

COPYRIGHT NOTICE:

**R. McNeill Alexander: Principles of Animal Locomotion**

is published by Princeton University Press and copyrighted, © 2002, by Princeton University Press. All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher, except for reading and browsing via the World Wide Web. Users are not permitted to mount this file on any network servers.

For COURSE PACK and other PERMISSIONS, refer to entry on previous page. For more information, send e-mail to [permissions@pupress.princeton.edu](mailto:permissions@pupress.princeton.edu)

## *Chapter One*

---

### *The Best Way to Travel*

**T**HIS BOOK describes the movements of animals and of the structures such as legs, fins, or wings that they use for movement. It tries to explain the physical principles on which their movements depend. And it asks whether the particular structures and patterns of movement that we find in animals are better suited to their ways of life than possible alternatives. This chapter will, I hope, help us when we come to ask these questions about the merits of particular structures and movements.

The structures of animals and some of their patterns of movement (the ones that are inherited) have evolved. Other patterns of movement may be learned afresh by successive generations of animals, by trial and error. Evolution by natural selection, and learning by trial and error, both tend to make the animals and their behavior in some sense better. What, in this context, does “better” mean?

#### 1.1. FITNESS

The most fundamental answer is that evolution favors structures and patterns of movement that increase fitness, and that the capacity for learning has evolved so that learning also can be expected to increase fitness. The fitness of an animal’s complement of genes (its genotype) is the probability of the same group of genes being transmitted to subsequent generations. Unfortunately for the purposes of this book, it is not generally easy to measure or calculate the effect on fitness of, for example, a change in the length of an animal’s legs or a modification of its gait. We can make more progress by looking at the effects of evolution in a less fundamental way.

Fitness depends largely on the number of offspring that animals produce, and on the proportion of those offspring that survive to breed. Thus, natural selection favors genotypes that increase fecundity or reduce mortality. This insight still seems rather remote from our discussions of locomotion. It seems helpful to ask at this stage, what aspects of an animal’s performance in locomotion are most likely to affect fecundity and mortality, and so fitness? What qualities, in the context of locomotion, can natural selection be expected to favor? Some suggestions follow.

## 1.2. SPEED

For many animals, natural selection may tend to favor structures and patterns of movement that increase maximum speed. A faster-moving predator may be able to catch more prey, which may enable it to rear and feed more offspring. A faster moving prey animal may be better able to escape predators, and so may live longer. However, we should not assume that speed is important for all animals. For example, tortoises are herbivores, with no need for speed to catch prey. Their shells are sufficient protection against most predators, so they do not need speed to escape. It seems clear that maximum speed has had little importance in the evolution of tortoises, so we need not be surprised that tortoises are remarkably slow.

It is probably generally true that most animals spend very little of their time traveling at maximum speed. Lions (*Panthera leo*) are idle for most of the day, but their ability to run fast occasionally is vital to their hunting success. The antelopes and zebra on which they feed spend nearly all their time quietly grazing or traveling slowly, but depend on their ability to run fast in emergencies, to escape from lions and other predators. Ability to travel fast may be highly important to animals, although it may seldom be used.

## 1.3. ACCELERATION AND MANEUVERABILITY

Acceleration may be even more important than speed for predators such as lions, which stalk antelopes and then make a sudden dash from a short distance; and pike (*Esox*), which hide among vegetation and dash out to catch small fish that swim past. Acceleration must be correspondingly important for the prey. Suppose a predator dashes with constant acceleration  $a_{\text{pred}}$ , starting from rest at zero time, at a distance  $d$  from its prey. At time  $t$  its speed is  $a_{\text{pred}}t$ , and it has traveled a distance  $0.5a_{\text{pred}}t^2$ . If the prey starts running at the same instant as the predator, with acceleration  $a_{\text{prey}}$ , it has traveled a distance  $0.5a_{\text{prey}}t^2$  at time  $t$ . If the predator's acceleration is greater than the prey's, and if the chase is short enough for neither animal to reach top speed, the predator catches the prey when

$$0.5 t^2 (a_{\text{pred}} - a_{\text{prey}}) = d$$

$$t = \left( \frac{2d}{a_{\text{pred}} - a_{\text{prey}}} \right)^{0.5} \quad (1.1)$$

by which time the predator has covered a distance  $a_{\text{pred}}d/(a_{\text{pred}} - a_{\text{prey}})$ . If the predator has twice the acceleration of the prey, it catches it after covering a distance  $2d$ ; but if its acceleration is only 1.1 times that of the prey it has to run a distance  $11d$ .

