

Locomotion is energetically expensive. Moving an animal's mass through space requires large increments in metabolic energy input, and these costs rise rapidly with increasing speed. Only thermoregulation by birds and mammals in very cold environments can cause a similar rise in acute energy expenditure. Locomotion may thus have a major impact on the energy budgets of animals, particularly animals that forage actively and continuously and animals that migrate.

Locomotory Costs and Metabolic Energetics

Whether a large or small proportion of the daily energy budget is spent on activity, the expense of locomotion greatly affects the behavior of all vertebrates. High or even moderate levels of movement may tax energy delivery systems to their limits and result in fatigue or inadequate performance. We can appreciate these relationships qualitatively in considering our own responses to activity. A steady walk of about 6 km/h can be undertaken by most people without noticeable difficulty. Doubling that rate to a run (12 km/h) requires considerable exertion with greatly increased rates of ventilation and circulation. This speed can be sustained only with difficulty. Increasing the rate again to a sprint of about 20 km/h exceeds our limits of sustainable activity and results in very rapid exhaustion. In many vertebrates the speeds at which pronounced exertion and exhaustion occur are considerably less than those of humans. These limits vary greatly among different vertebrate groups and also vary with

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such factors as body size and temperature. The failure of locomotory performance, either in maximal speed or stamina, can result in a spectrum of consequences up to and including death. Such factors as pursuit or escape from predation, territorial defense, and competition for a mate and courtship may require high or sustained levels of performance at the limits that an animal can undertake.

The energy demands even of resting vertebrates can be substantial. Protein synthesis, ion transport, and circulation of body fluids, along with other processes, use energy continuously. Minimal rates of energy use are designated standard metabolic rates or, for endotherms, basal metabolic rates. These depend on many factors, principally body size and temperature. In vertebrates this maintenance metabolism is fueled aerobically, that is, by complete combustion of foodstuffs with oxygen to carbon dioxide and water. These metabolic rates are generally determined by measurement of the rate of oxygen consumption (\dot{V}_{O_2}). During physical activity the contraction of skeletal muscle requires additional energy, and respiratory and cardiovascular systems must increase the rates of oxygen delivery to the metabolizing tissue. In turn, the increased activity of these systems themselves requires increased oxygen delivery and energy use.

The capacities of oxygen delivery in vertebrate systems are not enormously expandable. Maximal rates of oxygen consumption ($\dot{V}_{O_2, \max}$) exceed standard levels on the average by approximately 10-fold, varying in range in different animals from 4-fold to about 25-fold (Brett, 1972;

Lechner, 1978; Bennett, 1978). The functional basis of these limitations is not completely known. However, the use of a cardiovascular system to transport oxygen from the external environment to the tissues may be an important limiting factor. Insects, for instance, which have tracheal respiratory systems, may in some cases increase \dot{V}_{O_2} 100- or 200-fold above resting levels. For whatever reason, in vertebrates (particularly in ectothermic vertebrates) aerobic scope, which is the difference between $\dot{V}_{O_{2max}}$ and $\dot{V}_{O_{2standard}}$, may be rather low.

If energy demand exceeds aerobic energy supply, anaerobic metabolism is utilized. Over the period of a few seconds, muscle can sustain contractile function by the catabolism of endogenous stores of adenosine triphosphate and creatine phosphate. However, for longer periods, anaerobic metabolism in vertebrates primarily involves the production of lactic acid by carbohydrate catabolism. As these reactions do not depend on cardiovascular transport, they can be activated within a muscle and produce large quantities of available energy in a short time. The efficiency of production of energy per unit substrate traversed is considerably less than for aerobic metabolism, but energy conservation may not be foremost in the priorities of a fleeing animal. The behavioral repertoire and performance capacities of vertebrates, particularly those of ectothermic vertebrates, are considerably expanded by the use of anaerobic metabolism. However, activation of extensive anaerobiosis generally results in fatigue and decreased performance capacity. The physiological causes of these relationships are not well understood. For locomotory performance, however, the implications are clear.

Anaerobic metabolism may be used during the initial stages of activity, before oxygen consumption has risen to a new elevated level, or for short (approximately 1 min) bursts of intense activity. Activity of longer duration must be undertaken within aerobic limits or fatigue may result. The aerobic metabolic rate must lie within the boundaries set by maximal and standard levels of oxygen consumption. Maximal levels of oxygen consumption thus set limits on the sustained activities and behaviors of animals. Most of the locomotion

and locomotory energetics discussed in this chapter are carried out within those limits.

Metabolic energy expenditure may be regarded as the power input into locomotion. The power output, the rate of work actually performed by the locomoting animal, may be considerably less. Analysis of power output requires a detailed examination of the biomechanical performance of an animal and has not been attempted extensively. The ratio of power output to power input, the mechanical efficiency, has been commonly assumed to be about 20% to 25% for vertebrate skeletal muscle. Similar maximal values for mechanical efficiency have been found for swimming fish (Webb, 1975, 1977). However, recent determinations on terrestrial animals (Taylor, 1980; Taylor and Heglund, 1982; Heglund et al., 1982) have found that peak mechanical efficiency is size-dependent and varies from less than 10% in quail to approximately 70% in humans. The higher efficiencies are thought to be due primarily to storage and release of elastic energy during individual limb cycles. More information on locomotory efficiencies would be very helpful in understanding the return that animals receive for their metabolic energy expenditure. (The storage of elastic energy is discussed in Chapters 2, 3, and 4.)

