

# Optimization and Gaits in the Locomotion of Vertebrates

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I. Introduction .....	1199
II. Optimization Criteria .....	1200
III. Similarity Criteria .....	1204
IV. Walking and Running .....	1207
A. People and animals .....	1207
B. Robots .....	1216
V. Flight .....	1218
VI. Swimming .....	1221
VII. Conclusion .....	1224

## I. INTRODUCTION

People walk at low speeds and run to go faster. Quadrupedal mammals, such as horses, walk at low speeds, trot at intermediate speeds, and gallop at high speeds. These gaits are sharply distinct: a human run, for example, is not simply a walk performed quickly.

The concept of gaits has been applied principally to terrestrial locomotion on legs, but it seems useful to apply it also to other modes of locomotion. Its application to flight was justified when Rayner, Jones, and Thomas (78) showed that the pattern of vortices in the wake of a bat flying fast was strikingly different from the pattern behind the same bat flying slowly. It may be applied to the swimming of fish, such as *Lepomis*, that use their pectoral fins for swimming slowly and their tails for swimming fast (101). Crawling snakes use different patterns of movement in different circumstances (37), and these also may be regarded as gaits, but it is not clear whether the choice of pattern is governed by the speed of crawling. Indeed it seems to depend more on the nature of the substrate.

A slow human walk and a fast human walk are regarded as versions of the same gait, despite marked differences between them in features such as the pattern of force exerted on the ground (12) as well as in speed. This is because they merge into each other as speed changes: the quantities that describe the differences between them have intermediate values at intermediate speeds, as illustrated by Figure 1. The duty factor (the fraction of the duration of the stride for which each foot is on the ground) decreases slowly through the range of walking speeds and then drops abruptly at the onset of running. The ratio of Fourier coefficients  $q$  (which describes the pattern of

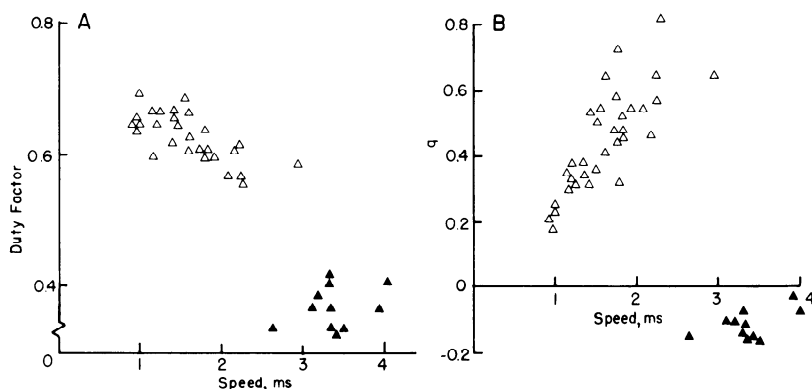


FIG. 1. Graphs showing how human locomotion changes with speed. *A*: duty factors used by adult men. *B*: ratio  $q$ , which describes pattern of force exerted on ground. These graphs are based on data of Alexander and Jayes (12), where  $q$  is referred to as  $-(a_3/a_1)$ .  $\Delta$ , Walking;  $\blacktriangle$ , running.

force exerted on the ground at each footfall) rises as walking speed increases but falls abruptly to a negative value at the onset of running. Quantities like these vary continuously with speed within each gait but may show discontinuities at gait changes. In this paper, I adopt the following definition of “a gait,” which I believe to be consistent with current usage.

A gait is a pattern of locomotion characteristic of a limited range of speeds described by quantities of which one or more change discontinuously at transitions to other gaits.

This definition admits application of the term to flight and swimming as well as to terrestrial locomotion. It also permits its application to intermittent styles of locomotion, such as bounding flight (76) and porpoising (17). In bounding flight, a bird alternates bursts of a few wing beats with intervals in which the wings are folded. In porpoising, a cetacean interrupts its swimming periodically by leaping out of the water. In both cases, and in other intermittent styles of locomotion, there is a pattern that repeats with a longer period than one cycle of limb or tail movements.

## II. OPTIMIZATION CRITERIA

Evolution and learning by experience are powerful optimizing processes. Animals tend to evolve the best possible structures and behaviors and to learn the best ways of doing things. Evolution tends to optimize fitness (a measure of the probability of the animal's genes being transmitted to future generations; for discussion of its precise meaning see Ref. 31). It does this by modifying structure and behavior, including (presumably) the manner of learning by experience. Thus animals tend to choose gaits for particular occasions so as to maximize fitness and also to refine each gait so as to maximize fitness.

It does not seem practicable to measure the effects of gait choice, and of the details of gait, on fitness. Instead we can assess the merits of gaits indirectly by considering their effects on other quantities that have predictable effects on fitness. Increases in maximum speed or endurance presumably tend to increase fitness by making animals better able to escape predators or catch prey. Reductions in the energy cost of locomotion increase fitness by making more energy available for reproduction or by reducing the time that must be spent in hazardous foraging (86). Alternatively, they may enable animals to travel faster for the same energy cost, making more time available for other activities.

A change that affects one of these quantities, in a way that tends to increase fitness, will not necessarily affect others in the same way. In attempting to discover why particular gaits are used at particular speeds, we must decide which of the optimization criteria are likely to be important. Speed maximization can apply only at the highest speeds and cannot be a criterion for slow gaits, such as walking. Minimization of energy seems more likely to be generally important, and I present several models that assess the effect of gait choice on energy cost. It must tend to be associated with maximization of endurance: an animal that needs less power to run should be able to run longer. However, there are difficulties in predicting the effect of gait changes on energy cost.

The principal problem is that models of locomotion generally predict the work required of the muscles, whereas fitness depends on metabolic energy cost. The relationship between the mechanical performance of a muscle and its metabolic energy consumption is not adequately understood. In particular, we cannot assume a constant efficiency (mechanical power/metabolic power). Taylor and co-workers (42) have measured both the mechanical and the metabolic power required for running by various birds and mammals and have found much lower efficiencies for small animals than for large animals. Similarly, investigations of fish swimming indicate lower efficiencies for small fish than for large fish (102). Aerodynamic theory predicts that the mechanical power required for flight will have a minimum value at a particular speed for any particular aircraft or animal. Graphs of oxygen consumption against speed show minima for some birds (81, 93) but not for others (92).

Taylor et al. (89) tried to explain the varying apparent efficiencies of running by suggesting that the main metabolic energy cost is associated with the generation of force in the muscles rather than the performance of work. The forces required for running are proportional to body weight, but smaller mammals use higher stride frequencies and need correspondingly faster muscle fibers with shorter cross-bridge cycling times. Force generation is more expensive of metabolic energy in faster muscles, so small animals have low apparent efficiencies of running. Taylor et al. (89) presented measurements of the metabolic cost of carrying loads for rats, dogs, humans, and horses. These data are consistent with their hypothesis but are not clear

evidence for it, because their experiment increased force and work in the same proportion (4).

Kushmerick and Paul (55) measured the oxygen uptake of isolated muscles that were stimulated to make a series of isometric tetanic contractions at short intervals. For any particular muscle, the metabolic energy cost ( $E$ ) of the contractions was found to be proportional to the time integral of the force  $F$  that the muscle developed

$$E_{\text{isometric}} \propto \int F \cdot dt \quad (1)$$

The energy cost of isometric contractions is higher for faster muscles (38, 41) and is probably about proportional to the intrinsic speed  $\dot{\epsilon}_{\text{max}}$  (the maximum rate at which the muscle can shorten, expressed in muscle lengths per unit time). It must also be proportional to the length  $l$  of the muscle fibers: it must be twice as expensive to maintain the same tension in twice the length of muscle. Thus we can write

$$E_{\text{isometric}} \propto l \dot{\epsilon}_{\text{max}} \int F \cdot dt \quad (2)$$

This proportionality is consistent with theoretical predictions (see Ref. 63).

Suppose, following Taylor et al. (89), that the metabolic energy cost of running is dominated by the cost of force generation, as shown by Eq. 2. This might be the case, if large forces are exerted principally when the muscles are changing length slowly compared with their intrinsic speed. If it is, then any adaptation that reduced the force required of the muscles, or made it possible to use shorter or slower fibers, would save energy. Shorter fibers can do less work in a contraction, and slower fibers can do less work in a given time. Thus adaptations that reduced the work required of the muscles would tend to reduce the metabolic energy cost, even though mechanical and metabolic energy costs were not directly linked. This rather elaborate argument tends to justify the intuitively obvious assumption that animals can be expected to adjust their gaits so as to minimize the work required of their muscles.

Gait variables, such as duty factor and stride length, may have different optimum values at different speeds. Changes of gait should occur when optimization demands a discontinuous change in one or more variables, that is, when the optimum displays a bifurcation.

