Locomotion: Energy Cost of Swimming, Flying, and Running

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The energy expended by animals as they swim through water, run on land, and fly in the air in the different kinds of locomotion is not immediately obvious to us. We know that a flying bird must continuously expend energy to keep from falling to the ground, and that in water many animals are neutrally buoyant and expend little effort to keep from sinking, but man has no experience in flying under his own power and he is a clumsy and ineffective swimmer. Walking and running we know more about, for man is our best and most cooperative experimental animal. Except for man and dog running animals have not received much attention, and studies of swimming and flying animals have only recently been carried out at a satisfactory level of success. In this article I shall compare the energy cost of these three kinds of locomotion.

Other types of locomotion exist, such as the hydraulic system of the earthworm, in which the body fluids in combination with the muscular body wall function as a "skeleton." Spiders lack extensor muscles in the limbs and use blood pressure to stretch their legs; the squid and octopus use jet propulsion in swimming. The mechanics of these types of locomotion have been well analyzed but their energy cost is completely unknown.

Differences in the physical qualities of the media in which animals move account for such structural adaptations as streamlining of the body in flying and swimming animals, and the use of levers for propulsion in running animals. The weight of most swimming animals is fully supported by the surrounding medium, but running and flying animals must support the full weight of their bodies. The running animal has a solid support, but the flying animal must support its weight against a fluid of low density and low viscosity. In contrast, when the aquatic animal swims through water, it meets the resistance of a medium of high viscosity and density; running and flying animals have the advantage of moving in a medium of low viscosity and low density.

Comparison of Energy Costs

To compare the energy cost of activities as different as swimming, flying, and running, we need a suitable basis for comparison. There are several variables that must be taken into consideration. (i) The amount of fuel an animal uses in moving, which is expressed as an increase in the metabolic rate. (ii) The cost of moving obviously depends on the animal's size or weight; and the power available for moving is related to muscle mass, which is a function of size. Although aquatic animals do not support their weight, their size is of importance to the resistance they meet in moving. (iii) The distance over which an animal moves influences the energy cost. (iv) The speed at which the animal moves may also be considered. What is the most suitable basis for comparison?

To calculate the energy cost of locomotion, I have chosen to use the amount of fuel (expressed as calories) it takes to transport one unit of body weight (in grams) over one unit of distance (1 kilometer) (*1*). For the calculation of the cost of transportation in these units, we can use the ratio of the metabolic rate in calories per gram per hour, at a given speed in kilometers per hour, to that speed.

$$\frac{\text{Metabolic rate}}{\text{Speed}} = \frac{\text{cal g}^{-1}\ \text{hr}^{-1}}{\text{km hr}^{-1}} = \text{cal g}^{-1}\ \text{km}^{-1}$$

We thus find that time has conveniently been eliminated, and that the speed is of no direct consequence for comparing the metabolic cost of locomotion. The animals can therefore move within the range of speeds natural to them. This convenience is, as we shall see later, well justified for mammals, but is less justified for birds for which the cost of moving is more speed dependent than for mammals (*2*).

Swimming

An animal swimming through water meets with resistance, or drag; to propel itself the animal must supply a force which equals the drag. The drag on an aquatic animal is a complex function of shape, size, and speed. The importance of shape is expressed in what is commonly known as "streamlining," so well known from fish and whales, and regrettably absent in man. The size of the animal enters primarily as the surface area in contact with the water, for as water moves over a surface, the boundary layer dissipates energy. An important consideration is whether the flow in the boundary layer is laminar or turbulent. Important variables that influence the nature of flow in the boundary layer are speed and length, as expressed in the well-known Reynolds number. At high Reynolds numbers the drag is approximately proportional to the square of speed, but at very low Reynolds numbers the laws of fluid dynamics seem to change and drag becomes primarily a function of viscosity and is directly proportional to speed (Stokes' law).

A knowledge of elementary fluid dynamics, however, is not sufficient to define what animals really do; we need actual determinations of the energy expenditure. The energy cost of swimming salmon has been extensively studied by Brett (*3*). Brett's observations cover a wide range of sizes, from about 3 grams to 1.5 kilograms, and a variety of swimming speeds. From his data I have selected salmon of five size groups, swimming at three-fourths of their fatigue speed, and have plotted the calculated cost of transportation on logarithmic coordinates (Fig. 1). The points fall very close to a straight line, which thus expresses the energy cost of swimming for salmon within the size range studied.