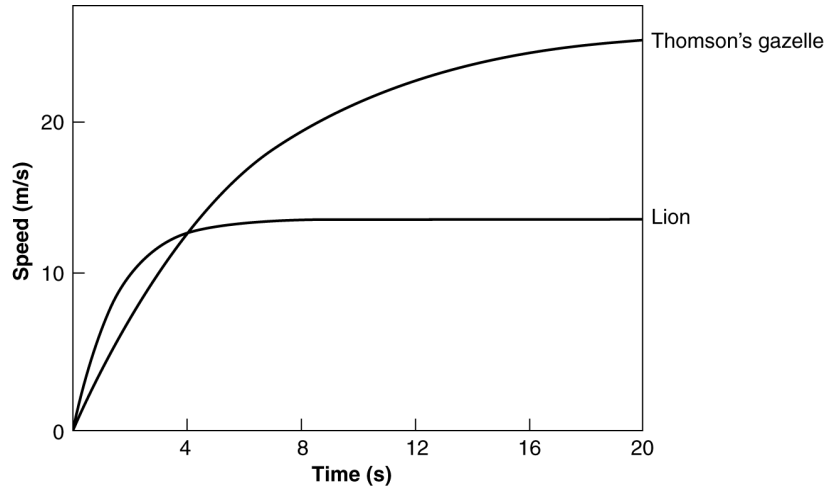


Fig. 1.1. Graphs of speed against time for lions and Thomson's gazelle, calculated from films of lions attacking prey. The curves were obtained by fitting to the data equations of the form  $v = v_{\max} [1 - \exp(-kt)]$ , where  $v$  is the speed at time  $t$ ,  $v_{\max}$  is the speed that is approached asymptotically, and  $k$  is a constant. Redrawn from Elliott et al. (1977).

That analysis is grossly simplified. It assumes that both animals start moving simultaneously, and that both animals have constant acceleration throughout the chase. Elliott et al. (1977) filmed lions hunting gazelles (*Gazella thomsoni*), and used his films to calculate graphs of speed against time. These graphs curve and level off, showing that both predator and prey accelerated at decreasing rates, as they gained speed (Fig. 1.1). However, the analysis is sufficient to show that the ability of a predator to catch prey may depend more on its acceleration than on its maximum speed. Indeed, a predator with superior acceleration may be able to catch prey, even if its top speed is lower than that of the prey. Elliott found that the initial accelerations of the lions averaged  $9.5 \text{ m/s}^2$ , and those of the gazelles only  $4.5 \text{ m/s}^2$ . He estimated that the speeds they would eventually have reached were  $14 \text{ m/s}$  for the lions, and a much faster  $27 \text{ m/s}$  for the gazelles. However, these estimates of top speed depended on extrapolation of his data, and may not be accurate.

The analysis also ignored the possibility that the prey might attempt to escape by swerving. Films of gazelles (*Gazella thomsoni* again) pursued by cheetah (*Acinonyx jubatus*) show the prey swerving when the predator is close behind. Children playing the game of tag (called tig in Britain) know that a well-timed swerve is a good escape strategy.

An animal traveling at speed  $v$  on a circular arc of radius  $r$  has an acceleration  $v^2/r$  toward the center of the circle. Thus, swerving involves sideways acceleration. Suppose that a predator running at speed  $v_{\text{pred}}$  is capable

of swerving with radius  $r_{\text{pred}}$ , and a prey animal running with speed  $v_{\text{prey}}$  swerves with radius  $r_{\text{prey}}$ . The prey can escape, even if  $v_{\text{prey}}$  is lower than  $v_{\text{pred}}$ , if its sideways acceleration  $v_{\text{prey}}^2/r_{\text{prey}}$  is greater than the predator's sideways acceleration  $v_{\text{pred}}^2/r_{\text{pred}}$ . Howland (1974) pointed this out, and went on to show that, to take full advantage of its superior sideways acceleration, the prey must delay swerving until the predator is very close behind. This is illustrated in Fig. 1.2, which shows the paths of predator and prey. The predator is represented as traveling faster than the prey, but with larger radius. Time intervals are marked on the animals' paths. Each animal has the same speed and radius in both diagrams. The prey escapes if it swerves at the last possible moment (B), but if it swerves too soon the predator cuts off the corner and intercepts it (A).

