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Support polygons and symmetrical gaits in mammals

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The symmetrical gaits of quadrupedal mammals are often described in terms of two variables: duty factor (S = the stance period of one foot, as a percentage of the gait cycle) and diagonality (D = the percentage of the cycle period by which the left hind footfall precedes the left fore footfall). We show that support polygons are optimized during walking (i.e. the percentage of the locomotor cycle spent standing on only two feet is minimized) for: (1) the diagonal-sequence, diagonal-couplets walks characteristic of primates ($50 < D < 75$) when D = [hindlimb S]; (2) lateral-sequence, lateral-couplets walks ($0 < D < 25$) when D = [hindlimb S] − 50; (3) lateral-sequence, diagonal-couplets walks ($25 < D < 50$) when D = 100 − [forelimb S]. To determine whether animal behaviour is optimal in this sense, we examined 346 symmetrical gait cycles in 45 mammal species. Our empirical data show that mammalian locomotor behaviour approximates the theoretical optima. We suggest that diagonal-sequence walking may be adopted by primates as a means of ensuring that a grasping hindfoot is placed in a protracted position on a tested support at the moment when the contralateral forefoot strikes down on an untested support. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **136**, 401–420

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INTRODUCTION

Background and concepts

The scientific study of mammalian gaits dates back to the work of Goiffon and Vincent in the 18th century (Gambaryan, 1974). Early students of gait (Marey, 1873; Muybridge, 1887; De la Croix, 1936; Howell, 1944) were interested primarily in describing and discriminating the traditionally recognized gaits of horses, and secondarily in extending their descriptive taxonomies to include the gaits of other tetrapods. Later scientific analyses of the gaits of mammals have made important technical advances in the collection and analysis of data (Manter, 1938; Hildebrand, 1965, 1966, 1967, 1968, 1976, 1980, 1985; Prost, 1965, 1969, 1970; Jenkins, 1974; Alexander, 1977a, 1981; Rollinson & Martin, 1981; Alexander & Jayes, 1983; Vilensky, 1983, 1989; Vilensky & Patrick, 1984, 1985; Vilensky, Gankiewicz & Townsend, 1988; Demes, Jungers & Nieschalk, 1990; Fischer, 1994). What is still lacking, however, is a generally accepted theory that can account for the patterned differences between an animal's gaits at different speeds, explain the differences in gait patterns between different groups of mammals, and allow us to derive expectations about an animal's gaits from our knowledge of other aspects of its biology. Although some previous studies (e.g. Hildebrand, 1968, 1980) have addressed some of these issues, no overall theory of gaits has emerged from them. In what follows, we offer such a theory and test it with new empirical data.

Gait analysis was first placed on a quantitative basis in the 1960s, when two researchers – V. Sukhanov in the U.S.S.R., and M. Hildebrand in the U.S. – independently noted that the distinctive properties of any symmetrical gait could be expressed as an ordered pair of numbers (Sukhanov, 1963, 1967) or as a point on a bivariate plot (Hildebrand, 1965, 1966). Hildebrand (1965) described the two dimensions of his bivariate plot as (1) "the percent of the stride interval that each hind foot is on the ground" and (2) "the percent of the stride interval that the footfall of a forefoot lags behind the footfall of the hind foot on the same side of the body." We will call these variables *duty*

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factor and *diagonality*, respectively. (Unless otherwise specified, we adopt Hildebrand's [1965, 1966, 1976, 1980, 1985] terminology for gaits and their associated variables.)

The meaning of these terms can be grasped intuitively if we model a quadrupedal gait as though it were being executed by two bipeds linked in tandem (Alexander, 1977a) – say, by two people walking or running in a horse costume (Fig. 1A). To stay linked, both bipeds must move forward at the same speed. It is assumed that both bipeds also have the same *stride period* (Hildebrand's 'stride interval'). The stride period is the time that elapses between two successive impacts of the same foot. In a repetitive gait at constant speed, this time is the same for all four feet. It would be possible in principle for one biped to take several small strides while the other took a few long ones, but in practice no real quadrupeds behave like this.

A *gait cycle* is the sequence of fore- and hindlimb movements that occur during one stride period. In the two-biped model, a *symmetrical* quadrupedal gait (Howell, 1944) is one in which each biped's successive footfalls are evenly spaced in time – that is, in which the time interval from each biped's left footfall to its next right footfall equals one-half of its stride period. Such gaits are called symmetrical because the second half of each quadrupedal gait cycle repeats the first half with left and right sides reversed.

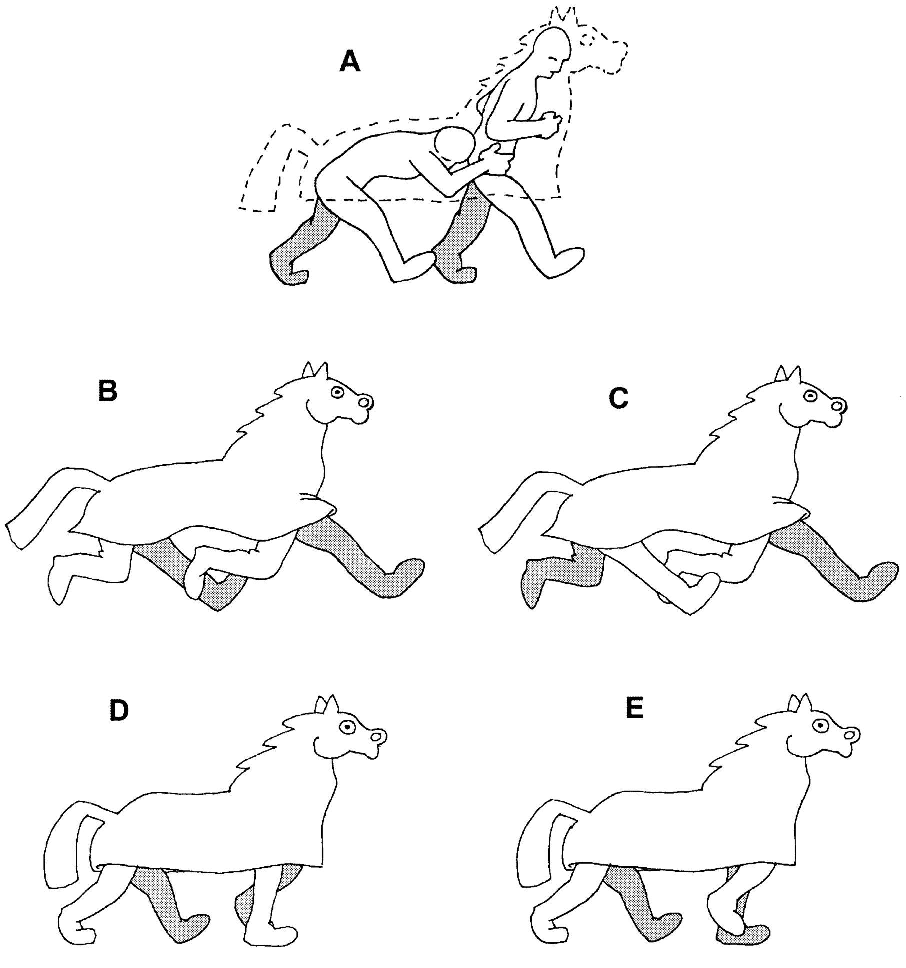

Figure 1. Quadrupedal gaits modelled as though being executed by two people in a horse costume. A, walking pace. The two bipeds are walking exactly in phase (diagonality = 0). B, running pace, shown during aerial phase (with all feet off the ground). The two bipeds are running in phase (diagonality = 0). C, running trot, shown during aerial phase. The two bipeds are running 180 ° out of phase; that is, the hind biped's cycle is running 50% of the cycle period ahead of the front biped's cycle (diagonality = 50). In a pace (A,B), both left feet (or both right feet) strike down together; in a trot (C), diagonally opposite feet strike down together. D, lateral-sequence (L-S) walk. The hind biped's cycle is running 25% of the cycle period ahead of the front biped's cycle (diagonality = 25%). E, diagonal-sequence (D-S) walk. The hind biped's cycle is running 75% of the cycle period ahead of the front biped's cycle (diagonality = 75%). In an L-S walk (D), the left hind footfall is followed by that of the left forefoot; in a D-S walk (E), it is followed by that of the right forefoot.

As an animal walks or runs along, each of its feet goes through a cycle in which the foot is placed on the ground (the *stance phase* of the cycle) and then lifted and swung forward (the *swing phase*). The *duty factor* (S) for any foot is the duration of its stance phase, expressed as a percentage of the stride period (that is, the percentage of time that the foot is on the ground during the gait cycle). Duty factor is the first of the two key variables defined by Hildebrand. Duty factor generally varies inversely with speed; as we walk faster, the stance phase of each foot's cycle gets shorter relative to the stride period (Prost, 1965, 1969, 1970; Grillner, 1975; Vilensky *et al*., 1988; Gatesy & Biewener, 1991; Demes *et al*., 1994).

When a biped's duty factor exceeds 50 ($S > 50$), each of its feet is on the ground most of the time. If its right and left footfalls are evenly spaced in time, the stance phases for its right and left feet must overlap by some percentage of the stride period. The duration, K, of each period of overlap equals $S - 50$. If $K > 0$, the biped will always have at least one foot on the ground. If a quadruped's gait is symmetrical and $K > 0$ for both the fore and hind pairs of feet, the animal must therefore have at least two feet on the ground at all times (i.e. at least one foot per biped in the two-biped model). Such quadrupedal gaits (symmetrical gaits in which $S > 50$ and therefore at least two feet are always on the ground) are called *walks*.

Using the two-biped model, *diagonality* (D) can be defined as the amount of time (as a percentage of the stride period) by which the left footfall of the front biped follows that of the rear biped. This number, which is the second of Hildebrand's two variables, measures how far out of step the two bipeds are. If the two bipeds are perfectly in step, so that their left feet strike down simultaneously, then $D = 0$ (Fig. 1A, B). (This can also be expressed by saying that $D = 100$). If the bipeds are exactly out of step, so that each biped's *left* footfalls are synchronized with the other's *right* footfalls, then $D = 50$ (Fig. 1C).