The mathematical concept of bifurcation may be unfamiliar to some readers, so it may be helpful to present an algebraic example. Consider the function

$$F_1 = x^4 + x^2 + ux \quad (3)$$

Suppose that we want to choose  $x$  so as to minimize  $F_1$ , for a given value of  $u$ . (This is analogous to the problem of choosing a gait variable so as to mini-

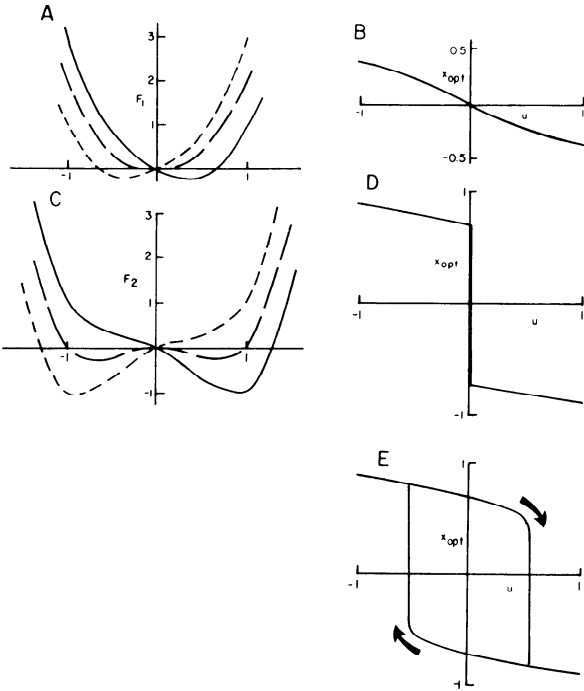
mize the power requirement at a given speed.) Figure 2*A* shows that for every value of  $u$ , there is an optimum value of  $x$  that minimizes  $F_1$ . Figure 2*B* shows that a graph of this optimum value against  $u$  has no discontinuities. Now consider the function

$$F_2 = x^4 - x^2 + ux \tag{4}$$

which differs from the previous function only by the reversal of a sign. Figure 2*C* shows that there is a range of values of  $u$  in which  $F_1$  has two minima: the optimum value of  $x$  is then the value that gives the lower of the two minima. Figure 2*D* shows optimum values chosen in this way. [This is described as choosing according to the Maxwell convention (82).] The optimum value changes continuously with increasing  $u$  until it reaches  $u = 0$  and then it makes a sudden jump, after which it changes continuously again. It is at  $u = 0$  that the left-hand minimum (in the graphs of  $F_2$  vs.  $x$ ) becomes the lower of the two.

Ideally, animals should use the Maxwell convention, always choosing the gait that minimizes the power requirement at their current speeds. Suppose, however, that animals controlled their gaits by continually testing the effects of small changes of gait variables. They would make each gait variable fluctuate slightly about the mean value that minimized power. This would keep them in a local power minimum that was not necessarily the global mini-

FIG. 2. Graphs illustrating the concept of bifurcation. *A*: graphs of  $F_1$  (Eq. 3) vs.  $x$  for various values of  $u$ . *B*: graph of optimum value of  $x$  (value that minimizes  $F_1$ ) vs.  $u$ . *C* and *D*: similar graphs for  $F_2$  (Eq. 4). *E*: behavior of a system that finds local minimum of  $F_2$  according to perfect delay convention.



imum. When they changed speed, they would not detect a second minimum until the minimum they were occupying disappeared. Consequently, they would change from walking to running at a higher speed than the one at which they made the reverse change. Figure 2E shows the equivalent behavior for our algebraic example. While  $u$  is increasing,  $x$  is chosen so as to keep it in the right-hand minimum until that minimum disappears (at  $u = 0.54$ ; see Fig. 2C). When  $u$  decreases,  $x$  is kept in the left-hand minimum until it disappears (at  $u = -0.54$ ). Between  $u = -0.54$  and  $u = 0.54$ , the chosen value of  $x$  depends on the system's recent history. This method of choice is described as the perfect delay convention, and the loop in Figure 2E may be regarded as an example of hysteresis.

Such behavior is not necessarily disadvantageous. Suppose (as seems likely) that every change from one gait to another implies an energy cost. An animal that used the Maxwell convention might find itself switching frequently between walking and running when traveling close to the transition speed and might use unnecessarily large amounts of energy. This could be avoided if it used the perfect delay convention or some strategy intermediate between the Maxwell and perfect delay conventions. It seems worth examining animal gaits to discover whether they show hysteresis.

The optimum strategy in our algebraic example would be changed if the requirement were not to maintain a particular value of  $u$  but to maintain a particular mean value. The minimum values of  $F_2$  are lower for positive and negative values of  $u$  than for  $u = 0$ . The mean value of  $F_2$  can be made lower if  $u$  alternates between positive and negative values (making the mean value of  $u = 0$ ) than if  $u$  is held constantly at zero. Similarly I argue that in a certain range of speeds it may be better for an animal to walk and run alternately than to maintain a constant speed.

### III. SIMILARITY CRITERIA

Animals of very different sizes use recognizably similar gaits: for example, mammals ranging from small rodents to rhinoceroses use the trot and the gallop (36). Our understanding of gaits as solutions to optimization problems will be much more general if we can make quantitative predictions that apply to animals of a wide range of sizes. The concept of dynamic similarity offers a means of so doing (2, 13).

This concept has the same role in studies of movement as geometric similarity has in the study of form. Two shapes are geometrically similar if one could be made identical to the other by multiplying all lengths by the same factor,  $\lambda$ . Two motions are dynamically similar if one could be made identical to the other by multiplying all lengths by a factor  $\lambda$ , all times by a factor  $\tau$ , and all forces by a factor  $\phi$ . Thus two rectangles of different sizes with the same ratio of length to breadth are geometrically similar. The motions of two pendulums of different lengths, swinging through the same angle, are dynamically similar.

Dynamic similarity is possible only in particular circumstances, which depend on the nature of the forces involved (32). If viscous forces are important, as they generally are in movement through fluids, dynamic similarity requires equal values of the Reynolds number  $ul/\nu$ . Here  $u$  and  $l$  are a speed and a length characteristic of the motion (for example, the forward speed and body length of a swimming fish) and  $\nu$  is the kinematic viscosity of the fluid. If gravitational forces are important (as in walking and running), dynamic similarity requires equal values of the Froude number  $u^2/gl$ . Here  $u$  and  $l$  are again a speed and a length characteristic of the motion (perhaps forward speed and leg length) and  $g$  is the gravitational acceleration. If elastic deformations are important (as I show them to be in running), dynamic similarity also requires equal values of the Strouhal number  $fl/u$ , where  $f$  is a natural frequency of vibration characteristic of the system. Strouhal numbers can be defined for all periodic motions, even if elasticity is not involved, by making  $f$  the frequency of the motion. Even in such cases, equality of Strouhal numbers is a condition for dynamic similarity, but the condition sometimes seems trivial. For example, consider the case of running, defining  $f$  as stride frequency,  $u$  as running speed, and  $l$  as leg length. To say that two running motions have equal Strouhal numbers is merely to say that the stride lengths ( $u/f$ ) are proportional to leg length. The reduced frequency  $2\pi fl/u$ , often used in discussions of flight, is  $2\pi$  times a Strouhal number.

Reynolds, Froude, and Strouhal numbers are dimensionless. They have no units, but the units of the quantities used to calculate them must be consistent. For example, if  $u$  is measured in meters per second,  $l$  must be in meters, not centimeters or inches.

In dynamically similar motions, all lengths are proportional to each other. Thus if an animal has legs twice as long as another that is running in dynamically similar fashion, it must take strides twice as long and must rise and fall twice as far in each stride. Consequently it does not matter how the lengths  $l$  used to calculate the dimensionless numbers are defined, provided they are defined in the same way for all the motions being compared. Similarly, all speeds and all frequencies are proportional to each other. It does not matter how the speed  $u$  and the frequency  $f$  are defined, provided they are defined in the same way for all the motions.

These statements require qualification if we are to deal with cases of imperfect dynamic similarity. Precise dynamic similarity between the motions of pendulums, for example, is possible only if the diameters of the bobs and of the strings are in the same proportion as the lengths of the strings. However, these diameters have far less influence on the motion than does pendulum length. If we are dealing with pendulums that may have different ratios of diameter to length, it is much more sensible to define  $l$  as the length of the pendulum rather than as either of the diameters. Similarly, if we are to compare the running of gazelles and buffaloes, it seems more sensible to define  $l$  as the length of the legs rather than as the length of the horns (15).

Animals of different sizes need not run in dynamically similar fashion, even when their speeds are in the ratio that make that possible, but they can

be expected to do so. For example, different-sized mammals can be expected to run in dynamically similar fashion when their Froude numbers are equal (13). Consider two mammals, one with legs  $\lambda$  times as long as the other. If they run in dynamically similar fashion, their Froude numbers ( $u^2/gl$ ) must be equal, so the ratio of their speeds ( $u$ ) must be  $\lambda^{1/2}$  and the ratio of their stride periods (stride length/speed) must also be  $\lambda^{1/2}$ . The forces they exert on the ground must be proportional to their weights. Consequently the factors  $\lambda$ ,  $\tau$ , and  $\phi$  by which lengths, times, and forces are multiplied, in dynamically similar motions, must be the same for all pairs of dynamically similar gaits. The mechanical powers (force  $\times$  velocity) that they use in any pair of dynamically similar gaits will be in the ratio  $\phi\lambda^{1/2}$ . If one animal has optimized power (or any other mechanical quantity), the other animal can optimize the same quantity by running in dynamically similar fashion when traveling with the same Froude number.