#### 1.4. ENDURANCE

Animals cannot maintain their top speeds indefinitely in a prolonged chase. Figure 1.3A shows the speeds at which human athletes have run races ranging from a 100-m sprint to a marathon, plotted against the time taken for the race. Figure 1.3B shows the maximum speeds maintained by trout (*Salmo irideus*) for different times. In each case speed falls as time and distance increase.

The graph for the fish (Fig. 1.3B) is plotted on ordinary linear coordinates. It shows, for example, that the 15-cm fish's maximum speed was 180 cm/s for one-second sprints, but fell, as time increased, toward an asymptote of about 40 cm/s. The graph for human running (Fig. 1.3A) would look very similar to the fish graph, if it had been plotted in the same way. However, it has been plotted on logarithmic coordinates, which have made it possible to display data for a much wider range of times. This graph shows not only that maximum speed declines markedly in the first 100 s of running time, but also that the decline continues over a period of several hours. The point for the 100-m race (triangle) is potentially misleading because sprinters are still accelerating over most of this distance. The remaining data, for races from 200 m to a marathon, form two straight lines meeting at an angle when plotted thus on logarithmic coordinates. This suggests that the decline in speed over short times (less than about 150 s) depends on a different phenomenon from the longer term decline in speed. We will find a likely explanation in Section 2.5.

Now suppose that a predator is chasing prey over a sufficient distance for us to ignore the acceleration period. We might, for example, be considering African hunting dogs (*Lycan*), which chase antelopes over distances of several kilometers (van Lawick-Goodall and van Lawick-Goodall 1970). Assume that both animals are able to estimate the duration of the