Other investigators, studying other species of fish, have obtained results that give an energy cost of swimming virtually identical to that for salmon. Grayling (*Thymallus*) and whitefish (*Coregonus*), studied by Soviet investigators (*4*), are salmonid fishes. Thus it

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is perhaps not surprising that the results are in accord with those obtained for the salmon, when they are recalculated to the same units. Similar results were obtained for the trout (*5*), another salmonid fish. It is interesting, however, that the energy cost of swimming for the goldfish (*6*), a carp, is so close to that of the trout that it could not be plotted as a separate point. Even the pinfish, *Lagodon rhomboides* (*7*), fits the curve for salmon, although its appearance and shape are quite different from the fast-swimming salmonids.

Even more interesting are the results obtained for the eel by Holmberg and Saunders (*8*). Their figures give a cost of transportation of 0.329 to 0.417 cal g^{-1} km^{-1}. Silver eel (mean weight, 248 grams) and green eel (mean weight 238 grams) gave similar results at swimming speeds ranging from 35 cm sec^{-1} to 65 cm sec^{-1}. Although the eel uses almost the entire body in propelling itself through water (anguilliform propulsion) and other fish use only the tail portion of the body (carangiform propulsion), the energy cost of swimming is similar.

It is worth noting that the investigators concerned with these different fish have worked independently and did not consider cost of transport in the terms used here. The close correspondence between their results therefore is striking.

To amuse my friends I have calculated the energy cost for 1 gram of mammalian sperm to travel 1 kilometer (*9*). The result is plotted in Fig. 1B, in which the points in the lower right hand corner and the regression line represent the data on salmon from Fig. 1A. A single bull sperm weighs 10^{-11} gram, and it takes a hundred thousand million sperm to make up the weight of the smallest salmon. The cost for this much sperm to swim 1 kilometer is nearly 10,000 times as high as for the one salmon. The coincidence between the sperm and the regression line for salmon should not be taken too seriously, however. The hydrodynamic considerations that govern the swimming of these two organisms are quite different; fish move at rather high Reynolds numbers, and the sperm at extremely low Reynolds numbers, of the order of 10^{-3}, where lift is negligible and viscous forces alone determine the drag.

The energy requirements of a swimming porpoise or dolphin have long been known among biologists as Gray's paradox. Dolphins can swim at high speeds; reliable determinations indicate that they readily swim at 15 knots, which is 28 kilometers per hour, and for short spurts they may reach 20 knots or 36 kilometers per hour (*10*). Gray (*11*) estimated the energy requirements of swimming dolphins by determining the drag on a model of the animal. He also calculated the drag from the area, the speed, and the drag coefficient, using a calculated Reynolds number of 1.6×10^7. Gray expressed the result in the following words: "If the resistance of an actively swimming dolphin is equal to that of a rigid model towed at the same speed, the muscles must be capable of generating energy at a rate at least seven times greater than that of other types of mammalian muscle" (*11*).

Gray's paradox is that the transition between laminar and turbulent flow takes place at Reynolds numbers of about 5×10^5, and at the speed dolphins swim, the calculated Reynolds number is more than 10^7. If the flow over the dolphin were laminar, however, the drag coefficient and thus the power requirement would be reduced to about one-ninth of the value estimated by Gray.

The oxygen consumption of swimming dolphins has not been determined. Let us instead compare the dolphin with the salmon and other fish, for which excellent information is available. Although we have no inherent right to extrapolate from the salmon to the dolphin, we can safely assume that both animals are highly adapted and effective swimmers, and extrapolating from a 1-kilogram salmon to a 90-kilogram dophin is not unreasonable. Gray's calculations were for the very high speed of 20 knots, but on the other hand, he did not include in his calculations that the efficiency of muscle in performing external work is not 100 percent, and the cost was therefore underestimated. Assuming an efficiency of 25 percent, I have obtained a metabolic rate of 18.1 kcal kg^{-1} hr^{-1}, which gives a cost of transport indicated by the upper open circle in Fig. 1C. (As a point of reference, the metabolic rate of man at rest is about 1 kcal kg^{-1} hr^{-1}, and during top athletic performances it is some 20 times as high.) If instead of turbulent flow we assume laminar flow, and if we assume that the dophin cruises at 10 knots, the power requirement is reduced accordingly. If we again assume 25 percent efficiency of the muscle in performing external work, we arrive at the lower open circle in Fig. 1C, which is located surprisingly close to the extended regression line for the salmon. In this case the extension of a regression line is better justified than it is in