The analysis of locomotory energetics requires the determination of \dot{V}_{O_2} of an animal moving at a steady rate. These measurements can be made on animals walking on a treadmill, flying in a wind tunnel, or swimming against a current. An effective method for measuring \dot{V}_{O_2} in aerial breathers entails fitting an animal with a light-weight, clear plastic mask (see Fig. 10-1). A pump draws room air into and through this mask. The animal consumes a portion of the oxygen passing in the air stream, lowering the oxygen content of the air in the flow stream below that of the room air. The animal's rate of oxygen consumption can be calculated from this differential in oxygen concentration and the rate of air flow through the mask. Speed can be set by regulating the rate of tread movement for terrestrial walkers or wind flow for flyers. Considerable perseverance and ingenuity are sometimes required to elicit cooperation from the subjects, but animals will often attempt

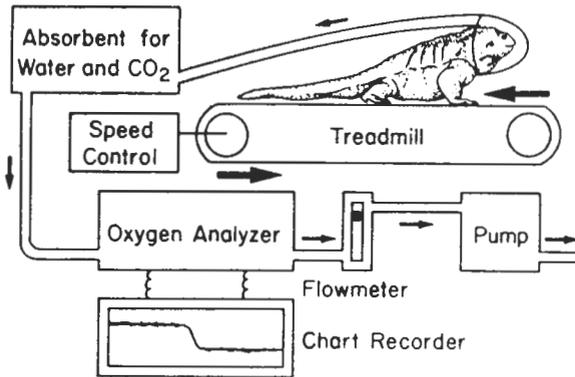


Figure 10-1 Measurement of oxygen consumption of an animal walking on a treadmill.

to match speed and maintain a constant station during the experiment. Data have been collected on a surprisingly large and diverse group of terrestrial animals. The logistical operations, including design concerns for laminar flow and drag, are more difficult for flying animals, and relatively fewer observations have been made on them.

Many fish will also maintain station against a current. If the oxygen content of the water upstream and downstream from the fish and the rate of the current flow are measured, \dot{V}_{O_2} can be calculated in a manner similar to that for aerial breathers.

Each locomotory mode, walking or running, flying, and swimming, has its own relationship between energy use and speed. The patterns are quite distinct and are discussed separately below, after which the relative costs of these different locomotory modes are compared.

Terrestrial Locomotion

As terrestrial animals walk and run, \dot{V}_{O_2} increases approximately linearly with speed (Taylor et al., 1970; Taylor, 1977; Taylor et al., 1982) until \dot{V}_{O_2max} is attained. This relationship between \dot{V}_{O_2} and walking speed is shown in Figure 10-2A for a lizard, the gila monster. Also shown (Fig. 10-2B) are a variety of terms that have been used to describe locomotory energetics of terrestrial ani-

mals (Tucker, 1970; Schmidt-Nielsen, 1972). The speed at which \dot{V}_{O_2max} is attained is the maximal aerobic speed, which is approximately 0.6 km/h in this lizard at 25°C. Speeds below this can be sustained for long periods because they are dependent only on aerobic metabolism. Walking at speeds greater than the maximal aerobic speed elicits the same aerobic power input, since it is already maximal. The additional power input required is provided anaerobically. These speeds cannot be sustained without resulting in fatigue.

If the values for \dot{V}_{O_2} are extrapolated to zero speed, they intersect the ordinate at levels considerably in excess of those measured for resting animals. This value of \dot{V}_{O_2} is called (accurately but somewhat inelegantly) the y-intercept. It ranges from 1.3 to 2.9 times resting metabolic rate and generally averages approximately 1.7 (Paladino and King, 1979). The functional basis of this increment is not well understood. It is often attributed to a "postural" component of locomotion,

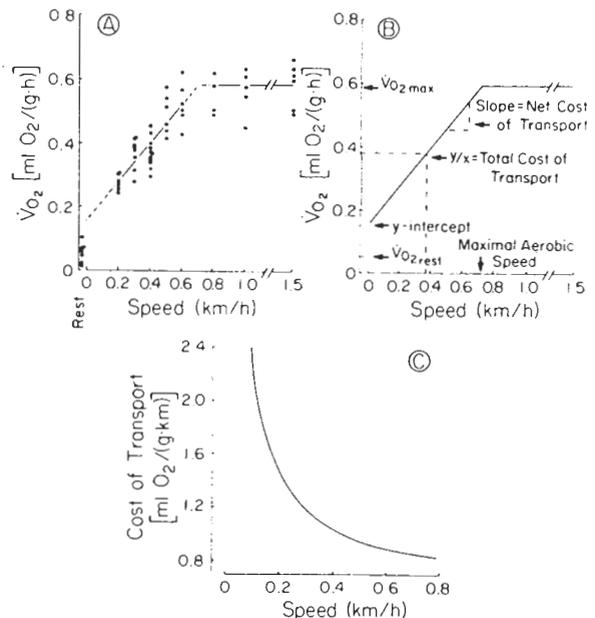


Figure 10-2 Locomotory energetics of the gila monster (*Heloderma suspectum*). A: Oxygen consumption at different walking speeds; B: locomotory terminology; C: total cost of transport at different speeds. (Data from John-Alder, Lowe, and Bennett, 1983.)

a cost associated with maintaining an upright stance. Whatever its cause, it greatly increases energy expenditure even during very slow locomotion. Its presence partly accounts for the high cost of locomotion in general and the narrow range of sustainable speed of animals with low aerobic scopes.

The slope of the relation of \dot{V}_{O_2} to speed between zero and maximal aerobic speed is defined as the net cost of transport. This quotient is expressed as volume of oxygen consumed (aerobic power input) per distance traveled, that is, volume of O_2 per unit time divided by distance per unit time, generally as ml or l of O_2 per km. It represents the amount of fuel that must be expended to traverse a given distance and is independent of time and speed. Because of this independence, it is widely used as the standard of comparison among animals of different taxonomic groups, body sizes, or body temperatures.

