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The Gaits of Bipedal and Quadrupedal Animals

Abstract

The gaits of reptiles, birds, and mammals are reviewed. It is shown that mammals of different sizes tend to move in dynamically similar fashion whenever their Froude numbers u^2/gh *are equal: here* u *is speed,* g *is the acceleration of free fall, and* h *is the height of the hip joint from the ground. The gaits of turtles and people are examined in detail. The gaits of turtles appear to reduce unwanted displacements (pitch, roll, etc.) to the minimum possible for animals with such slow muscles. The patterns of force exerted in human walking and running minimize the work required of the muscles at each speed. Much of the energy that would otherwise be needed for running, by people and other large mammals, is saved by tendon elasticity.*

1. Introduction

A designer of legged robots has to solve an optimization problem. He or she considers a variety of criteria, such as cost, reliability, and maneuverability, and aims to design a machine that is in some sense the best possible (McGhee 1976).

The legs and gaits of animals are the products of two very potent optimizing processes, the processes of evolution by natural selection and of learning by experience. Zoologists studying them are trying to solve inverse optimality problems: they are trying to discover the optimization criteria that have been important in the evolution of animal legs and in the evolution or learning of gaits (Alexander 1982*b*).

This paper aims to describe the gaits of two- and four-legged animals and to identify some of the important optimization criteria. It gives a general account of the gaits of reptiles, birds, and mammals, followed by more detailed discussions of turtles and people.

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2. Definitions

The technical terms needed to describe gaits must be defined before we can proceed further.

A *stride* is a complete cycle of leg movements, for example, from the setting down of a particular foot to the next setting down of the same foot. We will consider only gaits in which successive strides are more or less identical, and in which each foot is set down and lifted exactly once in each stride. The sustained gaits of animals are nearly always like this. *Stride frequency,* f, is the number of strides taken in unit time. *Stride length,* λ, is the distance traveled in a stride. Thus the mean speed u equals λf.

The *duty factor,* β, of a foot is the fraction of the duration of the stride for which it is on the ground. In nearly all the gaits used by animals, the left and right feet of a pair have approximately equal duty factors.

The *relative phase* of a foot is the stage of the stride at which it is set down, expressed as a fraction of the duration of the stride following the setting down of an arbitrarily chosen reference foot. Thus one foot is assigned relative phase 0 and the others have relative phases in the range 0–1. One option is to use the same foot (perhaps the left forefoot) as the reference foot in every case. An alternative (used in this paper) is to use the left or right foot, whichever is set down less than half a cycle (stride) before the other. The advantage of this method is that it avoids making gaits that are mirror images of each other seem grossly different.

The system of describing gaits in terms of duty factors and relative phases was proposed by McGhee (1968) and has proved convenient. Hildebrand (1977) designed an alterative system.

The patterns of force exerted by feet will be described, as well as footfall patterns. Consider a foot that is set down at time $-T/2$ and lifted at $+T/2$. The magnitude of the force exerted by it at any time t *in this interval* can be described by a Fourier series

$$F = a_1 \cos(\pi t/T) + b_2 \sin(2\pi t/T) + a_3 \cos(3\pi t/T) + b_4 \sin(4\pi t/T) + \dots \quad (1)$$

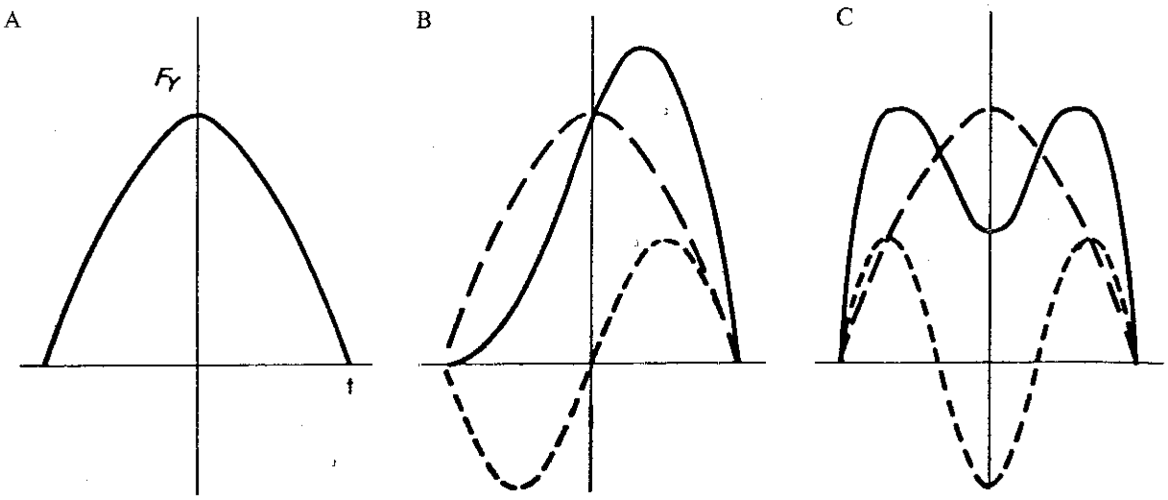


Fig. 1 Graphs of force against time simulated by (Eq. 2) using (A) r = q = 0, (B) r = 0.5, q = 0, and (C) r = 0, q = 0.5. Broken lines show the contributions of individual terms from the equation. (Reproduced from Alexander [1981], by permission of the Zoological Society of London.)

Any possible pattern of force can be described by choosing appropriate coefficients a_1, b_2, and so on. There are no even-numbered cosine terms or odd-numbered sine terms because the force must be 0 at times $-T/2$ and $+T/2$. Alexander and Jayes (1980) showed how (Eq. 1) can be used to describe human gaits.