Hildebrand's bivariate plot (Fig. 2) graphs diagonality (D) against duty factor (S). Each point on this

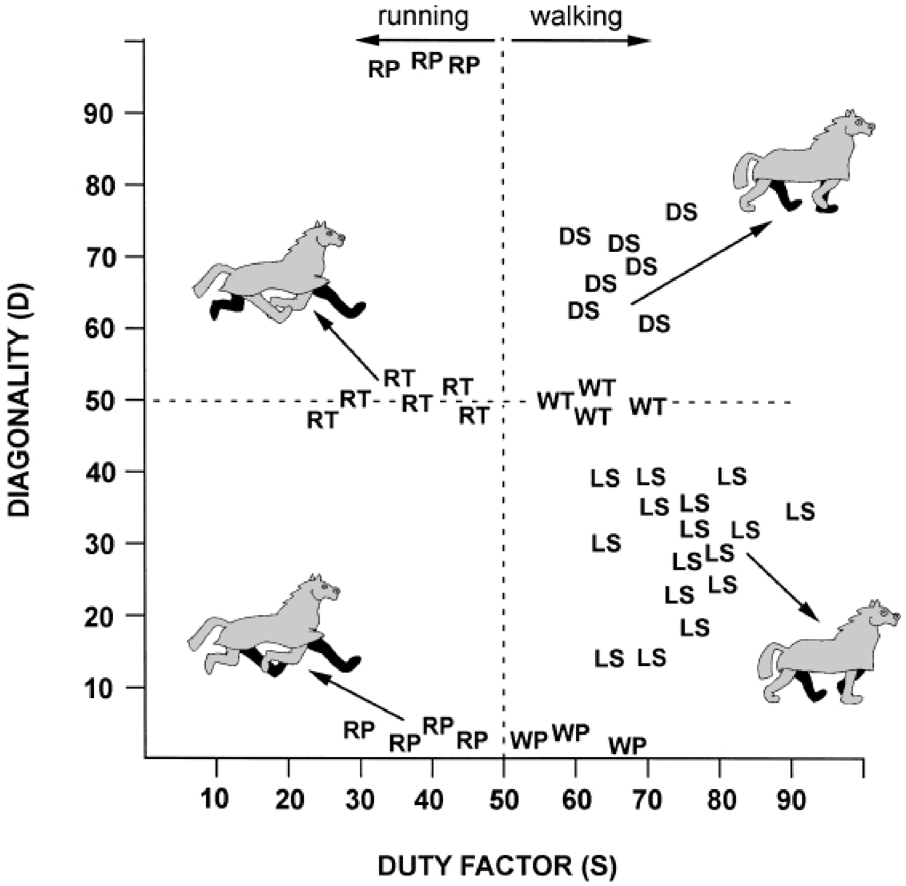

Figure 2. Plot of diagonality against (average) duty factor: the Hildebrand diagram. Positions of some mammalian gait types (two-letter codes) are plotted on the diagram. DS, diagonal-sequence walks; LS, lateral-sequence walks; RP, running pace; RT, running trot; WP, walking pace; WT, walking trot.

'Hildebrand diagram' represents a different gait. The S axis discriminates between running and walking gaits, while the D axis distinguishes various types of gaits within each category.

Four types of walking gait (S > 50) are commonly distinguished (Fig. 2). In a walking *pace*, the forelimbs are in phase with the hindlimbs (D = 0 or D = 100), so that both limbs on the same side touch down more or less simultaneously (Fig. 1A). In a walking *trot*, the fore- and hindlimb cycles are 180 ° out of phase (D = 50), so that diagonally opposite limbs touch down together. At these two values of diagonality, the animal spends a substantial percentage of the stride period (namely, twice the length of the swing phase) supported on only two feet.

Most tetrapods adopt intermediate values of diagonality (0 < D < 50, or 50 < D < 100) when they walk. Such values allow an animal to stand on three or four feet during most of the walk cycle. Other things being equal, this is an advantage to the animal, because standing on more than two feet increases the size of its *support polygon* (the minimum polygon bounding its support points), and thus makes its stance more stable as it moves forward When diagonality is between zero and 50% (0 < D < 50), the feet touch down in the order left hind, left fore, right hind, right fore (LH LF RH RF). This gait is called a *lateral-sequence* walk (Fig. 1D), because each hind footfall is followed by the ipsi*lateral* fore footfall. When diagonality is between 50 and 100% (50 < D < 100), the feet touch down in the order LH RF RH LF. This gait is called a *diagonal-sequence* walk (Fig. 1E), because each hind footfall is followed by the *diagonally* opposite fore footfall. These two gait types appear to have phylogenetic correlates, since most primates exhibit diagonal-sequence ('D-S') walks, whereas most other quadrupedal mammals use lateral-sequence ('L-S') walks instead (Hildebrand, 1967, 1985; Prost, 1965, 1969, 1970; Rollinson & Martin, 1981; Vilensky & Larson, 1989; Vilensky, 1989).

When a biped's duty factor is less than 50, the swing phases for its right and left feet must overlap in time. This implies that there must be an *aerial phase* of the cycle – a part of the stride period when both feet are off the ground. In our two-biped model, if the duty factors of all feet are less than 50, the animal will have an aerial phase for its front feet (the front biped) and another aerial phase for its hind feet (the rear biped). Quadrupedal gaits that meet this description are called *running* gaits. Most mammals have a symmetrical running gait in which the aerial periods for fore- and hindfeet roughly coincide, so that all four feet are off the ground at the same time. A running animal is in free flight during this part of the cycle. For a given duty factor, the period of free flight in running – the overlap between fore and hind aerial phases – is greatest when diagonality equals either zero or 50. When diagonality is approximately 0, so that the two feet on each side strike down together, the gait is called a *running pace* (Fig. 1B). When diagonality equals 50, so that diagonally opposite feet strike down together, the gait is a *running trot* (Fig. 1C).

At slow running speeds, with duty factors between 25 and 50, most mammals trot. Camels and a few others adopt a running pace instead (Muybridge, 1887; Hildebrand, 1968, 1980). At higher running speeds with lower duty factors (S < 25), almost all quadrupedal mammals shift to asymmetrical gaits like the gallop (Hildebrand, 1980). We will not be concerned here with asymmetrical gaits.

The symmetrical gaits of mammals are not randomly distributed on the Hildebrand diagram (Fig. 2). The central point on the diagram (S = 50, D = 50), which marks the transition from a walk to a running trot, is designated as 'B' in Figure 3. Hildebrand's (1976) data show that many nonprimate mammalian walks fall on his diagram roughly along a line drawn through point B downward and to the right with a slope approximating –1. Non-primate walks generally cluster near this line around the point at which D = 25. This point is designated as 'A' in Figure 3. Most of the remaining nonprimate walks lie near a different line sloping downward from point A to the left, with a slope approximating +1, ending in the walk-pace transition (S = 50, D = 0). From this point (point 'C' in Fig. 3), running paces lead off to the left (Fig. 2). The

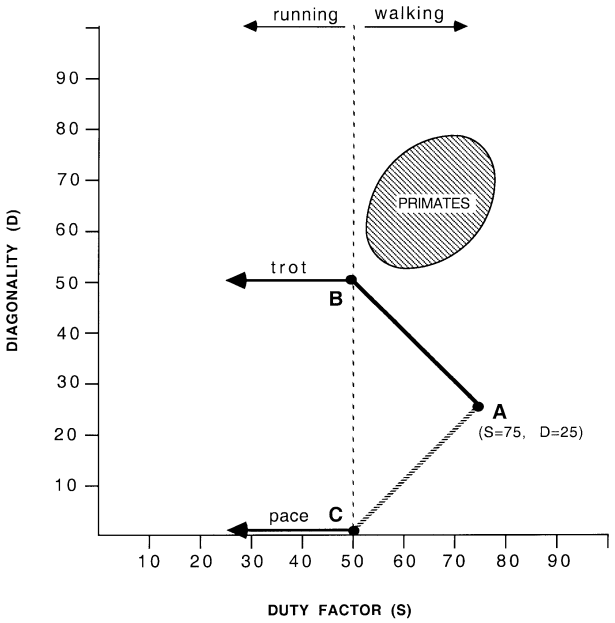

Figure 3. Distributions of mammalian gaits on the Hildebrand diagram.

D-S (diagonal-sequence) walks characteristic of primates fall in the upper right quadrant.

Although the parameters that distinguish one mammalian gait from another are all continuous variables, previous analyses have tended to regard different gaits as distinct entities – the walk, the trot, the pace, and so on – and to think of them in terms of separate clusters of data points rather than the continuous patterns of distribution seen in Hildebrand's data. Several factors have encouraged this habit of thought. Perhaps the most fundamental is a fact of animal behaviour: in accelerating and decelerating, mammals often (though not always) skip from one point on the Hildebrand diagram to another at some distance from the first, instead of executing a smooth transition running through all the intermediate points. Equestrians are trained to recognize and elicit these discontinuous gait transitions and to expect certain modal gaits from their mounts, adopting different postures, riding behaviour, and standards of judgement for each. The scientific study of mammalian locomotion has perpetuated the horseman's tradition of discrimination and description, and has accordingly not sought mathematical analyses couched in terms of continuous variables extending across gait modalities. A great deal of research has been directed toward discovering the factors that govern gait transitions (McMahon, 1975; Alexander, 1977b, 1981; Taylor, 1978, 1991; Hoyt & Taylor, 1981; Farley & Taylor, 1991). Mathematicians have posited discrete neural algorithms for different gait modalities to account for their supposed discontinuities (Golubitsky *et al*., 1999; Buono & Golubitsky, 2001). In analysing gaits, variants of a particular gait type are often averaged across strides, trials, or individuals in an attempt to determine the true or average properties of that gait modality (Hildebrand, 1966; Vilensky & Patrick, 1984; Vilensky *et al*., 1988).

Gait transitions are a fact of mammalian behaviour. But there are no boundaries or discontinuities in the distribution of mammalian gaits on the Hildebrand diagram (Fig. 2); and everyone from Muybridge on down who has undertaken to study and analyse the locomotion of mammals has encountered unclassifiable 'marginal' or 'transitional' gaits: slow walking trots that might equally well qualify as D-S walks, atypical L-S walks barely distinguishable from a walking pace, and so on.