It should be evident, however, that the real locomotory costs to animals are quite different from these values, which specifically exclude the portion of energy expenditure associated with maintenance and posture. The entire aerobic power input to locomotion is taken into account by the total cost of transport, the quotient of \dot{V}_{O_2} at any speed (between zero and maximal aerobic speed) and that speed. Although this value also has units of volume of O_2 consumed per distance traveled, it is highly speed-dependent. This dependence is shown in Figure 10-2C for total cost of transport in the gila monster. As the animal walks faster, the total amount of energy expended while traversing a given distance declines. As an animal spends less time crossing a given distance at a greater speed, maintenance and postural processes do not have to be sustained as long and consequently require less energy expenditure. Although maintenance energy costs continue whether the animal is locomoting or stationary, the postural costs do not. Therefore, the most economical transport is attained when an animal walks at close to its maximal aerobic speed.

The linear increment of aerobic power input with increasing speed is perhaps unexpected, as power inputs in mechanical vehicles must often increase exponentially as speed increases. A partial explanation for this linearity may be found in

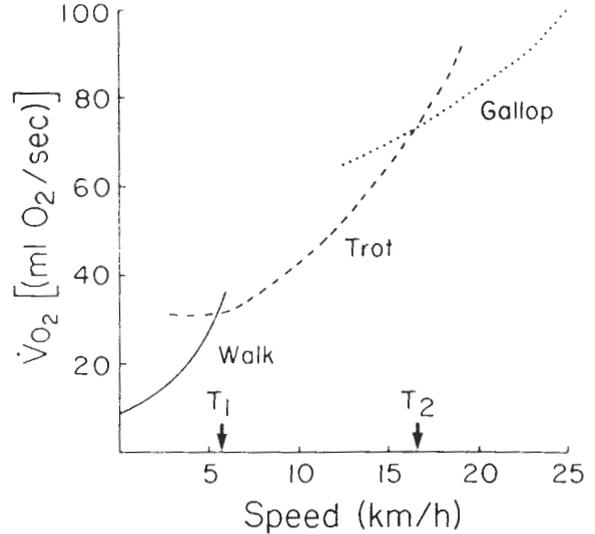


Figure 10-3 Oxygen consumption of a horse trained to continue different gaits beyond their normal range of speed. The horse normally changes from a walk to a trot at T_1 and from a trot to a gallop at T_2 . (Data from Hoyt and Taylor, 1981.)

gait transitions at different speeds (Hoyt and Taylor, 1981). As speed increases, quadrupeds often change gait from a walk to a trot to a gallop. Oxygen consumption in a horse trained to continue these gaits beyond their normal range of speeds is shown in Figure 10-3. Within each gait, \dot{V}_{O_2} increases exponentially with speed, but the horse naturally selects the gait that has the lowest energy expenditure at any given speed. The minimal cost of transport is the same in each gait. A linear approximation is an excellent description of the \dot{V}_{O_2} maintained over the entire range of speeds.

These relationships have proved highly useful in analytical and comparative studies of locomotory energetics. It is important to keep in mind, however, that they represent determinations based on steady rates of \dot{V}_{O_2} attained after several minutes of activity. When an animal is initially active, power output may increase almost immediately as a step function. Aerobic power input lags significantly for 1–2 min before a new level is attained. Anaerobic metabolism provides the differential energy requirement during this period. Often, \dot{V}_{O_2} will overshoot before settling at

an ultimate plateau level. After activity has ceased, oxygen consumption almost always remains elevated above resting levels for some time. This excess \dot{V}_{O_2} is termed the oxygen debt. Thus, the metabolic patterns and energetics of animals initiating activity, changing speeds, or recovering from activity are far more complex than the above relationships would suggest. These steady-state models attempt only to approximate natural activity and energy expenditures.

Quadrupedal Locomotion: Mammals and Lizards Endothermic (mammals and birds) and ectothermic (reptiles, amphibians, and fish) vertebrates have very different capacities for metabolic power input and consequently differ greatly in their locomotory capacities. These factors can readily be seen in comparisons of the locomotory energetics of lizards and mammals. Such direct comparisons can easily be undertaken in animals of similar body size and temperature. Mammals have considerably greater levels of resting \dot{V}_{O_2} , exceeding those of resting ectotherms of equal size and temperature by 6- to 10-fold (Benedict, 1932; Dawson and Bartholomew, 1956; Bennett, 1978, 1980a). This differential in metabolic rest and heat production is the basis of endothermy, and it represents a major energy commitment to this metabolic mode. Maximal oxygen consumption, too, is substantially greater in mammals, also exceeding \dot{V}_{O_2max} values of ectotherms by approximately 10-fold. Thus, oxygen processing abilities are nearly an order of magnitude greater in endotherms.

Mammals, with their greater aerobic scopes, are able to sustain substantially greater levels of metabolic power input and achieve greater maximal aerobic speeds (Fig. 10-4). Energy expenditure at rest or while walking at low speeds is substantially less in a lizard than in a mammal. The net cost of transport is very similar in both animals. Increments in speed thus require similar increments in energy input, indicating that the differences in limb configuration among these animals have no substantial energetic consequences (Bakker, 1972). However, a lizard of approximately 1 kg in mass reaches its aerobic limits at rather low speeds of 1 km/h or less. Maximal levels of aerobic energy expenditure are achieved

