A dynamic similarity hypothesis for the gaits of quadrupedal mammals

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(With 5 figures in the text)

The dynamic similarity hypothesis postulates that different mammals move in a dynamically similar fashion whenever they travel at speeds that give them equal values of a dimensionless parameter, the Froude number. Thus, given information about one species, it could be possible to predict for others relationships between size, speed and features of gait such as stride length, duty factor, the phase relationships of the feet and the patterns of force exerted on the ground.

Data for a diverse sample of mammals have been used to test the hypothesis. It is found to be tenable in many cases when comparisons are confined to quadrupedal mammals of the type described by Jenkins (1971) as "cursorial". Most mammals of mass greater than 5 kg are of this type. Although the hypothesis applies less successfully to comparisons between cursorial and non-cursorial mammals it is shown to be a reasonable approximation even for such comparisons and for comparisons between quadrupedal mammals and bipedal mammals and birds.

Contents

Introduction

When a dog and a horse travel side by side, at the same speed, the dog takes shorter strides than the horse, and may trot while the horse walks, or gallop while the horse trots. The differences between the gaits of the two animals are partly due to their different shapes, but

largely to their different sizes. This paper shows how account can be taken of differences of size, to obtain relationships between gait parameters and speed that apply widely among quadrupedal mammals of all sizes and taxa. It develops a hypothesis first formulated by Alexander (1976), explores its implications more thoroughly than previously and tests it more rigorously.

The hypothesis depends on the concept of dynamic similarity, which is closely related to the more familiar concept of geometric similarity. Two bodies are described as geometrically similar if the form of one could be made identical to that of the other by multiplying all its linear dimensions by some constant factor. 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:

   (i)   all linear dimensions by some constant factor;

   (ii) all time intervals by another constant factor; and

   (iii) all forces by a third constant factor

(Duncan, 1953, Newman & Searle, 1957). For example, pendulums of different lengths swinging through equal angles have dynamically similar motions.

For many motions, including the swinging of pendulums and the running of mammals, gravitational forces are important. In such cases, dynamic similarity is only possible if the systems have equal Froude numbers, u^2/gh. Here u is a speed characteristic of the motion, defined in the same way for the different systems being compared. It might, for instance, be the speed at mid-swing of pendulums. Similarly h is a characteristic length, perhaps the length from the pivots of the pendulums to their centres of mass. Finally, g is the acceleration of free fall. Since any speed is a distance divided by a time interval, this condition is equivalent to the condition that the systems must have equal values of $(h/t)^2/gh = h/gt^2$, where t is a characteristic time interval. Thus, systems moving in dynamically similar fashion under the influence of gravity must have corresponding velocities proportional to the square roots of their linear dimensions (to make u^2/gh equal, for equal values of g) and corresponding time intervals also proportional to the square roots of their linear dimensions (to make h/gt^2 equal).

The hypothesis to be tested is that different mammals tend to move in dynamically similar fashion, whenever they walk or run with equal Froude numbers u^2/gh or equal values of the parameter h/gt^2. The mean speed of locomotion will be used as the characteristic speed u and the height of the hip joint from the ground (in normal standing) as the characteristic height h. These conventions were also adopted by Alexander (1976, 1977a, b). Some mammals do not often adopt a standing posture: for them, h is measured while the hind foot is on the ground in locomotion. Further, the stride period (the duration of one complete cycle of leg movements) will be used as the characteristic time t. Initially, the hypothesis will be applied only to quadrupedal mammals.

The hypothesis generates the following predictions.

(i) Different mammals will move their legs in the same phase relationships, when moving with equal Froude numbers or values of h/gt^2. Thus if one mammal sets down one fore foot 0·4 of a stride period after the other, another mammal running at the same Froude number will do the same. Any abrupt changes of phase relationships (changes of gait) will occur at equal Froude numbers and equal values of h/gt^2 in different mammals. They will therefore occur at speeds proportional to (hip height)$^{\frac{1}{2}}$ and at stride periods also proportional to (hip height)$^{\frac{1}{2}}$.

(ii) The relative stride lengths of different mammals will be equal, at any particular Froude number. Stride length is the distance travelled during one complete cycle of leg movements, and relative stride length is (stride length)/(hip height).

(iii) Corresponding feet of different mammals will have equal duty factors, at any particular Froude number. The duty factor is the fraction of the stride period, for which the foot is on the ground.

(iv) Corresponding feet of different mammals walking or running at any particular Froude number will exert forces that are equal multiples of body weight, at corresponding stages of the step. This follows from the third point in the definition of dynamic similarity (above): the gravitational forces on the animals are their weights so all other forces must be proportional to their weights. It applies both to the vertical and to the horizontal components of the forces.

(v) When different mammals walk or run with equal Froude numbers, the power outputs of corresponding muscles, at corresponding stages of the stride, will be proportional to (body weight) × (running speed). This follows from the hypothesis because the power output of a muscle is the force it is exerting multiplied by the speed at which it is contracting. In dynamically similar motions all forces are proportional to body weight and all speeds are proportional to running speed.

Alexander (1976) was concerned only with prediction (ii). He demonstrated quite good agreement with the prediction, for a selection of mammals that included both bipeds and quadrupeds, and ranged in size from a small rodent (*Meriones*) to an elephant (*Elephas*). Alexander (1977b) presented some evidence for prediction (i) but used a quantity $\hat{u}$ which is the square root of the Froude number, instead of the Froude number itself. His data showed that a selection of mammals changed from a walk to a run at Froude numbers around 0·6 and (in the case of quadrupeds) from a trot to a gallop at Froude numbers between 2 and 4. These papers presented only a limited amount of evidence for only two of the predictions. This one assembles a much larger body of evidence from the literature and from unpublished observations.

Precise dynamic similarity between the motions of different animals would be possible only if they were geometrically similar and had corresponding body segments representing equal fractions of total body mass. A dog cannot move in precisely similar fashion to a horse because (among other reasons) its joints are differently placed in its legs. If the geometric differences are not too severe, the dynamic similarity hypothesis may, nevertheless, be useful for making comparisons between horses, dogs and other animals. A section of this paper enquires how closely quadrupedal mammals are geometrically similar to each other, in features that seem relevant to locomotion.