Hildebrand himself made use of the continuity of his variables chiefly to postulate evolutionary pathways leading from one sort of locomotor repertoire to another (Hildebrand, 1976). However, some of his analyses partition the continuous space of the Hildebrand diagram into a network of triangular compartments separating gaits distinguished by different patterns of support (on 2, 3, and 4 legs) over the course of the gait cycle. These analyses of Hildebrand's, and his observations on how support patterns change when forelimb duty factors differ from those of the hindlimb (Hildebrand, 1966, 1976), furnished insights leading us toward a more algebraic analysis of symmetrical mammalian gaits that helps to account for their patterned distribution on the Hildebrand diagram – and for some patterned deviations from Hildebrand's assumptions.

THE SUPPORT-POLYGON MODEL

The Hildebrand diagram assumes that duty factor is a single quantity for any symmetrical gait. This implies that the duty factor of the hindlimb (S_h) is the same as that of the forelimb (S_f). This is not always the case, and the differences between fore and hind duty factors can affect both footfall sequences and support patterns. As Hildebrand (1966, 1976) pointed out, a change in the S_h/S_f ratio can in principle transform an L-S gait into a D-S gait or vice versa. Although Hildebrand did not offer a detailed analysis of the effects that such changes have on support patterns, he noted that it would be possible "to recover from the gait graph the relative durations of the various combinations of supporting feet" (Hildebrand, 1976: 222). This is possible because the sequences of footfalls and support patterns throughout a symmetrical gait cycle can be deduced if we know forelimb duty factor, hindlimb duty factor, and diagonality.

This fact can be demonstrated with reference to Fig. 4, which presents a conventional diagrammatic representation of two gait cycles in which hindlimb duty factor (S_h) exceeds forelimb duty factor (S_f). In both of the diagrammed cycles, $S_f = 54$ and $S_h = 64$. However, the two cycles differ with respect to diagonality (D). When D = 26 (Fig. 4A), the gait is an L-S walk. The animal spends 40% of the stride period supported on two ipsilateral legs only (20% on the right legs and 20% on the left), 24% of the interval supported on two diagonally opposite legs only, and the remaining 36% of the cycle supported on three legs. When D is increased to 56 (Fig. 4B), the gait becomes a D-S walk. The periods of unilateral bipedal support disappear, diagonal bipedal support rises to 72% of the cycle, and the remaining 28% of the cycle comprises periods of support on three or four legs.

Such changes in the support pattern can affect an animal's stability. An animal becomes unstable, and will tend to fall over, if its line of gravity falls outside its support polygon. This is not always undesirable. A running quadruped has to be unstable, since it must have both hindlimbs and/or both forelimbs off the ground at some point in the gait cycle. Moreover, falling in a forward direction contributes to forward movement. An animal can initiate or continue such movement by lifting and dropping its feet in a

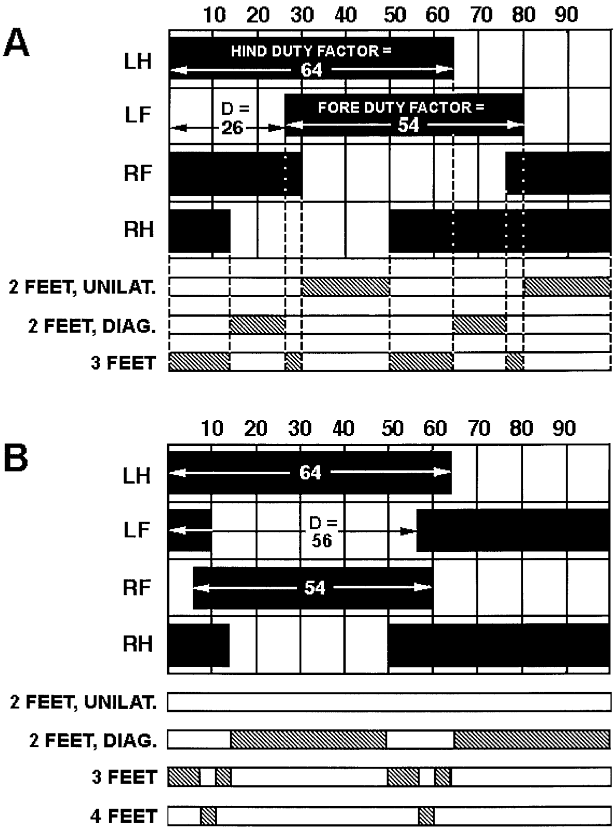

Figure 4. Support patterns for two gait cycles with similar duty factors but different diagonalities. In each diagram, the horizontal axis represents time, expressed as a percentage of stride period. Horizontal black bars represent stance phase (period of ground contact) for each foot (LH, left hind; LF, left fore; RF, right fore; RH, right hind). Duty factors are 64 for hind feet and 54 for fore feet. Since the gait is symmetrical, LH and RH footfalls differ by exactly 50% of the cycle, as do LF and RF footfalls, and left and right duty factors are the same. Each cycle starts with the LH footfall. Diagonality (percentage of cycle by which LF footfall trails LH footfall) equals 26 in cycle A and 56 in cycle B. Hatched bars below each diagram show periods of different support patterns (by 2 feet on the same side, 2 diagonally opposite feet, 3 feet, and 4 feet) during each cycle. The lengths and timing of these periods can be inferred from the timing of the liftoff and touchdown of each foot (vertical dashed lines), which can in turn be inferred from duty factors and diagonality.

sequence that keeps the line of gravity moving along near the front edge of a shifting support polygon, so that it moves forward in a continual but controlled forward fall. This description applies, for example, to human locomotion (Alexander, 1976, 1977a, b, 1992; Cavagna, Heglund & Taylor, 1977).

Stability is therefore not the only desideratum in positional behaviour. We do not subscribe to James Gray's contention that "four-legged animals, when moving slowly, move their legs in such a way that it is possible for the body to stop at any instant without falling over" (Gray, 1959: 76). As Vilensky & Larson (1989) note, a table is not an appropriate model for analysing quadrupedal locomotion. Still, other things being equal, it seems reasonable to expect that moving animals would deploy their limbs in such a way as to maximize their support polygons over the stride period. Doing so not only contributes to stability, especially at walking speeds, but also affords more options in making abrupt changes of speed or direction.

Because the percentage of the cycle that exhibits a particular support pattern can be inferred from S_h, S_f, and D (Fig. 4), we can calculate the value(s) of D that will optimize the support pattern for a given S_h and S_f. In a quadrupedal walking gait, there will be at least two legs on the ground at every point in the gait cycle. Sometimes both supporting legs will be on the same side (*unilateral bipedality*: RH + RF or LH + LF). At other times, the two supporting legs will be diagonally opposite (*diagonal bipedality*: RH + LF or LH + RF). The relative durations of the periods of unilateral and diagonal bipedality depend on diagonality and on the duty factors of the fore- and hindlimbs (Fig. 4). Figure 5 shows how periods of unilateral bipedality (B_u) and of diagonal bipedality (B_d) vary with diagonality (D) for the simplest case, in which hind and fore duty factors are identical ($S_h = S_f$). The curves for B_u and B_d have the same shape and dimensions, but with a 180 ° phase shift. Unilateral bipedality peaks when diagonality equals zero (the walking pace), whereas diagonal bipedality is maximal when diagonality equals 50 (the walking trot).

Unilateral and diagonal bipedality therefore vary more or less inversely in walking gaits. But their sum is not constant. When $S_h = S_f$ (Fig. 5), each curve has a sharp peak but a flat trough, so that the percentage of the cycle spent on each type of bipedality falls to zero over a range of D-values, in the centre of which the other type of bipedality reaches its peak (highest percentage of the cycle). Total bipedality ($B_u + B_d$) is maximal at each peak and minimal between the two flat troughs. There are thus two ranges of D-values over which total bipedality is minimized. We assume that diagonality values in these ranges are optimal, because they maximize the average area of the polygon of support over the extent of the gait cycle.

The extent, amplitude, and position of these two zones of minimal bipedality can be expressed algebraically as functions of K (the duration of overlap between right and left stance phases for a given pair of limbs). Depending on the value of D (diagonality), total bipedality ($B_u + B_d$) can assume values between a maximum of $2(50 - K)$ and a minimum of $2(50 - 2K)$. It reaches a minimum in two zones of minimal bipedality: (1) at D-values between K and $50 - K$, and (2)