Dynamic similarity is impossible in some cases, even between geometrically similar animals. Consider the case of ducks swimming at the surface of the water. Two ducks have hull lengths  $l_1$  and  $l_2$  and swim at speeds  $u_1$  and  $u_2$ . Viscous forces in the water boundary layer are important, so dynamic similarity requires equal Reynolds numbers

$$\begin{aligned} u_1 l_1 / \nu &= u_2 l_2 / \nu \\ u_2 &= u_1 (l_1 / l_2) \end{aligned} \quad (5)$$

Gravitational forces are also important because surface swimming generates a bow wave, so dynamic similarity requires equal Froude numbers (71)

$$\begin{aligned} (u_1)^2 / gl_1 &= (u_2)^2 / gl_2 \\ u_2 &= u_1 (l_2 / l_1)^{1/2} \end{aligned} \quad (6)$$

Equations 5 and 6 cannot be satisfied simultaneously for different-sized ducks, which cannot therefore swim in dynamically similar fashion. It might nevertheless be possible to argue that ducks should change gaits at equal Froude numbers, if it could be shown that the pattern of water flow was much less sensitive to changes of Reynolds number than to changes of Froude number. (This example is imaginary. I am not aware of any suggestion that ducks have more than one swimming gait.)

Some similarity criteria that have been applied to locomotion do not directly invoke dynamic similarity. The theory of elastic similarity postulates that animals of different sizes are constructed so as to deflect under gravity in geometrically similar fashion (61, 75). I show in the next section that elastically similar animals can be expected to move in approximately dynamically similar fashion when running with equal Froude numbers. Another hypothesis that has been applied to walking and running is that approximately equal strains and stresses occur in corresponding parts of the skeletons and muscles of different mammals in corresponding gaits (20, 70).



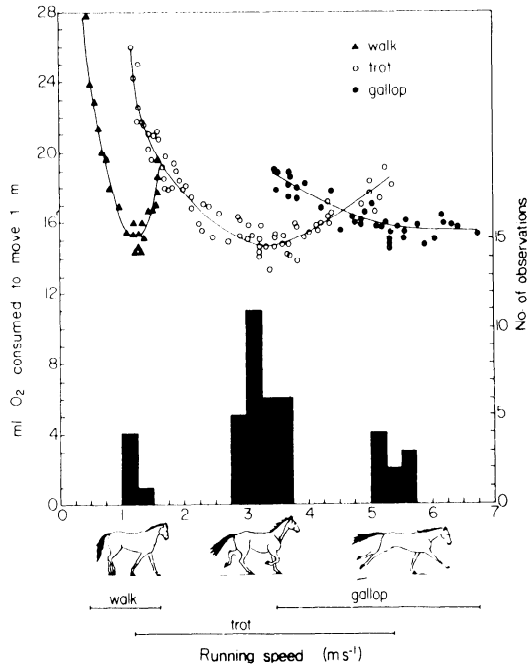
IV. WALKING AND RUNNING

A. People and Animals

I argue in this section that minimization of energy costs is predominantly important in determining terrestrial gaits. The most direct evidence comes from measurements of oxygen consumption, but it is rather sparse and is necessarily limited to the range of speeds in which oxygen balance can be maintained.

Many measurements have been made of the oxygen consumption of animals trained to run on treadmills, matching their speed to that of the belt (88). Hoyt and Taylor (50) used ponies trained to walk, trot, or gallop on command, even at speeds at which they would normally have used other gaits. Figure 3 shows the cost of traveling a unit distance plotted against speed. The lines for walking and trotting intersect at a speed of 1.8 m/s, and the lines for trotting and galloping intersect at 4.7 m/s. Walking is the most economical gait below 1.8 m/s, trotting is most economical between 1.8 and 4.7 m/s, and galloping is most economical at higher speeds. The histograms show that when the ponies were moving spontaneously in their field, they always used the gait that was the most economical for their current speed. Also, they preferred the speeds at which the lowest values of cost per unit distance can be attained. A pony that set out to travel a given distance at a mean speed of 2 m/s could do so most economically by walking part of the way at  $\sim 1$  m/s and trotting the rest at  $\sim 3$  m/s.

FIG. 3. Oxygen consumption of ponies in 3 gaits. Volume of oxygen (ml) used per meter traveled is plotted vs. speed (m/s). Histograms show frequencies with which animals moved spontaneously at different speeds. [From Hoyt and Taylor (50); reprinted by permission from *Nature*. Copyright © 1981 Macmillan Magazines Ltd.]



Measurements of the oxygen consumption of adult humans show that walking is more economical than running at speeds below  $\sim 2.2$  m/s and that running is the more economical at higher speeds (59). The oxygen required to travel a unit distance has a minimum value at a walking speed of  $\sim 1.0$  m/s and is more or less independent of speed in running. Average adult walking speeds range from 0.8 m/s in small villages to 1.7 m/s in large cities (24). Mean speeds near 2 m/s can be achieved most economically by walking for part of the time at speeds around 1 m/s and running for the rest at higher speeds. "Ultrarunners," who run 100-mile (161 km) races, alternate spells of walking with their running (79). Thorstensson and Roberthson (90) measured the speeds at which men changed gaits on an accelerating or decelerating treadmill. The change from walking to running occurred at a mean speed of 1.92 m/s, and the reverse change occurred at 1.85 m/s. The small difference between these speeds was statistically significant. This seems to be the only published observation of hysteresis in a terrestrial gait transition.

Not only do humans choose walking or running so as to minimize oxygen consumption at their current speed, they also seem to choose the optimum stride frequency. This was shown in experiments in which men and women walked on a treadmill, matching their speed to that of the belt and their stride frequency to the beat of a metronome (106). The stride frequency that minimized oxygen consumption at each speed was approximately equal to the frequency that the subjects used voluntarily when the metronome was not used.

Cavagna and Franzetti (28) sought to discover why a particular stride frequency minimizes oxygen consumption at given speed. They investigated the mechanical work required for walking. Very little net work is required for a stride at constant speed over level ground, merely enough to overcome friction and air resistance. However, people perform this small net work by doing much larger quantities of positive work and almost equal negative work. They must do positive work whenever the (kinetic plus potential) energy of the body increases and negative work whenever it decreases. Cavagna and Franzetti (28) used a force plate to record the forces exerted on the ground by men walking at various speeds, with various stride frequencies. From the records, they calculated the fluctuations of the potential energy and external kinetic energy of the body. (External kinetic energy is the kinetic energy associated with movement of the body's center of mass.) They also analyzed films and calculated the fluctuations of internal kinetic energy (associated with movement of parts of the body relative to the center of mass). As stride frequency increased, at any given speed, the fluctuations of (potential plus external kinetic) energy decreased but those of internal kinetic energy increased. Their data seemed to show that the positive and negative work requirements of walking were minimized at a stride frequency 20–30% lower than the preferred stride frequency at any particular speed. They offered a possible explanation for the discrepancy. Mochon and McMahon (66) had shown that the legs swing forward passively, like pendulums

hinged at the knees. No work would be required of the muscles to swing them forward if the internal kinetic energy of the swing were supplied by a fall in the (potential plus external kinetic) energy of the body. Cavagna and Franzetti's (28) calculations did not admit the possibility of such energy transfers. If they had, they would have predicted higher optimum stride frequencies closer to the preferred frequencies.

It was argued in section III that to minimize mechanical power (or any other mechanical quantity), different-sized animals traveling with the same Froude number should move in dynamically similar fashion. This involves moving their feet in the same phase relationships, using the same duty factors, and making their stride lengths proportional to their leg lengths.

The gaits of different mammals are not identical (46, 47). Primates walk with unusual phase relationships between their feet. Camels pace instead of trotting. Horses tend to use the transverse gallop, and giraffes use the rotary gallop. Despite these differences there are marked similarities. Most mammals use gaits recognizable as walks at low speeds, trots at intermediate speeds, and gallops at high speeds. Alexander and Jayes (13) examined the gaits of mammals ranging from small rodents to rhinoceroses and showed that there is a strong tendency for different mammals to move their feet in about the same phase relationships and with about the same duty factors when traveling at equal Froude numbers. They make corresponding gait changes at about equal Froude numbers. For example, Figure 4 shows that a very diverse selection of mammals change from a symmetrical gait (a trot or pace) to an asymmetrical gait (one of the forms of the gallop) at Froude numbers between 2 and 3. The change of gait is marked by an abrupt change in the phase difference between the fore feet, from near 0.5 to below 0.3. In this graph, and throughout this section, the measure of leg length used to define the Froude number is the height of the hip joint from the ground in normal standing.