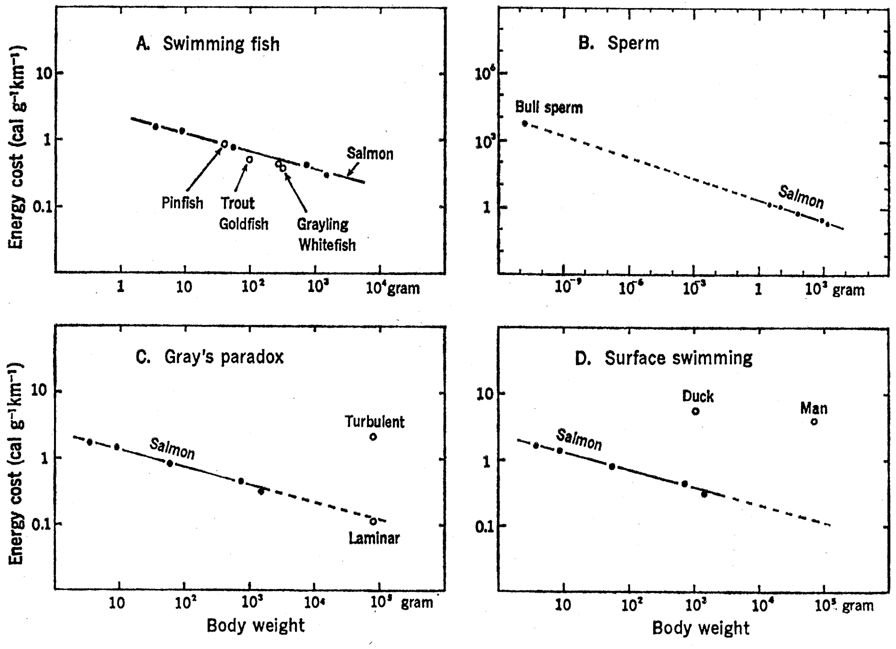

Fig. 1. Energy cost of swimming. (A) Cost of swimming for various fish relative to body size. Coordinates are logarithmic. Solid circles and regression line, represented in each graph, represent salmon with body weights of 3 to 1500 grams [data from Brett (*3*)]; open circles, other fish [data from (*4–8*)]. (B) Estimated energy cost for propulsion of bull sperm (*9*). Data for salmon and regression line are the same as in (A); the coordinate scales are different. (C) Estimated cost of swimming for dolphins, based on the assumption of turbulent flow or laminar flow of water over the body. Actual measurements on dolphins have been made. (D) Cost of propulsion for two surface swimmers. Data for salmon are repeated from (A).

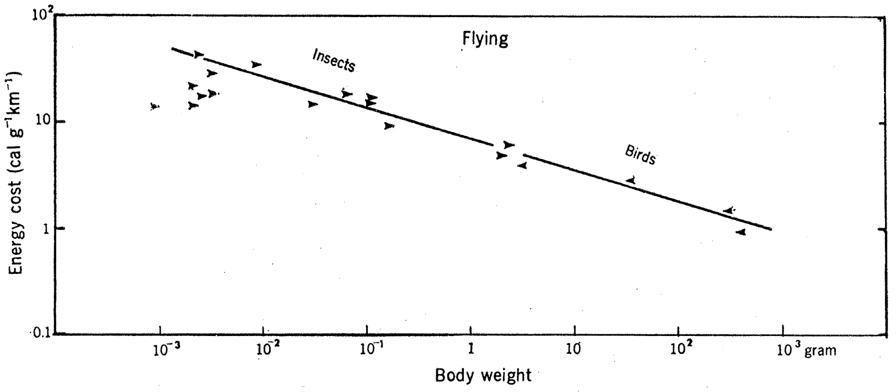

Fig. 2. Energy cost of flying relative to body size of insects (*23, 24*) and birds (*2, 16, 17, 22*). The regression line is based on birds and is arbitrarily extended to cover the size of insects.

the case of the sperm, because the fluid dynamics for salmon and dolphin should be similar. The calculated metabolic rate of the dolphin cruising at 10 knots, if we still assume laminar flow, is 2 kcal kg^{-1} hr$-^{1}$, about twice the resting metabolic rate of man. In other words, if the dolphin swims as effectively as a salmon, it should be able to cruise at 10 knots with little effort, and this is precisely the impression we gain when we observe these delightful animals from the deck of a ship.

The question of whether the flow can be laminar at this speed has not been resolved. The fluid dynamics of an oscillating body is not fully understood, but in popular terms we could say that as the tail undulates, perhaps it constantly moves out of the area of potential turbulence. Also, the thickest part of the dolphin's body is well behind the midpoint from snout to tail, and this aids in reducing a potentially turbulent boundary layer. An interesting but little-noticed observation was made some years ago by Steven (*12*). He noted that dolphins swimming at night in a phosphorescent sea produced a wake of two clean diverging lines of luminescence stretching behind the animal with very little luminescence, and therefore turbulence, in between. If two dolphins crossed each other's paths at close range, a definite pattern of crossing clean lines could be observed. These wakes indicate low turbulence, and are very different from the boiling mass of turbulence produced by a seal swimming at speed.