Jenkins (1971) distinguished "cursorial" mammals such as dogs, cats and horses from "non-cursorial" mammals such as opossums, rats and ferrets. Cursorial mammals stand and run with the humerus and femur more nearly vertical than horizontal. They move the bones of each leg in (more or less) a parasagittal plane. In contrast non-cursorial mammals stand and run with the humerus and femur more nearly horizontal than vertical. The movements of their legs deviate considerably from parasagittal planes. Nearly all terrestrial mammals with masses greater than 10 kg are probably best described as cursorial, and nearly all with masses less than 1 kg as non-cursorial.

The walking and running movements of cursorial mammals are plainly not dynamically similar to those of non-cursorial mammals, though some gait parameters may have approxi-

mately equal values, in the two groups, at equal Froude numbers. The gaits of cursorial and non-cursorial mammals will be considered separately.

There is a reason why animals might be expected to behave according to the dynamic similarity hypothesis. Cost of transport is the energy required to move unit weight of animal through unit distance, so it is (power)/(body weight × speed). Prediction (v) tells us that different animals moving in dynamically similar fashion have equal costs of transport. Consequently, if geometrically similar animals move in such a way, as to minimize their costs of transport at the particular speeds at which they have chosen to travel, they must behave according to the dynamic similarity hypothesis. This is also evident from mathematical models of walking (Alexander, 1980) and running (Alexander, Jayes & Ker, 1980). It seems likely that animals tend to move so as to minimize cost of transport.

Materials and methods

The principal sources of data for this paper are listed below. Some other (published) sources are cited at appropriate points in the Results section.

Gaits of cursorial mammals

Dogs (*Canis familiaris* L.)

(a) Films and force platform records of 2 dalmatians walking and running at low to moderate speeds in a gymnasium. Further details of experimental method and analysis are given by Jayes & Alexander (1978).

(b) Films of the same 2 dogs galloping fast on a running track. The scale of distance was given by white lines painted transversely across the track. The cine camera was run at a nominal framing rate of 64 frames/s, and the actual rate was determined by means of a Stevenson-Milburn timing light (Stevenson & Milburn, 1977).

Cats (*Felis catus* L.)

Data on the gaits of cats walking and running on the ground (not on treadmills) from Goslow, Reinking & Stuart (1973) and Wetzel, Atwater, Wait & Stuart (1975). Hip height was estimated from Manter (1938) to be 0·22 m.

Sheep (*Ovis aries* L.)

(a) Films and force platform records of a sheep walking and running at low to moderate speeds in a gymnasium (Jayes & Alexander, 1978).

(b) Films of several sheep running fast over short grass, taken in the course of research by Dr R. F. Ker. Vertical posts at measured intervals on the side of the path that was further from the camera, and corresponding pegs driven into the ground on the near side, were used to establish a scale of length. The framing rate of the electrically-driven camera was determined to be 91 frames/s, by filming a stopwatch.

Wildebeest (*Connochaetes taurinus* Thomas) and Thomson's gazelle (*Gazella thomsoni* Gunther)

Observations by Pennycuick (1975) of antelopes moving spontaneously on the Serengeti plains. It was assumed in analysing these data that the hip height of the wildebeest was 0·96 m and of the gazelles 0·55 m, as estimated by Alexander, Langman & Jayes (1977).

Arabian camels (**Camelus dromedarius** *L.*)

Films of camels walking and running at various speeds (Alexander, Maloiy, Ker, Jayes & Warui, 1982).

Great Indian rhinoceros (**Rhinoceros unicornis** *L.*)

Films of adult rhinoceros walking and running at low to moderate speeds in a zoo enclosure (Leyhausen, 1959). Framing rates are specified in the films, and the lengths of the animals are included in information supplied with them. The films were analysed by the methods of Alexander, Langman & Jayes (1977). Film sequences of a juvenile had to be excluded from the analysis because several months (during which it presumably grew) intervened between filming and measurement of its length.

White rhinoceros (**Diceros simus** (*Burchell*))

A film of adult rhinoceros running, pursued by a vehicle, in a very large paddock at Whipsnade Park. They were filmed from a position just outside the paddock, by means of an electrically-driven camera running at 62 frames/s. This framing rate was determined by filming a digital clock. The lengths of the animals were determined from the film, by comparison with the vehicle. The film was analysed by the methods of Alexander, Langman & Jayes (1977).

Horse (**Equus caballus** *L.*)

(a) Sequence of photographs of horses, taken in rapid succession by a row of cameras, by Muybridge (1887). The time intervals between exposures are known, and the scale is given by a background grid. Some of the sequences used for analysis show horses with riders, and others without, but sequences showing horses pulling carts were excluded.

(b) Observations of the speeds and gaits of a small (140 kg) horse (Hoyt & Taylor, 1981). The hip height of this horse was estimated to 1·0 m.

(c) Force platform records of horses walking and trotting by Schryver, Bartel, Langrana & Lowe (1978).

(d) Force records obtained from instrumented horse shoes by Björck (1958).

Gaits of non-cursorial mammals

Ferrets (**Putorius putorius** (*L.*))

Films of ferrets running on a thin rubber mat in a laboratory. The camera, which was fitted with a Stevenson-Milburn timing light, ran at 70 frames/s. The scale was given by a grid close behind the animals' path. Sequences of 2 or more successive strides were analysed.

Rats (**Rattus norvegicus** (*Berkenhout*))

Films taken at about 67 frames/s of laboratory rats running on a hard, rough surface.

Jirds (**Meriones unguiculatus** (*Milne-Edwards*))

Films taken at 70 frames/s of 2 jirds running on a treadmill. A scale was mounted close behind them, and a timing device was included in the field of view of the camera. Sequences of 3–9 successive strides were analysed.

Coypu (Myocaster coypus Molina)

Films and force platform records of 2 coypu, obtained by the methods of Jayes & Alexander (1978).

Anatomical data

The lengths of head plus body, and body masses, of terrestrial quadrupedal mammals were taken from Walker (1968). The data used were geometric means of ranges given for genera, or typical values for particular species representing their genera. Bipeds, and non-terrestrial mammals such as bats, seals and whales were excluded. Five other genera were excluded because inconsistencies in Walker's book, or gross disagreement with other publications, suggested that an error had been made. All 290 other genera for which Walker supplied the required data were included.