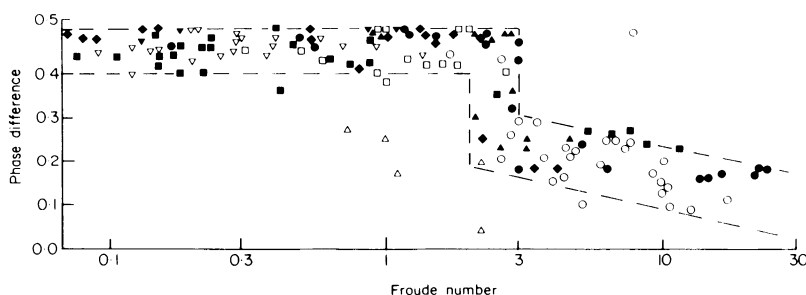


FIG. 4. A graph of phase difference between fore feet vs. Froude number for quadrupedal mammals. Scale of Froude number is logarithmic. Filled symbols are used for cursorial mammals and open symbols for noncursorial mammals. ●, Dog (*Canis*); ■, sheep (*Ovis*); ◆, camel (*Camelus*); ▲, ▼, rhinoceros (*Rhinoceros* and *Ceratotherium*); ○, ferret (*Putorius*); □, rat (*Rattus*); △, jird (*Meriones*); and ▽, coypu (*Myocaster*). [From Alexander and Jayes (13).]

Bipeds change from walking to running or to hopping at about the same Froude number as quadrupedal mammals change from walking to trotting. Adult men break into a run at a mean Froude number of 0.37 (calculated from the data of Ref. 90), crows (*Corvidae*) start hopping at a Froude number of  $\sim 0.5$  (Ref. 40), and dogs and sheep start trotting at Froude numbers  $> 0.3$  (Ref. 52).

Mammals generally increase their stride lengths as they increase speed. In reviewing stride lengths, Alexander and Jayes (13) found it necessary to distinguish between noncursorial mammals, such as most rodents, that run on strongly bent legs (54) and cursorial mammals, such as large carnivores and ungulates. Within each of these groups, different-sized mammals running with equal Froude numbers tend to use equal relative stride lengths (stride length/leg length), but noncursorial mammals use longer relative stride lengths than cursorial ones. Alexander and Maloiy (16) showed that quadrupedal primates use still longer relative stride lengths. Hayes and Alexander (40) showed that bipedal hopping mammals of grossly different sizes use about equal duty factors and relative stride lengths when hopping with equal Froude numbers.

When animals travel with equal Froude numbers,  $u^2/gl$ , their speeds  $u$  are proportional to the square root of leg length, i.e.,  $u \propto l^{0.5}$ . If they are moving in dynamically similar fashion, their stride lengths  $L$  are proportional to leg length. Therefore stride frequency ( $u/L$ ) is proportional to  $l^{-0.5}$ . Pennycuik (69) measured the stride frequencies of African cursorial mammals moving spontaneously in their natural habitat and found them proportional to  $l^{-0.57}$  in walking,  $l^{-0.53}$  in trotting, and  $l^{-0.49}$  in galloping, in good agreement with the dynamic similarity hypothesis (Fig. 5). Subsequent investigators (16, 43, 44) found that mammals ranging from mice to rhinoceroses use stride frequencies approximately proportional to  $(\text{body mass})^{-0.15}$  in corresponding gaits. If their leg lengths were proportional to  $(\text{body mass})^{0.33}$ , as required for geometric similarity, the frequencies were proportional to  $l^{-0.45}$ . Primates, however, used lower frequencies than other mammals of the same mass (16).

McMahon et al. (65) treated running as the bouncing of a mass on a spring (Fig. 6A) and defined a dimensionless number to describe it. Their "Groucho number" is  $2\pi f_0 v/g$  where  $f_0$  is the natural frequency of the spring-mass system,  $v$  is the vertical component of the body's velocity when the foot hits the ground, and  $g$  is the gravitational acceleration. It can be written  $2\pi(v^2/gl)(f_0 l/v)$ , which makes it apparent that it is  $2\pi$  times the product of a Froude number (although not the same Froude number as we have been using) and a Strouhal number. If two animals run in dynamically similar fashion, they must have equal Froude numbers, equal Strouhal numbers, and (therefore) equal Groucho numbers.

The theory of elastic similarity has been applied largely to the structure of animals, and such applications do not concern us here, but McMahon (62) applied it also to running. It postulates that animals tend to be constructed so

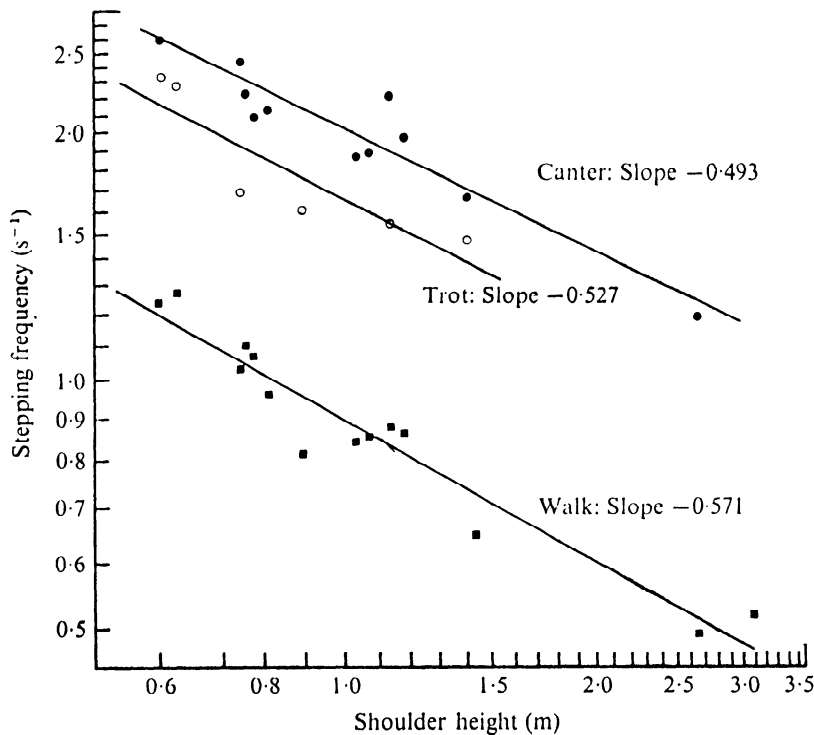


FIG. 5. Stride frequencies of mammals moving spontaneously in their natural habitat. Stride frequency is plotted vs. shoulder height on logarithmic scales. Different symbols are used for 3 gaits. Animals range in size from Thomson's gazelle (*Gazella thomsonii*) to elephant (*Loxodonta africana*). [From Pennycuik (69).]

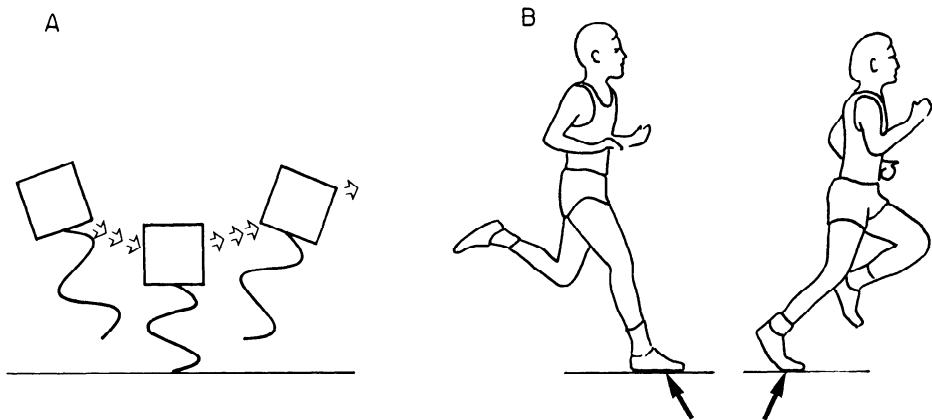


FIG. 6. A: a mass bouncing on a spring: a simple model of running. B: outlines of a man walking, showing directions of forces on feet.

as to deform under gravity in geometrically similar fashion. This is consistent with the dynamic similarity hypothesis and indeed is required by it. In dynamically similar motions for which gravitational forces are important, deformations are geometrically similar and forces are proportional to body weight. Animals must be elastically similar to move in dynamically similar fashion. By this, I do not mean that the lengths and diameters of bones and body segments must scale as postulated by McMahon (61), merely that the tendons and muscles must allow the joints of different-sized animals to move through equal angles, when forces proportional to body weight act on the feet. The anatomic consequences of elastic similarity, as postulated by McMahon (61), are inconsistent with strict dynamic similarity, which implies geometric similarity. Heglund, Taylor, and McMahon's (44) observation that stride lengths of different-sized animals (at the trot-gallop transition) are proportional to (body mass)<sup>0.38</sup> is consistent with the theory of elastic similarity, as McMahon (62) presents it, but the exponent is a little higher than expected for dynamic similarity.