In this paper, (Eq. 1) will be used to describe only the vertical component F_Y of the force on the ground. Only the first three terms will be used, and the equation will be rewritten

$$F_Y \approx A[\cos(\pi t/T) + r\sin(2\pi t/T) - q\cos(3\pi t/T)]. \tag{2}$$

The negative sign of the q term conforms with an established convention. Figure 1 shows the effects of different values of r and q. Nonzero values of r skew the force pattern (Fig. 1B). Positive values of q tend to generate force patterns with two maxima (Fig. 1C), and negative values generate bell-shaped curves.

3. Gait and Posture

Gaits are classified as walks or runs. The distinction generally made is that walks have duty factors greater than 0.5 (so there must be stages in the stride when both feet of a pair are on the ground simultaneously), and runs have duty factors less than 0.5 (so there must be stages when both feet of a pair are off the ground). This distinction works well for some mammals, including humans, but not for others, such as sheep, which show no discontinuity between walking and running gaits.

Gaits are also classified as symmetric or asymmetric. A symmetric gait is one in which the left and right feet of each pair have equal duty factors and relative phases differing by 0.5. Thus human walking and running are symmetric gaits, but the hopping of kangaroos, in which the left and right feet move in unison, is paradoxically considered asymmetric.

There are special names for many rather precisely defined quadrupedal gaits. In Fig. 2, the amble, trot, and pace are symmetric gaits, and the others are asymmetric. The names do not imply precisely the relative phases shown: the same names would also be given to gaits with slightly different relative phases. When they walk, mammals generally use relative phases close to those shown in Fig. 2 for the amble, but reptiles generally use relative phases closer to those shown for the trot (Hildebrand 1976). Walking is performed only at low speeds. Quadrupedal mammals generally use symmetric gaits for slow running and asymmetric gaits for fast running. The trot is the commonest symmetric run, but camels pace, elephants amble, and wildebeests change directly from a walk to a canter. A horse increasing speed will first walk, then trot, then canter, and finally gallop. Most reptiles trot at running

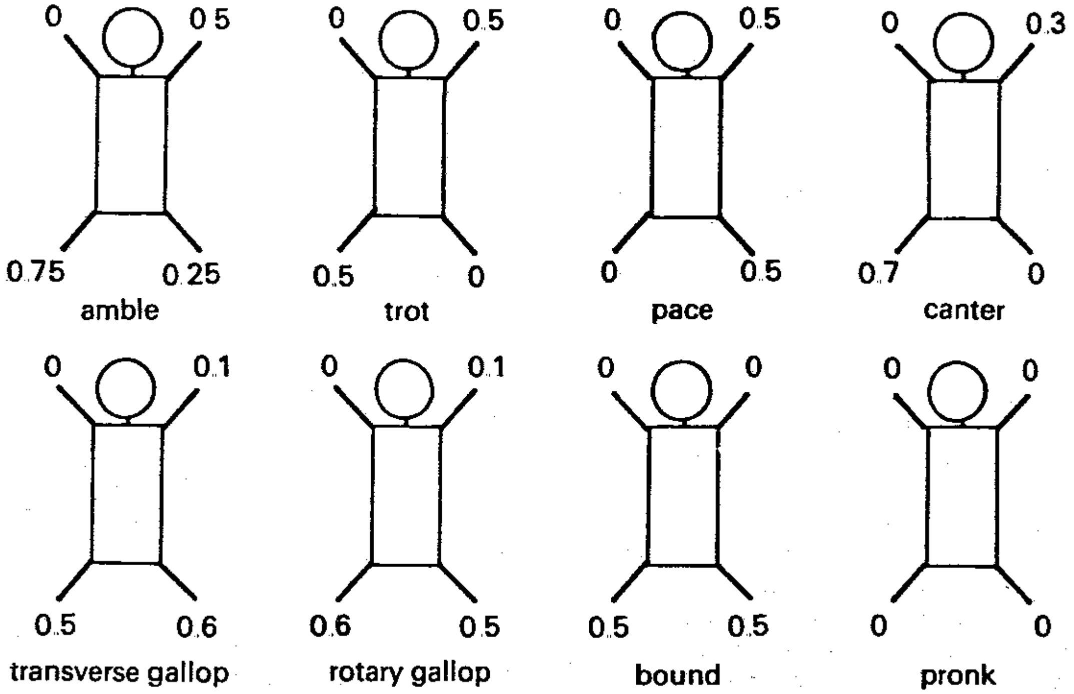


Fig. 2 Diagrams of quadrupedal running gaits showing typical relative phases of the feet. (From Alexander 1982a.)

speeds, but some lizards run bipedally on their hind legs (Sukhanov 1974), and crocodiles occasionally gallop (Zug 1974).

Quadrupeds adopt three main postures when they stand, walk, or run. Reptiles and newts generally keep their feet well out on either side of the body (Fig. 3A) (Rewcastle 1981). Small mammals (e.g., rats) generally keep their feet close under the body, but run on strongly bent legs (Fig. 3B) (Jenkins 1971). Only larger mammals (e.g., cats and horses) stand and run on relatively straight legs (Fig. 3C). Mammals that adopt the posture of Fig. 3B are described as noncursorial, and those that adopt the posture of Fig. 3C as cursorial.

4. Effects of Size

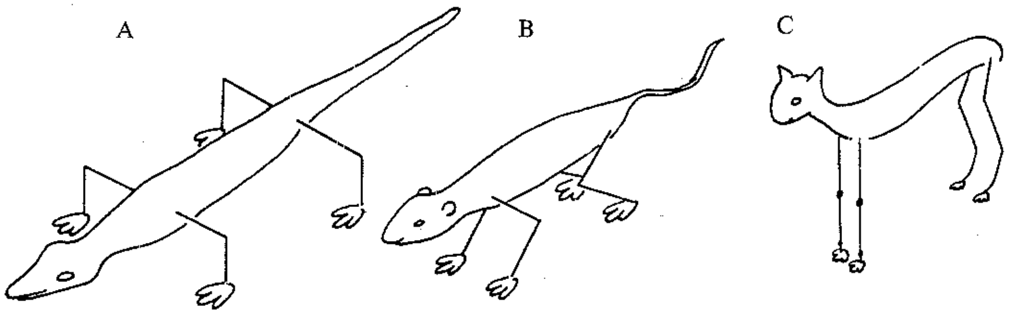
Small shrews have masses around 3 g but large elephants are over one million times heavier, with masses around 5 t. Some of the principal leg bones of elephants are well over 100 times as long as the corresponding bones of shrews. Such differences of size have to be taken into account in describing gaits.