The lengths of limb bones, and body masses, of terrestrial quadrupedal mammals were taken from the data of Alexander, Jayes, Maloiy & Wathuta (1979). Two bipeds (man and springhare) were excluded, leaving 39 mammals of 34 species, ranging in mass from 0·003 to 2500 kg.

Statistical analysis

The dynamic similarity hypothesis predicts that various gait parameters x will have equal values for quadrupedal mammals of all sizes and taxa, whenever they walk or run with equal Froude numbers u^2/gh. This implies that each x is related to Froude number by a unique function F,

$$x = F(u^2/gh). \tag{1}$$

The hypothesis does not specify the nature of the function F, but we have found that in many cases the data are well fitted by power-law equations

$$x = a(u^2/gh)^b, \tag{2}$$

where a and b are constants. Such equations have been fitted to the data by model II (geometric mean) regression after transformation to logarithms (Sokal & Rohlf, 1981).

If the predictions of the hypothesis were precisely true, all the data would lie on the line represented by equation (1). In practice, the data are scattered about all lines fitted to them. The inaccuracy of the predictions can be measured, by measuring the scatter of the data about the best-fitting line.

The scatter could be measured by calculating the standard deviation of $(x - \hat{x})$, *where x* is the observed value of the parameter and $\hat{x}$ is the value predicted by the regression equation, for the same Froude number. In the case of power law equations, the standard deviation of $(\log x - \log \hat{x})$ seems more appropriate. We have preferred to use the antilogarithm of the standard deviation of $(\log x - \log \hat{x})$, a quantity that we call the standard deviation factor. Its merit is that it gives an immediate impression of the scatter. Remember that 68% of the values of a normally-distributed variable lie within one standard deviation of the mean. Similarly, a standard deviation factor of (for instance) 1·2 suggests that 68% of the values lie between $\hat{x}/1·2$ and $1·2\hat{x}$. If there were no scatter, the standard deviation factor would be 1·0.

This measure of scatter treats x as a dependent variable, so it seems appropriate to obtain $\hat{x}$ from a model I regression equation. The equations that are presented in the Tables, however, have been obtained by model II regression, because they are intended to show functional relationships between two variables, both of which are subject to error (Sokal &

Table I

Exponents (with 95% confidence limits), and standard deviation factors, for allometric equations relating various lengths to body mass in quadrupedal mammals

	Exponent	Standard deviation factor
Head plus body length	0·33 ± 0·01	1·18
Femur length	0·37 ± 0·02	1·25
Tibia length	0·32 ± 0·02	1·22
Humerus length	0·37 ± 0·02	1·24
Ulna length	0·36 ± 0·02	1·22

Sources of data are specified in the Materials section.

Rohlf, 1981). If there were no scatter, the model I and model II equations would of course be identical.

Allometric equations have been derived, relating the lengths of body segments to body mass, to test how close mammals of different sizes and taxa are to geometric similarity. These equations have been obtained in the same way as the power-law equations relating gait parameters to Froude number, and standard deviation factors have also been calculated.

Results and discussion

Shapes of mammals

Quadrupedal mammals are obviously not all geometrically similar to each other. For instance, giraffes are so different in shape from rhinoceros that they have twice the shoulder height of rhinoceros of equal mass (Sachs, 1967, on *Giraffa*; Meinerzhagen, 1938, on *Diceros*). This is, however, an extreme example. Most pairs of quadrupedal mammals are much more similar in shape.

Table I shows relationships between segment lengths and body mass, for quadrupedal mammals varying widely in size and taxonomic affinity. If these mammals were all geometrically similar to each other, all the exponents would be 0·33 and all the standard deviation factors would be 1·00. None of the exponents are grossly different from 0·33. All the standard deviation factors are 1·25 or less. Thus mammals tend to be reasonably close to geometric similarity, in some of their principal linear dimensions.

There are considerable differences between mammals, in the distribution of mass between body segments. Thus the limbs total 40% of body mass in cheetahs (*Acinonyx*) but only 31% in gazelles (*Gazella*) and 19% in domestic goats (*Capra*) (Taylor, Shkolnik, Dmi'el, Baharav & Borut, 1974). They total 35% of body mass in *Macaca* but only 21% in *Tupaia* (Grand, 1977). There are also marked differences of mass distribution within limbs.

These deviations from geometric similarity need not destroy the usefulness of the dynamic similarity hypothesis. There is obvious resemblance between giraffes, rhinoceros, cheetahs,
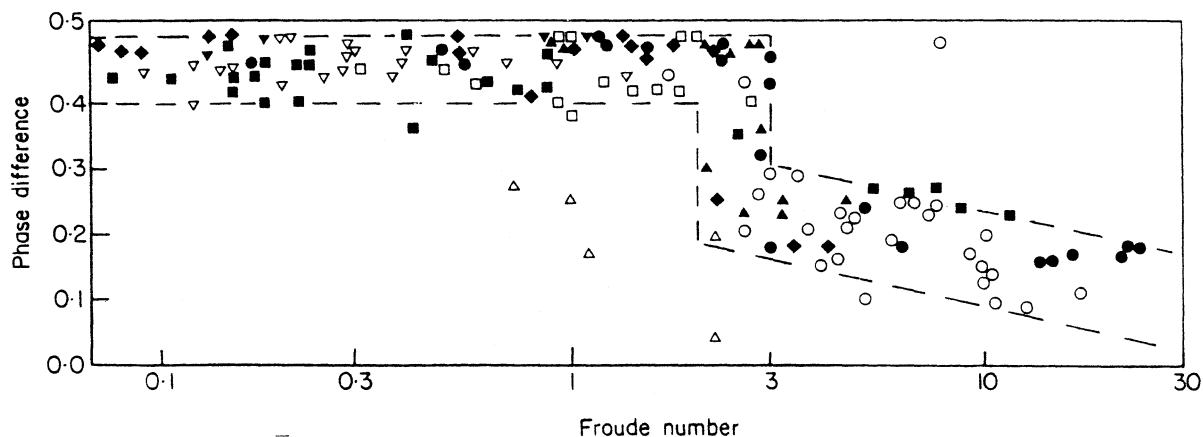
FIG. 1. A graph of phase difference between the fore feet, against Froude number, for quadrupedal mammals. The scale of Froude number is logarithmic. Filled symbols are used for cursorial mammals and hollow symbols for non-cursorial ones, as follows. ●, Dog; ■, sheep; ♦, camel; ▼, Indian rhinoceros; ▲, White rhinoceros; ○, Ferret; □, rat; △, jird; ▽, Coypu.

goats and all other quadrupedal mammals, despite differences of build and mass distribution. The usefulness of the hypothesis depends on the accuracy and scope of its predictions.