We have seen that the evidence from oxygen consumption suggests that horses and humans (and probably other animals) choose their gaits to minimize the metabolic energy cost of locomotion. Also, the evidence of a tendency to dynamic similarity is consistent with the hypothesis that walking and running animals choose their gaits so as to optimize some mechanical property of locomotion. Now I attempt to explain why the chosen gaits minimize power requirements. I assume that for any individual animal the metabolic power required for locomotion is proportional to the positive mechanical power, as suggested by the discussion after *Eq. 2*.

People and animals perform the small quantity of net work needed for each stride by doing large quantities of positive work and almost equal quantities of negative work (3). This is not an inevitable consequence of using legs rather than wheels but could be avoided by using pantograph mechanisms, such as are used in some legged robots (97). Animals seem not to use pantographs but use different methods to reduce the positive work requirement for locomotion. They do not keep the forces on their feet vertical, which would involve some muscles doing positive work while others simultaneously did negative work (10). Instead, they keep the forces roughly in line with their legs (Fig. 6*B*): the force on a foot slopes backward, tending to decelerate the animal in the first half of each step, and forward, tending to accelerate the animal in the second half of each step. The resulting kinetic energy changes are largely balanced in walking by potential energy changes and in running by changes of elastic strain energy (29). Thus the positive work required of the muscles is reduced in walking by the principle of the pendulum and in running by the principle of the bouncing ball. Tendons are the most important strain energy stores in running (10).

Alexander (5) devised a model of walking that calculated the positive work required of the muscles of each leg. He sought to explain the changes of duty factor and force pattern that occur with increasing speed, as illustrated

for human gaits in Figure 1. Figure 7 shows how the positive work requirement of the model depends on the duty factor  $\beta$  and on the quantity  $q$  that describes the force pattern. At low walking speeds (Fig. 7A), minimum work is required at high values of  $\beta$  and fairly low values of  $q$ . As speed increases (Fig. 7, B and C), the optimum value of  $\beta$  decreases to  $\sim 0.55$  and the optimum value of  $q$  rises toward 1. At a critical speed (4 m/s for humans of leg length 0.9 m), a bifurcation occurs and the optimum shifts suddenly to the lowest attainable values of  $\beta$  and  $q$  (Fig. 7D): running becomes preferable to walking. The points in Figure 7, A and B, show that at 0.9 and 1.8 m/s, humans walk with values of  $\beta$  and  $q$  quite close to the optima predicted by the model. Mean values for fairly slow running are  $\beta = 0.37$ ,  $q = -0.10$  (data from Ref. 12). The model suggests that  $\beta$  should be reduced to zero once the critical speed has been exceeded, but zero duty factor would require infinite force on the foot. The observed values of  $q$  are reasonably near the minimum possible value of  $-0.33$ .

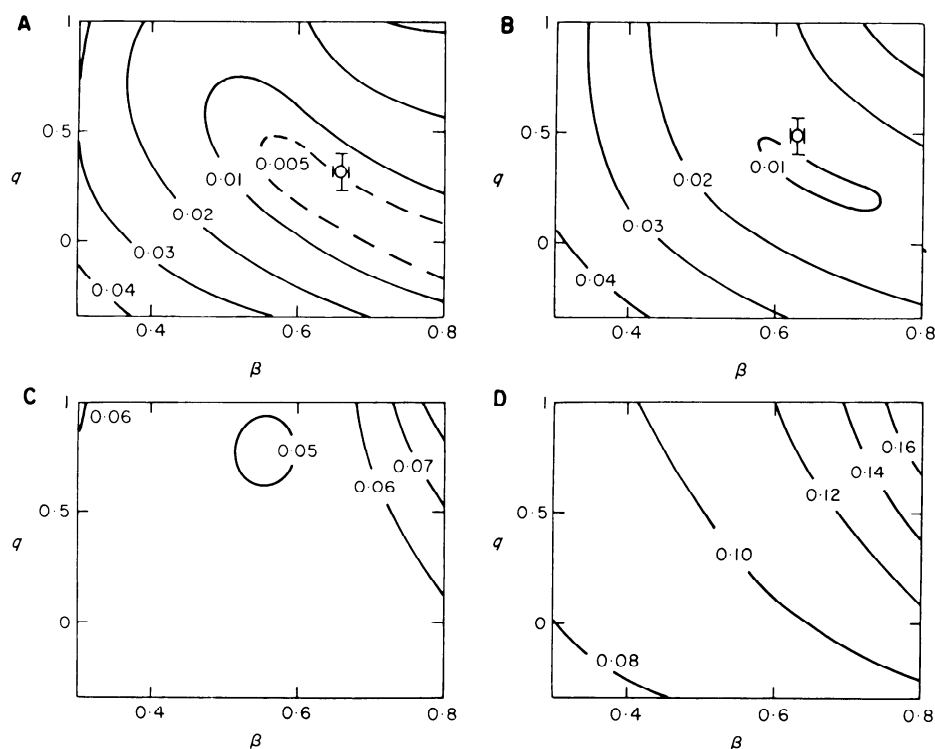


FIG. 7. Graphs showing positive work required for each step of a biped. Quantity  $q$  that describes force pattern is plotted against duty factor  $\beta$ , with contours showing work requirement in arbitrary units. Each graph represents a different Froude number, corresponding to the following speeds for a man of leg length 0.9 m: 0.9 m/s (A), 1.8 m/s (B), 3.6 m/s (C), and 5.1 m/s (D). Points in A and B are observed values for humans  $\pm 2$ SE. [From Alexander (5).]

The model is quite successful in explaining the values of  $\beta$  and  $q$  that humans use when they walk and the changes of  $\beta$  and  $q$  that occur with increasing speed within the walking range. It also shows correctly that there is a critical speed at which an abrupt change should be made from walking to running. However, the critical speed that it gives is approximately double the speed at which humans break into a run. This is probably because it ignores the energy savings that can be made in running by storage of elastic strain energy in tendons. Very little energy can be saved by elastic mechanisms in fast walking with high values of  $q$ , but large savings can be made in running (5). A model that incorporated tendon elasticity would give a lower critical speed.

The model was also applied to quadrupedal gaits. It showed, as for bipeds, that walking is more economical at low speeds and running gaits are more economical at high speeds, but it predicted higher values of  $q$  than are generally observed for walking by dogs and sheep (5). The model failed to show any advantage of galloping over trotting at high speeds (14), but a plausible explanation for galloping emerged later (11). In trotting and other symmetrical gaits, the two feet of each pair move one-half a cycle out of phase with each other. In galloping the two feet of each pair are more nearly in phase. The fore feet are brought forward while the hind feet are on the ground, and the hind feet are brought forward while the fore feet are on the ground. This makes it possible for elastic structures in the back to be used to store up energy taken from the legs at the end of their swing and restore it to set them swinging in the opposite direction.

A simple argument shows that galloping should become more economical than trotting above a critical speed. The positive work done during each stride can be divided into two parts: a part  $W_{\text{on}}$ , done by the muscles of the legs while their feet are on the ground, and a part  $W_{\text{off}}$ , done while their feet are off the ground to accelerate the legs at the beginning of each forward or backward swing. The kinetic energy associated with the movement of each leg relative to the body is greatest during its backward swing when it is proportional to the square of the running speed  $u$ , so  $W_{\text{off}}$  is about proportional to  $u^2$ .  $W_{\text{on}}$  increases much more slowly with speed and is larger for galloping than for symmetrical gaits (from calculations of Ref. 14).  $W_{\text{off}}$  can be supplied in part by recoil of elastic structures in the back in galloping but not in symmetrical gaits. Above a critical speed this saving more than compensates for the additional  $W_{\text{on}}$  that galloping requires.

McMahon (64) presented a simple model of quadrupedal gaits in which the legs were represented as springs subjected to vertical forces only. He compared a trot with a gallop that included only one interval in each stride, during which all four feet were off the ground. He assumed, without specifying the mechanism that would make this possible, that as each leg was lifted, its strain energy was transferred to any other legs that were then on the ground. This led him to the conclusion that, for the same leg stiffness, galloping should be 2.8 times as fast as trotting. The unspecified mechanism for



transferring strain energy seems to me to be the most serious problem with this model.

Lizards run in bursts of movement, stopping briefly between bursts (18). This must increase the work required for running, because the kinetic energy of the body is lost at each stop. It may perhaps be easier for them to detect moving objects visually, while the head is stationary. A similar function has been proposed for the "head bobbing" of running birds (34, 72).

Considerations that have been ignored so far arise in very slow walking, for example, by tortoises (53). Any departure from equilibrium during a stride results in an unwanted displacement: for example, the animal will rise and fall if the total vertical force exerted by its feet fluctuates. Excessive unwanted displacements would be troublesome: a tortoise that repeatedly hit the ground with its shell would not be walking satisfactorily. The need to control unwanted displacements can be assessed by calculating the dimensionless parameter  $g/(f_s)^2 h$ , where  $f_s$  is the stride frequency and  $h$  is the height of the hip joint from the ground (6). An animal falling from rest for the duration of a stride would fall  $g/2(f_s)^2$ . The maximum acceptable displacement is presumably proportional to hip height  $h$ , and the parameter has been obtained by dividing  $g/2(f_s)^2$  by  $0.5 h$ . The larger it is, the more troublesome unwanted displacements are likely to be. It is very much larger for a slow, low-slung turtle than for a brisk mammal (see Table 1), so tortoises and turtles must keep much closer to equilibrium than mammals.