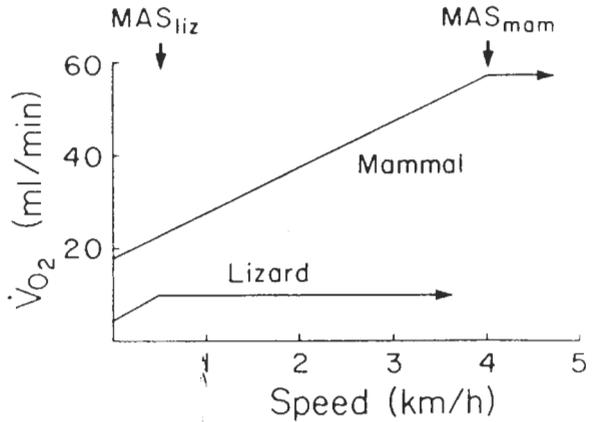


Figure 10-4 Oxygen consumption of a 1-kg mammal and a 1-kg lizard (35°C) walking on a treadmill. MAS = maximal aerobic speed. (Redrawn from Bennett and Rubin, 1979.)

by a mammal of similar size at 4-5 km/h. There is thus a substantial range of locomotory activities that is sustainable by endothermic vertebrates but cannot be maintained by ectotherms.

Maximal burst speeds, however, are similar in both mammals and lizards. Since these are fueled primarily by anaerobic metabolism, the greater aerobic power inputs of mammals do not greatly affect this aspect of locomotion. Ectotherms may thus be equally fast and may escape from endotherms during brief periods of rapid pursuit.

Size and Locomotory Energetics One might reasonably expect that the energy cost of locomotion should increase directly as body mass increases. That is, a doubling of body size might be expected to double locomotory costs. In fact, energy expenditure does not increase in proportion to mass, but rather as $mass^{0.7}$. Allometric equations have been calculated summarizing the net cost of transport for many species of mammals (Taylor et al., 1982) and lizards (Gleeson, 1979):

$$\dot{V}_{O_2} = 0.53 m^{0.68} \quad (\text{mammals})$$

$$\dot{V}_{O_2} = 0.67 m^{0.75} \quad (\text{lizards})$$

where \dot{V}_{O_2} is l O_2 /km and m is mass in kg. As there is considerable scatter about these regressions, they are not significantly different and net costs of transport of equal-sized mammals and lizards

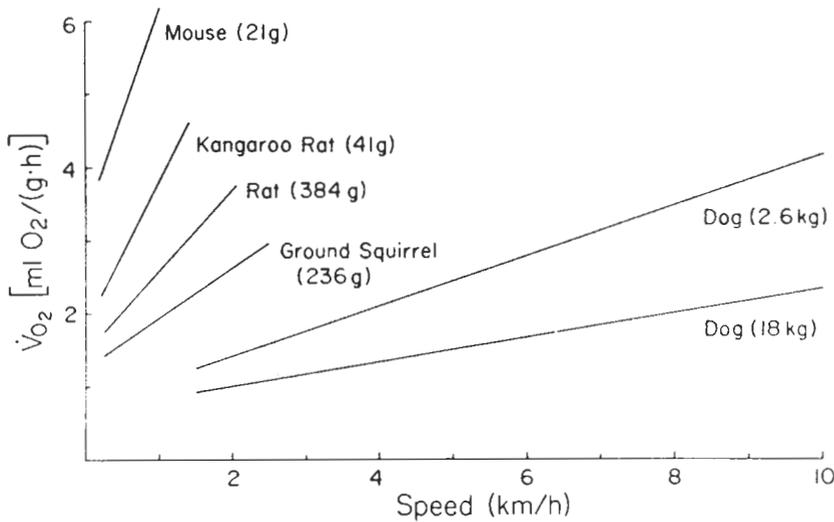


Figure 10-5 Mass-specific rates of oxygen consumption of different-sized mammals running on a treadmill. (Redrawn from Taylor, Schmidt-Nielsen, and Raab, 1970.)

are not different. Total locomotory costs may be estimated by adding the y-intercept value to the product of speed and net cost of transport. For mammals, this relationship is

$$\dot{V}_{O_2} = 1.09 m^{0.69} + 0.53 m^{0.68} S,$$

where \dot{V}_{O_2} is l O₂/h, m is mass in kg, and S is speed in km/h (Taylor et al., 1982).

Net costs of transport have been found to be very similar among several groups of terrestrial vertebrates. Transport costs are, for instance, indistinguishable between quadrupedal and bipedal walkers (Fedak and Seeherman, 1979; Paladino and King, 1979), contrary to an earlier report based on fewer observations (Fedak, Pinshow, and Schmidt-Nielsen, 1974). Even within single species of primates, quadrupedal and bipedal gaits have equal transport costs (Taylor and Rowntree, 1973). The relationship of oxygen consumption, speed, and transport costs in most hopping mammals are also adequately described by these equations (Thompson et al., 1980). The evolution of bipedality or bipedal hopping was probably not, therefore, based on energetic grounds. One conspicuous exception to these general patterns of energetics of both bipedal and quadrupedal locomotion is the red kangaroo. It maintains a constant oxygen consumption over a broad range of hopping speeds while altering stride length (Dawson and Taylor, 1973). Elastic storage in the conspicuous tendons of the hind

limbs may be involved in this unique pattern of locomotory energetics (see also Chapter 3).

If these relations are expressed on a mass-specific basis, it is clear that the cost of moving a unit of mass is less in larger organisms and is approximately proportional to body mass^{-0.3}. Thus, at equal speeds a mouse or rat must utilize more energy and consume more oxygen per gram body mass than does a dog or human (Fig. 10-5). The functional basis of this allometry is not understood completely, but it may reflect differences in the inherent contractile properties of muscle tissue between large and small animals (Taylor et al., 1980).