Prediction (i): phase relationships

It is predicted that different mammals will move their legs in the same phase relationships when they walk or run with equal Froude numbers.

Figure 1 shows the phase difference between the fore feet plotted against Froude number. This phase difference is the fraction of the stride period elapsing between the setting down of one fore foot and the setting down of the other. Plainly, if the left foot is set down 0·4 of a stride period after the right, the right foot is set down 0·6 of a period after the left. Whichever interval is less than 0·5 of the stride period has been used in plotting the graph. This convention has been adopted to avoid making trivial distinctions between gaits that are mirror images of each other. The phase difference thus defined is identical with the parameter γ of Alexander, Jayes & Ker (1980).

Almost all the points in Fig. 1 lie within the band outlined by broken lines. At Froude numbers below 2, almost all the phase differences lie between 0·4 and 0·5. At Froude numbers above 3, almost all the phase differences lie below 0·3, and they tend to decrease as the Froude number increases further. There is an abrupt transition at Froude numbers between 2 and 3. The phase difference between the hind feet changes in the same way. Thus at Froude numbers below 2, mammals use symmetrical gaits (gaits such as the walk, trot and pace, in which the feet of each pair move approximately half a cycle out of phase with each other). At Froude numbers above 3, mammals use asymmetrical gaits (the various kinds of canter and gallop). Most of the points outside the broken lines in Fig. 1 refer to jirds, which use asymmetrical gaits at unusually low Froude numbers.

Figure 1 shows remarkable uniformity between very diverse mammals. There is published data showing that various other mammals change from symmetrical to asymmetrical gaits at Froude numbers around 2 or 3. Hoyt & Taylor (1981) observed that a horse walked or trotted at speeds below 3·75 m/s but galloped at speeds above 5 m/s. We estimate that the corresponding Froude numbers were 1·4 and 2·5. Goslow et al. (1973) observed that cats
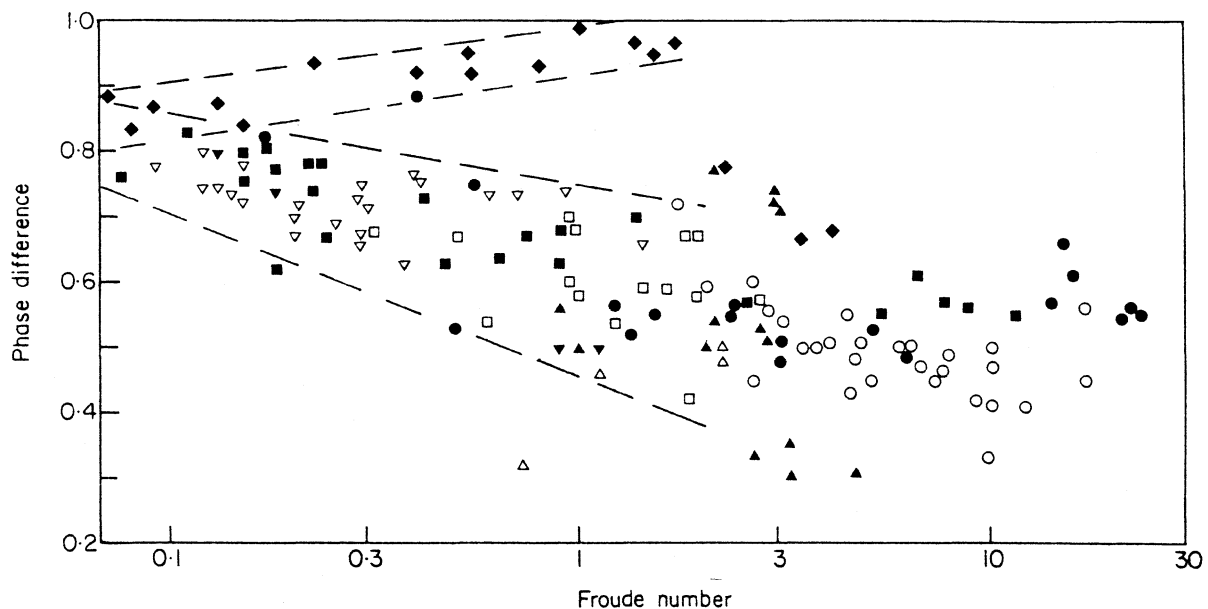
FIG. 2. A graph of phase difference between fore and hind feet (as defined in the text) against Froude number, for quadrupedal mammals. Symbols as in Fig. 1.

change from trotting to galloping at 6 miles/h (2·7 m/s), at an estimated Froude number of 3. Pennycuick (1975) found that Thomson's gazelle changes from symmetrical to asymmetrical gaits within the range 3·7–5·3 m/s (Froude numbers 2·5 to 5·2). However, he also observed that the wildebeest (which does not trot) uses asymmetrical gaits at speeds down to 2 m/s (Froude number 0·4).

Figure 2 shows the phase difference between the fore and hind feet of the same side of the body. This is the time interval from the setting down of the fore foot, to the next setting down of the hind foot of the same side, expressed as a fraction of the stride period. It has been calculated for both sides of the body, and a mean taken. The values for the two sides are identical in precisely symmetrical gaits but may be very different in asymmetrical gaits.