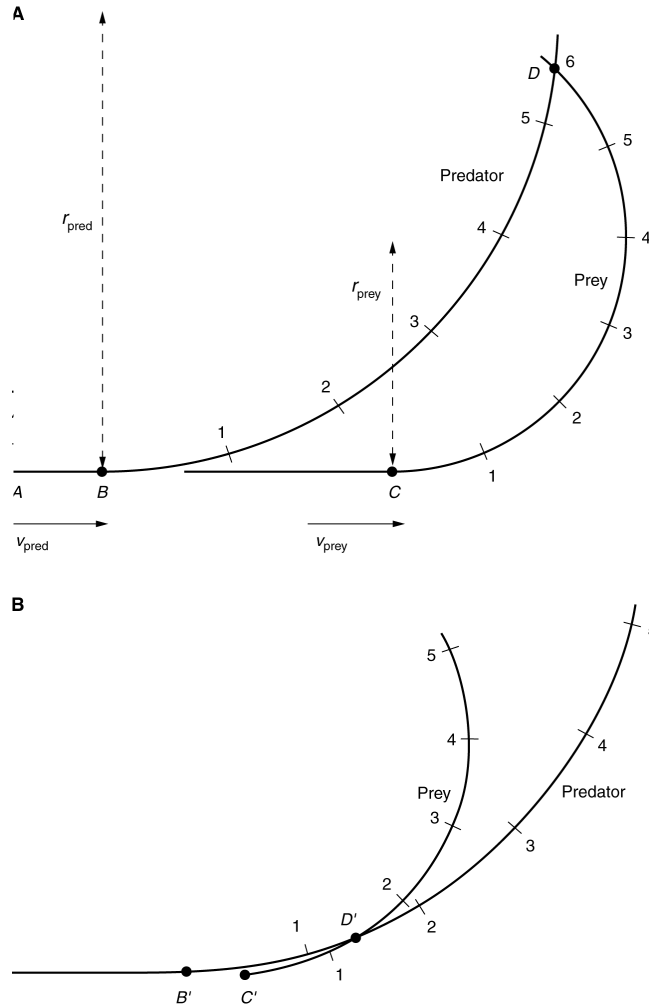


Fig. 1.2. Diagrams of a predator chasing swerving prey. The paths of the animals are seen in plan view, with the animals' positions after successive intervals of time numbered 1, 2, etc. The prey is slower than the predator ( $v_{\text{prey}} = 0.75v_{\text{pred}}$ ), but can execute a tighter turn ( $r_{\text{prey}} = 0.5r_{\text{pred}}$ ). In (A) the animals were initially running along the line  $ABC$ . At time zero, when both animals started swerving, the predator was at  $B$  and the prey at  $C$ . The prey reaches point  $D$  after 6 units of time. The predator would pass  $D$  after 5.4 units of time if it continued running at maximum speed, but by slowing down a little it can intercept the prey there. In (B) swerving starts when the animals are at  $B'$ ,  $C'$ . The prey passes point  $D'$  after 1.3 units of time, and the predator arrives there only after 1.4 units of time, so in this case the prey escapes. Modified from Alexander (1982).

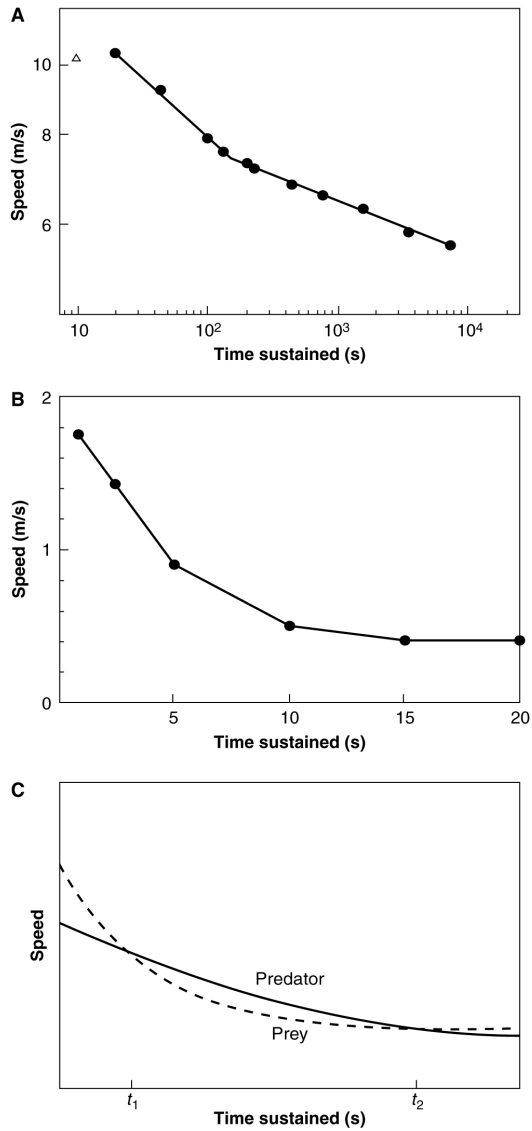


Fig. 1.3. Graphs showing how the speed at which an animal can travel falls, as the time for which it has to be sustained increases. (A) World record speeds for male human athletes in races of different lengths, plotted against the time for the race, redrawn from Savaglio and Carbone (2000). (B) The highest speeds that a trout (*Salmo irideus*) maintained for different times when swimming spontaneously in an annular tank, redrawn from Bainbridge (1960). (C) A schematic graph, which is explained in the text, showing how a predator with good endurance may be able to catch faster prey.

chase in advance, and choose the speeds that will take them furthest in that time. Though its sprinting speed may be less than that of the prey, the predator will eventually overtake the prey if its sustainable speed is greater than that of the prey. Less obviously, even though its sprinting speed and its maximum speed over long distances may be less than those of the prey, it may be able to catch the prey if it fatigues less quickly than the prey. Figure 1.3C is a schematic graph illustrating this possibility; notice how the lines cross, showing that there is a range of chase times for which the predator can travel faster than the prey.

### 1.5. ECONOMY OF ENERGY

Measurements of the oxygen consumption of many animals have been made, to find out how much energy they use in locomotion; the principal methods will be outlined in Section 5.3. Some striking differences have been observed. For example, Taylor et al. (1982) found that walking penguins (*Pygoscelis*) use energy about 60% faster than turkeys (*Meleagris*) of the same mass, walking at the same speed. In another comparison, this time of the energy cost of swimming at the surface of water, penguins (*Eudyptula*, in this case) performed much better; they used only 0.72 times as much energy as ducks (*Anas*) of equal mass, swimming at the same speed (Baudinette and Gill 1985). In a second comparison of swimmers, squid (*Illex*) used energy 1.75 times as fast as salmon (*Onchorhynchus*) of comparable mass, although they were swimming at only 0.6 times the speed of the fish (Webber and O'Dor 1986). Are these differences likely to be important to the animals?

