in an hour—a speed faster than that attained by the world's fastest sprinter over a distance of only 100 meters.

## Muscle efficiency

From the above discussion it is clear that high costs of transport for running are related to low mean muscular efficiency. But why should running stand out in this regard from other forms of locomotion? The explanation involves the mechanics of active muscles. Although muscles are often thought of

as tissues that are specialized for shortening and doing work, active muscles in the body also normally lengthen. They are better thought of as tissues that, when active, are specialized to maintain a controlled tension, whether they shorten or lengthen in doing so.

When an active muscle shortens, it does mechanical work. When it lengthens, work is done on it. Work, by definition, is the product of the force applied to a point and the displacement of the point in a direction parallel to that of the applied force. An active muscle develops tension and hence applies a force to part of, say, a tendon. If the muscle shortens, so that the tendon moves in the same direction as the force, then work is positive—the muscle “does work.” If the muscle lengthens while exerting tension, because the bone at the other end of the tendon is exerting more force than the muscle, then the region of the tendon moves in the direction opposite to the force applied by the muscle. The work is negative—work is done on the muscle. In the jargon of physiology, the muscle “does negative work.” The phrase is unfortunate, for, taken literally, it describes the nonsense situation of a muscle doing work that is done on itself. An inactive muscle at its normal length devel-



ops insignificant tension and thus neither does work nor has work done on it. As an example of active muscle both shortening and lengthening, consider a man chinning himself. As he raises his chin to the bar, his arm and shoulder muscles shorten and do work. As he lowers himself slowly from the bar, his arm and shoulder muscles are still active but are now stretching, and work is done on them.

Active muscles stretching as well as shortening during locomotion are characteristic of walking and running in humans and in other terrestrial bipeds and quadrupeds. The necessity for muscle stretching seems to be associated largely with the cyclic acceleration and deceleration of the animal's center of mass during running. The leg muscles shorten, accelerating the animal upward and forward; later in the step cycle, the center of mass falls and the active muscles are stretched as they slow its rate of descent and forward motion. To begin a new cycle, the muscles then shorten again.

The stretching of active muscles explains the low mean muscular efficiencies that I have described for walking and running animals. The efficiency of an active muscle at any instant depends on the speed and direction of movement. When the muscle shortens, efficiency varies from near zero at low and high shortening speeds to a maximum value near 0.2 to 0.3 at intermediate speeds (Hill 1950; Woledge 1968). During stretching, the efficiency of an active muscle becomes negative. That is, the power input of the muscle remains positive, but since work is being done on the muscle, the power output of the muscle becomes negative. Hence the efficiency, or the ratio of power output to power input, is also negative. Efficiency values for stretching muscles depend on several factors, among them the speed of stretching. Values in the vicinity of  $-1.2$  are often measured (Magaria 1968). A comprehensive summary of the mechanical and energetic properties of muscle can be found in Carlson and Wilkie (1974).

The average efficiency of a muscle involved in a cyclic motion can be positive, negative, or zero for an in-

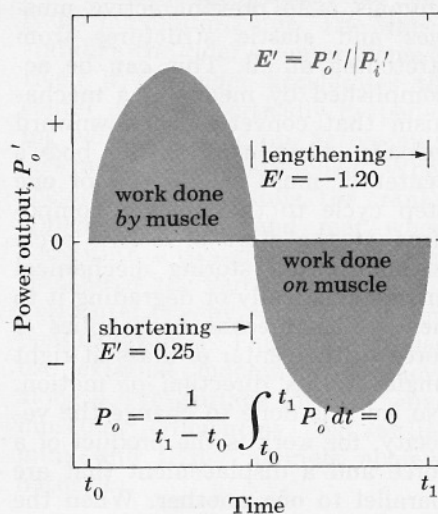


Figure 4. An active muscle can have a mean efficiency of zero over the cycle of a step during which it shortens and then lengthens. The curve shows the instantaneous power output of the muscle at any instant in the cycle is the ratio  $P_o'/P_i'$ . In this example, the instantaneous efficiency has the constant value 0.25 when the muscle is shortening and the constant value  $-1.2$  when the muscle is lengthening. The mean power output ( $P_o$ , defined by the integral equation) during the time interval between  $t_0$  and  $t_1$  is zero, because the work done by the muscle is equal to the work done on the muscle. The instantaneous power input is always positive, and so is the mean power input. Thus the mean muscular efficiency, which is the ratio of the mean powers, is zero.

tegral number of cycles (Fig. 4). Consider the calf muscle during walking. As it shortens its power output is positive, but as it stretches its power output is negative, and its mean power output could be zero for the period of a step cycle. In this case, the mean efficiency of the muscle would be zero.