Large animals generally take longer strides than small ones traveling at the same speed and may use different gaits. To keep up with a walking horse, a dog would probably have to trot and a mouse would have to gallop.

Alexander (1976) formulated a hypothesis about the relationship between size, speed, and stride length, in a discussion of the speeds of dinosaurs. This was the origin of a hypothesis applied by Alexander and Jayes (1983) to many aspects of the gaits of quadrupedal mammals. It depends on the concept of *dynamic similarity*.

Two systems of moving bodies are described as dynamically similar if the motion of one could be made identical to that of the other by multiplying (1) all linear dimensions by some constant factor, (2) all time intervals by another constant factor, and (3) all forces by a third constant factor. For example, two pendulums of different lengths swinging through the same angle have dynamically similar motions. The dynamic similarity hypothesis predicts that animals of different sizes tend to move in dynamically similar fashion whenever the ratio of their speeds allows it.

Fig. 3 Diagrams illustrating typical postures of (A) a reptile, (B) a noncursorial mammal, and (C) a cursorial mammal (From Alexander 1982a.)



Plainly, animals cannot move in precisely dynamically similar fashion unless their bodies are geometrically similar. It might be argued that the hypothesis should be discarded, because animals of different species are different shapes. However, comparisons of related animals of grossly different sizes show remarkably little deviation from geometric similarity. The (head plus body) lengths of mammals ranging from shrews to elephants are approximately proportional to (body mass)$^{0.33}$ (Alexander and Jayes, 1983), and the lengths of their principal leg bones are approximately proportional to (body mass)$^{0.35}$ (Alexander et al. 1979). The lengths of the leg bones of flying birds are approximately proportional to (body mass)$^{0.35}$ (Alexander 1983). If geometric similarity held, all these lengths would be proportional to (body mass)$^{0.33}$. McMahon (1973) argued that mammals of different sizes ought to deviate strongly from geometric similarity. His predictions are quite accurate for hoofed mammals but not for other groups of mammals or for mammals in general.

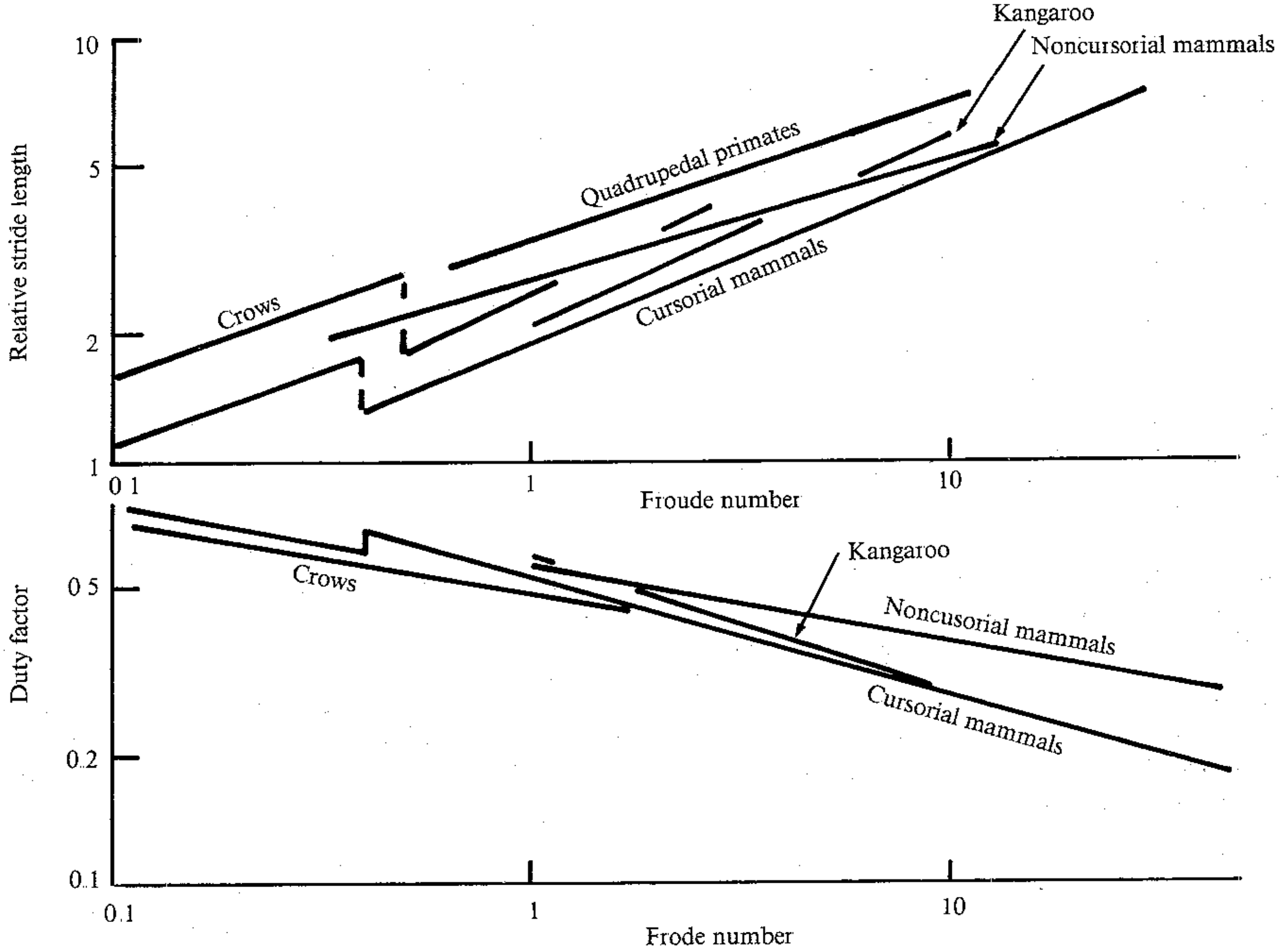
We want to know the ratios of speeds at which animals can move in dynamically similar fashion. These ratios of speeds are given by a standard result from the theory of physical similarity. For motions in which gravitational forces are important (as in walking and running), dynamic similarity is possible only if the motions have equal Froude numbers u^2/gh (Duncan 1953). Here u is a speed characteristic of the motion, defined in the same way for the systems being compared; g is the acceleration of free fall; and h is a characteristic length. In discussions of walking and running the speed of travel is the obvious choice for u, and some measure of leg length is the obvious choice for h: the length used here is the height of the hip joint from the ground.