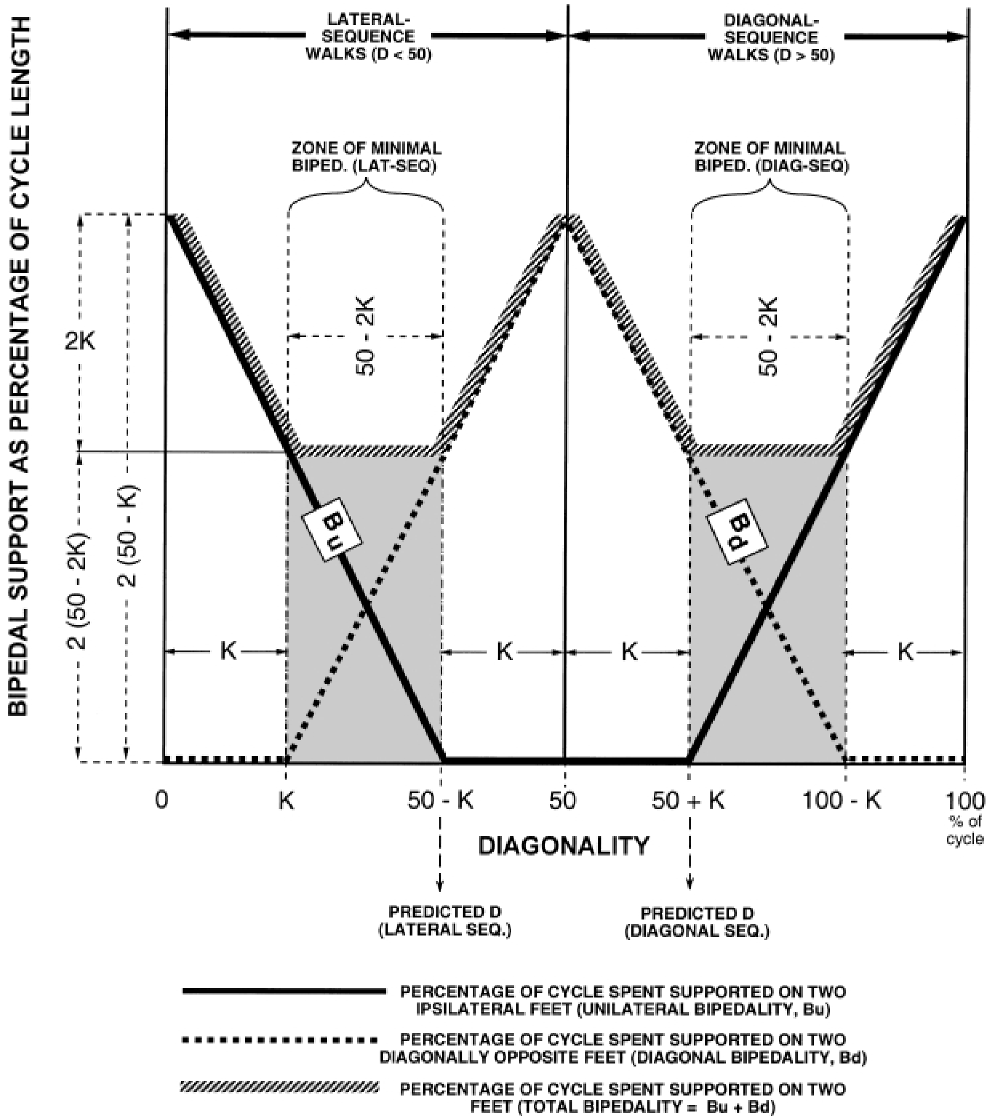

Figure 5. Curves of unilateral bipedality (B_u) and diagonal bipedality (B_d) against diagonality (D) for the case where the duty factors of the hind- and forelimbs are equal ($S_h = S_f = S$). $K = S - 50$. All variables (B_u, B_d, D, K, S) represent durations expressed as percentages of the stride period (time between two successive falls of the same foot).

at D-values between 50 + K and 100 – K. The first of these zones corresponds to L-S walks (D < 50); the second, to D-S walks (D > 50). Selecting any value of D within either of these zones will yield a walk in which bipedal support periods have a minimal value, thereby optimizing support polygons over the stride period as a whole.

However, within each zone where total bipedality assumes a minimal value, that minimal value is differently apportioned between the two bipedal support patterns at different values of D. B_u has a value of zero at one end of each zone; B_d equals zero at the other end. This difference is important. Although any bipedal stance is unstable, some are more unstable than others. A mammal's centre of mass lies near the body's midsagittal plane, and so a quadruped is likely to be more nearly balanced over a line passing through diagonally opposite feet than over one passing through the two feet on one side. Although the breadth and length of an animal's stance and the shifting position of its centre of mass will affect its balance, it seems reasonable to assume that most quadrupeds are further out of equilibrium during unilateral bipedality than during diagonal bipedality in most locomotor postures (Fig. 6). If so, then a quadruped will do best to maximize B_d while minimizing total bipedalism. This means selecting a diagonality value ('predicted D' in Fig. 5) as close as possible to D = 50 within either minimal-bipedality zone. An animal moving with an L-S walk can achieve this by making D equal (50 – K);

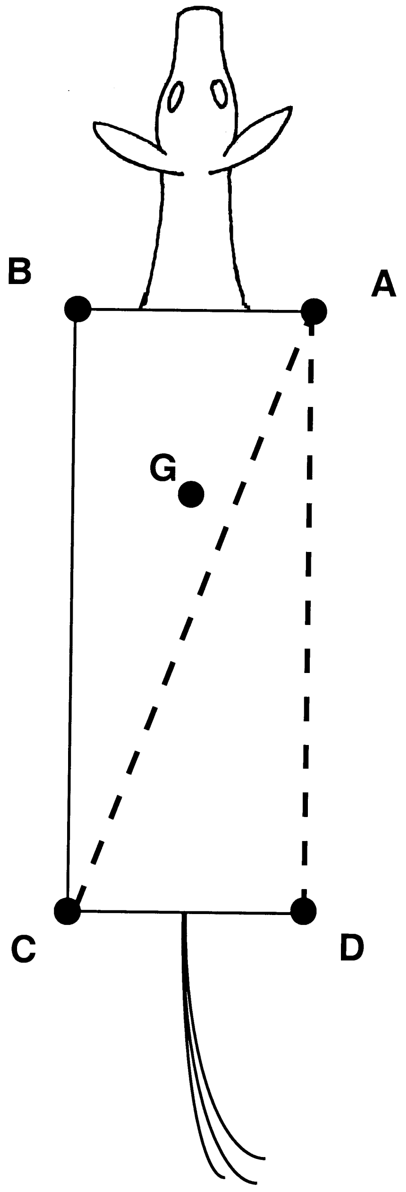

Figure 6. Diagrammatic quadruped seen from above. Points A-D represent the animal's four feet; point G represents the vertical drawn through its centre of gravity. The animal will be more nearly balanced when standing on two diagonally opposite feet (A, C) than when standing on two ipsilateral feet (A, D), as long as G is closer to line AC than to line AD – which will be the case in most situations.

an animal moving with a D-S walk can do it by making D equal (50 + K).

When hind and fore duty factors are unequal ($S_h \neq S_f$), the picture becomes more complicated (Fig. 7). Periods of maximum B_u and B_d now extend across a range of D-values; that is, the zigzags have flat plateaus as well as flat troughs. The values of D at which the B_u and B_d curves inflect now depend on both S_h and S_f. The inflection points are expressed in Figure 7 in terms of the separate values of the overlap term K for the fore- and hindlimbs ($K_h = S_h - 50$: $K_f = S_f - 50$).

The key fact to be drawn from Figure 7 is that the optimum value of D for L-S walks ($D = 50 - K_f$) depends entirely on the forelimb duty factor, whereas that for D-S walks ($D = 50 + K_h$) depends entirely on the hindlimb duty factor. The pattern seen when fore and hind duty factors are equal (Fig. 5) represents a special case of the general relationship (Fig. 7).

We base our predictions concerning symmetrical gaits on the following two assumptions:

A1. Animals will select a value of diagonality (D) that minimizes the percentage of the gait cycle spent on minimal polygons of support.

For walking gaits, this entails minimizing bipedality (since two is the minimum number of feet that can be on the ground at any time in a symmetrical gait where $S_h > 50 < S_f$). For running gaits, it entails *maximizing* bipedality (since two is the *maximum* number of feet that can be on the ground at any time in a symmetrical gait where $S_h < 50 > S_f$).

A2. If an animal can substitute diagonal for unilateral bipedality without altering the overall percentage of bipedality, it will do so. That is, diagonal bipedal support is preferable to unilateral bipedal support, all other things being equal (Fig. 6).

Taken together with the support-polygon model sketched above, these assumptions yield the following predictions:

P1. In L-S walks, D will equal $50 - K_f$. Since $K_f = S_f - 50$, this implies that *diagonality in L-S walks should equal 100 minus the forelimb duty factor* (Fig. 8A). D will therefore vary inversely with S_f, with a slope of -1 and an intercept of 100 on the S_f axis.

P2. In D-S walks, D will equal $50 + K_h$. Since $K_h = S_h - 50$, this implies that *diagonality in D-S walks should equal the hindlimb duty factor* (Fig. 8B). D will therefore vary directly with S_h, with a slope of +1 and an intercept of zero on the S_h axis.

P3. In running gaits (with an aerial phase), animals will choose values of D approximating either zero or 50 (to maximize bipedality).

P4. The running trot (D = 50) will be chosen in preference to the running pace (D = 0), in order to minimize B_u in running.

To determine how and why actual behaviour differs from these theoretical predictions, we undertook an empirical study of duty factors and diagonality in the symmetrical gaits of mammals.