There are two reasons why the stretching of active muscles causes the mean efficiency of the muscles to be low over a cycle of motion. First, in running humans, about half or more of the work that is done in stretching the muscles is converted to heat (Cavagna et al. 1964). The remainder is stored in stretched elastic elements. Since heat cannot be used by animals as an energy source for mechanical work, it is wasted for the purposes of locomotion. Second, as muscles stretch, they consume extra metabolic energy at the same time that they are absorbing work. The consumption of metabolic energy amounts to about 0.8 units for

every unit of work energy absorbed, corresponding to the previously mentioned figure of  $-1.2$  for the efficiency of stretching muscles.

## How to improve it

By engineering standards of energy conservation, the evolutionary process has done a pretty poor job on walking and running animals—they spend a lot of energy without getting much work done. Let us examine some alternatives.

Since low muscular efficiencies arise when active muscles are stretched, the problem is to design a running animal in which muscles are not stretched. Suppose for example that the work done to stretch a vertebrate muscle was applied instead to a passive elastic structure. Then the work done to decelerate the center of mass could be stored as elastic energy and used to reaccelerate the center of mass in a new direction to initiate a new step cycle. Since the elastic structure would be located between two bones, the minimum force required to stretch it would depend on the positions of the bones and hence on the posture of the animal. And the force applied by the elastic structure as it shortened would also depend on the animal's posture. The difficulty is that the forces an animal might wish to apply to its bones depend on factors other than posture—for example, on whether the animal is accelerating, turning, or correcting for the fact that its left hind foot has inadvertently stepped in a gopher hole.

In fact, animals do use elastic structures to store mechanical energy. In running humans about half the work done as the muscles shorten is accounted for by energy stored in elastic structures. The arrangement of these structures in series with the muscles enables the muscles to control the length and tension of the elastic structure. The system works at the expense of muscle efficiency, however, since the muscle is called upon to stretch while active.

The evolutionary process has not yet come up with a mechanism for storing mechanical energy for indefinite periods and releasing it later at controlled rates. Human

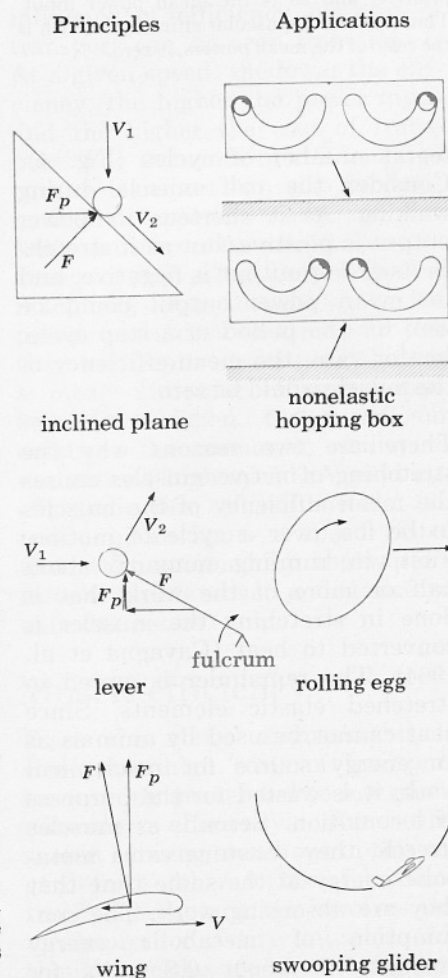
technology has risen to the same challenge, with somewhat better success. Perhaps the most commonly used man-made storage devices are wind-up springs connected to gear boxes, used in clocks, or the combination of electric generator, storage battery, and electric motor, used for starting automobile engines. In the latter system, mechanical work done by the automobile engine is stored as chemical energy in the battery. After the engine stops, chemical energy is used to do mechanical work, which then restarts the engine. Spinning flywheels can also be used to store mechanical energy. When installed in an automobile or bus, they can drive the vehicle for practical distances (Post and Post 1973). Flywheel-driven vehicles (and some electrically driven ones) promise to have considerably lower costs of transport than conventional automobiles, because they can store the mechanical energy that ordinarily would be lost as heat when the vehicle brakes to a stop. The energy can then be used to reaccelerate the vehicle. If running animals could store the mechanical energy that is degraded to heat as muscles are stretched during deceleration at each step, and use it for reacceleration, they could similarly decrease their costs of transport.