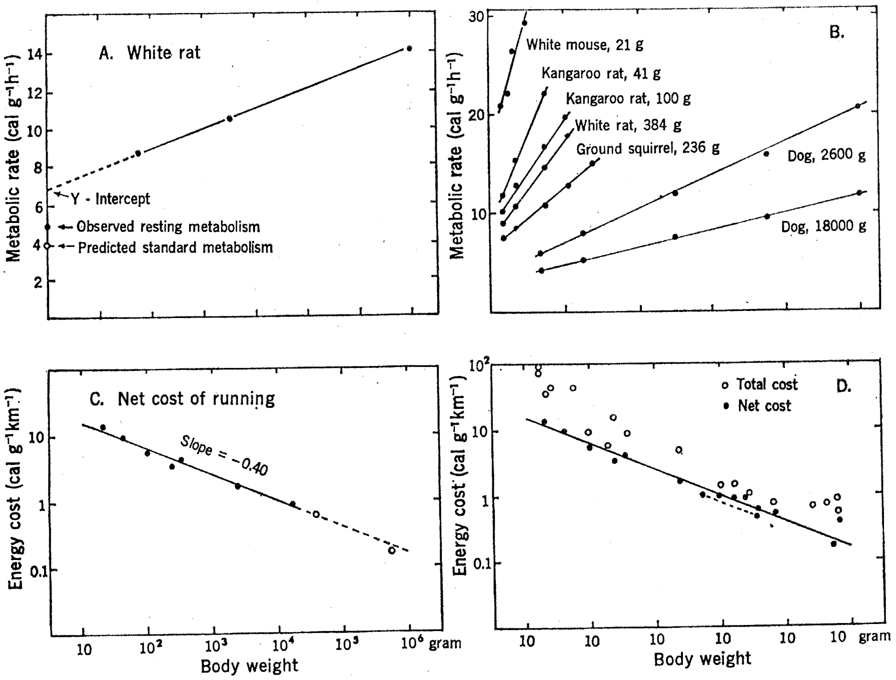

Fig. 3. Energy cost of running. (A and B) Metabolic rate (measured as oxygen consumption) of running animals relative to speed of running. Data for the white rat (*33*) shown in (A) are repeated in (B). Note the linear relationship between metabolic rate and speed, and that in (A) the regression line does not extrapolate to resting metabolic rate. (C) Net energy cost of running for mammals of different body size. Solid circles represent the slopes of each regression line in (B), and thus give the net cost of locomotion for the species in question. Open circles, sheep and horse (*33*). (D) Solid circles, net cost of running for mammals, same data as in (C), with additional data from (*39*). Open circles, total cost of locomotion [data from (*39, 40*)]. The dotted line represents an historical curiosity; it is the calculated regression line for all the data on dogs published by Slowtzoff in 1903 (*28*). This line has a slope of − 0.40, exactly the same value as that obtained in 1970 for animals ranging in size from 21 grams to 1.8 kilograms (*33*).

Before leaving the subject of swimming, I shall compare two surface swimmers to the salmon. The mallard duck, which Prange and I studied (*13*), swims at an energy cost which is nearly 20 times as high as that for a salmon of the same size (Fig. 1D). There are two important differences, the duck propels itself by paddling, and it swims on the surface where it sets up a wake of gravity waves. For a ship, a major cost of propulsion goes into surface waves, which contain both kinetic and potential energy, but how important this energy loss is for the duck we do not know.

The duck is a natural swimmer, but this cannot be said for man. The energy cost of swimming for man (*14*) is also high, and compared to the extrapolated cost of swimming for salmon, man struggles along at a cost which seems to be about 30 times as high as what we might expect for a fish of his size.

Flying

The medium in which flying animals move is much less dense and viscous than water, but flying animals must support the weight of their bodies. They must overcome drag, and this has several components. Friction drag is caused by the viscosity of the air in the boundary layer and depends on the shear rate. Friction drag occurs because the fluid in immediate contact with the surface of a moving body is dragged along with the body and establishes a velocity gradient in the boundary layer. What is meant by pressure drag can be described by imagining a flat plate moving perpendicularly to its plane through a fluid. It leaves a highly turbulent wake, and the work dissipated in this way represents the pressure drag. If we were to move the plate along its own plane, however, pressure drag would be negligible and friction drag would dominate. Induced drag can perhaps best be understood by reference to an airplane or a bird moving horizontally through the air. To move horizontally it needs lift which must equal the weight of the body. Lift is produced as air moves over the wing or airfoil, and the necessary force to move the wing in the direction of flight, to achieve this lift, is known as induced drag. Induced drag therefore represents the force necessary to support the body in the air.