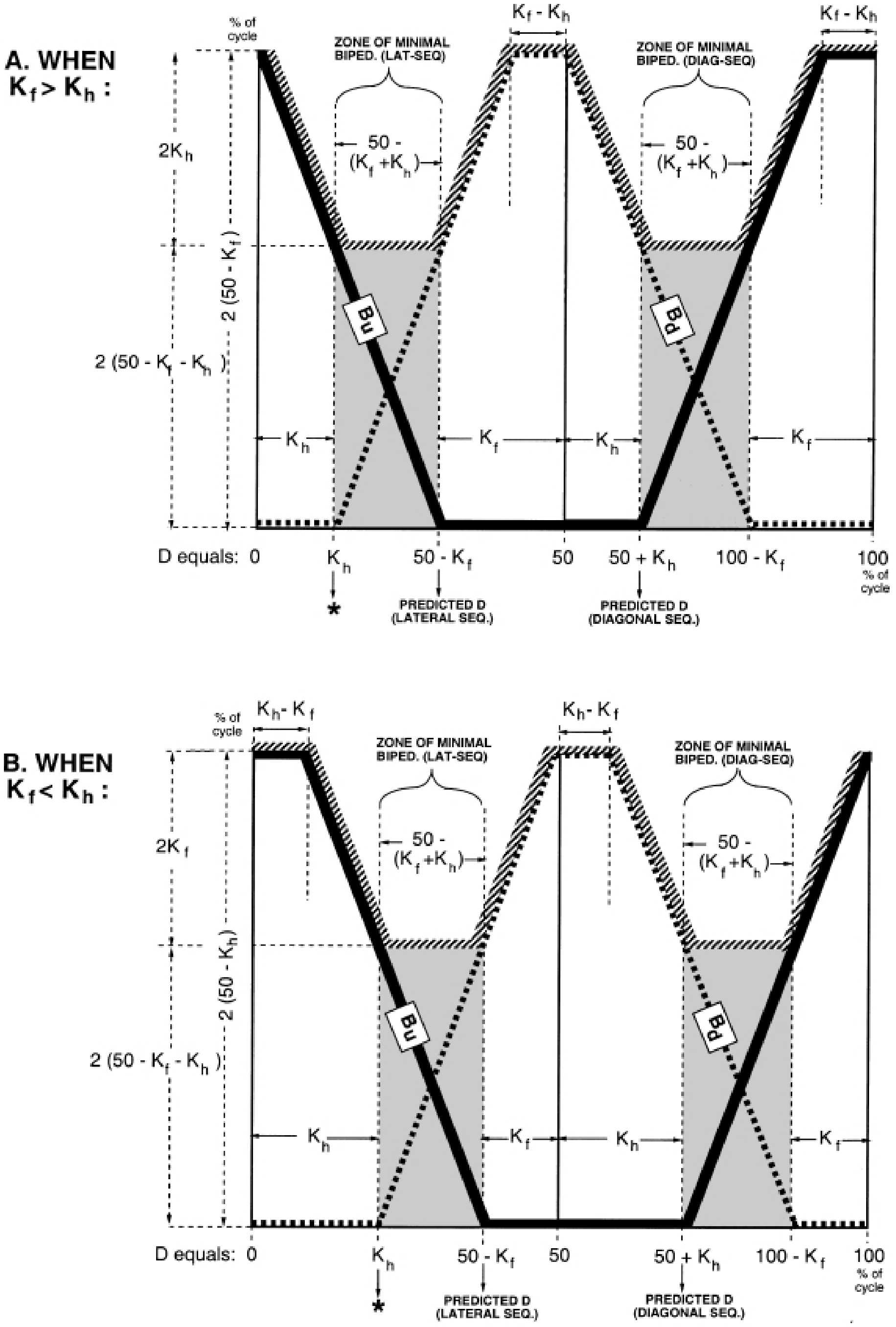

Figure 7. Curves of unilateral bipedality (B_u) and diagonal bipedality (B_d) against diagonality (D) for the general case where the duty factors of the hind- and forelimbs (S_h, S_f) are unequal. $K_h = S_h - 50$; $K_f = S_f - 50$. All variables represent durations expressed as percentages of the stride period (time between two successive falls of the same foot). See text for explanation.

MATERIAL AND METHODS

Species and individuals included in the study are listed in Table 1. All subjects were captive animals housed in zoos or other approved animal facilities, or domestic animals living on farms. Subjects were videotaped at 60 fields per second using industrial-quality Panasonic camcorders or cameras. The two horses (*Equus caballus*), the llama (*Lama glama*), and one of the domestic dogs (*Canis familiaris*) were

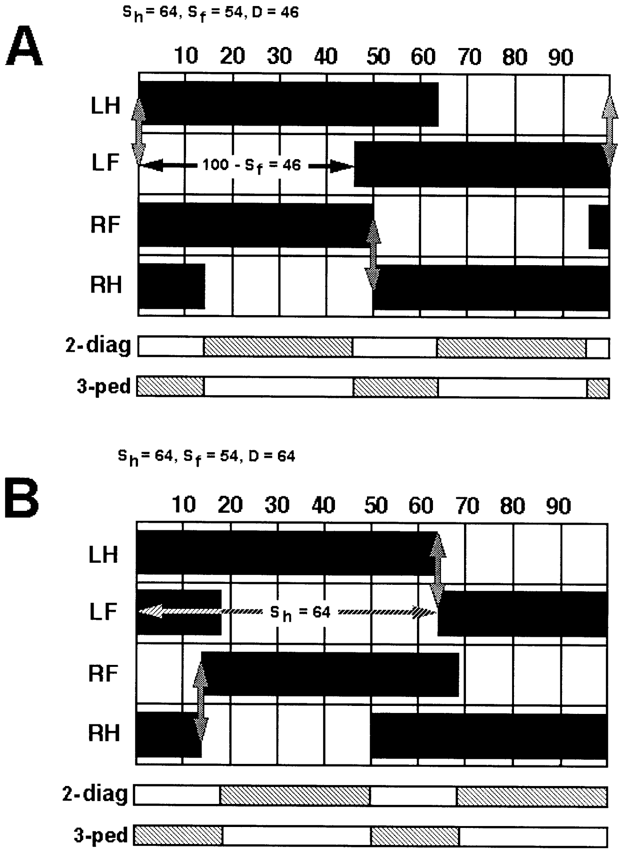

Figure 8. Values of diagonality predicted from the support-polygon model. Duty factors and graphic conventions as in Figure 4. To minimize overall bipedality while maximizing diagonal bipedality ('2-diag'), a quadruped walking with a lateral-sequence gait (A) should adopt a D-value equal to 100 minus the forelimb duty factor ($100 - S_f$: horizontal arrows). A quadruped using a diagonal-sequence walk (B) should adopt a D-value equal to the hindlimb duty factor (S_h: horizontal arrows). In A, this entails that forefoot liftoffs and ipsilateral hind footfalls should be simultaneous; in B, fore footfalls and ipsilateral hindfoot liftoffs should be simultaneous (vertical arrows). In both A and B, diagonal bipedality ('2-diag') comprises the minimal percentage (64%) of the stride period possible for these duty factors. The animal is supported on 3 legs ('3-ped') for the remaining 36% of the stride period.

'lunged' (run in circles on a long hand-held tether) or led (along a linear course) in front of the camera at various speeds on a line attached to a collar or a halter. The lead line was slack at all speeds. All other subjects were videotaped walking or running under their own control. Most of the subjects, including certain primates (*Pan*, *Papio*, *Erythrocebus*, six of the cycles for *Lemur catta*, six for *Eulemur fulvus*, and 10 for *Callithrix jacchus*), were videotaped moving on flat ground or other horizontal surfaces. *Caluromys*, *Arctictis*, and the remaining primates were videotaped moving on raised horizontal poles or bars made of wood or PVC (with a roughened surface) from 1 to 10 cm in diameter. From 10 to 20 steps were recorded for most of the subjects. To assess the intraindividual variability of gaits, larger samples were collected for one dog subject (52 cycles, of which 41 were symmetrical) and one horse subject (24 cycles, all symmetrical).

Video images of gait cycles were imported into a Motus 2000 gait analysis system (Peak Performance Technologies Co., Englewood, Colorado, U.S.A.). In all cycles chosen for analysis, the animal was travelling at an apparently steady speed and at least one complete stride occurred both before and after the stride that was analysed. Each chosen cycle was cropped beginning and ending at touchdown for the same hind foot. The frame number was then noted for the touchdown and liftoff of each foot during the cycle. The nine frame numbers thus identified were entered in a spreadsheet to calculate the duration of the cycle (stride period), duration of the stance and swing phases for each foot, and diagonality. If the time from the first hind footfall to the next (contralateral) hind footfall was greater than 55% or less than 45% of the total stride period (±5% deviation from symmetry), the cycle was rejected as asymmetrical. Of the 416 cycles analysed, 70 were rejected for this reason. The remaining 346 cycles constitute our data set (Table 1).

RESULTS AND DISCUSSION

The model outlined above assumes that the duty factor of the forelimb (S_f) in symmetrical gaits may differ significantly from that of the hindlimb (S_h). Figure 9 presents a plot of our data displaying diagonality (D) vs. the *duty-factor index*, which we define as $100S_h/S_f$ – that is, average hindlimb duty factor over a given gait cycle expressed as a percentage of average forelimb duty factor. The 100% line, along which the two are equal ($S_f = S_h$), represents the plane of the Hildebrand diagram, seen edge-on. Our data deviate substantially from the Hildebrand plane. The average deviation has an absolute value of 7.2%, and 55% of the data are separated from the plane by five or more percentage points. Most of the L-S walks ($D < 30$) closely approximate the Hildebrand plane. More diagonal gaits ($D > 40$), including both trots (nonprimates) and D-S walks (primates other than *Callithrix*), deviate more markedly, lying both below and above the Hildebrand plane.

In an earlier study (Lemelin, Schmitt & Cartmill, 1999), we conjectured that the D-S walking gaits characteristic of primates might be explained as a result of an increase in the duration of the stance phase of the grasping hind foot relative to that of the generally less prehensile forefoot. Our present data show that S_h/S_f

Table 1. Materials used in this study

Order & Family	Genus & Species	Individuals	Cycles
POLYPROTODONTIA			
Didelphidae	*Caluromys philander*	2	9
	Monodelphis domestica	1	9
PRIMATES			
Loridae	*Nycticebus coucang*	1	6
	Perodicticus potto	1	2
	Loris tardigradus	1	6
Galagonidae	*Otolemur garnetti*	1	10
Cheirogaleidae	*Microcebus murinus*	1	6
	Mirza coquereli	1	8
Lemuridae	*Lemur catta*	1	10
	Eulemur fulvus	1	7
	Eulemur mongoz	1	9
	Hapalemur griseus	1	8
	Varecia variegata	1	6
Daubentoniidae	*Daubentonia madagascariensis*	1	6
Callitrichidae	*Callithrix jacchus*	2	17
Cebidae	*Cebus capucinus*	1	8
Atelidae	*Ateles geoffroyi*	1	9
Cercopithecidae	*Erythrocebus patas*	1	10
	Papio anubis	1	7
	Macaca fascicularis	1	10
Hominidae	*Pan troglodytes*	1	5
CARNIVORA			
Ursidae	*Ursus thibetanus*	1	5
Canidae	*Canis familiaris*	2	49
Procyonidae	*Procyon lotor*	1	2
	Potos flavus	1	1
Mustelidae	*Galictis vittata*	1	7
Felidae	*Felis catus*	1	8
	Felis serval	1	3
	Felis concolor	1	2
	Felis caracal	1	2
	Neofelis nebulosa	1	3
	Panthera tigris	1	8
Viverridae	*Suricata suricatta*	1	1
	Arctictis binturong	1	5
RODENTIA			
Muridae	*Rattus norvegicus*	1	2
PROBOSCIDEA			
Elephantidae	*Loxodonta africana*	1	2
PERISSODACTYLA			
Equidae	*Equus caballus*	2	35
Rhinocerotidae	*Ceratotherium simum*	1	4
ARTIODACTYLA			
Giraffidae	*Giraffa camelopardalis*	2	7
Bovidae	*Antilope cervicapra*	1	2
	Capra hircus	1	1
	Ovis aries	1	3
Camelidae	*Camelus dromedarius*	2	13
	Lama glama	1	10
Cervidae	*Muntiacus muntjak*	1	3
TOTALS	45 spp	51	346