Figure 2 shows that, at very low Froude numbers, mammals use fore-hind phase differences around 0·8. Increases of Froude number tend to be accompanied by decreases of the phase differences except in camels, in which they are accompanied by an increase in the phase difference. At Froude numbers approaching 2, camels use fore–hind phase differences approaching 1·0 (i.e. the hind foot moves just *before* the fore foot of the same side) and other mammals use fore–hind phase differences around 0·55. Remember that it has already been shown that symmetrical gaits are generally used at all Froude numbers below 2. A typical quadrupedal walk (the lateral sequence, single-foot walk of Hildebrand, 1976) has a fore–hind phase difference of 0·75, a trot has a phase difference of 0·5 and a pace has a phase difference that can be expressed either as zero or as 1·0. Thus, quadrupedal mammals in general seem to use gaits very close to the lateral sequence, single-foot walk at very low Froude numbers, but change gradually as they increase speed and approach an ideal trot (or pace, in the case of camels) as they approach the Froude number at which transition to an asymmetrical gait occurs. Some mammals, including dogs, generally make an abrupt change in the fore–hind phase difference as they change from a walk to a trot, but others, including sheep, make a more gradual change (Jayes & Alexander, 1978). A horse walked at Froude numbers up to about 0·2 and trotted at Froude numbers from 0·8 upwards (calculated from Hoyt & Taylor, 1981). Cats change from walking to trotting at a Froude number of about 0·4 (Goslow
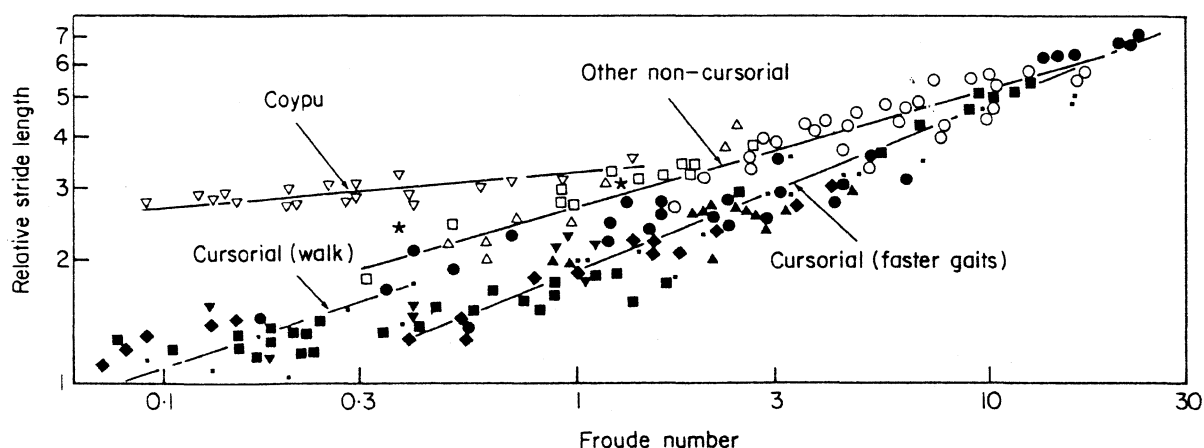
FIG. 3. A graph on logarithmic coordinates of relative stride length against Froude number, for quadrupedal mammals. The equations of the lines are given in Table II. Symbols as in Fig. 1 except ★, cat; ■, horse.

et al., 1973). Thomson's gazelle walk at Froude numbers up to 0·3 and trot at Froude numbers from 1·0 upwards (Pennycuick, 1975).

Figures 1 and 2 show that a diverse sample of mammals change the phase relationships of their feet in broadly similar fashion, as they change Froude number. They also show differences between species, especially in the fore–hind phase differences used at high Froude numbers. Further information about the differences between the gaits used by different species is given by Hildebrand (1976, 1977) who does not, however, specify speeds.

Prediction (i) requires the stride periods at which mammals change gaits to be proportional to (hip weight)$^{0.5}$. For geometrically similar mammals, this would also be proportional to (body mass)$^{0.167}$. Heglund, Taylor & McMahon (1974) found that the stride periods at which mice, rats, dogs and horses changed from trotting to galloping were proportional to (body mass)$^{0.14}$, which is reasonably close to the prediction. However, as they emphasize, it is also close to proportionality to (body mass)$^{0.125}$, as predicted by McMahon's theory of elastic similarity.

Pennycuick (1975) observed large mammals moving spontaneously in their habitat in East Africa. He found that they walked with stride periods proportional to (shoulder height)$^{0.57}$, trotted with periods proportional to (shoulder height)$^{0.53}$ and cantered or galloped with periods proportional to (shoulder height)$^{0.49}$. The exponents are close to the exponent of 0·5 predicted by the dynamic similarity hypothesis.

Prediction (ii): relative stride length

The hypothesis predicts that different mammals will use equal relative stride lengths when travelling with equal Froude numbers. However, Fig. 3 shows marked differences between species. At all but the highest Froude numbers, non-cursorial mammals (hollow symbols) use larger relative stride lengths than cursorial mammals (filled symbols). At low Froude numbers, Coypu use relative stride lengths more than twice those of camels, sheep and horses. The Coypu were far from tame, and behaved in an apparently nervous manner. We are not satisfied that they were using a normal gait.

The points for cursorial mammals in Fig. 3 cannot be fitted closely by any single straight line. Two lines have therefore been fitted, one for walks and one for faster gaits. Almost all points representing Froude numbers below 0·4 have been identified as walks, and almost all above 0·4 as faster gaits. The division has been made largely by considering the phase

TABLE II

Equations of the form $x = a(u^2/gh)^b$ relating gait parameters x to Froude number u^2/gh for quadrupedal mammals

	Factor a	Exponent b and 95% confidence limits	Standard deviation factor
Relative stride length			
Cursorial mammals, walking	2·4	0·34±0·10	1·16
Cursorial mammals, faster gaits	1·9	0·40±0·03	1·14
Wildebeest walking*	2·4	0·31	
Wildebeest cantering*	1·7	0·42	
Coypu	3·3	0·09±0·03	1·05
Other non-cursorial mammals	2·7	0·28±0·03	1·10
Fore duty factor			
Cursorial mammals, walking	0·52	−0·14±0·05	1·07
Cursorial mammals, faster gaits	0·52	−0·28±0·03	1·14
Coypu	0·57	−0·10±0·04	1·06
Other non-cursorial mammals	0·52	−0·17±0·03	1·07
Hind duty factor			
Cursorial mammals, walking	0·51	−0·18±0·08	1·10
Cursorial mammals, faster gaits	0·53	−0·28±0·03	1·16
Coypu	0·61	−0·10±0·03	1·05
Other non-cursorial mammals	0·56	−0·18±0·03	1·08

*Data from Pennycuick (1975).

relationships of the feet. There are a few points that could have been assigned almost equally plausibly to either group, but the regression lines would have been altered very little if they had been assigned differently. The equations of the lines are given in Table II. Notice that their standard deviation factors are reasonably small and that both equations are very similar to the corresponding equations calculated from Pennycuick's (1975) data for wildebeest. In the narrow range of Froude numbers in which walks and faster gaits both occur, the walks tend to involve larger relative stride lengths.