An alternate strategy for running animals is to prevent active muscles and elastic structures from stretching at all. This can be accomplished by means of a mechanism that converts the downward velocity component of the body's center of mass at the end of one step cycle to the upward component at the start of a new cycle without either storing mechanical energy elastically or degrading it to heat. The mechanism applies a force to the center of mass at right angles to its direction of motion. No work is done to change the velocity, for work is the product of a force and a displacement that are parallel to one another. When the force is at right angles to the displacement, the muscles that supply the force can neither do work nor have work done on them. The result is that the body is accelerated—that is, its velocity is changed to a new direction—at no expense for muscular work. This principle is used by birds and bicyclists to at-

tain their high muscular efficiencies during locomotion, and probably by walkers and runners to a lesser extent.

Mechanical devices for applying force components perpendicular to the direction of motion include levers and inclined planes (Fig. 5). For example, a pole vaulter uses his pole as a lever to convert horizontal velocity to vertical velocity. He runs at high speed and thrusts the pole into a box set into the ground. If the pole is not horizontal, a force develops along the pole that has a component perpendicular to the direction in which the vaulter is running. The perpendicular force accelerates the vaulter upward, and no muscular work is needed to achieve this acceleration. The same principle is illustrated by a rolling egg in Figure 5. The lever extends from the center of mass to the point where the egg contacts the surface. The egg could roll along a level surface indefinitely, except for frictional forces. Its center of mass continually accelerates and decelerates, due to the shape of the egg, but no work is done to keep the egg rolling. Cavagna et al. (1964) have compared a walking human to a rolling egg; and the legs of the walker serve to some extent the function of the vaulter's pole, although they apparently are not used in this way during running.

Figure 5. If a force ( $F_p$ ) is applied perpendicular to the direction of movement of a body, the body can change direction at no energetic expense. The mechanical principles involved and some applications are shown. Through interaction with an inclined plane (top left) the direction of the velocity ( $V_1$ ) of a body is changed (to  $V_2$ ); the magnitude of the velocity remains constant.  $F$  is the force applied to the body by the plane. This principle is exemplified in the hopping box (top right), a light, frictionless cage containing 2 heavy balls. The hopping box is dropped with the balls at the tops of the slots; when the cage hits a fixed surface and stops, the balls roll to the other ends of the slots, hit the top of the cage, and accelerate it upward again. The principle of the lever (middle left) is used by a pole vaulter to convert the horizontal velocity of running to a vertical velocity sufficient to carry him over the crossbar. It is also exemplified by a rolling egg (middle right), whose ellipsoidal shape gives its center of mass both horizontal and vertical components. The shape of the wing (shown in cross section, bottom left) produces a very large perpendicular force component. The wing's ability to change the downward motion of its center of mass to a forward motion with only a small energy expenditure is illustrated by the glider (bottom right), which converts its velocity from a dive to a climb.



An inclined plane can also develop a force perpendicular to an object. Inclined planes formed by the bones are not found in animals as devices for changing the direction of motion. But the principle can be used to design a device that will move indefinitely along a level, frictionless surface while its center of mass continually accelerates and decelerates. The nonelastic hopping box illustrated in Figure 5 is such a device. It bounces somewhat like a rubber ball but does not store energy elastically.