These regression equations may be used to predict transport costs of a previously uninvestigated animal or to compare differences in locomotory modes. For instance, the net cost of transport of a garter snake is only one third that predicted by the equation for lizards (Chowdrow and Taylor, 1973), indicating that crawling may be considerably less expensive than walking. These equations are powerful in theoretical or generalized analyses of locomotory or energetic costs. However, there is real variability among species that is obscured by these regressions, and predictions should be made with a note of caution for any particular species.

Carrying external loads, such as food or an infant, also increases locomotory costs. Oxygen consumption rises in direct proportion to the per-

centage mass increment (Taylor et al., 1980). If a load equivalent to 10% of its mass is placed on a walking animal, its oxygen consumption will rise 10%. This relationship has interesting allometric implications. A smaller animal expends more energy per unit mass walking at a given speed than does a larger animal. If a load representing an equal percentage of body mass is placed on each, the amount of energy input per unit mass must rise a greater amount in the smaller animal to sustain the load. A smaller animal must consequently expend more energy to produce an equivalent force at a given speed than does a larger animal.

Body Temperature and Locomotion Most metabolic processes are directly temperature-dependent. As body temperature changes, $\dot{V}_{O_2\text{rest}}$ and $\dot{V}_{O_2\text{max}}$ are markedly affected and are substantially lower at low body temperatures. Changes in these aerobic metabolic factors may be expected to produce changes in locomotory capacities and patterns. Endotherms generally avoid these fluctuations by maintaining constant body temperature, although there is much more variability in mammalian muscle temperature than is generally appreciated. Body temperature changes may, however, be pronounced in ectotherms. Relatively few analyses of the effects of temperature on locomotory capacities and energetics have been undertaken.

The contrasting advantages and disadvantages of different body temperatures for locomotory performance are shown in the desert iguana (Fig. 10-6; John-Alder and Bennett, 1981). Low body temperatures permit energy conservation and economical locomotion: resting or walking at any given speed costs less at the lower temperature. However, the range of aerobically sustainable behaviors is relatively low because of low $\dot{V}_{O_2\text{max}}$. At 40° C, lizards can walk three times faster without tiring than at 25° C. Thus, the higher body temperature permits a greater range of sustainable behaviors while requiring a greater energy input. These increased costs of the higher temperature can be somewhat offset by the expanded behavioral capacity. The minimal total cost of transport, that is, the least amount of energy required to traverse a given distance, is equal at both tem-

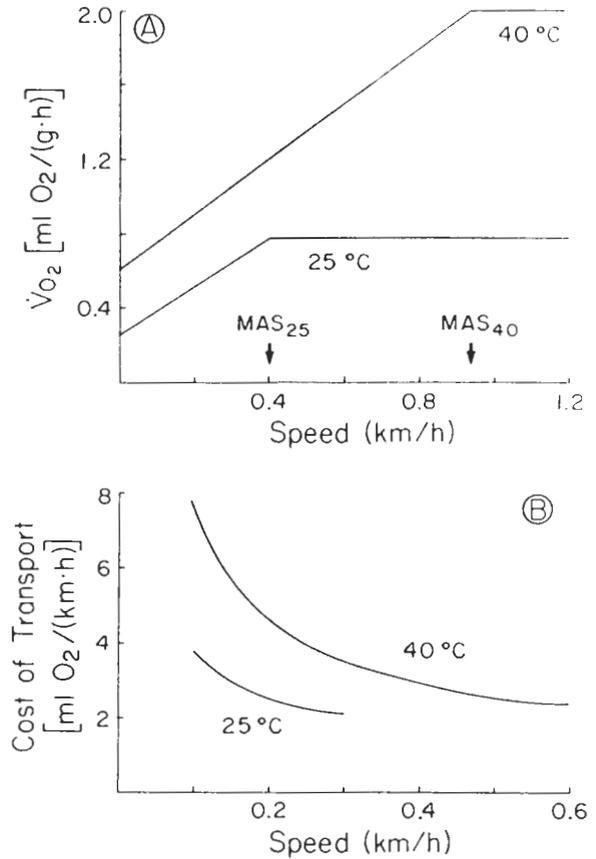


Figure 10-6 Locomotory energetics of a lizard (*Dipsosaurus dorsalis*) on a treadmill at two body temperatures. A: Oxygen consumption; B: total cost of transport. (Data from John-Alder and Bennett, 1981.)

peratures (Fig. 10-6B). Thus, an animal with a high body temperature may reduce its transport cost by traveling at a faster speed. Behavioral thermoregulation permits an ectotherm to take advantage of both aspects of the thermal dependence of locomotory energetics: energy conservation at low temperatures and expanded locomotory capacities at high temperatures.

In contrast to the thermal dependence of oxygen consumption and transport, anaerobic metabolism in ectothermic vertebrates can be relatively independent of body temperature (Bennett, 1978). The rate of lactic acid formation during intense activity in small lizards is nearly constant between 20° and 40° C (Bennett and Licht, 1972). Burst speeds show a similar lack of

thermal dependence in these animals (Bennett, 1980b). Anaerobic metabolism provides a capacity for rapid activity and escape over short distances over a considerable range of body temperatures. Locomotory capacity in ectotherms is thus not completely tied to the strict thermal dependence of aerobic metabolism.

Flight

Flight requires high levels of power input. Although brief bursts of flight might be fueled anaerobically, sustained flight of more than a minute's duration must be supported aerobically. Among the vertebrates only birds and mammals possess levels of oxygen consumption capable of sustaining flapping flight. Among the mammals, only bats, which have particularly high levels of $\dot{V}_{O_{2max}}$, fly. Although it requires high energy expenditure, flight is a relatively economical way of covering long distances, particularly during migration.