Table 1. Metabolic rate during steady-state horizontal flight. (Information for hummingbird is for hovering flight.)

Flying animals	Body weight (g)	Metabolic rate (cal g^{-1} hr^{-1})		
		Rest	Flight	Increase
		Birds		
Hummingbird (*16*)	3	14.3	204	14 ×*
Budgerigar (*2*)	35	15.8	105	6.7 ×
Gull (*17*)	300	7.3	54	7.4 ×
		Bats		
Phyllostomis (*18*)	90	3.8	94	25 ×*

* Resting values for the hummingbird and bat are not well defined because these animals readily undergo torpor.

The total drag is a complex function of air density and viscosity, and is related to area, shape, and speed of the flying animal. In spite of the complexities, the aerodynamics of bird flight has recently been successfully analyzed by Pennycuick (*15*).

Direct measurements of the energy cost of flying have been made for only a small number of birds, ranging from 3 to 300 grams (*2, 16, 17*), and quite recently for a medium-sized tropical bat (*18*). Table 1 shows that the metabolic rate during flight is quite high, but decreases with increasing body size. The bat, the only flying mammal that has been studied, falls within the range of the birds. Compared with the metabolic rate at rest, the increase in metabolic rate during flight for the budgerigar (parakeet) and the gull (*2, 17*) is about sevenfold, which is similar to the maximum increase obtained for running animals of similar size, such as mice and rats (*19*). Since the resting metabolic rate of birds in general is of the same magnitude as that of mammals of equal size, we can see that horizontal flight does not require extraordinary feats of power output (*20*). The apparently much higher increase factors for hummingbirds and bats are misleading because the resting metabolic rates for these animals are atypical; both hummingbirds and bats readily undergo torpor with considerable drops in body temperature and oxygen consumption. Therefore resting values are difficult to define accurately, and the increase factors are correspondingly uncertain.

Tucker's studies of flying birds are extraordinarily informative. By using a wind tunnel that could be tilted, Tucker determined the energy cost of flight at a variety of speeds for horizontal as well as for ascending and descending flight. The budgerigar had a definite minimum in the rate of oxygen consumption at a speed of 35 km hr^{-1}; when it flew faster or more slowly the rate of oxygen consumption increased (*2*). For the laughing gull (*17*) the cost of flying was far less dependent on the flying speed, however, and this difference points out the need for more extensive information for birds of various body sizes and different flight patterns. Most recently Bernstein *et al.* (*21*) have studied the fish crow, which has shorter, broader wings than gulls and in nature mostly uses continuous flapping flight while gulls use soaring as well as flapping flight. Despite these differences the energy cost of horizontal flight for the crow did not differ strikingly from the means reported for the gull (*17*).

A particularly interesting aspect of the flying budgerigar was pointed out by Tucker (*2*). In analyzing the partial efficiency (the ratio of change in external work done to change in energy expenditure) for flight at different angles, he reached the conclusion that a flying budgerigar could ascend from and again descend to a given altitude and use no more energy than if it had spent the same time in horizontal flight at the same speeds. Furthermore, the budgerigar is a ground-feeding bird and does much of its ascending flight immediately after takeoff when it has not yet accelerated to normal flight speed. At these slow speeds the partial efficiency for ascent is greater than for descent, so that a combination of ascending and descending flight is more economical than horizontal flight over the same distance. These observations may explain why some birds seem to prefer an undulating flight pattern.

Oxygen consumption is technically far easier to determine for flying insects than for birds, and a larger number of such determinations is available. Information about birds and insects is combined in Fig. 2. In addition to the three birds in Table 1, a fourth (the point to the far right) refers to pigeons, in which metabolic turnover during flight was derived from an ingenious double-labeling technique with ^{2}H and ^{18}O (*22*). The bat is not included in the graph because the determinations were made on tethered animals that were flying in circles, and their speed therefore did not represent free or natural flight. The oxygen consumption of hummingbirds was determined for hovering flight; the calculation of cost of transport is based on an assumed flying speed of 50 km hr^{-1}.

The flying insects for which data are given in Fig. 2 cover a 1000-fold range of body weights, from a few milligrams to 3 grams (*23*). The two points to the right represent the desert locust and the cecropia moth, at the other end are mosquitoes that weigh less than 2 milligrams (*24*). The regression line is an arbitrary extension of the line for birds and some points for the smallest insects fall distinctly below this line. Some of these are based on older determinations that may be less reliable than more recent data. Whether or not we disregard these deviations, the overall conclusion is that all flying animals fall amazingly close to one straight regression line, in spite of the vast differences in size, anatomy, flight pattern, speed, body temperature, and so on, between insects and birds.