A wing is a device that, in a fluid medium, can generate forces having large components perpendicular to the direction of the wing's motion (Fig. 5). Wings are usually long and narrow—that is, the mean distance between the leading and the trailing edges of the wing is a small fraction of the wing span. Typically, wings produce a perpendicular



force component that is 20 or more times larger than the force component parallel to the direction of movement. Wings are found not only on flying animals but also on swimming animals. The flippers of whales and penguins and the fins of many fishes are examples.

In its wings, a flying animal has a mechanism for changing the downward motion of its center of mass to a forward motion without doing muscular work and without stretching elastic structures or active muscles. As a dramatic example of the benefits of developing a perpendicular force, consider the results of dropping a pigeon and a rat from a height of, say, 100 meters. The pigeon merely extends its wings and the perpendicular force changes its motion from vertical to horizontal. The rat, however, is faced with absorbing its kinetic energy at the bottom of the fall by stretching elastic structures and active muscles. In this case, the kinetic energy is more than can be absorbed without dire consequences for the rat.

A final method of preventing muscle stretch during locomotion would be to prevent vertical movement of the center of mass. This is achieved by the many teleost fish that have swimbladders. The force of gravity is constantly balanced by the buoyancy of the swimbladder, so that no vertical force components exist to accelerate the center of mass. Snakes, having no legs, support their centers of mass continuously, but they must pay the price of energy loss due to sliding friction between their bodies and the substrate. Their costs of transport appear to be lower than those of runners and more like those of fliers (see Figure 2). Animals with very large numbers of legs—millipedes, for example—can also support their centers of mass at all times. This strategy carried to an extreme leads to the wheel, in which some point on the circumference is always in contact with the substrate.

We can now appreciate why bicycle riders are willing to propel the extra weight of a bicycle, even when going uphill. The cost of transport on a bicycle is low because active muscles are not stretched while pedaling, and mean

muscle efficiency is about .25, nearly its maximum value. The wheels stabilize the rider's center of mass. Even if the rider accelerates the center of mass vertically by pedaling while standing up, active muscles need not be stretched. When the center of mass falls, the cranks, sprockets, chain, and rear wheel constitute a system of levers that transposes the vertical motion to a horizontal one by supplying a perpendicular force. Thus, humans can use external machinery to move along a level surface with the same muscular efficiencies that swimming and flying animals achieve naturally.

## References

Asterisked references were used in the compilation of Figure 2.

Carlson, F. D., and D. R. Wilkie. 1974. *Muscle Physiology*. Englewood Cliffs: Prentice-Hall.

Cavagna, G. A., F. P. Saibene, and R. Margaria. 1964. Mechanical work in running. *J. Appl. Physiol.* 19:249-56.

\*Chodrow, R. E., and C. R. Taylor. 1973. The cost of limbless locomotion in snakes. *Fed. Proc.* 32:422.

\*Dawson, T. J., and C. R. Taylor. 1973. Energetic cost of locomotion in kangaroos. *Nature* 246:313-14.

\*DiPrampo, P. E., D. R. Pendergast, D. W. Wilson, and D. W. Rennie. 1974. Energetics of swimming in man. *J. Appl. Physiol.* 37:1-5.

\*Elsley, G. H., and A. J. Devereaux. 1968. *Hovercraft Design and Construction*. Cambridge, MD: Cornell Maritime Press.

\*Fedak, M. A., B. Pinshow, and K. Schmidt-Nielsen. 1974. Energy cost of bipedal running. *Amer. J. Physiol.* 227: 1038-44.

\*Gabrielli, G., and Th. von Karman. 1950. What price speed? Specific power required for propulsion of vehicles. *Mech. Engr.* 72:775-81.

Hill, A. V. 1939. The mechanical efficiency of frog muscle. *Proc. Roy. Soc. Lond., ser. B.*, 127:434-51.

Hill, A. V. 1950. The dimensions of animals and their muscular dynamics. *Proc. Roy. Inst. Great Britain* 34:450-71.

\*Hughes, C. H. 1942. *Handbook of Ship Calculations, Construction and Operation*. New York: McGraw-Hill.