Economy of energy can affect fitness in various ways, of which the most generally important is probably this: energy that is not used for locomotion is available for growth and reproduction. For example, birds rearing nestlings may have to spend all the daylight hours foraging for food, flying for much of the time. A substantial proportion of the food they collect has to be used to fuel flight, and so is not available to feed the nestlings. House martins (*Delichon urbica*) are small birds that feed on insects, which they catch on the wing. In field experiments in Scotland, Bryant and Westerterp (1980) set up nest boxes that were used by house martins. Trapdoors on the boxes enabled them to capture the birds, to make the injections and (a day or two later) collect the blood samples needed to measure their metabolic rates by the doubly labeled water technique, which is explained in Section 5.3. While they had young in the nest, the birds spent an average of 14 h per day off the nest, flying all the time, and their metabolic rates were 3.6 times the resting rate. For part of the time, the nestlings were temporarily fitted with collars that prevented them



from swallowing, so that the experimenters could recover and weigh the mouthfuls of food that their parents gave them. The brood was found to be receiving food from each parent at a rate equivalent to 3.0 times the parent's resting metabolic rate, while the parents (as we have seen) were using energy at 3.6 times the resting rate for their own metabolism. A very large fraction of the energy that the parents were using, in excess of the resting rate, must have been used to power flight; and if they could have flown more economically they would have had more food to spare for the young. They might have been able to rear a larger brood, and so pass on more of their genes to the next generation.

As another example to show how economy of energy can affect fitness consider a typical fish, which, unlike the birds we have been considering, does not care for its young. The more eggs it lays (of given size and quality), the more offspring it will have and the more genes it is likely to contribute to successive generations; but the number of eggs it can produce is limited by its size. As a rough general rule, a mature female fish of mass  $m$  can be expected to produce a mass of 0.1 to 0.2 $m$  of eggs in the course of the season (Le Cren and Holdgate 1962). Other things being equal, the less energy it has had to use for locomotion in the course of its life, the more of its food energy intake will have been available for growth, the bigger it will have grown, and the more eggs it can lay. Alexander (1967) made a simple calculation to assess the likely effect of energy economy on fitness. I estimated that 20% of the energy content of the food eaten by a typical fish would be lost in feces and urine; 34% would be used for resting metabolism; 34% would be used to power swimming; and 12% would be available for growth and reproduction. If these estimates are realistic, three times as much energy is used for swimming as for growth and reproduction, so a 1% improvement in the efficiency of swimming can be expected to make 3% more energy available for growth and reproduction.

## 1.6. STABILITY

We have already noted that tortoises walk very slowly. The likely reason is that, if speed is unimportant, an animal can make do with very slow muscles. These can be very economical of energy, as will be explained in Section 2.5. Experiments with tortoise muscle have shown that it is remarkably economical (Woledge et al., 1985). We will see in Section 7.9 that stability is a problem for walking animals with very slow muscles, but that the problem can be alleviated by appropriate choice of gait. Natural selection seems to have optimized the gait of tortoises to obtain adequate stability with the slowest possible muscles.

### 1.7. COMPROMISES

The discussion so far may suggest that animals should evolve to be as fast as possible, to have the best possible acceleration, maneuverability and endurance, and to be as economical as possible of energy. However, these objectives are not always compatible. The example of tortoises has already shown us that an animal designed to walk as economically as possible cannot be fast. Similarly, no human athlete is a champion both in sprinting and in distance running, and an animal adapted to sprint as fast as possible would be unlikely to have good endurance. Sprinters and distance runners differ markedly in physique, the sprinters having well-developed muscles and the distance runners being less muscular, with bigger hearts capable of pumping a greater volume of blood at each stroke (Reilly et al., 1990). Evolution can be expected to favor compromises between the requirements of speed, endurance, economy, etc.