Length multiplied by frequency has the dimensions of speed, so hf (where f is stride frequency) could be used instead of the characteristic speed in the Froude number. Thus the parameter $(hf)^2/gh = hf^2/g$ could be used instead of the Froude number.

The dynamic similarity hypothesis predicts that animals will tend to move in dynamically similar fashion when they have speeds proportional to the square roots of their legs lengths (giving them equal values of u^2/gh). Dynamic similarity requires their stride frequencies to be inversely proportional to the square roots of their leg lengths (giving them equal values of hf^2/g).

The hypothesis predicts that animals of different sizes will use the same gait when traveling with equal Froude numbers. Alexander and Jayes (1983) examined the gaits of various mammals over a wide range of speeds. A Froude number of 0.1 corresponds to a speed of 0.5 m/s for a cat ($h = 0.22$ m), but 1.3 m/s for a camel ($h = 1.7$ m). At Froude numbers around 0.1, all the species for which data were obtained used quadrupedal walks with relative phases approximately as for the amble (Fig. 2). However, very small mammals, such as rats, did not use such low Froude numbers and did not walk. At Froude numbers around 1.0 (1.5 m/s for a cat; 4 m/s for a camel) almost all the species used symmetric running gaits. Most of them trotted, but camels paced. The change from walking to running was abrupt in some species, but gradual in others. Almost all the species changed from a symmetric to an asymmetric gait (canter or gallop) at a Froude number between 2 and 3.

Fig. 4. Graphs on logarithmic coordinates of (A) relative stride length against Froude number and (B) duty factor against Froude number (Based on the data of Alexander and Jayes [1983], Alexander and Maloiy [in press], and Hayes and Alexander [1983.])



To move in dynamically similar fashion, animals must use stride lengths λ proportional to leg length h. The dynamic similarity hypothesis predicts that animals of different sizes will use equal relative stride lengths λ/h when traveling with equal Froude numbers. Figure 4A shows that this prediction does not hold universally. At any particular Froude number, quadrupedal primates (monkeys, etc.) take strides about 1.5 times as long as typical cursorial mammals. Noncursorial nonprimates take strides of intermediate length. Though the prediction does not hold universally, it holds quite well within each of these groups. For example, dogs, camels, and rhinoceroses (all of them cursorial mammals) use approximately equal relative stride lengths at any given Froude number.

The dynamic similarity hypothesis also predicts equal duty factors at any given Froude number. This prediction is fairly successful (Fig. 4B).

Alexander and Jayes (1983) applied the dynamic similarity hypothesis only to quadrupedal mammals, but Fig. 4 shows that the stride lengths and duty factors of birds and a bipedal mammal (kangaroo) are related to Froude number in much the same way as for quadrupedal mammals. Also, bipeds change from walking to running or hopping at Froude numbers near 0.5, like quadrupedal mammals (Hayes and Alexander 1983; Alexander and Maloiy, in press).

The dynamic similarity hypothesis tells us nothing about the optimization criteria that have molded gaits, but it is consistent with the idea that gaits have been optimized by evolution or learning. If a particular gait optimizes a particular mechanical property (e.g., economy of energy, or stability), a dynamically similar gait will generally optimize the same quantity for a different-sized animal traveling with the same Froude number.

The next two sections try to identify important optimization criteria for the gaits of particular animals.

5. Turtles

The movements of turtles are proverbially slow. Turtles must keep very close to equilibrium throughout each stride, for the following reason.

Consider an animal walking or running with constant velocity (i.e., with the same mean velocity in successive strides). The mean forces on its body, averaged over a complete stride, must be in equilibrium. There is no requirement to be in equilibrium at every instant, and a galloping horse is obviously not in equilibrium at the stage of its stride when all four feet are off the ground. However, any temporary departure from equilibrium causes an unwanted displacement of the body, making it rise or fall, pitch or roll, and so on. If the amplitudes of these displacements become too large, the animal's belly may hit the ground at some stage and the gait will (presumably) be unsatisfactory. The greater the duration of the stride, the more troublesome unwanted displacements are likely to be, because a small unwanted component of velocity can result in a large displacement if it continues for a long time.

Let the animal have stride frequency f, so that the duration of its stride is $1/f$. If it fell freely for the whole of this time, starting from rest, it would lose height $g/2f^2$. The distance it could fall before hitting the ground would be proportional to h: suppose that it is $h/2$. Thus $(g/2f^2)/(h/2) = g/hf^2$ can be used as a measure of the need to maintain equilibrium. Note that this is the reciprocal of the parameter introduced earlier as an alternative to the Froude number. Its value is about 10 for a dog walking slowly and about 400 for a turtle (*Geoemyda*) walking at normal speed (Jayes and Alexander 1980). The turtle needs to keep much closer to equilibrium than the dog.