\*Jagger, J. A., C. R. Taylor, and A. W. Crompton. 1974. The tenrec, a primitive mammal with reptilian energetics. *Fed. Proc.* 33:349.

\*Maksud, M. G., R. L. Wiley, L. H. Hamilton, and B. Lochart. 1970. Maximal  $\dot{V}_{O_2}$  ventilation, and heart rate of Olympic speed skating candidates. *J. Appl. Physiol.* 29:186-90.

Margaria, R. 1968. Positive and negative work performances and their efficiencies in human locomotion. *Int. Z. angew. Physiol. einsch. Arbeitsphysiol.* 25:339-51.

\*Moberly, W. R. 1968. The metabolic re-

sponses of the common iguana, *Iguana iguana*, to walking and diving. *Comp. Biochem. Physiol.* 27:21-23.

\*Nayar, J. K., and E. van Handel. 1971. The level for sustained mosquito flight. *J. Insect Physiol.* 17:471-81.

\*Nayar, J. K., and D. M. Sauerma, Jr. 1973. A comparative study of flight performance and fuel utilization as a function of age in females of Florida mosquitoes. *J. Insect Physiol.* 19:1977-88.

Pennycuik, C. J. 1968. Power requirements for horizontal flight in the pigeon *Columba livia*. *J. Exp. Biol.* 49:527-55.

Pennycuik, C. J. 1969. The mechanics of bird migration. *Ibis* 111:525-56.

Post, R. F., and S. F. Post. 1973. Flywheels. *Sci. Am.* 229:17-23.

\*Prange, H. D., and K. Schmidt-Nielsen. 1970. The metabolic cost of swimming in ducks. *J. Exp. Biol.* 53:163-77.

\*Schmidt-Nielsen, K. 1972. Locomotion: Energy cost of swimming, flying, and running. *Science* 177:222-28.

Stainsby, W. N., and J. K. Barclay. 1972. Oxygen uptake for brief tetanic contractions of dog skeletal muscle *in situ*. *Am. J. Physiol.* 223:371-75.

\*Taylor, C. R. 1973. Energy cost of animal locomotion. In *Comparative Physiology*, ed. L. Bolis, K. Schmidt-Nielsen, and S. H. P. Maddrell. Amsterdam: North-Holland. pp. 23-42.

\*Taylor, C. R., and V. J. Rowntree. 1973. Running on two or on four legs: Which consumes more energy? *Science* 179:186-87.

\*Taylor, C. R., K. Schmidt-Nielsen, and J. L. Raab. 1970. Scaling of energetic cost of running to body size in mammals. *Amer. J. Physiol.* 219:1104-07.

\*Taylor, C. R., K. Schmidt-Nielsen, R. Dmi'el, and M. Fedak. 1971. Effect of hyperthermia on heat balance during running in the African hunting dog. *Amer. J. Physiol.* 220:823-27.

Tucker, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* 48:67-87.

\*Tucker, V. A. 1970. Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.* 34:841-46.

\*Tucker, V. A. 1973a. Bird metabolism during flight: Evaluation of a theory. *J. Exp. Biol.* 58:689-709.

\*Tucker, V. A. 1973b. Aerial and terrestrial locomotion: A comparison of energetics. In *Comparative Physiology*, ed. L. Bolis, K. Schmidt-Nielsen, and S. H. P. Maddrell. Amsterdam: North-Holland. pp. 63-76.

\*Utter, J. M., and E. A. LeFebvre. 1970. Energy expenditure for free flight by the purple martin (*Progne subis*). *Comp. Biochem. Physiol.* 35:713-19.

Woledge, R. C. 1968. The energetics of tortoise muscle. *J. Physiol.* 197:685-707.

\*Wunder, B. A. 1970. Energetics of running activity in Merriam's chipmunk, *Eutamias merriami*. *Comp. Biochem. Physiol.* 33:821-36.

\*Wunder, B. A., and P. R. Morrison. 1974. Red squirrel metabolism during incline running. *Comp. Biochem. Physiol.* 48A:153-61.

\*Yust, W., ed. 1956. *Encyclopedia Britannica*. 1:468, 18:932. Chicago: Encyclopedia Britannica.