If we were to try to express the relationship between the locomotion of animals and their fitness in mathematical terms, we would have to conclude that fitness is a function of speed, acceleration, maneuverability, endurance, energy economy, and a great many other properties. It would not be at all obvious what the function should be, and if we were to try to assess the effect on fitness of some change (for example, longer legs or bigger thigh muscles) we would find ourselves doing elaborate and highly unreliable calculations. To make our discussions manageable, we must try to identify the properties that are most important, and concentrate on the effects that adaptations have on them. We can safely assume that racehorses have been selected for speed over distances of the order of a few kilometers, but for animals designed by natural selection, as distinct from selective breeding, the criteria for selection are generally less clear-cut.

### 1.8. CONSTRAINTS

We will have to remember in our discussions that evolution cannot bring about every imaginable change. We have already seen that squid are less economical swimmers than salmon. They are also slower; the maximum sustainable speeds of a 0.5-kg salmon and a similar-sized squid were 1.35 and 0.76 m/s, respectively (Webber and O'Dor 1986). Squid might be faster and more economical if they had evolved fishlike tails, but their evolution has been constrained by their molluscan ancestry. Evolution proceeds by relatively small steps, and there does not seem to be any conceivable evolutionary route from a squid to a fishlike animal that would not involve passing through a stage less fit than either. Again, the

walking of tortoises would be more stable if they had six legs instead of four, but the evolution of tortoises has been constrained by their four-legged ancestry.

To understand how these constraints operate, think of a walker in a hilly landscape, who walks always uphill. He or she may reach the highest summit, but is much more likely to finish on some subsidiary peak. There is no route from a lower peak to a higher one that does not involve first going downhill. Similarly, an evolutionary path along which an animal species changed progressively, increasing fitness at every stage, would not necessarily lead to the fittest imaginable structure.

### 1.9. OPTIMIZATION THEORY

Optimization theory is the branch of mathematics that finds the best possible solutions to problems. Here is a simple example. Consider a bird gliding with fully spread wings, aiming to glide at the shallowest possible angle and so to travel as far as possible for given loss of height. It can glide faster or slower by holding its wings in slightly different positions, and this will affect its angle of descent. This angle  $\theta$  is given by an equation that applies also to man-made gliders:

$$\sin \theta = Av^2 + B/v^2 \quad (1.2)$$

where  $v$  is the speed, and  $A$  and  $B$  are constants that depend on the size and shape of the wings (Equation 10.18). Figure 1.4A is a graph of  $\sin \theta$  against speed  $v$ . It shows that the angle is steep if the bird glides very slowly or very fast, and is least at an intermediate speed.

The same result can be obtained without drawing a graph. Notice that at low speeds the graph slopes downhill, and at high speeds uphill. The minimum angle of glide is obtained where the graph runs level, with zero slope. We can find the minimum by deriving an equation that gives the slope, which can be done by the mathematical process of differentiation, and then finding the value of  $v$  that makes the slope zero. Readers who do not know how to differentiate can take the process on trust, or consult a textbook of calculus or (for a very quick explanation) read Section 1.2 of my book *Optima for Animals* (Alexander 1996). The slope of a graph of  $\sin \theta$  against  $v$  is represented by the mathematical expression  $d(\sin \theta)/dv$ . Differentiation of Equation 1.2 tells us that the slope is