It is, in principle, possible for a quadruped to maintain equilibrium throughout the stride if it moves its feet one at a time. It must move them in appropriate order to keep its center of mass over the triangle of support formed by the feet remaining on the ground. Moving the feet one at a time obviously requires a duty factor of at least 0.75. When the duty factor is 0.75, the only possible relative phases are those shown in the turtle diagram in Fig. 5A. When it is higher, slightly different relative phases become possible and it is arguably better to increase the relative phases of the hind feet (McGhee and Frank 1968). However, turtles actually use relative phases approximately as shown below the graph in Fig. 5C. Consequently they rise and fall, pitch and roll, as they walk. Why do they not maintain constant equilibrium?

A likely answer can be found by calculating the forces that the feet would have to exert to maintain equilibrium. These are shown in Fig. 5A. Note that at some stages of the stride, large instantaneous changes of force are required. Turtles have slow-acting muscles (Woledge 1968), which could not produce the required force pattern. They could conceivably evolve faster-acting muscles, but their slow muscles have the advantage of extremely economical energy consumption.

Equations (1 and 2) show how a Fourier series can be used to describe the pattern of force exerted by a foot. The faster the muscles, the more terms are required in the series to describe the patterns of force that can be produced. Very slow muscles might allow only the first term, in which case the force would rise and fall like a half-cycle of a cosine curve (Fig. 1A). Jayes and Alexander (1980) formulated a mathematical model of a turtle that behaved like this. They assumed (fairly realistically) that the forces exerted by the feet were precisely vertical. They calculated the amplitudes of unwanted displacements for different sets of relative phases of the feet. To simplify the problem, they considered initially only gaits in which the phase difference between the hind feet was the same as between the forefeet. Thus the relative phases were 0, γ for the forefeet and δ, $(\delta + \gamma)$ for the hind feet. They allowed γ to take any value between 0 and 0.5 (a convention explained in the Section 2 forbids larger values) and δ to take any value between 0 and 1.

Figure 6 shows ranges of unwanted displacements for all possible combinations of γ and δ. The only gait

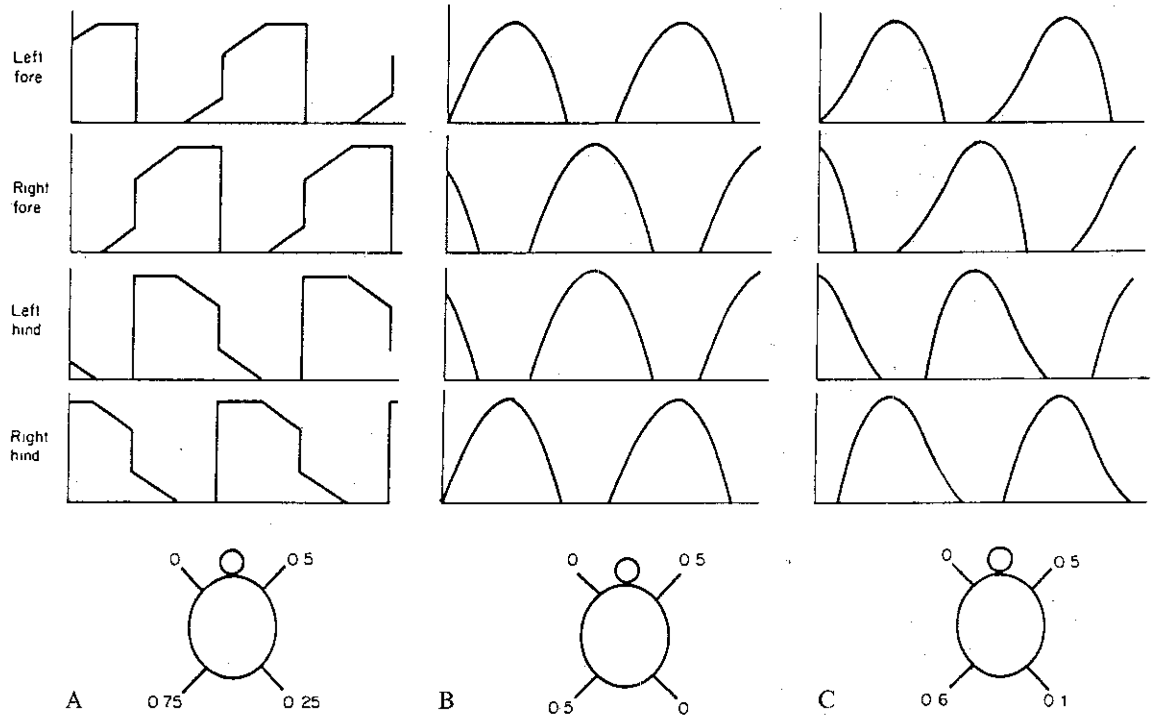


*Fig 5 Graphs of vertical forces exerted by the feet of hypothetical turtles, against time The diagrams below the graphs show the relative phases of the feet A. The gait required for perpetual equilibrium B The optimum gait for a turtle with very slow muscles. C. The gait used by turtles. (From Alexander 1982*b.)