Quadrupeds could eliminate unwanted displacements entirely by moving one foot at a time and adjusting the forces on the other three to keep the body in equilibrium. Moving one foot at a time means that the duty factor of the feet must be at least 0.75. If it is 0.75 (or any other value up to 0.83), the feet must move in the order shown in Figure 8A, because any other order would move the center of mass outside the triangle of support formed by the three feet on the ground at some stage in the stride (60). The gait shown in Figure 8A maintains perfect equilibrium throughout the stride, eliminating unwanted displacements. However, it is impossible, because it requires infinitely fast muscles, capable of increasing and decreasing the forces on the feet instantaneously. Even a reasonable approximation to it would require very fast muscles.

Jayes and Alexander (53) postulated a tortoise with very slow muscles, capable only of exerting forces that rose and fell like a one-half cycle of a sine wave. They calculated its unwanted displacements for different phase relationships of the feet and showed that these could be minimized by using the gait shown in Figure 8B. Notice that this requires the feet to move, not one at a time, but in diagonally opposite pairs. They also considered the case of a tortoise with slightly faster muscles, capable of exerting a pattern of force described by a one-half cycle of a two-term Fourier series ( $a_1 \cos\theta + b_2 \sin 2\theta$ ). This made it possible to reduce the unwanted displacements further and gave an optimum gait very like the gaits that tortoises and turtles were observed to use (Fig. 8C).

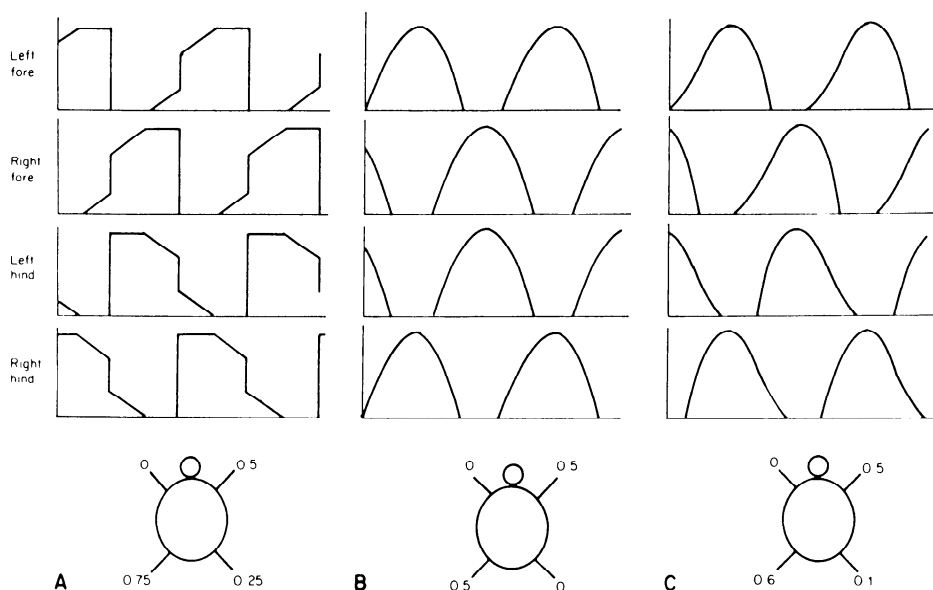


FIG. 8. Graphs of vertical forces exerted by feet of hypothetical tortoises vs. time. Diagrams below graphs show relative phases of feet. A: gait required for equilibrium. B: optimum gait for a tortoise with very slow muscles. C: gait used by tortoises. [From Alexander (7).]

Adoption of this gait should probably be regarded as an adaptation to minimize the metabolic cost of standing and walking. The slower the muscles, the less the metabolic cost (*Eq. 2*). To walk with the slowest muscles capable of reducing unwanted displacements to an acceptable level, a tortoise must use this gait.

### B. Robots

The principles presented in this section apply also to legged robots. So far, most legged robots have been experimental rather than working vehicles (91), and the cost of fuel has presumably been trivial in comparison with the cost of construction. Nevertheless, their designers have shown some concern for economy of energy, if only to avoid the problems that would result from excessive generation of heat. The pantograph legs of the Adaptive Suspension Vehicle (ASV; Ref. 97) and of Perambulating Vehicle II (PV II; Ref. 48) are designed to avoid having actuators do work against each other. The ASV is a human-carrying robot, large and fast enough for unwanted heat production to be a potential problem, but PV II is small and slow (Table 1).

Table 1 compares a few legged robots with animals. Most of the robots travel with Froude numbers  $<0.5$ , that is, at speeds at which animals of equal hip height would walk, but two of them reach slightly higher Froude num-

TABLE 1. *Locomotion on legs by animals and robots*

	No. of Legs	Hip Height ( <i>h</i> ), m	Speed ( <i>v</i> ), m/s	Frequency, ( <i>f<sub>s</sub></i> ), Hz	Froude No.		Reference
					( <i>v<sub>s</sub></i> ) <sup>2</sup> / <i>gh</i>	<i>g</i> / <i>f</i> <sup>2</sup> <i>h</i>	
Man walking	2	0.9	1.6	1.0	0.3	11	12
Man jogging	2	0.9	3.3	1.6	1.2	4	12
Dog walking	4	0.5	1.3	1.6	0.4	8	52
Dog trotting	4	0.5	2.7	2.2	1.5	4	52
Turtle	4	0.07	0.1	0.6	0.02	400	53
Three-dimensional hopper	1	0.6	2.2	1.5	0.9	8	74
Kenkyaku 1	2	0.6	0.8	1.1	0.1	13	35
PV II	4	0.4	0.02		10 <sup>-4</sup>		48
NCTU quadruped	4	0.6	0.01	0.02	2 × 10 <sup>-5</sup>	4 × 10 <sup>4</sup>	56
Running quadruped	4	0.7	0.75	2.2	0.09	3	74
Sutherland hexapod	6	0.2	0.1		5 × 10 <sup>-3</sup>		87
ASV	6	1.8	3.6		0.7		97
ReCUS	8	3.5	0.07	0.03	10 <sup>-4</sup>	4000	91

Many of the speeds given for robots are maximum speeds. Information about other walking robots can be found in Todd (91).

bers. These are Raibert's (74) small one-legged hopping robot and the six-legged ASV(97). Hopping is the only possible gait for a one-legged robot. Raibert's (74) quadruped trots with a duty factor of ~0.25, although its Froude number at a normal speed is only ~0.1. All the other robots in Table 1 walk. Both PV II and the North Carolina Technical University (NCTU) quadruped walk with the gait shown in Fig. 8A, moving their legs one at a time. The very low stride frequency of the latter makes  $g/(f_s)^2h$  very large (much larger even than for turtles), so it must use a gait that can keep it very close to equilibrium throughout the stride. The Ohio State University (OSU) hexapod (68) also moves its legs one at a time. This ensures that a vertical line through the center of mass is always well within the polygon of support marked by the feet on the ground, giving the robot a substantial margin of stability. A six-legged robot can maintain equilibrium throughout the stride by moving three legs at a time in an alternating tripod gait (legs 1 and 3 of one side moving with leg 2 of the other). The OSU hexapod uses a follow-the-leader gait, placing foot 2 in the footprint of foot 1, and foot 3 in the footprint of foot 2. If it continued to do that while using an alternating tripod gait with a duty factor of 0.5, it would bring the center of mass to the extreme edge of the triangle of support, leaving no margin of stability whatever. The Sutherland hexapod (87) used an alternating tripod gait and ReCUS (a large octopod designed for use on the sea bed) uses groups of four legs alternately (91).

Vertebrates seem limited by their evolutionary history to a maximum of four legs, but if an extra pair were possible they could give a substantial advantage to turtles that walk with large values of  $g/(f_s)^2h$ . A quadruped using the gait of Figure 8A with a duty factor of 0.75 would need infinitely

fast muscles (capable of developing force instantaneously) to maintain constant equilibrium. A hexapod using an alternating tripod gait with the same duty factor would have all six feet on the ground for two periods of one-quarter stride in the course of each stride. These periods would be available for it to transfer the load from one set of three feet to the other set, so it would not need particularly fast muscles to maintain perpetual equilibrium.

Because the OSU hexapod moves its legs one at a time, their duty factor must be at least 0.83. Turtles use duty factors between 0.68 and 0.89 (Ref. 53). Very high-duty factors require each leg to be swung forward in a very small fraction of the stride period.