Running

More adequate physiological information is available for running than for swimming and flying. When an animal, including man, runs horizontally, he performs no useful external work. Energy loss due to frictional resistance against the ground is minimal, and work performed against air resistance is in most cases very small. Only when a man runs a sprint at top speed does the air resistance account

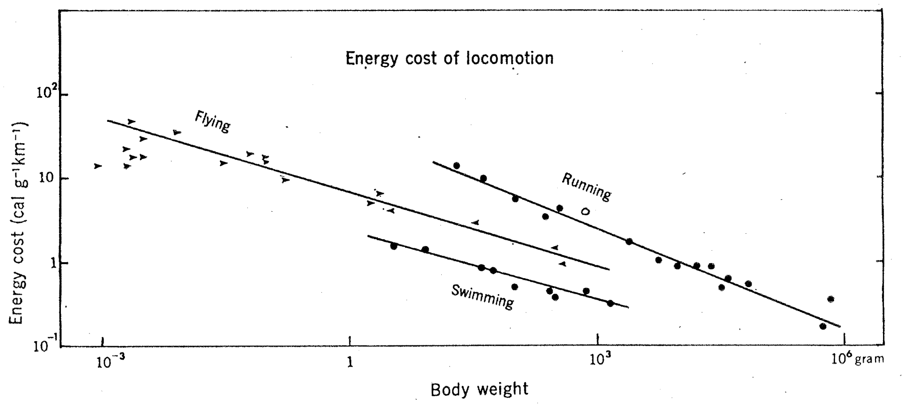

Fig. 4. Energy cost of locomotion for swimming, flying, and running animals, related to body size. Data are from Figs. 1A, 2, and 3D (net cost only). (The single open circle among the running animals refers to the cost of locomotion for the swimming duck.)

for more than a few percent of his total energy output (*25*); usually wind resistance is negligible compared to the common inaccuracies of measurements of oxygen consumption.

We know, however, that running fast requires a great deal of energy, and since it is not dissipated as work done on the environment, it must be dissipated internally. It can be divided into two categories, energy dissipated because of frictional and viscous resistances in joints and muscles, and energy used in the continuous accelerations and decelerations of the mass of the body and of the limbs. An exact analysis of these requirements is difficult because of geometrical complexities, such as the steadily changing angular momentum, the changing radius of curves followed by the center of mass of the different portions of the limbs, and so on. In spite of these difficulties an excellent kinematic analysis of running man was made by Wallace Fenn as early as 1930 (*26*). More recently, further analyses of the mechanical work of walking and running have been made at Margaria's laboratory in Milan (*27*). Such studies are essential for the analysis of the energy cost of locomotion in man, and studies extending to body shapes and sizes other than man's are much needed.

Running uphill, as we know, requires additional energy. A body that has been moved uphill has acquired potential energy, which is the product of its weight and the vertical distance through which it has moved. As we might predict, the cost of moving one unit of body weight uphill is similar for animals of widely different body sizes. This has been amply documented by many investigators; an early demonstration of this simple fact was given in 1903 by Slowtzoff (*28*), who studied dogs ranging in size from 5 to nearly 40 kilograms.

An animal moving downhill, on the other hand, loses potential energy, and there is some question of whether this energy can be usefully recovered by the organism. Conceptually, physiologists have attached the term "negative work" to this matter of events. To the physicist the term sounds appalling, for in actuality work cannot be negative; use of the term comes from the simple fact that work equals force times distance. For an animal moving downhill as opposed to uphill, the vertical distance is given a negative sign and the work therefore also gets a negative sign. The term is convenient and is likely to remain in use in physiology.

The question of whether any negative work can be recovered in the reversal of energy-yielding biochemical processes in the muscles has been seriously considered since the 1920's, when Fenn observed that lengthening of a muscle during contraction decreases the heat production in the muscle. In other words, to quote Fenn, "When the work done by the muscle is negative, the excess energy is also negative" (*29*).

An experiment as amusing as it is simple can be used to demonstrate that a given force can be exerted with less effort when the work is "negative." It is described in A. V. Hill's words as follows: "Two bicycles were arranged in opposition; one subject pedaled forward, the other resisted by back-pedaling. The speed had to be the same for both, and (apart from minor loss through friction) the forces exerted were the same. All the work done by one subject was absorbed by the other; there was no other significant resistance. The experiment was shown in 1952 at the Royal Society in London and was enthusiastically received, particularly because a young lady doing the negative work was able quickly, without much effort, to reduce a young man doing the positive work to exhaustion" (*30*).