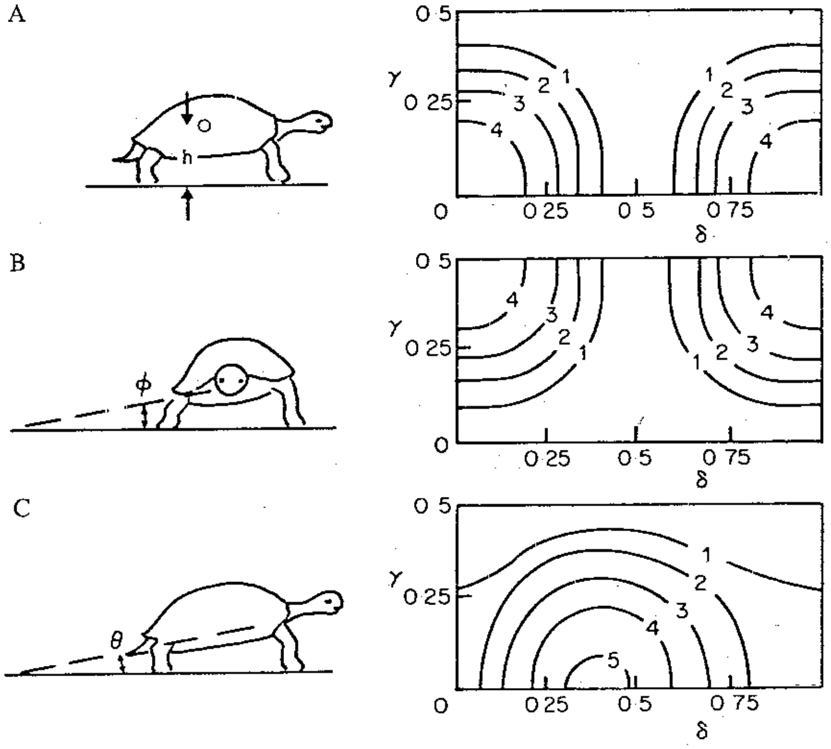


Fig 6. Unwanted displacements of a walking turtle for different combinations of the relative phases γ and δ The contours on the graphs show ranges in arbitrary units of (A) the height h *of the center of mass (circle); (B) the angle of roll ϕ, and (C) the angle of pitch θ All duty factors are 0 83 (From Alexander 1982*b)

for which the ranges of vertical movements, rolling, and pitching are all small has $\gamma = \delta = 0.5$: it is the gait illustrated in Fig. 5B This has relative phases that differ from the constant-equilibrium walk (Fig. 5A) and are more like those used by turtles (Fig. 5C). Calculations were also made for gaits for which the relative phase of the second hind foot was $(\delta - \gamma)$ instead of $(\delta + \gamma)$, and the same conclusion was reached. The gait shown in Fig. 5B minimizes unwanted displacements for turtles with muscles so slow that the force exerted by a foot can be represented by the first term only of a Fourier series.

Jayes and Alexander (1980) then considered a turtle with slightly faster leg muscles, requiring two terms of a Fourier series to describe the forces exerted by the feet. Thus they allowed r (Eq. 2) to take nonzero values (but kept $q = 0$). Thus they permitted skewed patterns of force, as in Fig. 1B (and as observed in force records made by turtles walking over force platforms). The relative phases γ and δ and the parameter r were all varied, and unwanted displacements were calculated. The gait represented in Fig. 5C seemed more satisfactory than any other: it gave less vertical movement and pitch than the gait shown in Fig. 5B, but a little more roll. It is very similar, both in relative phases and in Fourier spectra, to the gaits actually used by turtles.

This finding is consistent with the suggestion that minimization of unwanted displacements (subject to the constraints imposed by slow muscles) may have been predominantly important in the evolution of turtle gaits. However, this criterion is unlikely to have been important in other vertebrates, which move with much smaller values of the parameter g/hf^2.

6. People

Alexander (1980) argued that the walking gaits of mammals (including people) tend to minimize energy costs. We will consider how these costs arise.

Active muscles exert tension. When they shorten, they do work When they are forcibly stretched they exert a braking action, degrading mechanical energy to heat. It is convenient to regard this as negative work performance. Food energy is used both when muscles do positive work and (paradoxically) when they do negative work. Thus negative work performance has negative efficiency.

The leg joints of people (and other vertebrate animals) are well lubricated. The work we have to do against air resistance, when walking in still air, is negligible. It might therefore be argued that level walking at constant speed should require negligible quantities of energy. This is not the case, because our leg muscles do positive work at some stages of each stride and negative work at others.

Consider a man with frictionless joints moving in a perfect vacuum. In a time interval δt, his left and right leg muscles do work δW_l and δW_r. These quantities may be positive or negative. In a complete stride, numerically equal quantities W of positive and negative work are done. They are

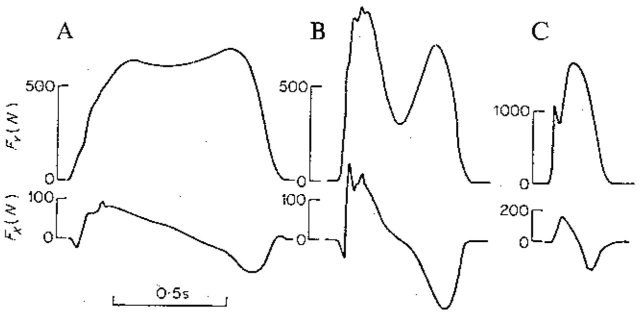
$$W = 0.5[\Sigma|\delta W_l| + \Sigma|\delta W_r|]. \tag{3}$$

The summations refer to one complete stride. We will examine the hypothesis that people walk so as to minimize W

First, we must examine the walking techniques that people actually use. Figure 7 shows typical force records made by a man walking over a force platform set into the floor In slow walking (Fig. 7A), the vertical component of force rises rapidly, plateaus, and then falls. In fast walking (Fig. 7B), there are two well-defined peaks of force. The pattern of force changes gradually and systematically throughout the range of walking speeds The duty factor falls a little as speed increases, but remains close to 0.6. When the subject breaks into a run, the duty factor falls abruptly and peak forces consequently increase. (Note the different scale of force in Fig. 7C.) The pattern of vertical force also changes abruptly to one with only a single major peak. (The small subsidiary peak at the beginning of the record in Fig. 7C will be ignored in this analysis. It is probably due to the foot striking the ground with finite velocity and being brought suddenly to rest.) The records of F_Y in Fig. 7 can be imitated quite closely by (Eq. 2), with the parameters shown in Table 1. Note particularly that q is positive in walking, with values that increase with increasing speed, but negative in running.