The points for Coypu in Fig. 3 stand apart from the points for other non-cursorial mammals. Separate lines have therefore been fitted. Their equations are given in Table II, and also their standard deviations factors, which are satisfactorily small.

Thus, prediction (ii) is reasonably accurate for the cursorial mammals considered alone, or for the non-cursorial mammals excluding Coypu considered alone, but it is rather inaccurate if applied to all the quadrupedal mammals as a single group.

The discrepancy between the long relative stride lengths of non-cursorial mammals and the generally shorter ones of cursorial mammals could be reduced by re-defining h as the extended length of the leg (which is a larger multiple of hip height in non-cursorial than cursorial mammals). It seems doubtful whether it would be useful or sensible to try to conceal the difference between cursorial and non-cursorial mammals in this way. The difference of posture is a clear departure from dynamic similarity.
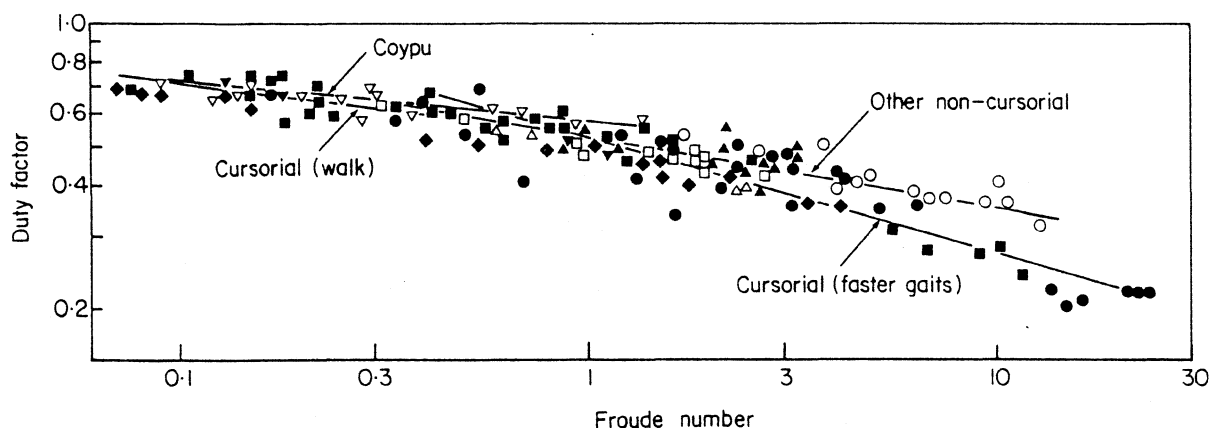
FIG. 4. A graph on logarithmic coordinates of duty factor for fore feet against Froude number, for quadrupedal mammals. The equations of the lines are given in Table II. Symbols as in Fig. 1.

Prediction (iii): duty factors

It is predicted that different mammals will use equal duty factors, when travelling with equal Froude numbers. Figure 4 shows that this is fairly true for the fore feet, except that, at high Froude numbers, non-cursorial mammals (rats) use larger duty factors than cursorial mammals. The equations of the regression lines drawn on Fig. 4 are given in Table II. Notice that the standard deviation factors are reasonably small.

Table II also shows that the duty factors of the hind feet are generally about equal to those of the fore feet.

Prediction (iv): forces on the feet

It is predicted that the forces on the feet of mammals travelling with the same Froude number will be equal multiples of body weight, at corresponding stages of their strides. This implies that the task of supporting body weight will be divided in the same way between the four feet.

Björck (1958) found that when horses walk without a cart, their fore legs support about 58% of body weight and their hind legs 42%. Similarly, Jayes & Alexander (1978) found that the fore legs of dogs and sheep support about 61% and 57% of body weight, respectively, during locomotion. A similar calculation based on three suitable force records of Coypu shows that their fore feet support about 53% of body weight. Rollinson & Martin (1981) collected data on the distribution of weight between the feet of standing mammals. They showed that the fore feet support about 60% of body weight in many quadrupedal mammals, but considerably less in monkeys and a few others. The lowest value was found in a highly specialized arboreal monkey (Ateles), but even so terrestrial a monkey as Papio had only 44% of its weight supported on its fore feet.

The preceding paragraph suggests that in many and perhaps most quadrupedal mammals, the mean vertical force exerted over a complete stride is 0·3 of body weight for each fore foot and 0·2 of body weight for each hind foot. This is not sufficient to satisfy prediction (iv). It is also necessary that corresponding feet should have equal duty factors, in mammals running with the same Froude number, so that the mean force during the period of contact with the ground is the same. This is also required by prediction (iii), and has already been discussed. Further, the detailed pattern of rise and fall of the force exerted by each foot