$$\frac{d(\sin \theta)}{dv} = 2Av - 2B/v^3$$

which is zero when

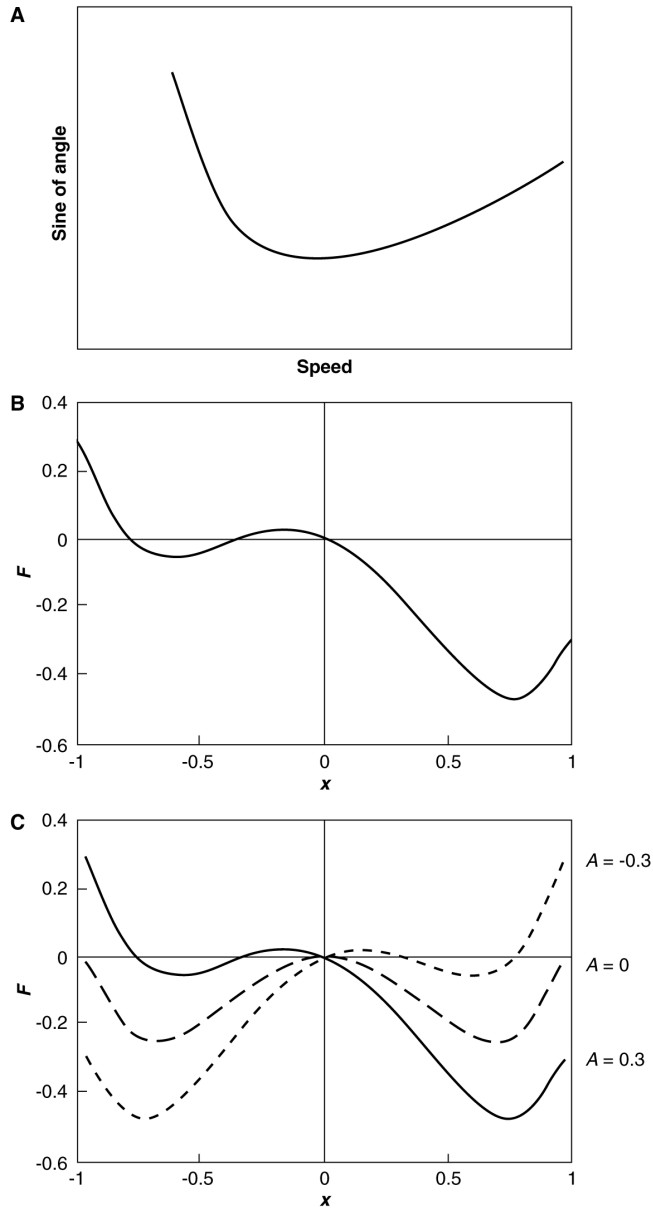


Fig. 1.4. Graphs illustrating an explanation of the basic principles of optimization theory: (A) Equation 1.2; (B) Equation 1.3 with the parameter  $A$  given the value 0.3; and (C) the same equation for several different values of  $A$ .

$$v = \left( \frac{B}{A} \right)^{0.25}$$

Thus, the speed at which the angle of glide is least is  $(B/A)^{0.25}$ . We will use a more complicated form of this equation in Section 10.6, when we discuss how the wings of soaring birds are adapted to their ways of life.

Instead of a graph of the sine of the angle of descent against speed, we might have drawn a graph of the distance traveled per unit loss of height. This would have shown a maximum, instead of a minimum. The slope is zero at the top of a hill, as well as at the bottom of a valley, so the speed that gives maximum glide distance could be found by differentiating the appropriate equation, in the same way as we found the (identical) speed that gives minimum glide angle.

When we discuss gaits, we will encounter more complex situations, involving graphs with more than one maximum or minimum. Figure 1.4B illustrates this possibility, by showing a graph of the function

$$F = x^4 - x^2 - Ax \tag{1.3}$$

where  $A$  is a constant that has been given the value 0.3. The previous graph had one minimum but this has two, at  $x = 0.8$  and at  $x = -0.6$ . At both minima the graph runs level, and both would be found by differentiation. However, if the aim is to make  $F$  as small as possible, the deeper minimum should be chosen, at  $x = 0.8$ . This is described as the global minimum, and the other as a local minimum.

Figure 1.4C shows graphs of Equation 1.3 for several different values of  $A$ . When  $A = 0.3$ , the global minimum is at a positive value of  $x$  and the local minimum at a negative one, as we have already seen. As  $A$  is reduced, the minima become more equal, and when  $A = 0$  they are equal. When  $A$  is negative, the global minimum is found at a negative value of  $x$  and the local minimum at a positive value. This phenomenon, in which a small change of a parameter results in an abrupt shift of the global minimum (or maximum), is called bifurcation.

### 1.10. GAITS

People walk to go slowly and run to go fast. Walking and running are quite different patterns of movement, which do not merge into each other; as we increase speed, we make the change from walking to running within a single stride. Similarly, horses change from walking to trotting and then to galloping as they increase speed. Walking, running, trotting, and galloping are described as gaits, and in later chapters we will see that flying birds and swimming fishes also use several distinct gaits.