Several models have been advanced to predict the requisite power input for avian flight (for example, Tucker, 1973; Pennycuik, 1975; Greenewalt, 1975; Rayner, 1979; see also Chapter 8). Although these differ in several details, they all predict a U-shaped relationship between power input and speed (see Fig. 10-7A). That is, power requirements for hovering flight (stationary flight with no forward velocity) are predicted to be high. As speed increases, costs decrease to a minimal value at velocity V_0 , the minimum power speed. At greater speeds, power input increases again. Thus, there is a predicted minimal cost associated with flight, for if a flier attempted to minimize its rate of energy expenditure, it would fly at V_0 . This speed is not, however, the most economical in terms of energy expended per distance traveled (that is, the minimal cost of transport). This is obtained at the V_1 , the maximum range speed, at which a line from the origin is tangent to the power curve. Distance traveled per unit fuel would be minimal at V_1 , and a flier traveling long distances might be expected to fly at this speed.

The predicted speed dependence of locomotory costs in fliers is thus fundamentally different from that of terrestrial animals. In the latter min-

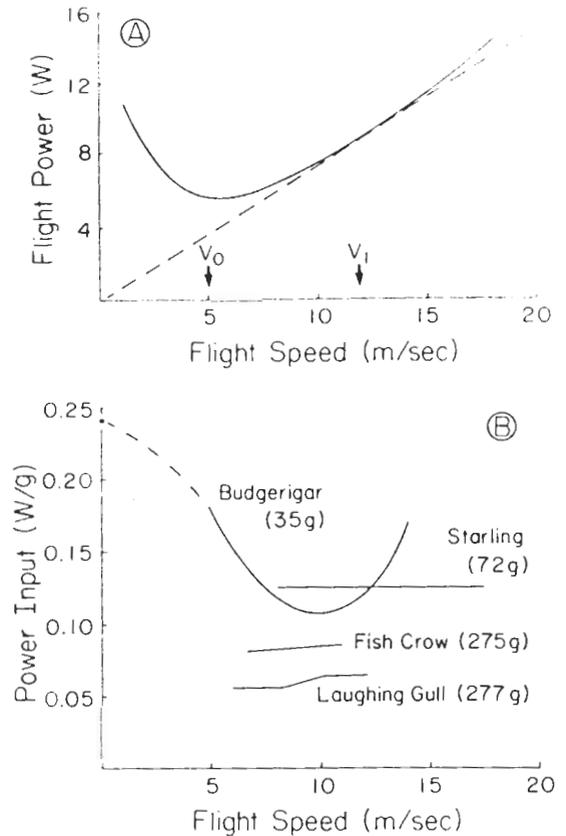


Figure 10-7 Flight energetics of birds. A: Theoretical predicted power input required for flight by a 330-g pigeon. V_0 = minimum power speed; V_1 = maximum range speed. (Redrawn from Rayner, 1979.) B: Observed power requirements for four species of birds. (Redrawn from Bernstein, Thomas, and Schmidt-Nielsen, 1973.)

imal rates of energy expenditure are obtained while standing still, and minimal total cost of transport occurs at maximal aerobic speed. In fliers flight is least expensive and minimal transport costs occur at intermediate speeds.

Relatively few measurements of oxygen consumption as a function of speed have actually been made on flying birds (budgerigar and laughing gull, Tucker, 1968, 1972; fish crow, Bernstein, Thomas, and Schmidt-Nielsen, 1973; starling, Torre-Bueno and Larochelle, 1978; see Fig. 10-7B). A distinct U-shaped relationship between oxygen consumption and flight speed is seen only for the budgerigar. Oxygen consumption increases slightly with increasing speed in the

laughing gull, but it is independent of speed in the fish crow and starling. The data do not correspond well to model predictions. Many variables are built into such models, and flying birds alter these variables so as to minimize energy expenditure. Moreover, the efficiency of energy generation may be changing as a function of speed. At any rate, the predictions concerning a minimal cost of flying at a specific speed (V_0) and an intermediate speed (V_1) with a minimal total cost of transport are not found in any bird examined besides the budgerigar. Total cost of transport is minimal at the fastest speeds flown for the other species. Further observations on the actual cost of avian flight and the reconciliation of the models with empirical data are required before we can understand avian flight energetics.

These data and models refer to the cost of level, continuous flapping flight, but other patterns of flight are also commonly seen in some birds. Gliding flight on air currents with fixed and extended wings can be used by birds with large wingspans. The cost of gliding as estimated for vultures (Pennycuik, 1972) and measured for gulls (Baudinette and Schmidt-Nielsen, 1974) is less than one third that of flapping flight. Gliding approximately doubles energy expenditure above basal metabolic levels, whereas flapping flight requires a substantially greater increment. It has also been proposed (Tucker, 1968) that undulating flight, which is seen in many small birds, may be more economical than level flight (Rayner, 1977).

Determination of the energetics of bat flight has received relatively less experimental attention. Maximal oxygen consumption, net cost of transport, and total cost of transport are similar in birds and bats, indicating a convergence of locomotory energetics and physiological capacity in these groups (Thomas and Suthers, 1972; Thomas, 1975). Oxygen consumption is relatively independent over a range of flight speeds in two species of bats examined (Thomas, 1975).