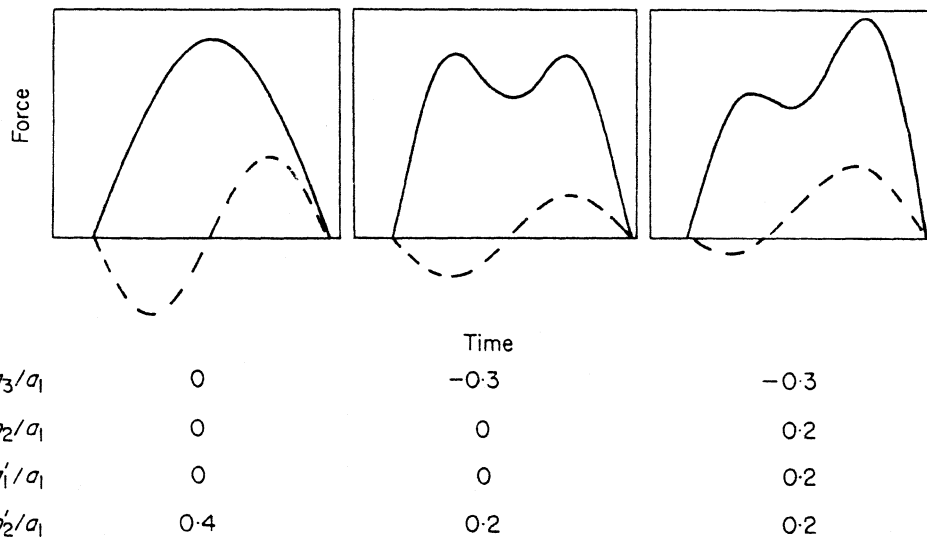|			
a_3/a_1	0	−0·3	−0·3
b_2/a_1	0	0	0·2
a_1'/a_1	0	0	0·2
b_2'/a_1	0·4	0·2	0·2

FIG. 5. Schematic graphs of forces exerted by feet on the ground, against time, during a step. Continuous lines represent vertical components and broken lines represent horizontal components. These graphs illustrate how different ratios of Fourier coefficients (given below them) describe different patterns of force.

(represented by the shape of a force record) must be the same, for different mammals running with equal Froude numbers.

This pattern can be described by means of Fourier analysis, as explained by Alexander & Jayes (1980). The analysis gives a set of coefficients a_1, b_2, a_3, b_4, etc. describing each record of the vertical component of force exerted during each footfall, and another set a_1', b_2', etc. describing each record of the horizontal component. Prediction (iv) requires the ratios of the coefficients to be the same, for different mammals running with equal Froude numbers.

Figure 5 shows how the ratios of coefficients describe the shapes of force records. In record (i), a_1 is the only non-zero coefficient for the vertical component and b_2' is the only non-zero coefficient for the horizonal component. The graphs of both components are segments of sine waves. In record (ii), the graph of the vertical component has been given a two-humped shape by giving a_3 a negative value. (A positive value would have made the graph bell-shaped.) Also, the amplitude of the horizontal component has been halved by halving b_2'. In record (iii) the values of a_1, a_3 and b_2' remain as in (ii), but b_2 has been given a positive value, making the graph of the vertical component asymmetrical and a_1' has been given a positive value, making the positive and negative impulses unequal. Negative values of b_2 and a_1' would have distorted the graphs in the opposite direction. Further explanation of the meanings of the coefficients is given by Alexander & Jayes (1980).

We have calculated the first few Fourier coefficients for suitable force records, using either the five-point method described by Alexander & Jayes (1980) or an equivalent method using more points. Some records were unsuitable because several feet were on the force platform simultaneously, and the forces exerted by them could not be determined separately (Jayes & Alexander, 1978, showed how vertical components of force can be determined separately for two feet simultaneously on a force platform, but we cannot do the same for longitudinal components).

Scrutiny of the data showed differences between walking and running, but no other systematic relationships between ratios of Fourier coefficients and Froude number. The ratios are therefore presented in Table III as means for walking (identified by the phase relationships of the feet) and for faster gaits. The ratio $-a_3/a_1$ is generally negative for walking but close

TABLE III

Ratios of Fourier coefficients for force records of mammals. Mean values are given $\pm$ one standard deviation

		a_3/a_1	b_2/a_1	b'_2/a_1
Walking				
Dog	fore	-0.18 ± 0.05	0.08 ± 0.16	0.14 ± 0.02
	hind	-0.39 ± 0.03	-0.22 ± 0.06	0.14 ± 0.00
Sheep	fore	-0.07 ± 0.04	0.14 ± 0.02	0.13 ± 0.01
	hind	-0.20 ± 0.02	-0.15 ± 0.12	—
Horse*	fore	-0.10	-0.03	0.09
Coypu	fore	-0.11 ± 0.03	-0.05 ± 0.06	0.08 ± 0.03
	hind	-0.14 ± 0.03	-0.07 ± 0.06	0.08 ± 0.02
Faster gaits				
Dog	fore	0.14 ± 0.05	-0.05 ± 0.08	0.13 ± 0.04
	hind	0.11 ± 0.05	-0.16 ± 0.11	0.12 ± 0.04
Sheep	fore	0.03 ± 0.04	0.14 ± 0.14	0.11 ± 0.01
	hind	-0.01 ± 0.03	-0.22 ± 0.05	0.09 ± 0.01
Horse*	fore	0.09	-0.18	0.07

*Data from Schryver, Bartel, Langrana & Lowe (1978).

The ratios for dogs walking and the ratio b_2'/a_1 for sheep walking are means from only two or three force records each. All other ratios are based on four to 12 records. One record of sheep, showing a gait intermediate between walking and trotting, was discarded.

to zero or positive for faster gaits. This was previously observed by Alexander & Jayes (1978). Their parameter q is $-a_3/a_1$). The ratio b_2/a_1 is rather variable between species and in some cases within species. The ratio b_2'/a_1 is close to 0·1 for all species and gaits. The ratios of Fourier coefficients seem not to be identical, for different mammals travelling with the same Froude number, but show a fair degree of similarity between the species included in the Table.

Prediction (v): power outputs

Let P be the power output of a particular muscle or group of muscles, at a particular stage of the stride. Let mg be body weight and let u be running speed. Prediction (v) requires different mammals running with equal Froude numbers to have equal values of the dimensionless quantity P/mgu.