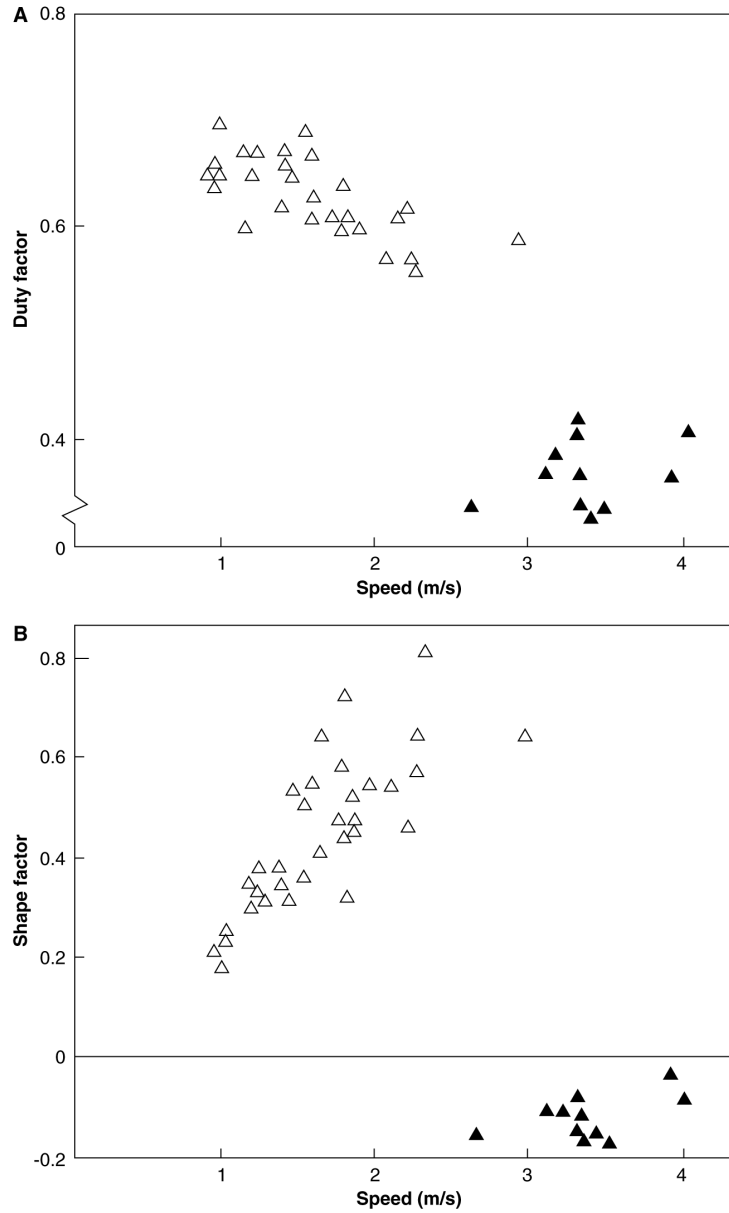


Fig. 1.5. Graphs showing how the gait of adult humans changes with increasing speed. (A) Duty factor and (B) shape factor plotted against speed. Note the abrupt changes at about 2 m/s, at the transition from walking (open symbols) to running (filled symbols). From Alexander (1989a).

The formal definition of a gait is as follows: “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” (Alexander 1989a). Figure 1.5 shows graphs of two of the quantities that change, when people change gait. Duty factor (Figure 1.5A) is the fraction of the duration of the stride, for which each foot is on the ground. In walking, each foot is on the ground for more than half the time, and in running for less than half the time. As speed increases, the duty factor falls gradually from about 0.65 in slow walks to about 0.55 in the fastest walks; but at the change to running it drops abruptly, to around 0.35. The shape factor  $q$  (Figure 1.5B) describes the pattern of force exerted on the ground; it will be explained in Section 7.3. As speed increases, it rises smoothly from about 0.2 in slow walking to about 0.8 in very fast walking; but then drops abruptly to negative values at the transition to running.

I will show in Section 7.7 that people seem to adjust their gaits so as to minimize the energy cost of traveling at their chosen speed. Thus, our gaits are solutions to optimization problems. The abrupt shift of the optimum from walking to running is a bifurcation.

Thus speed, acceleration, maneuverability, endurance, energy economy, and stability are aspects of locomotion that are likely to be important to animals in different circumstances. Natural selection can be expected to act on structures and patterns of movement that affect them, but the course of evolution is constrained by the animal’s ancestry.