Swimming

Energy expenditure during swimming has been measured for several species of teleost fish, and its speed dependence is different than that of either flying animals or terrestrial walkers. Oxygen con-

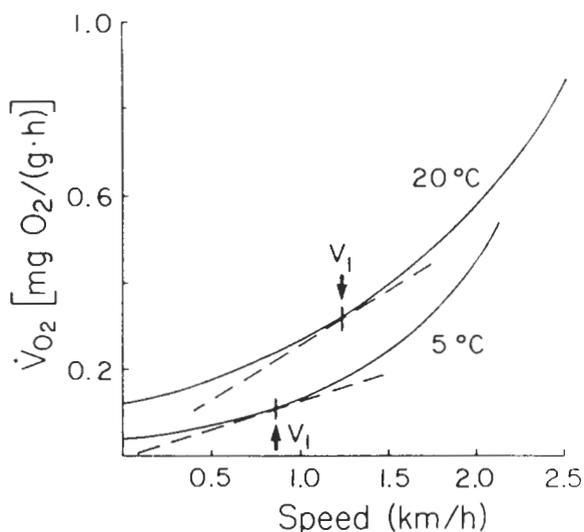


Figure 10-8 Oxygen consumption of a 50-g salmon acclimated to two temperatures. (Data from Brett, 1964.) V_1 = speed at which the normal cost of transport is attained at each temperature.

sumption increases exponentially with increasing speed (Fig. 10-8) and is generally best described by the relation $Y = ae^{bx}$, where Y is \dot{V}_{O_2} , x is swimming speed, and a and b are constants (Brett, 1964). More specifically, \dot{V}_{O_2} often increases approximately as the square of swimming speed (Fry, 1957). Standard metabolic rate is often measured in fish by extrapolating \dot{V}_{O_2} to zero swimming speed, as it is operationally difficult to measure this rate directly (Fry and Hochachka, 1970). Under these circumstances, there would be by definition no "postural" costs associated with swimming locomotion. In some fish standard metabolic rate is less than that observed by extrapolation to zero speed (Puede and Holliday, 1980; Duthie, 1982). The basis of this cost, designated as "postural" by analogy with terrestrial animals, is unknown. Oxygen consumption increases with increasing speed up to the critical swimming speed, the equivalent of maximal aerobic speed in terrestrial animals. This is the greatest speed at which activity can be sustained and is used to determine \dot{V}_{O_2max} . Very active fish, such as salmon (*Oncorhynchus*), have greater levels of \dot{V}_{O_2max} and can attain greater critical swimming speeds than more sluggish species such as goldfish (*Carassius*) (Fry, 1947; Brett, 1964). Swimming at

levels in excess of critical speeds, fish activate anaerobic metabolism and very rapidly accumulate high levels of lactic acid. Exhaustion ensues rapidly and recovery from burst activity may be protracted, particularly at low body temperatures.

The minimal cost of transport in fish, as in birds, is attained at some intermediate locomotory speed V_1 (Fig. 10-8), determined by a line through the origin and tangent to the curve relating oxygen consumption to speed. This is the most economical speed for traversing a given distance. From the limited data available the minimal cost of transport does not appear to vary greatly with structure or swimming mode among fish of different families: anguillids, sparids, and salmonids, for instance, have similar locomotory costs (Brett, 1964; Rao, 1968; Wohlschlag, Cameron, and Cech, 1968; Schmidt-Nielsen, 1972). Difference in body form and locomotory mode may, however, influence other aspects of locomotory performance, such as burst speed.

Body size greatly influences locomotor capacities of fish. Larger fish can sustain substantially greater critical swimming speeds than can smaller fish (Brett, 1965; Webb, 1975; Hoar and Randall, 1978; Wardle, 1977; Weihs, 1977). For example, at 15° C a 3-g salmon has a critical swimming speed of 1.9 km/h, whereas that of a 1400-g fish is 6.4 km/h (Brett and Glass, 1973). Speeds measured in body lengths decrease with increasing size: in the former examples, the speed of the smaller fish is 6.7 body lengths/sec and that of the larger is 3.3 body lengths/sec. The minimum cost of transport per unit mass in salmon decreases as $\text{mass}^{-0.24}$ (Brett, 1965; Schmidt-Nielsen, 1972). As in terrestrial animals, the speed dependence of mass-specific metabolic rate is less in larger fish.

As in locomotion in terrestrial ectotherms, temperature exerts a controlling influence on energy expenditure and performance capacity. For experiments on thermal influences fish are previously acclimated to all experimental temperatures. Consequently, the resulting patterns are not strictly comparable to those determined during the acute temperature exposure of terrestrial ectotherms. As in the latter group, activity at any given speed is more expensive at a higher temperature (Fig. 10-8). For example, \dot{V}_{O_2} of a salmon

swimming at 1 km/h is approximately twice as high at 20° C as at 5° C (Brett, 1964). Critical swimming speed also increases at higher temperatures, but this increment is relatively small in comparison with that in terrestrial ectotherms. In salmon critical speed increases from 2.1 km/h at 5° C to only 2.5 km/h at 20° C (Fig. 10-8; Brett, 1964). For several species of fish examined, $\dot{V}_{O_{2max}}$ and maximal critical swimming speeds are attained at intermediate acclimation temperatures and not at maximal temperatures (15° C in salmon, Brett, 1964; 20° C in goldfish, Fry and Hochachka, 1970; 30° C in bass, Beamish, 1970). Critical swimming speeds and $\dot{V}_{O_{2max}}$ remain relatively constant as temperature is increased above these levels. These plateaus in performance and $\dot{V}_{O_{2max}}$ may be the result of a limitation on environmental oxygen availability in some species (Brett, 1964).

The energetics of fish locomotion has received considerable theoretical attention (Weihs, 1973a,b, 1974, 1977; Webb, 1975, 1977; Wardle, 1975, 1977; Alexander, 1977; Wardle and Videler, 1980; Videler and Weihs, 1982). Several of these authors have proposed models for power input necessary at different speeds. Some have suggested that schooling (Weihs, 1973a) or burst-and-coast swimming behavior (Weihs, 1974; Videler and Weihs, 1982) can substantially reduce energy expenditure over solitary or steady-rate swimming. These models now require empirical testing.