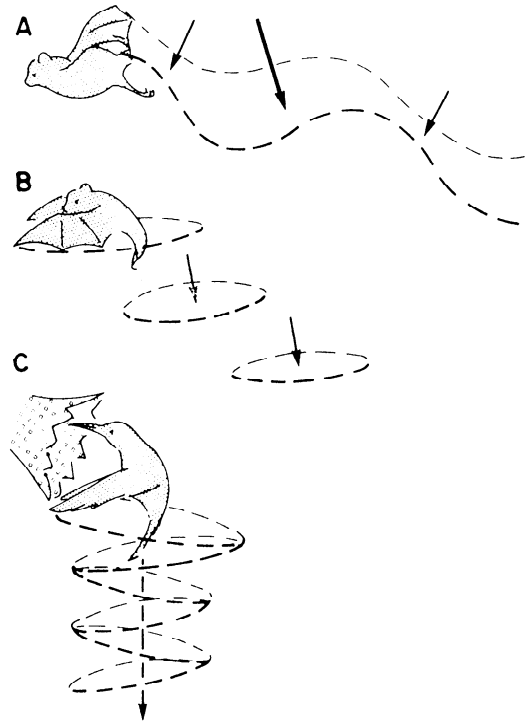
Most animals walk forward, in the direction of the long axis of the body, but crabs walk sideways. The PV II is designed to walk in any direction. When it walks forward it moves its feet in the order left fore, right hind, right fore, left hind, in the gait shown in Figure 8A. When it walks sideways toward its left, it has to change the order to left fore, right hind, left hind, right fore to keep the center of mass always over the triangle of support. As it changes direction, it has to change the order of moving the feet whenever its direction of walking crosses one of the diagonals defined by the feet (48).

## V. FLIGHT

Brown (27) realized that the pattern of wing movement of pigeons (*Columba*) flying slowly was quite different from when they flew fast, but our appreciation of gait differences in flight has been made much clearer by recent flow-visualization experiments (Ref. 85 and references given below). Birds and bats have been flown through clouds of helium-filled soap bubbles. These bubbles had the same density as air so their movements, seen in multiple-flash photographs, showed the air movements in the animal's wake. The animals obtained the lift needed to support their weight by driving air downward, as aircraft also do. Vortices were formed around the downward-moving air and were made visible by the soap bubbles. Two distinct patterns were found.

The pattern shown in Figure 9A was seen when a kestrel (*Falco*) and noctule bats (*Nyctalus*) flew at 7–8 m/s (78, 84). There is a vortex behind each wing tip, like the vortices that sometimes become visible as vapour trails behind aircraft. These vortices undulate up and down, following the up and down movement of the wings. They also undulate in and out, because the wing tips come closer together in the upstroke than in the downstroke. This is necessary because the air driven downwards by the wings moves roughly at right angles to their path through it. The downstroke drives air downwards and backwards (as shown by the large arrow in Fig. 9A), providing weight support and thrust. The upstroke drives air downward and forward (small arrows), contributing to weight support but also producing a retarding force. The retarding force must not cancel out the thrust, so the forces produced in

FIG. 9. Diagrams showing vortices generated by flying animals in 3 gaits described in text. [From Alexander (9); reprinted by permission from *Nature*. Copyright © 1986 Macmillan Magazines Ltd.]



the upstroke must be reduced either by driving the air less fast (which would involve making the vortices weaker) or by driving less air. The latter alternative is adopted: the wing tips are brought closer together so that the band of downwardly directed air is narrower.

The pattern of vortices shown in Figure 9A was produced by a kestrel and by noctule bats, both flying at 7–8 m/s. The pattern shown in Figure 9B was produced by a pigeon (85), by a jackdaw (83), and by noctules and long-eared bats (*Plecotus*) (78), all flying at 1–3 m/s. Instead of undulating wing-tip vortices the animal leaves a series of vortex rings, each produced by a downstroke of its wings. These rings are formed like smoke rings, each by a discrete puff of air. Only the downstrokes drive air downward, and only they produce lift.

The vortex patterns shown in Figure 9, A and B, have been demonstrated only for fast and slow flight, respectively, but the noctule bat is the only species to have been shown (so far) to produce both patterns. (The other species flew fast or slow through the bubble cloud, but not both.) It seems very likely that many species use both gaits, changing from Figure 9B to 9A at some critical speed. We do not know whether the transition is an abrupt one (as required by the definition of gaits, adopted in section 1) or whether one merges into the other. If the upstroke vortices were brought progressively closer together, in gait as in Figure 9A, they would eventually merge,

and the wake would become a series of vortex rings. Aldridge (1) found no abrupt changes in the wing beat kinematics of the horseshoe bat *Rhinolophus*, flying at speeds between 2 and 5 m/s.

It seems likely that each gait is the more economical of energy in the range of speeds in which it is used, but there are no metabolic data to test this hypothesis. The mechanical power requirements of the two gaits could be calculated by means of the model outlined by Spedding (84), but the following crude argument suggests that each is likely to be the more economical in the range of speeds at which it is used. In the gait as in Figure 9A, air is driven in two different directions (represented by the two directions of arrows), so more work is needed to drive it than if all of it were driven in the direction of the required force. In the gait as in Figure 9B, this disadvantage is avoided but work is needed to produce the starting and stopping vortices that open and close the vortex rings. The disadvantage of the gait as in Figure 9A is more serious at low speeds, because the animal travels less far in each wing beat cycle, increasing the angle between the upstroke and the downstroke (for a given amplitude of wing beat).

Many birds seem to produce lift on the downstroke only when they hover, so their hovering gait is simply a stationary version of the gait seen in Figure 9B (30). Hummingbirds and many insects beat their wings horizontally, turning them upside down for the upstroke and generating lift and presumably a vortex ring in every stroke (33, 106). Thus they produce a stack of linked vortex rings enclosing a downward jet of air (Fig. 9C). This may be regarded as a third flapping gait.

If hummingbirds minimize the mechanical power required for hovering, different-sized hummingbirds should hover as nearly as possible in dynamically similar fashion. In particular, they should hover with equal Strouhal numbers  $fr/v$ , where  $f$  is wing beat frequency,  $r$  is wing length, and  $v$  is the speed of the downward jet of air. (This means that the spacing of the vortex rings,  $v/f$ , should be proportional to their radius.) The theory of helicopters tells us that  $v$  is proportional to  $m^{0.5}/r$ , where  $m$  is body mass (8), so the requirement of equal Strouhal numbers implies equal values of  $fr^2m^{-0.5}$ . Hummingbirds of different sizes have wing spans proportional to  $m^{0.53}$  and hovering wing beat frequencies proportional to  $m^{-0.60}$  (Ref. 77), so  $fr^2m^{-0.5}$  is about proportional to  $m^{-0.60} \cdot m^{1.06} \cdot m^{-0.50} = m^{-0.04}$ , which is close to the prediction of constancy.

Perfect dynamic similarity between flying animals of different sizes is, however, impossible, because viscous and gravitational forces are both important. It would require both the Reynolds and the Froude numbers to be identical, which is impossible for different-sized animals for the reason explained in the discussion of ducks in section III. A Reynolds number  $vr/\nu$  ( $\nu$  is the kinematic viscosity of air) and a Froude number  $v^2/gr$  can be defined for hummingbird hovering, but the data above show that neither is independent of body mass: they are proportional to  $m^{0.5}$  and  $m^{-0.6}$ , respectively. (Discussions of flight generally use lift coefficients rather than Froude numbers.

Dynamically similar flight motions of geometrically similar animals of equal density, in the same air, would have lift coefficients inversely proportional to the Froude numbers.)

Many passerines and other small birds use bounding flight, alternating short bursts of wing beating with intervals in which the wings are folded against the body and the bird travels as a projectile. For example, Pye's (73) radar records of sparrows (*Passer*) show bursts of about six wing beat cycles, lasting  $\sim 0.3$  s, with 0.3-s periods in which the wings are folded. Many larger birds, including crows (*Corvidae*) and gulls (*Laridae*), and some bats use undulating flight, alternating bursts of wing beats in which they fly upwards with downward glides for which they keep their wings spread. Rayner (76) discussed both these intermittent gaits and reviewed the earlier literature.

A simple model based on the aerodynamics of fixed-wing aircraft indicates that bounding can reduce the mechanical power requirement for flight but only above a critical airspeed, estimated to be 6 m/s or more for small finches. We might expect to find birds beating their wings continuously at low speeds and bounding only at high speeds. However, many species bound during slow flight and some even when hovering. Rayner (76) suggested that the advantage of bounding flight might be physiological rather than mechanical: it might enable the muscles to work at the high rate at which they were most efficient, even at flight speeds that do not require maximum effort. The pectoralis muscles of many birds consist entirely of fast fibers (80), but it is not clear whether all the fibers have the same intrinsic speed.

## VI. SWIMMING

Vertebrate animals use many different swimming techniques (25), but only a few cases have been described of different gaits being used at different speeds.

Some acanthopterygian fishes use their pectoral fins to swim slowly but undulate the whole body to swim fast. Brett and Sutherland (26) reported this for *Lepomis* and Blake (21) reported it for *Pterophyllum*, but the most thorough study seems to be an unpublished one by P. W. Webb (Fig. 10). *Salmo* and *Esox* (which are not acanthopterygians) swam only by undulating their bodies, even at very low speeds. *Lepomis*, however, used its pectoral fins alone at low speeds, used body undulations alone at high speeds, and used both at intermediate speeds. Similar gait changes have been described for squid (67).