Whether the biochemical events of muscular contraction actually can be reversed by stretching the muscle during contraction—that is, by performing work on the muscle, has not been finally resolved (*31*). The question is not without importance to locomotion, however. Let us consider the end of a single step of a running man. As the foot hits the ground, kinetic energy from the moving body is taken up by the partly contracted muscles of the leg. Part of the kinetic energy is stored as elastic energy in the contracted muscles, part of it seems to be recovered as the increased external work that the muscles can perform because of being stretched. The external work done by a muscle which has been stretched immediately before contraction has been found to be up to 2.5 times the work that the same muscle would perform during shortening from a state of isometric contraction (*32*), and only part of this increase can be accounted for by the elastic energy stored in the stretched muscle.

The physiological role of negative work is still very much in dispute, both at the molecular level and in studies of the energetics of the whole organism. I shall not attempt a further review of this particular field, instead I shall return to the energy expenditure of animals running horizontally.

The metabolic rate of a running animal increases with speed. For the white rat, as well as for other mammals, the relationship gives a straight line, as shown in Fig. 3A (*33*). It is now commonly agreed that within a wide range of speeds, the metabolic rate of a running man shows a similar straight line relationship (*34*). [For a walking man the relationship is distinctly nonlinear (*35*)]. The straight line in Fig. 3A does not extrapolate to the resting metabolic rate of the animal in question; the *Y*-intercept for zero running speed is higher than the value for the resting metabolism. However, the metabolic rate for a man who stands quietly on the treadmill instead of walking, or who is sitting passively on the bicycle ergometer (*36*), is close to the *Y*-intercept. The simplest interpretation of this observation is to consider that the difference between intercept and resting metabolism is due to the cost of maintaining the posture of locomotion, and the term "postural effect" seems acceptable.

To calculate the energy cost of running, we could use the total metabolic rate at a given speed, or we could subtract the resting (or standard) metabolic rate and say that the remainder goes into locomotion, or we could subtract the *Y*-intercept from the metabolic rate at a given speed and say that the excess energy is the cost of moving at that speed.

For my purposes this procedure is the simplest, for when the *Y*-intercept is subtracted, we obtain the metabolic cost of running as the slope of the line. Because the line is straight, the net cost of locomotion remains constant and does not change with the speed of running.

Determinations of the metabolic rate of animals of various body sizes in relation to the running speed shows that smaller animals have steeper regression lines than those of large animals (Fig. 3B). The slopes of these lines make it possible to compare animals running at quite different speeds, even though the maximum speed reached by the white mouse is less than the slowest speed of the dogs.

The slopes, calculated by dividing metabolic rate less intercept, by speed, indicate the cost of locomotion in the same units as used throughout this article. These slopes, the energy cost of moving 1 gram of animal over 1 kilometer, plotted against the body weight on logarithmic coordinates, yields a straight line as shown in Fig. 3C (*37*). The slope of the best-fitting straight regression line for these mammals is -0.40. Thus the cost of locomotion, per unit weight, is lower for larger animals, but the meaning of the exact numerical value of the slope has so far not been analyzed successfully.

Additional available data on the cost of locomotion in mammals are compiled in Fig. 3D. The solid circles repeat the data from Fig. 3C, with additional points from other studies which permit a reasonably accurate calculation of the net cost of locomotion, obtained either by plotting the rate of metabolism against speed, or by subtracting an observed nonrunning metabolic rate. The open circles are for the total cost of running, obtained from the total oxygen consumption while the animal was moving. Since no intercept has been subtracted, these points fall above those for the net cost. Furthermore, the distribution of these points seems to be curved upward at both ends. This is probably because these animals were not running very fast, and their nonrunning metabolism therefore was a large fraction of the total. If the nonrunning metabolism or the *Y*-intercept were subtracted, the points would be displaced downward, toward the regression line for the net cost of running, and the curved distribution might disappear.

In Fig. 3D the energy cost of locomotion for the swimming duck is also inserted, in this case the total rather than the net cost. Is is interesting, although perhaps fortiutious, that a swimming duck moves across the surface of the water at a cost similar to that of a mammal of the same body size running on land.

The energy costs of swimming, flying, and running are compared in Fig. 4 [see also (*38*)]. The points used for running animals represent the net cost of running, but for flying animals, the total cost at the most economical speed has been used. Since the flight metabolism is a high multiple of the resting metabolism, subtraction of the latter would have only minor influence on the points. It is interesting that for a given body size, flying is a far cheaper way to move to a distant point than is running. This is not intuitively obvious to us, for man has no experience in flying under his own power and it seems that the mere cost of staying up in the air would be excessive. If we consider a migrating bird, however, things appear more reasonable. A migrating bird can fly nonstop for more than 1000 kilometers, but it is hard to imagine a small mammal, say a mouse, running 1000 kilometers without stopping to eat and drink. The energy cost of swimming appears to be lower again. Man, however, is so ill-adapted to moving in water that swimming costs him five or ten times as much energy as does running the same distance on land. If the dolphin had a similar energy expenditure while swimming, its ability to live in the ocean would indeed be a paradox.