Energetic measurements have also been made on locomotory costs of several nonpiscine swimmers (humans, Andersen, 1960; ducks, Prange and Schmidt-Nielsen, 1970; sea turtles, Prange, 1976; marine iguana, Gleeson, 1979; Vleck, Bartholomew, and Gleeson, 1981). In all cases energy expenditure during swimming is substantially in excess of the costs measured or estimated for fish of similar size. The cost of swimming in ducks and humans is 20 to 30 times higher than levels predicted for fish (Schmidt-Nielsen, 1972). These values do reflect also the greater metabolic costs associated with endothermy in these species, but even in ectothermic turtles and lizards, metabolic costs are 2 to 3 times those anticipated for fish. Surface swimming involves considerable wake formation, which should increase power

input requirements, but this undoubtedly does not account for all the energetic differential. It is clear that the other vertebrates measured have not been able to reduce swimming costs to those characteristics of fish. Presumably, marine mammals such as cetaceans have substantially lower locomotory costs during swimming (Schmidt-Nielsen, 1972), but these have not been examined.

Locomotory Costs and Evolution of Energetic Patterns

A comparison of the energy costs of different locomotory modes was undertaken by Tucker (1970) and Schmidt-Nielsen (1972), revealing striking differences in the levels of energy expenditure associated with walking, flying, and swimming (Fig. 10-9). (See Chapter 6 for the energetics of fossorial vertebrates.) Terrestrial locomotion is by far the most expensive way of getting around. Much of the energetic input is expended in raising the center of mass and accelerating and decelerating the limbs through successive limb cycles. Flight is a less expensive way of traversing a given distance, despite the relatively large amounts of energy input required. Swimming by fishes is the least expensive of the three locomotory modes, requiring only about one half to one third the input required for flight and only one eighth that for walking. In view of these large differentials it is not surprising that most animals that undertake long distance movements are swimmers or flyers.

Locomotory energetics undoubtedly played a significant role in shaping the evolution of vertebrate metabolic and behavioral patterns. Levels of standard and maximal oxygen consumption are similar throughout the ectothermic vertebrates and most invertebrate groups (Hemmingen, 1960; Bennett, 1978), suggesting a similar pattern of energy use and capacity for oxygen transport in ancestral forms. Likewise, anaerobic capacities of the vertebrates have been well developed since their very early evolution (Ruben and Bennett, 1979). Since ancestral vertebrate systems evolved in aquatic environments, costs of transport must have been relatively low for an-

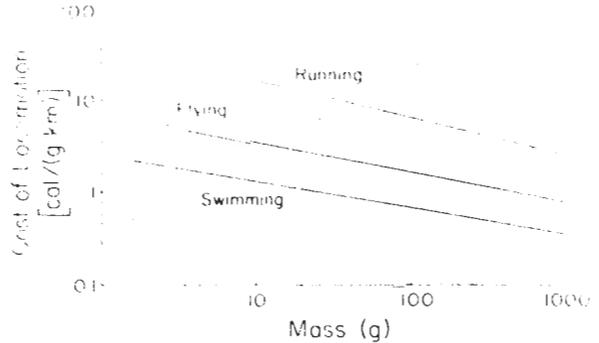


Figure 10-9 Cost of locomotion of running, flying, and swimming animals. (Redrawn from Schmidt-Nielsen, 1972.)

cestral fish, as they are for modern fish. The low cost of swimming permits high cruising speeds and a great range of aerobically sustainable behavior, even though V_{O_2max} is relatively low in fish in comparison with modern birds and mammals. A salmon of 1-2 kg, for instance, can swim at nearly 5 km/h for long periods (Brett and Glass, 1973). This speed is fully equivalent to the maximal aerobic speeds of terrestrial mammals of equal size, animals that possess substantially greater aerobic power inputs. The well-developed anaerobic capacities of modern fish increase capacities above sustainable levels of performance. Burst speeds are approximately four times critical swimming speeds in modern fish (Brett, 1965; Wardle, 1975). Thus, in extant fish anaerobic metabolism plays a supplementary role for escape or pursuit on top of a substantial behavioral repertoire that is supported aerobically. These energetic relationships were probably similar in ancestral fish.

These metabolic patterns and capacities would then have characterized the vertebrate groups that colonized the land. However, their range of sustainable levels of activity could have been severely constrained because of the greater transport costs associated with terrestrial locomotion. Similar aerobic scopes could no longer provide previous levels of activity. This condition may be exemplified by modern lizards, which have maximal aerobic speeds of only 0.5-1 km/h in animals of 1-2 kg and even lower capacities at low

body temperatures. Anaerobic capacities would still have been well developed and would have necessarily provided a much greater margin of behavioral capacity than previously. Burst speeds in lizards this size may be 15–20 km/h, increasing performance levels by 15- to 40-fold. Activation of this anaerobic metabolism results, however, in rapid exhaustion and loss of performance capacity.

With the evolution of higher rates of metabolism associated with endothermy, aerobic capacities greatly expanded. These permitted high levels of sustainable behavior during terrestrial locomotion in spite of the high cost of transport. Additionally, sufficient aerobic power was then available to permit flapping flight, with its advan-

tages of low locomotory costs, once a certain level of aerobic power input was attained. In endotherms anaerobic metabolism was again relegated to use only during the initial stages of activity or under very substantial exertion, and it provided support for a relatively smaller proportion of maximal behavioral performance. In mammals, for instance, burst speeds are only 2 to 3 times maximal aerobic speeds. The evolution of endothermy thus substantially altered patterns of locomotion and metabolic support among the evolving groups. The expanded capacities for sustainable behavior were undoubtedly significant selective factors in promoting development of greater aerobic levels (Bennett and Ruben, 1979).

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