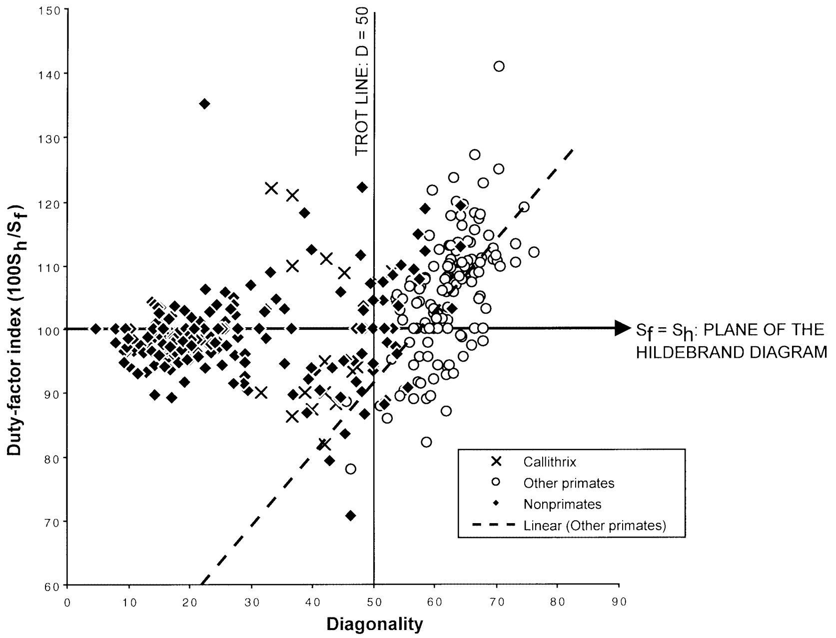

Figure 9. Diagonality (D) plotted against the duty-factor index. The 100% line, along which $S_f = S_h$, represents the plane of the Hildebrand diagram, here seen edge-on. The diagonal black line is the bivariate least-squares regression line for all primate data (circles), excluding *Callithrix* (crosses). Black diamonds represent nonprimate data.

ratios are significantly correlated with diagonality in walking gaits of noncallitrichid primates ($P < 0.001$). The high S_h/S_f ratios seen in many primate walks can thus be regarded as causing an exaggerated diagonality (Fig. 9). But the details of this correlation show that primate D-S walks are not (as we first thought) simply the result of high S_h/S_f ratios. If they were, then primate walks in which the duty-factor ratio is 100 ($S_h = S_f$) should be walking trots (D = 50), and the least-squares regression line for the primate data in Figure 9 should intersect the plane of the Hildebrand diagram at the trot line. In fact, all our primate data for which $S_h = S_f$ have D-values greater than 50 (Fig. 9), and the primate regression line crosses the Hildebrand plane at D = 57.5. Prolonged hindlimb contact evidently enhances the diagonality of primate walks, but it is not solely responsible for their diagonal sequence.

Of the 346 cycles in our data set, only 17 qualified as running gaits in the sense of having an aerial phase for both the fore- and hindlimbs. On the Hildebrand diagram (Fig. 10), these 17 cycles are clustered around the trot line (D = 50) on the vertical axis, as predicted (P3 and P4, above). Twenty-six other cycles exhibited an aerial phase for one pair of limbs but not the other. In 5 of these 26 cycles (1 *Canis*, 2 *Monodelphis*, 1 *Mirza*, and 1 *Otolemur*), there was an aerial phase for the forelimb but not for the hindlimb; in the other 21 (7 *Canis*, 3 *Galictis*, 1 *Monodelphis*, 2 *Equus*, 7 *Callithrix*, and 1 *Microcebus*), there was an aerial phase for the hindlimb but not for the forelimb. These 26 cycles can be described in terms of the two-biped model as gaits in which one biped is walking very fast and the other is running very slowly. We will call such gaits *half-runs*. Twenty-one of the 26 half-runs in our sample are near-trots, with the diagonally opposite limbs striking down close together in time (40 < D > 60). Eighteen of the 26 half-runs have average duty factors of 50 or more, and are scored hereafter as walking gaits.

Including these 18 half-runs, our data set contains 321 walking gait cycles (with average duty factors of 50 or more). These data are plotted in Fig. 11 on a modified Hildebrand diagram, in which the horizontal axis represents, not the average duty factor or the hindlimb duty factor, but the *relevant* duty factor in the terms prescribed by our initial model – that is, S_h for D-S walks and S_f for L-S walks. Although the scatter of data points conforms roughly to our predictions, there are significant and systematic deviations. The D-S walks (almost all of which represent primates) are clustered around the predicted line ($D = S_h$). However, our data for L-S walks do not conform to the predictions of the support-pattern model. Almost all the L-S walks lie below the predicted line ($D = 100 - S_f$). The deviation is especially marked for duty factors between 60 and 70.

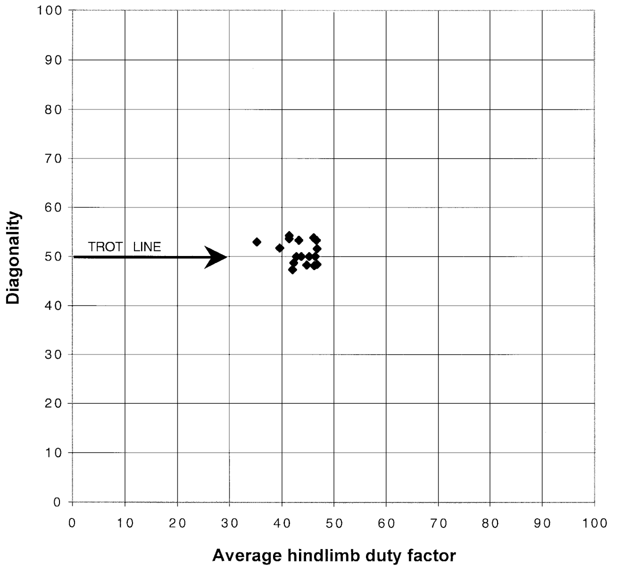

Figure 10. Running gaits ($S_h < 50 > S_f$) in our data, plotted on the Hildebrand diagram. The arrow ('trot line') indicates the diagonality predicted for running gaits ($D = 50$).

These deviations from predictions for L-S walks may represent a way of evading the potential problem of interference between fore- and hindlimbs in quadrupeds with long legs. Hildebrand (1968) analysed 207 symmetrical gaits of pedigreed domestic dogs moving at various speeds. His sample was divided into 19 'long-legged' breeds (e.g. German Shepherd, Great Pyrenees) and 6 'short-legged' breeds (e.g. Dachshund, Corgi). He found that short-legged dogs always trotted when running, whereas long-legged dogs tended to pace in running and frequently approached a walking pace in their faster walks. Hildebrand suggested that quadrupeds with long legs (relative to trunk width) can afford to pace, because they tend to roll less (around the fore-and-aft axis) when standing on two ipsilateral feet than does an an animal with shorter legs and a proportionately wider stance. He argued further that animals with long legs (relative to trunk *length*) should prefer to pace rather than trot, because pacing minimizes the risk of interference between the fore- and hindlimbs.

It is useful in this context to introduce the distinction (Hildebrand, 1965) between *lateral-couplets* (L-C)

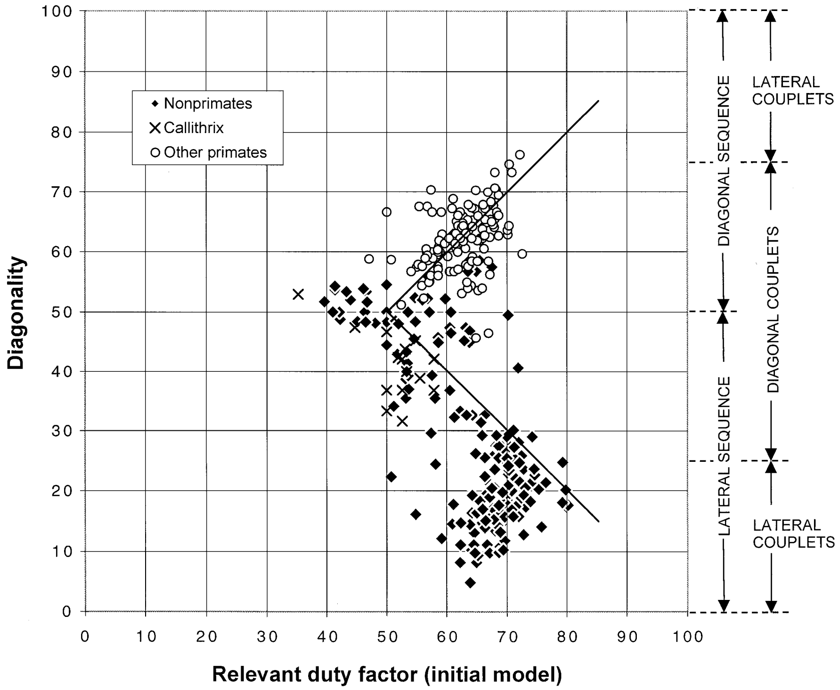

Figure 11. Modified Hildebrand diagram for the walking gaits (average duty factor ≥ 50) in our data set. The theoretically relevant duty factor in each case – S_h for diagonal-sequence walks, S_f for lateral-sequence walks – is plotted against diagonality. The diagonal lines show the distribution predicted by the support-polygon model as initially formulated.

gaits and *diagonal-couplets* (D-C) gaits. This distinction, like that between lateral sequences ($D < 50$) and diagonal sequences ($D > 50$), partitions the vertical or D axis of the Hildebrand diagram into two discrete ranges (Fig. 11). Our usage differs slightly from that of Hildebrand (1965), who represented the trot, pace, and L-S and D-S singlefoots on the original Hildebrand diagram as horizontal bands (about 12 units in width). We treat these modal gaits as ideal types conforming to specific integral values (50, 0, 25, and 75, respectively) of D, represented by horizontal lines on the Hildebrand diagram.

L-C gaits are those in which D is less than 25 or more than 75, so that the two ipsilateral feet touch down close together in time. In D-C gaits, the diagonally opposite feet touch down close together in time ($25 < D < 75$). (Gaits in which $D = 25$ or $D = 75$ are so-called single-foots, in which each footfall is separated by the same interval from the one preceding and from the one following.) L-C gaits approximate the pace; D-C gaits approximate the trot. D-C gaits minimize unilateral bipedality, but increase the risk of interference between fore and hind feet. L-C gaits minimize the chance of interference, albeit at the cost of increasing B_u. In the terms of the two-biped model: the hind biped can best avoid stepping on or kicking the fore biped's feet (Fig. 1C) by staying roughly in step with the fore biped – implying a lateral-couplets gait.