Webb (98) made a kinematic analysis of *Salmo* swimming and used Lighthill's (57) theory to calculate the mechanical power that they exerted. He found that this was several times the power that would have been required to propel a rigid body of the same size and shape. A later study of cod (*Gadus morhua*) led to a similar conclusion (94), but a study of saithe (*Pollachius virens*) showed no drag enhancement (45). This discrepancy has not

been explained. Body undulation might be expected to thin the boundary layer and so increase drag (58). If it does, the principal advantage of using the pectoral fins for slow swimming may be that the body can be kept rigid, keeping the drag low. It is probably necessary to use the tail for fast swimming, so as to involve a larger mass of muscle. However, 14-cm Shiner sea-perch (*Cymatogaster aggregata*) swam by means of their pectoral fins alone at speeds up to 0.5 m/s (99), whereas 16-cm *Lepomis* swam predominantly by body undulation at speeds  $>0.2$  m/s. The pectoral muscles of *Lepomis* may possibly not be large enough for swimming faster than this, but, if swimming with the fins is more economical than body undulation, it is not clear why *Lepomis* has not evolved larger fins and fin muscles.

The fish studied by Webb (Fig. 10) usually used a beat-and-coast technique when swimming moderately fast. They alternated bursts of tail beating with periods of coasting with the body held straight. More power must be needed during the bursts than in continuous undulatory swimming at the same speed, but the mean power is probably reduced because there is less drag on the body while it is being held rigid during coasting (23, 96, 104). This suggests that beat-and-coast should be used even at the lowest speeds of swimming by body undulation, but Figure 10 shows it being used only at fairly high speeds. The explanation may be that the red and white muscles each have rates of contraction at which they work most efficiently (96).

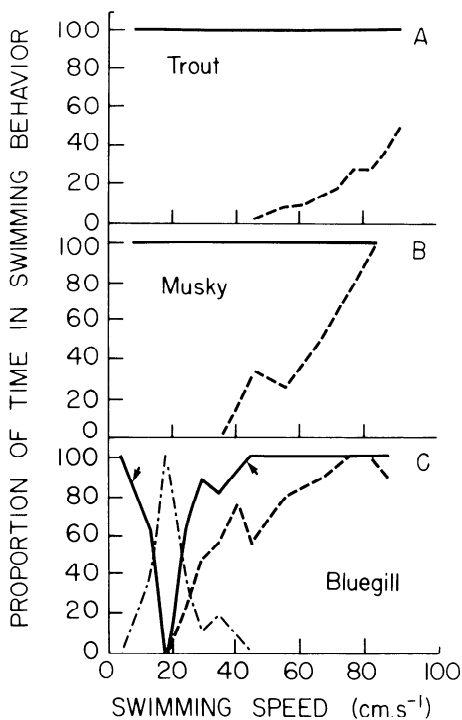


FIG. 10. Graphs showing frequencies with which different gaits were used at different swimming speeds by 20-cm total length trout (*Salmo gairdneri*) (A), 18-cm musky (*Esox lucius*  $\times$  *E. masquinongy*) (B), and 16-cm bluegill (*Lepomis macrochirus*) (C). A and B: —, body; ---, beat and coast, C: —, 1st arrow is fins, and 2nd arrow is body; ---, beat and coast; -.-, fins and body. (From P. W. Webb, unpublished observations of 10 specimens of each species.)



Continuous undulatory swimming may be powered by the red muscles alone. At higher speeds it becomes necessary to recruit white muscle, which will work most efficiently if used in short bursts at its optimum rate of contraction rather than continuously at lower rates. This seems consistent with the observations that the maximum aerobic speed of 29-cm trout is 0.58 m/s (99) and that 20-cm trout use beat-and-coast at speeds of 0.4 m/s and upward (Fig. 10). It could make beat-and-coast swimming advantageous, even if undulating swimming did not incur enhanced drag.

It has been suggested that fish that are denser than water may use another intermittent technique (103). They may swim for a while on an upward-sloping path and then glide down. This would save energy if drag were reduced during the glide. The authors who have suggested this swimming technique offer no evidence that it is actually used.

There seems to be only one steady undulatory swimming gait in carangiform teleosts (19, 95, 102) and sharks (101). Tail beat amplitude, the wavelength of the body waves, and the distance traveled in each tail beat cycle change a little as swimming speed increases but without any apparent discontinuities. A small fish swimming fast and a large one swimming more slowly might have equal Reynolds numbers and could swim in dynamically similar fashion, but they seem not to do so. Drag coefficients calculated from kinematic data plotted against Reynolds number give different graphs for different-sized trout (101).

Small whales use the intermittent gait called porpoising, alternately swimming and leaping out of the water. Au and Weihs (17) suggested that this might save energy because the drag that acts on the animal in water is greatly reduced while it is traveling through air. They presented a model that predicted that porpoising would save energy only when the speed was above some critical value. Their model is modified here in the light of Gordon's (39) criticisms.

A whale of mass  $m$  leaving the water with speed  $u$  has kinetic energy  $0.5 mu^2$ . Some of this is temporarily converted to potential energy during the leap but (since drag in air is small) the whale reenters the water with almost the same kinetic energy as it left. While in the water, it can use its flippers as hydrofoils to change its direction in time for the next leap, at the cost of a little induced power. [This is the power that must be used to obtain lift (8).]

The whale in water has an "added mass" of water traveling with it as a boundary layer. This is carried into the air as the whale leaps but falls off as spray. When the whale reenters the water, it must accelerate a new added mass to speed  $u$ , giving it the necessary kinetic energy. This may be the main energy cost of the leap. The added mass is proportional to the volume  $V$  of the body in whales of different sizes so its kinetic energy is proportional to  $Vu^2$ . The length of a leap is  $u^2 \sin 2\theta / g$  (where  $\theta$  is the take-off angle), so the work required for leaping unit distance is proportional to  $Vg / \sin 2\theta$ . The work required to swim unit distance is the drag in water, which is proportional to  $Au^2 C_D$ , where  $A$  is the surface area of the animal and  $C_D$  is the drag coefficient.

cient. (The constant of proportionality is hard to estimate because body undulation and proximity to the water surface both enhance drag.) Porpoising saves energy if the cost of leaping a unit distance is less than the cost of swimming a unit distance, that is, if  $Au^2C_D\sin 2\theta/Vg$  exceeds some critical value. For geometrically similar whales,  $V/A$  is proportional to length  $l$ , and the condition is that  $(u^2/gl)C_D\sin 2\theta$  should exceed a critical value. This expression includes a Froude number ( $u^2/gl$ ) and a drag coefficient that is a function of Reynolds number.

The theory suggests that porpoising should occur only above a critical speed, which would be larger for larger whales. Ten-meter killer whales (*Orcinus*) porpoise (22), but larger whales do not, possibly because they cannot swim fast enough.

That interpretation of porpoising has been challenged by Hui (51), who observed the swimming behavior of penguins. They porpoise like whales, but their leaps occupy only a small fraction of their swimming time. Hui suggested that the leap enabled the bird to breathe without spending much time close under the surface, where drag would be increased because a bow wave would develop. The penguins do not porpoise at low speeds, possibly because if they did they would not be in the air long enough to take a breath.

Human swimming styles might be regarded as gaits, but they do not seem to be adapted to different speed ranges. Measurements of oxygen consumption show that the front crawl uses less power than back crawl or breast stroke over a wide range of speeds (49).

## VII. CONCLUSION

The theme of this paper is that vertebrate animals adjust their patterns of locomotion so as to minimize power requirements at their chosen speeds. Gait changes are responses to bifurcations at which the optimum style of locomotion changes discontinuously with changing speed. The gaits of terrestrial locomotion are well known. Two styles of continuous, flapping flight used by birds and bats have been described as gaits (Fig. 9, *A* and *B*), but it is possible that they may grade into each other at intermediate speeds. Some fish swim slow by pectoral fin movements and fast by body undulation, and these may be regarded as gaits. Some gaits repeat with a period that is longer than the cycle of limb movements. These intermittent gaits include bounding and undulating flight, beat-and-coast swimming, and porpoising.

It has been shown that horses and humans each choose the gait that requires the least oxygen consumption for their current speed. Also, humans adjust their walking stride lengths to minimize oxygen consumption. The gaits of many other animals seem adapted to minimize metabolic power, but the evidence is less direct. The gaits of turtles seem adapted to make walking feasible with the slowest possible (therefore the most economical) muscles. The intermittent gaits of birds and fishes may be adapted to use fast muscles

at their most efficient rates of contraction. It has been argued that walking, trotting, and galloping each minimize mechanical power requirements (and so, indirectly, metabolic power) in the ranges of speed in which they are used. The same has been suggested rather tentatively for the flying gaits of Figure 9, *A* and *B*. However, the relationship between mechanical and metabolic power requirements is inadequately understood, as explained in section II.

Many legged robots have been built, but none known to me change gaits as they change speed. Comparison with animals, as in Table 1, may aid robot design. However, economy of energy seems less important in the present, experimental phase of robot development than it has been in the evolution of animals.

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