Heglund, Cavagna & Taylor (1982) examined the fluctuations of potential and external kinetic energy of various mammals (External kinetic energy is energy associated with movement of the centre of mass). They summed all positive increments of the total of these energies over a series of strides and calculated a mean positive power $\bar{P}$. (They considered positive increments only because positive and negative increments cancel out over a complete stride.) The prediction requires $\bar{P}/mgu$ to be equal, for different mammals running at the same Froude number. Heglund and his colleagues found that $\bar{P}/mgu$ tended to be fairly close to 0·07 for all the animals they investigated, at all speeds. (Note that the intercept of

their general equation is small.) The prediction did not require $\bar{P}/mgu$ to be independent of speed, but merely to have equal values for different mammals at the same Froude number. The finding does, however, satisfy the prediction. The animals investigated included quadrupeds ranging from 0·1 kg chipmunks (*Tamias*) to 70 kg sheep, and also various bipedal mammals and birds.

Fedak, Heglund & Taylor (1982) measured the fluctuations of internal kinetic energy of mammals and birds. (Internal kinetic energy is the energy associated with movements of parts of the body relative to the centre of mass.) The calculated a quantity $\dot{E}'_{EK,\ tot}$ which they regarded as their best estimate of the mean positive power required to accelerate body segments relative to the centre of mass. The prediction requires $\dot{E}'_{KE,\ tot}/mgu$ to have the same value for all quadrupedal mammals at any particular Froude number. We have used the equations given by Fedak *et al.* (1982, Table 3) to calculate this quantity for a Froude number u^2/gh of 2, using "height at hip" given in their Table 1 as the characteristic length h. The values thus obtained are 0·12 for a 0·1 kg chipmunk, 0·07 for a 5 kg dog and 0·06 for a 100 kg horse.

It would be interesting to have data for more species, in order to discover whether the difference between the high value for the chipmunk and the relatively low values for dog and horse is a consistent difference between non-cursorial and cursorial mammals.

Comparisons with bipeds

A biped cannot move in dynamically similar fashion to a whole quadruped, though its legs might conceivably move in dynamically similar fashion to the hind legs of a quadruped. This subsection looks for resemblances between bipedal and quadrupedal techniques of locomotion.

Men break into a run and kangaroos and crows change from walking to hopping at Froude numbers around 0·6, about the same as the Froude numbers at which quadrupedal mammals change from walking to a faster symmetrical gait (Alexander, 1977*b*; Hayes & Alexander, 1983). Note, however, that hopping is an asymmetrical gait, like galloping.

Men and kangaroos use relative stride lengths similar to, or a little longer than, those used by cursorial quadrupeds at the same Froude number (Alexander, 1977*b*). Smaller bipedal mammals and birds seem to use longer relative stride lengths, as might be expected on account of the more bent attitude of their legs, rather like non-cursorial quadrupeds (Hayes & Alexander, 1983). Bipeds generally seem to use about the same duty factors as quadrupeds at the same Froude number.

Force platform records of human walking and running have ratios of Fourier coefficients much like those observed for cursorial quadrupeds walking and running, except that the values of a_3/a_1 used in fast walking are more strongly negative than for quadrupeds (Alexander & Jayes, 1980). The force records of birds (*Meleagris* and *Rhea*) walking, made by Cavagna, Heglund & Taylor (1977) are difficult to interpret because they consist of overlapping records of several successive footfalls, but they do seem to show that a_3/a_1 was negative, as for walking quadrupeds. Their records of the same species running show just one maximum in each record of a footfall, indicating a near-zero or positive value of a_3/a_1. Force records of bipedal hopping by mammals also resemble records of quadrupeds trotting or galloping, in this respect (Alexander & Vernon, 1975; Cavagna *et al.*, 1977; Biewener, Alexander & Heglund, 1981).

Heglund, Cavagna *et al.* (1982) found that rates of performance of positive work were about the same multiple of (body weight) × (speed) for men, hopping mammals and birds, as for quadrupedal mammals. It can be calculated from the equations of Fedak *et al.* (1982) that $\dot{E}_{KE, tot}/mgu$ at a Froude number of 2 ranges from 0·04 to 0·06 for four species of birds with masses ranging from 40 g to 90 kg. Most of the values are a little lower than the values given above for dog and horse.

Thus, in many respects, the techniques of walking and running of bipedal mammals and birds are much as would be predicted from the techniques of quadrupedal mammals, by extending the dynamic similarity hypothesis to them.

Maximum speeds

Though mammals of different sizes apparently tend to move in dynamically similar fashion, when their Froude numbers are equal, the ranges of Froude numbers at which they are capable of moving are unlikely to be the same. Suppose first that speed is limited by the maximum power output available from unit mass of muscle. Animals moving in dynamically similar fashion have equal values of (power)/(body weight × speed), as shown in the Introduction. However, a larger animal needs a higher speed, to attain the same Froude number. Hence (power)/(weight) at any given Froude number should be greater for larger animals, and larger animals are unlikely to be able to attain maximum Froude numbers as high as similar small animals.

Now suppose that speed is limited by the stresses developed in muscles or in the skeleton. Compare geometrically similar animals of different sizes moving in dynamically similar fashion. Corresponding forces in their bodies are proportional to body weight and so to the cube of linear dimensions, but corresponding areas are proportional to the square of linear dimensions. Hence stresses are proportional to linear dimensions. Larger stresses will act in a large animal than in a smaller one, at any given Froude number. Therefore if maximum possible or acceptable stresses are identical for animals of different sizes, large animals cannot be expected to attain maximum Froude numbers as high as small ones.

Alexander, Langman & Jayes (1977) found that maximum Froude numbers are lower for larger ungulates, as these arguments suggest they should be. In contrast, the dogs whose gaits are recorded in Figs 1 to 4 attained higher maximum Froude numbers than could be elicited from the (much smaller) Ferrets, but this is a comparison between a cursorial and a non-cursorial mammal.

Conclusions

This survey has shown strengths and limitations of the dynamic similarity hypothesis. There seems to be a strong tendency for cursorial quadrupeds to move as nearly as possible in dynamically similar fashion, when they travel with equal Froude numbers. The hypothesis is capable of predicting many features of the walking and running techniques of one quadruped from those of another, even when the animals being compared are as diverse as dogs, camels and rhinoceros. Speeds of gait changes, stride lengths, duty factors, shapes of force records and rates of performance of work are all predicted fairly well. The hypothesis is less useful for comparison of cursorial with non-cursorial mammals but still has some value for that, and even for comparisons of quadrupeds with bipeds.

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