Hildebrand's (1968, 1976) data show that certain long-legged ungulates (camels, giraffes, gerenuks, pronghorns) and carnivorans (long-legged dog breeds, hyenas, and some felids and viverrids) not only pace at the run, but adopt L-C walking gaits as well. These L-C walks fall roughly along line AC in Figure 3, which is the line on the Hildebrand diagram connecting the L-S singlefoot point (point A: $S = 75$, $D = 25$) with the walk-pace transition point (point C: $S = 50$, $D = 0$). Gaits that lie on this line minimize overall bipedality, but *maximize* unilateral bipedality (B_u). They represent the minimal-diagonality edge of the zone of minimal bipedality for L-S gaits (asterisks, Fig. 7), described by the equation $D = K_h = (S_h - 50)$.

Since some mammals adopt lateral-couplets gaits, our initial assumption that B_u is always minimized (A2, above) is false. When modified to take the existence of L-C gaits into account, the support-polygon model yields the following revised predictions:

P5. In D-S D-C walks ($50 < D < 75$), D will equal $50 + K_h$. Since $K_h = S_h - 50$, this implies that diagonality in D-S D-C walks should equal the hindlimb duty factor (Fig. 8B). D will therefore vary directly with S_h, with a slope of +1 and an intercept of zero on the S_h axis.

P6. In L-S D-C walks ($25 < D < 50$), D will equal $50 - K_f$. Since $K_f = S_f - 50$, this implies that diagonality in L-S D-C walks should equal 100 minus the forelimb duty factor (Fig. 8A). D will therefore vary inversely with S_f, with a slope of -1 and an intercept of 100 on the S_f axis.

P7. Animals with walking gaits that obey (P5) or (P6) will adopt the trot at slow running speeds. Conversely, animals that run at the trot will obey (P5) or (P6).

P8. In L-S L-C walks ($0 < D < 25$), D will equal K_h. Since $K_h = S_h - 50$, this implies that diagonality in L-S L-C walks should equal the hindlimb duty factor minus 50. D will therefore vary directly with S_h, with a slope of +1 and an intercept of 50 on the S_h axis.

P9. Animals with walking gaits that obey (P8) will adopt the pace at slow running speeds. Conversely, animals that run at the pace will obey (P8).

These predictions constitute the *revised support-polygon model*. We can sum them up by saying that mammals should obey one of three rules:

RULE 1 (*Monkey rule*, D-S D-C): $D = S_h$ at the walk, $D = 50$ at the run.

RULE 2 (*Horse rule*, L-S D-C): $D = 100 - S_f$ at the walk, $D = 50$ at the run.

RULE 3 (*Camel rule*, L-S L-C): $D = S_h - 50$ at the walk, $D = 0$ at the run.

A fourth rule is implicit in the revised support-polygon model – namely, that D-S L-C walks should conform to the equation $D = 50 - S_f$ (modulo 100). However, no D-S L-C gaits have ever been reported.

Lines representing these equations are superimposed on our data for walking gaits (average $S > 50$) in Figure 12 on a modified Hildebrand diagram, in which the horizontal axis represents the relevant duty factor in terms of the revised model – that is, S_f for L-S D-C walks and S_h for other walking gaits.

Some animals are apparently able to switch from one rule to another. Horses can be trained to pace at the run, and some breeds do so more or less naturally. (The walking gaits of these breeds have not been systematically studied.) Hildebrand (1968) observed that some long-legged dog breeds may run at either the pace or the trot. To determine whether this was a matter of inter- or intraindividual variation, we obtained a large sample of gaits ($N = 41$) of different speeds from a single individual of one of the dog breeds identified by Hildebrand as 'long-legged' (Great Pyrenees). These data are shown in Figure 13, plotted against Hildebrand's (1968) data on a standard Hildebrand diagram on which we have superimposed the predicted regression lines for Rules 2 and 3 (substituting S_h for S_f in Rule 2 to accommodate Hildebrand's data). Both our data and Hildebrand's cluster around the

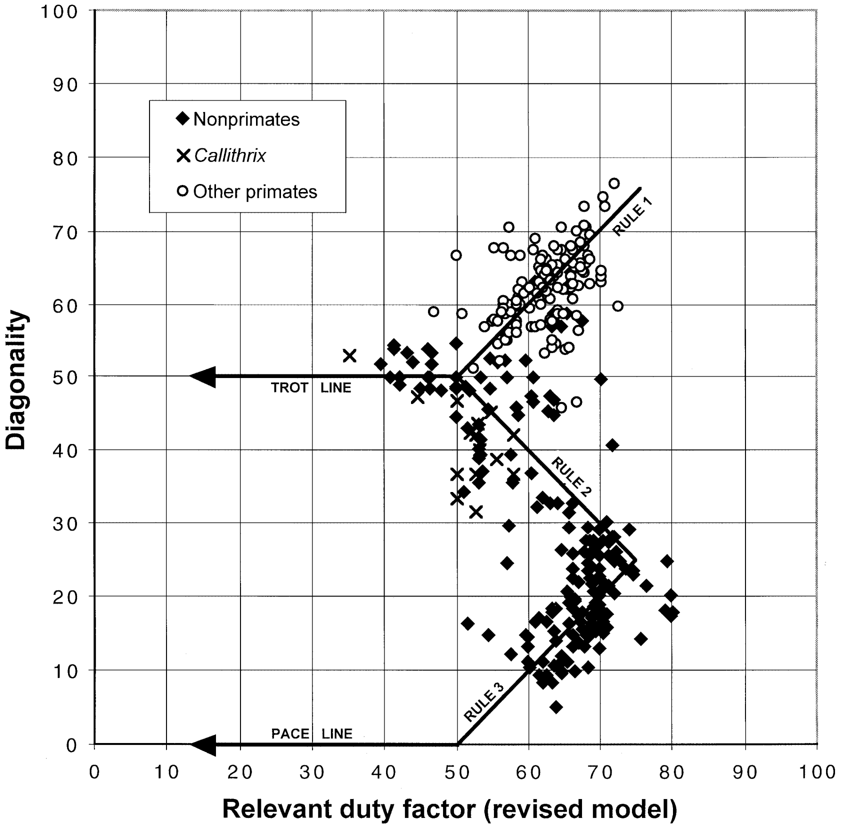

Figure 12. Modified Hildebrand diagram for our data set: revised support-polygon model. The relevant duty factor in each case – which is now S_f for L-S, D-C gaits (Rule 2: D = 100 – S_f) and S_h for the others – is plotted against diagonality. The diagonal lines show the distribution predicted for walking gaits by the revised support-pattern model. Compare Figs 3 and 11.

two lines predicted by our revised theory. Our data for this individual's D-C walks more closely approximate the predicted line for L-S D-C gaits (Rule 2) when plotted using the theoretically relevant duty factor S_f instead of S_h (Fig. 14). Of this animal's fast walks (with an average S between 50 and 60), all were half-runs; two were near-paces (approximating Rule 3) and the others were near-trots (approximating Rule 2). These data demonstrate that for a given set of duty factors, an individual dog can follow either Rule 2 or Rule 3, in effect choosing to walk either like a horse or like a camel.

CONCLUSIONS AND PROSPECTS

Once it is known which of three diagonality ranges an animal's walking gait falls into (above 50, below 25, or intermediate), the revised support-pattern model allows us to predict diagonality from duty factors within that range. For lateral-sequence gaits, we may eventually be able to to predict the diagonality range (i.e. the choice of Rule 2 or Rule 3) from an animal's relative limb length. However, the fact that some individuals are capable of switching from one L-S rule to another (Fig. 14) implies that the choice of rules must depend in part on variables other than limb length. This fact is also evident in the behaviour of some relatively short-legged carnivorans – e.g. raccoons (*Procyon*) and coatimundis (*Nasua*) – that use exclusively lateral-couplets gaits (McClearn, 1992).

How does an individual animal, or an evolving species, go about shifting from one rule to another? The animals that obey these rules are presumably not solving equations in their heads to determine when they should drop and lift their feet in order to optimize their support polygons, but exactly what they are doing remains to be determined. As a working hypothesis, we suggest that mammals follow these rules by synchronizing certain events as they alter speed and duty factors. An animal with a symmetrical walking gait can follow Rule 1 (the monkey rule) simply by lifting each hindfoot whenever the forefoot on that side touches down (Fig. 8B, vertical arrows). Likewise, it

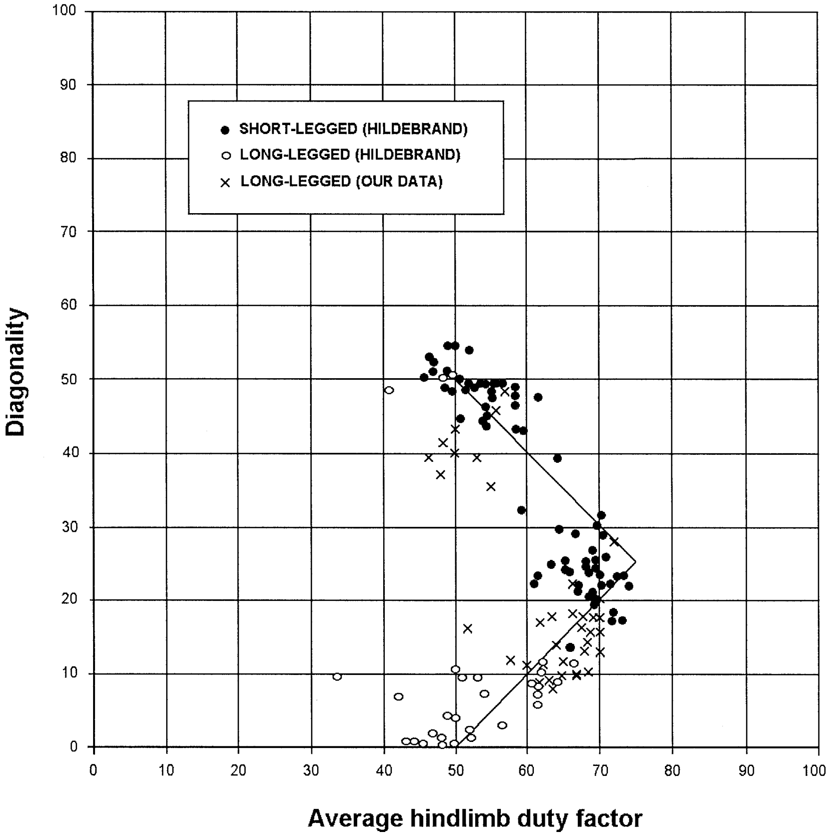

Figure 13. Standard Hildebrand diagram, comparing Hildebrand's (1968) dog data with our data for 41 gait cycles of a single long-legged dog. Diagonal lines represent the relationships between duty factor and diagonality predicted by the revised support-polygon model (using hind-limb duty factor throughout to accommodate Hildebrand's data).

can follow Rule 2 (the horse rule) by lifting each forefoot when the ipsilateral hindfoot touches down (Fig. 8A, vertical arrows), or Rule 3 (the camel rule) by synchronizing the touchdown of each forefoot with the lifting of the contralateral hind foot (Fig. 15, vertical arrows). An animal that is able to switch from one rule to another presumably has neural mechanisms that can enforce either of two different patterns of simultaneity, depending on circumstances. The coexistence of two rules in the behaviour of a single individual indicates one possible way in which one locomotor pattern might evolve into another – that is, by the phylogenetic addition of a new rule, followed by the gradual suppression or disappearance of the original rule.