References and Notes

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or to subtract the resting metabolism from the total and consider the remainder as the energy used in running, or, as I have done here, subtract value for the *Y*-intercept. The procedure must depend on the purpose we have in mind. I have discussed the net cost of locomotion—that is, the cost of locomotion per se. The total energy expenditure during locomotion is higher, but equally correct. For example, a migrating bird uses its fat reserves for flying, and the distance it can cover on the available fuel is determined by its total metabolic rate. Likewise, a grazing sheep must obtain enough food to cover, not only the energy cost of walking, but enough for its total metabolic needs. Therefore, there is no reason for controversy, so long as we have defined the terms in estimating the cost of locomotion.

38. A comparison with man-made machines shows that automobiles use about twice as much energy in locomotion, per unit weight, as a horse (about 0.5 cal g^{-1} km^{-1}). Big jet airplanes use about the same amount of energy as a horse per unit weight, but smaller planes use progressively more energy, and helicopters use nearly ten times as much as a horse. Ships use less energy, however, and an economical long distance freighter may, per unit weight, use almost as little as one-tenth the energy used in locomotion of a horse.
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The Evolutionary Taxonomy of Culture

A few behavioral factors account for the regional variation and evolutionary development of culture.

Alan Lomax with Norman Berkowitz

The grand theme of anthropology is that man, to a far greater degree than the other animals, adapts to his environment by means of changes in socially transmitted, rather than biologically inherited, patterns of action and interaction. The ways of a people—its economic, affective, political, communicative, and expressive systems—are learned and may be changed by each succeeding generation. Margaret Mead tells how the Manus, a Stone Age people, were so impressed by Western culture that they decided to get rid of their own and straightway threw much of it into the sea (*1*). This instance illustrates the malleability of culture. It is this flexibility of cultural, as compared to biological, systems that gave man an advantage over other species and enabled him, early in his history, to occupy every zone of the globe.

Since cultures consist of enormous complexes of customs, beliefs, institutions, and modes of communication, they could only be transmitted, before the invention of written language, by whole societies. An ideal cultural taxonomy should, therefore, discover a series of geographically continuous culture regions, each explicable as a pattern of adaptation that was carried from its zone of origin to others along feasible land or sea routes. The borders of a given culture region should be defined by physical barriers or by the limits of other such culture regions. Any breaks in the distribution of such a culture continuum should be explained by the intrusion of another, more productive and better adapted cultural system. It should be possible to arrange these geographically bounded cultural taxa in a developmental sequence that would account for their boundaries and their discontinuities. Thus, human subspeciation could be viewed as a continuum of cultural adaptions with several regional specializations.

The factored cultural taxonomy presented here meets those requirements. Its weak spots occur exactly in those places where it lacks data, which may, with further effort, be supplied. Otherwise, its inclusiveness and its parsimony recommend it. First, the scheme accounts for most of the variation in human cultures by a small number of discrete cultural zones (Fig. 1) organized into three large regional clusters (Fig. 2): (i) the simple producers; (ii) the tropical gardeners; and (iii) the Eurasian agriculturalists. Each of these regions represents a decisive adaptive development. Second, factor analysis clusters the measures of culture themselves around two main vectors: (i) economic and social control of the environment, and (ii) organization and integration of teams. Vector 1 orders the main zones of culture on a steadily rising curve of socioeconomic development. Vector 2 (which depicts the form of team organization each subsistence level requires) oscillates in a regular, wavelike fashion along the curve of progress as the species deploys, again and again, its limited repertory of organizational resources (Fig. 5). A third group of factors, which includes the organization of kin and family, shows no clear vectored relation to evolutionary development.

The data for this evolutionary taxonomy came from two sources—a comparative survey of world song styles and a similar survey of ethnography: namely, G. P. Murdock's *Ethnographic Atlas* (*2*). Murdock encodes from the literature of ethnology the economic, social, and political features of more than 1000 societies. In some cases, these codes formed scales—for example, the one concerning the number of levels of political authority outside the local community, from 0 among hunters to 4 for Oriental empires. In other cases, Conrad Arensberg and I arranged the codes into scales in order to measure the relative frequency of certain kinds of behaviors or features of culture, such as level of

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