The records of the horizontal component of force could also be represented by a Fourier series, but it

Fig 7 Records of the vertical (F_Y) *and horizontal* (F_X) *components of the force exerted by one foot of a man (A) walking slowly, (B) walking fast, and (C) running. (From Alexander and Jayes 1978.)*



will be more convenient to use a different description. In each case the foot exerts a forward force on the ground (tending to decelerate the body) when it is first set down. It exerts a backward (accelerating) force later in the step. It is found that the records can be imitated closely by giving the constant k an appropriate value in the equation

$$F_X = ut\,F_Y/k, \tag{4}$$

where u is the speed and t (as in Eqs 1 and 2) is time from the midpoint of the step. If the resultant force acted at a fixed point on the sole of the foot, it would keep in line with a point at a height k from the ground, moving with the speed of the body. For humans $k \approx 1.7\,h$, but the point of application of the force moves from heel to toe during the step and the force keeps almost in line with the hip joint. Consequently, moments about the hip (and the knee) are kept fairly small.

Alexander (1980) sought to explain the changes of q and of duty factor that people make when they walk and run at different speeds. His simple model had legs of zero mass and exerted forces according to (Eqs. 2 and 4), but with $r = 0$. From the patterns of force, he calculated the instantaneous velocity of the center of mass for each stage of the stride. From the forces and velocities together, he calculated the instantaneous power outputs of each leg and hence the total positive and negative work done in a stride (W, Eq. 3).

Results are shown in Fig. 8. The whole of the possible range of q is included: values outside this range would make the vertical component of force negative at some stage of the step. Each graph refers to a different speed. At the slowest (Fig. 8A), the contours show minimum work at high duty factors, β (i.e., for walking) and for fairly low values of q. At the higher speeds represented in Figs. 8B and C, the minimum remains in the walking range ($\beta > 0.5$) but with higher values of q. At a still higher critical speed a catastrophe occurs and the minimum shifts suddenly to the left of the graph (Fig. 8D). It becomes advantageous to run with the lowest possible values of β and q.

Table 1. Parameters from (Eq. 2)

	A	B	C
Speed (m/s)	0.9	1.9	3.7
Duty factor	0.64	0.59	0.40
r	0.05	−0.10	−0.24
q	0.22	0.55	−0.12

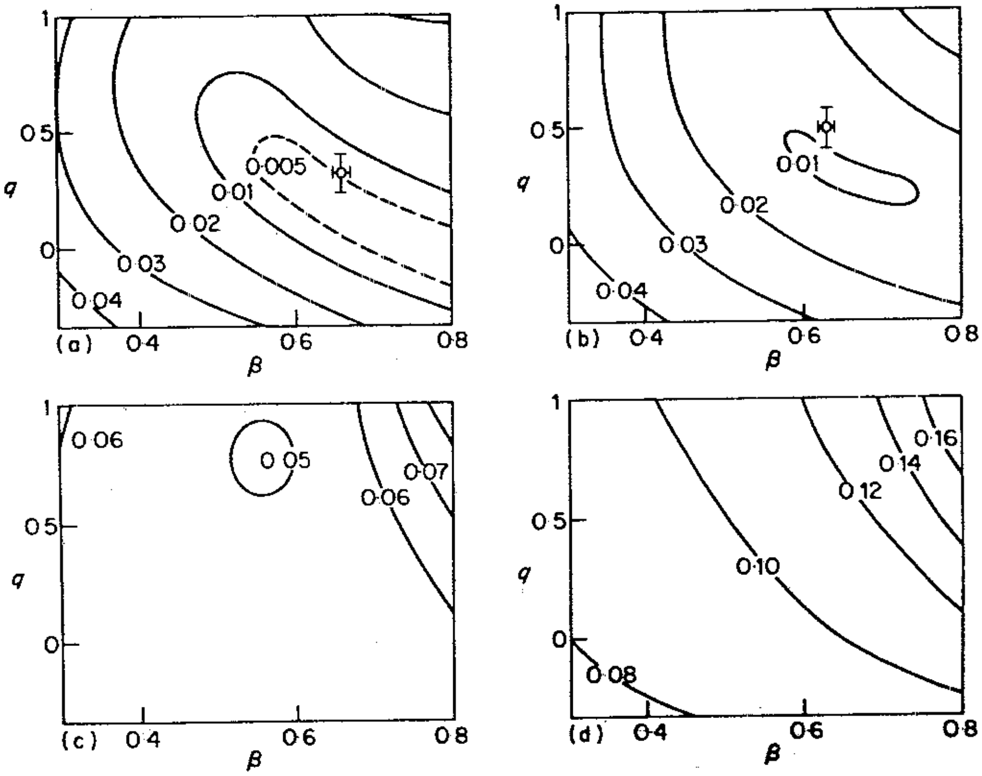
Points in Fig. 8A and B show observed values of β and q for men walking at the appropriate speeds. They lie close to the theoretical optima. The theory suggests that adult men should change from walking to running at 4 m/s, but men actually change at about 2.5 m/s. An explanation for the discrepancy will be offered in the next section.

The theory that has been presented ignores the mass of the legs. Mochon and McMahon (1980) used a theory that took into account the mass of the legs to calculate the optimum time for the forward swing of the legs. That theory gave no insight into the pattern of force on the feet, however.