Our data represent only a preliminary sample of the variety of mammalian gaits. They do not sample some of the symmetrical gaits that other researchers have reported, including certain gait patterns that violate the three rules articulated here or extrapolate them into unexpected ranges – e.g. running gaits with diagonalities around 25 or 75, respectively, attributed to elephants and muntjacs (Hildebrand, 1976). We hope in the future to collect data that will allow us to analyse these reported patterns.

The distribution of diagonal-sequence walking gaits also remains to be explained. Several ideas have been put forward to attempt to explain why most primates usually adopt D-S walks and most other mammals do not (Vilensky & Larson, 1989). However, all of the explanations thus far proposed remain controversial. Our working hypothesis is that primates adopt D-S walking gaits as a means of ensuring that one of their grasping hindfeet is placed in a protracted position (and thus lies roughly underneath the animal's centre of mass) on a tested support at the moment when the contralateral forefoot strikes down on an untested support (Fig. 16, top) during arboreal locomotion. In a slow L-S walk with a diagonality around 25 (Fig. 16, bottom), the supporting hindfoot lies considerably behind the centre of mass at the moment of forefoot touchdown. If the forelimb of a primate walking with a typical D-S gait comes down on an insecure support,

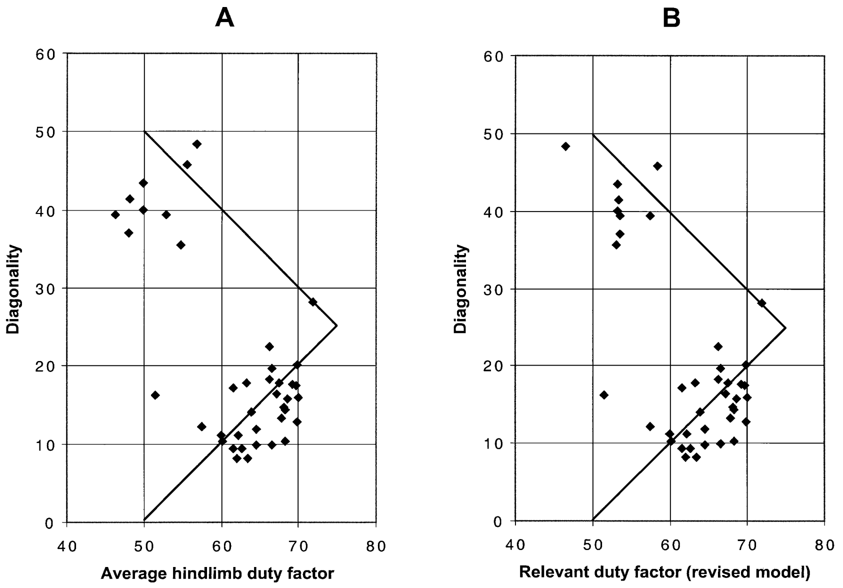

Figure 14. Our gait data for a single long-legged dog, displayed (A) on the standard Hildebrand diagram and (B) on the modified diagram, in which the relevant duty factor specified by the revised support-pattern model – S_f for L-S, D-C walks, S_h for other gaits – is plotted on the horizontal axis.

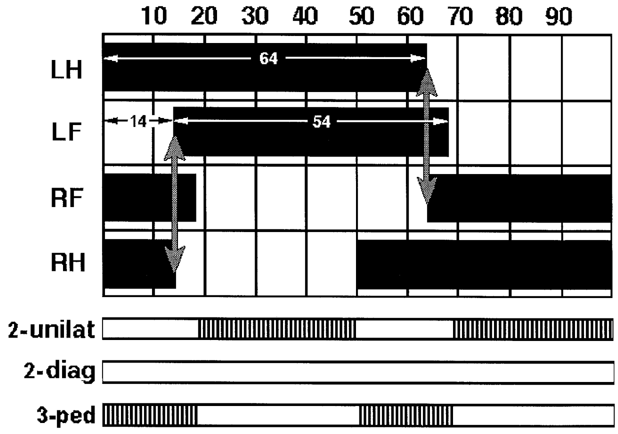

Figure 15. Values of diagonality predicted for lateral-sequence, lateral-couplets walks from the revised support-polygon model. Duty factors and graphic conventions as in Figure 4. To minimize overall bipedality while maximizing unilateral bipedality ('2-unilat'), a quadruped walking with an L-S, L-C gait should adopt a D-value equal to the hindlimb duty factor minus 50 (horizontal arrows). This entails that fore footfalls and contralateral hind liftoffs should be simultaneous (vertical arrows). Compare Figure 8.

the animal is still roughly balanced on its grasping hindfoot, and can pull back or right itself more easily than an animal that walks like a horse can.

Our preliminary conclusion is that D-S gaits in primates are correlates of their arboreal habits and grasping hindfeet, and that the disproportionately large duty factors and vertical reaction forces found in the hindlimbs of walking primates (Fig. 9; Kimura, Okada & Ishida, 1979; Reynolds, 1985; Demes *et al.*, 1994; Schmitt, 1999) are aspects of the same adaptive complex. We conjecture that this explains why *Callithrix*, which employs a claw grip in climbing trees, has a secondarily reduced hallux, and confines its arboreal activity chiefly to large, secure branches and trunks (Pocock, 1917; Lessertisseur & Jouffroy, 1973; Sussman & Kinzey, 1984; Garber, 1992; Hamrick, 1998), has apparently reverted to L-S walking gaits (Fig. 12; Schmitt, 2002). It also explains the primate-like D-S gaits reported for arboreal marsupials (Hildebrand, 1976; White, 1990; Pridmore, 1994; Lemelin, 1996; Lemelin *et al.*, 1999, 2002; Schmitt & Lemelin, 2002). The only D-S walks that we recorded for nonprimates occurred in the didelphid marsupial *Caluromys*. This arboreal fruit-and-insect-eater has been proposed as a living model for the way of life of the ancestral primates (Cartmill, 1972, 1974; Charles-Dominique, 1983; Rasmussen, 1990). Its morphological and behavioural similarities to small living strepsirhine primates extend to its D-S gaits, which cluster unequivocally with our primate data on the modified Hildebrand diagram. The few gait cycles we have analysed for its more terrestrial relative *Monodelphis* are either L-S walks or walking trots (Lemelin *et al.*, 2002; Schmitt & Lemelin, 2002). It seems probable that the resemblances in gait between *Caluromys* and typical

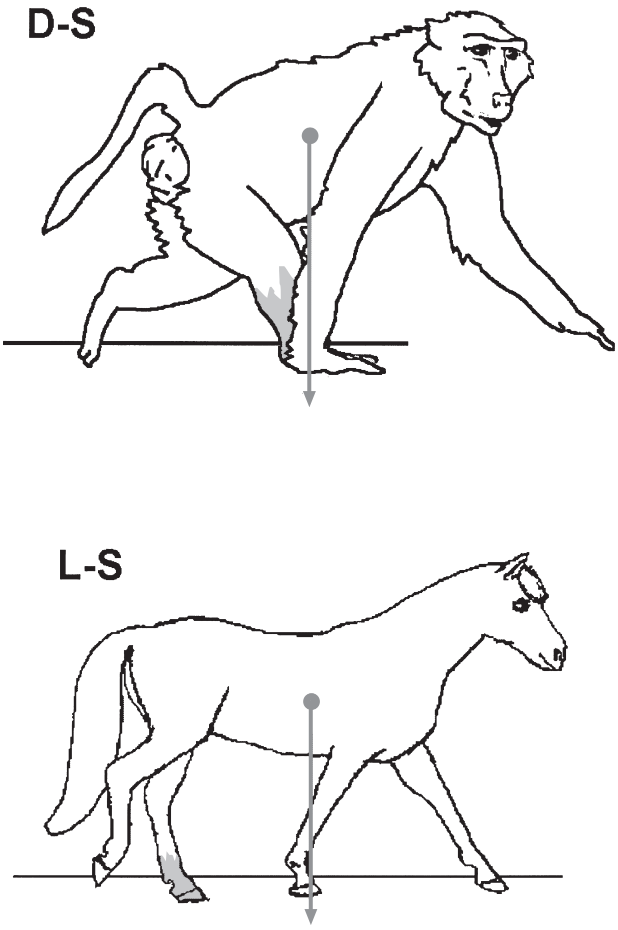

Figure 16. Possible adaptive value of diagonal-sequence walking gaits in primates. At the moment of forefoot touchdown, when weight is about to be transferred to a new and untested substrate, the line of gravity (grey arrow: the vertical through the body's centre of mass, estimated here as the vertical through the midpoint of an ischium-to-occiput line) passes approximately through the supporting hindfoot (grey tone) in the D-S walk of the baboon (top), but not in the L-S walk of the horse (bottom). In primates or other arboreal animals with marked grasping specializations of the hind foot, the primate support pattern allows the animal to draw back or regain its balance if the new support breaks or bends precipitously.

primates represent evolutionary convergences, arrived at independently in the two groups for similar adaptive reasons.

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