7. Elastic Mechanisms

Consider a muscle that is required to extend (doing negative work) while the force on it increases, and then to shorten (doing a numerically equal quantity of positive work) while the force falls. It consumes food energy in both phases of its action. However, it could in principle be replaced by a perfect spring of appropriate compliance, which would achieve the same effect with no energy cost whatsoever. Particular muscles may not be required to exert precisely equal quantities of positive and negative work, but there may nevertheless be considerable scope for saving energy by means of springs. Muscles themselves have elastic properties, but their compliance is too low to have much importance (Alexander and Bennet-Clark 1977)

Fig 8 Graphs showing energy costs of bipedal walking and running at four different speeds The axes show duty factor β and the parameter q *The contours show a quantity proportional to the work done in each stride (It is* Wf^2/mg^2, *where* W *is the quantity given by [Eq 3],* f *is stride frequency,* m *is body mass, and* g *is the acceleration of free fall) The speeds are defined in terms of the parameter* u^2/gk, *where* u *is speed and* k *is the constant from (Eq. 4). For adult men, these speeds would be about (A) 0.9 m/s, (B) 1.8 m/s, (C) 3.6 m/s, and (D) 5.1 m/s Points in A and B show mean values of β and* q *(± two standard errors) observed for adult men walking at the appropriate speeds. (From Alexander [1980], by permission of the Zoological Society of London.)*



Their length changes in locomotion are largely inelastic, due to sliding of myofilaments past each other. Muscle fibers behave as actuators incorporating low compliance. Some of the tendons, which are attached in series with muscles, connecting them to the skeleton, are much more important springs. Tendon elasticity apparently saves a large fraction of the energy that would otherwise be needed for running, in people and other large mammals. Tendon is an excellent material for this function. Dynamic tests on sheep tendons have shown that it is capable of returning, in an elastic recoil, 93% of the work expended to stretch it (Ker 1981)

Alexander (1980) showed that large savings of energy by elastic storage were possible for some combinations of speed, duty factor, and the parameter *q*, but not for others. This is because only some combinations require springlike behavior of the muscles. Large savings are possible for running, but not for fast walking with high values of *q*.

Look again at Fig 8C, which suggests a walk as the optimum gait at a speed at which people normally run. It is based on a model that ignores the possibility of energy saving by elastic storage Note that the minimum is a very shallow one. If account were taken of elastic storage, which is much more effective for running than for fast walking, the optimum would be shifted into the part of the graph that represents running.

The results presented in this and the previous section are consistent with the suggestion that people adjust their gaits to minimize energy costs They contrast with the data of an earlier section, which showed that turtle gaits appear to minimize not energy costs, but unwanted displacements.

8. Conclusion

This paper has shown how the gaits of animals seem designed to minimize unwanted displacements (in the case of slow-moving turtles) or energy costs (in the case of mammals). It may interest robot engineers if (as seems likely) they are concerned with the same optimization criteria. The conclusions for animal gaits apply equally to robot gaits, provided only that the assumptions about permissible patterns of force hold for robots, as for animals. The assumption that the force patterns can be represented by truncated Fourier series (Eq 2) implies only that they have no high-frequency components This assumption may be novel to robot engineers, who are accustomed to using fast-acting actuators, but they may find it useful to consider the possibility of using slower, more economical devices The assumption of vertical ground forces (for the turtle model) or forces tilting according to (Eq. 4) (for the mammal model) may well be as realistic for some robots as they are for animals

REFERENCES

Alexander, R McN. 1976 Estimates of speeds of dinosaurs. *Nature* 261:129–130

Alexander, R. McN. 1980 Optimum walking techniques for quadrupeds and bipeds *J. Zool* (Lond.) 192:97–117.

Alexander, R. McN. 1981. Tetrapod gaits: adaptations for stability and economy. *Symp Zool Soc. Lond* 48:269–287.

Alexander, R. McN. 1982*a*. *Locomotion of animals*. Glasgow: Blackie.

Alexander, R. McN. 1982*b*. *Optima for animals* London: Arnold

Alexander, R. McN. 1983. Allometry of the leg bones of moas (Dinornithes) and other birds. *J Zool* (Lond) 200:215–231.

Alexander, R McN, and Bennet-Clark, H. C. 1977 Storage of elastic strain energy in muscle and other tissues *Nature* 265:114–117

Alexander, R McN., and Jayes, A. S. 1978. Vertical movements in walking and running. *J. Zool.* (Lond.) 185:27–40.

Alexander, R McN, and Jayes, A. S. 1980. Fourier analysis of forces exerted in walking and running. *J. Biomechan* 13:383–390.

Alexander, R. McN., and Jayes, A. S 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals *J Zool* (Lond) 201:135–152

Alexander, R. McN., et al. 1979. Allometry of limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J. Zool.* (Lond.) 189:305–314

Alexander, R. McN, and Maloiy, G. M. O. 1984. Stride lengths and stride frequencies of primates *J Zool* (Lond.) 202

Duncan, W. J 1953 *Physical similarity and dimensional analysis*. London: Arnold.

Hayes, G., and Alexander, R. McN. 1983. The hopping gaits of crows and other bipeds *J. Zool* (Lond) 200:205–213.

Hildebrand, M 1976 Analysis of tetrapod gaits: general considerations and symmetrical gaits. *Neural control of locomotion*, ed. R M Herman et al New York: Plenum, pp 203–236

Hildebrand, M. 1977. Analysis of asymmetrical gaits *J Mammal.* 58:131–156.

Jayes, A S., and Alexander, R. McN 1980. The gaits of chelonians: walking techniques for very low speeds. *J Zool* (Lond.) 191:353–378.

Jenkins, F A. 1971. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *J Zool.* (Lond.) 165:303–315

Ker, R F. 1981. Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *J. Exp Biol.* 93:283–302.

McGhee, R. B. 1968. Some finite state aspects of legged locomotion. *Math Biosci* 2:67–84

McGhee, R. B 1976. Robot locomotion. *Neural control of locomotion*, ed. R. M Herman et al New York: Plenum, pp. 237–264.

McGhee, R. B., and Frank, A. A. 1968. On the stability properties of quadruped creeping gaits. *Math Biosci* 3:331–351.

McMahon, T. A. 1973. Size and shape in biology. *Science* (Washington) 179:1201–1204.

Mochon, S., and McMahon, T. A 1980. Ballistic walking: an improved model. *Math Biosci.* 52:241–260

Rewcastle, S C 1981. Stance and gait in tetrapods: an evolutionary scenario. *Symp Zool. Soc Lond* 48:239–267.

Sukhanov, V. B. 1974. *General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods*. New Delhi: Amerind.

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

Zug, G. R. 1974 Crocodilian galloping: an unique gait for reptiles. *Copeia* 1974:550–552.