

Lateral Sequence Walking in Infant *Papio cynocephalus*: Implications for the Evolution of Diagonal Sequence Walking in Primates

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ABSTRACT One of the most distinctive aspects of primate quadrupedal walking is the use of diagonal sequence footfalls in combination with diagonal-couplets interlimb timing. Numerous hypotheses have been offered to explain why primates might have evolved this type of gait, yet this important question remains unresolved. Because infant primates use a wider variety of quadrupedal gaits than do adults, they provide a natural experiment with which to test hypotheses about the evolution of unique aspects of primate quadrupedalism. In this study, we present kinematic data on two infant baboons (*Papio cynocephalus*) in order to test the recent hypothesis that diagonal sequence, diagonal couplets walking might have evolved in primates because their limb positioning provides stability in a small branch environment (Cartmill et al. [2002] *Zool J Linn Soc* 136:401–420). To assess hind-

limb position at the moment of forelimb touchdown, we measured hindlimb angular excursion and ankle position for 84 walking strides, across three different types of gaits (diagonal sequence, diagonal couplets (DSDC); lateral sequence lateral couplets (LSLC); and lateral sequence diagonal couplets (LSDC)). Results indicate that if a forelimb were to contact an unstable substrate, LSLC walking provides as much, and perhaps more, stability when compared to DSDC walking. Therefore, it appears that this moment in a stride was unlikely to be a particularly important selective factor in the evolution of DSDC walking. Further insight into this issue will likely be gained by observations of primate quadrupedalism in natural environments, where the use of lateral sequence gaits might be more common than currently known. *Am J Phys Anthropol* 126:205–213, 2005. © 2004 Wiley-Liss, Inc.

The quadrupedal walking style of primates is characterized by several distinct kinematic and kinetic characteristics when compared to that of most other mammals. For example, primates employ relatively large limb angular excursions, highly protracted forelimbs and humeri at touchdown, relatively long strides, low stride frequencies, and a compliant gait, while exhibiting reduced vertical substrate reaction forces on their forelimbs (Alexander and Maloiy, 1984; Kimura et al., 1979; Demes et al., 1994; Larson, 1998; Schmitt, 1998; Larson et al., 2000, 2001). In addition, one of the most easily recognizable characteristics of primate quadrupedalism is the sequence in which the limbs touch the ground. Primates, though flexible in their footfall sequence (Vilensky and Larson, 1989), clearly prefer a diagonal sequence/diagonal couplets gait when walking quadrupedally (a foot touches the ground, followed by the contralateral, or opposite-side hand, with diagonal limbs related in time as a pair). Almost all other mammals prefer a lateral sequence gait in which a foot touches the ground, followed by the same side, or ipsilateral hand, with either diagonal limbs or same-side limbs related in time as a pair (Hildebrand, 1967).

Recently, several researchers (e.g., Larson, 1998; Larson et al., 2000, 2001; Cartmill et al., 2002, in

press; Schmitt and Lemelin, 2002; Lemelin et al., 2003; Schmitt, 2003) have shown how many of the kinematic and kinetic aspects of primate quadrupedalism can be viewed as part of a functional package that facilitated the early evolution of primates in a small branch niche by providing locomotor stability on flexible branches. This view has been reinforced by the existence of similar features in arboreal marsupials (Hildebrand, 1976; White, 1990; Pridmore, 1994; Larson et al., 2000; Schmitt and Lemelin, 2002; Lemelin et al., 2003). While this adaptive scenario provides a convincing explanation for many of the distinct aspects of primate quadrupedalism listed above, the selective pressures that might have led specifically to the evolution of diagonal sequence,

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diagonal couplets walking in primates remain less obvious.

Numerous hypotheses have been put forth to explain why primates prefer a diagonal sequence, diagonal couplets gait, none of which are mutually exclusive. These include the neurological view that diagonal sequence gait is a by-product of increased supraspinal control over locomotion (Vilensky and Larson, 1989; Vilensky, 1989), as well as the biomechanical view that diagonal sequence gait is the most stable choice for primates whose body center of mass is presumably more posterior than that of other mammals (Rollinson and Martin, 1981; but see Vilensky and Larson, 1989).

More recently, in a detailed analysis of mammalian symmetrical gaits, Cartmill et al. (2002) demonstrated that overall stability is best achieved by the use of diagonal couplets, whether in lateral or diagonal sequence. Diagonal couplets minimize the overall amount of time an animal spends on only two limbs during walking, while maximizing support by (more stable) diagonal limb pairs during portions of the step cycle when the animal does use only two limbs. In this respect, then, diagonal sequence does not provide an advantage in overall stability over lateral sequence walking, as long as the couplets are diagonal. However, Cartmill et al. (2002) also provided an ecologically based hypothesis to suggest a possible evolutionary advantage to diagonal sequence/diagonal couplets gait. They suggested that diagonal sequence/diagonal couplets gait evolved in primates because it allows stable positioning of the hindlimb under the body's center of mass at the moment when the contralateral forelimb contacts a potentially unstable branch within a small branch niche. In lateral sequence/diagonal couplets gait, the hindlimb in contact with the substrate is not in this stable position. For example, the position of a primate's body and limbs at forelimb touchdown stands in stark contrast to that of the horse illustrated by Cartmill et al. (2002, their Fig. 16), walking in a lateral sequence gait.¹ When the horse's forelimb touches down, neither hindlimb is underneath the assumed center of mass of the body. Therefore, the authors concluded that although both diagonal sequence/diagonal couplets (DSDC) and lateral sequence/diagonal couplets gaits (LSDC) (ideally) minimize the total amount of time the body is supported by only two limbs while maximizing support by diagonal limbs, DSDC walking has the extra advantage of stability on unstable branches.

These combined explanations provide a reasonable scenario for the selection of DSDC gaits in primate evolution. The minimization of bipedality and the maximization of contralateral bipedality

brought about by the employment of diagonal couplets during quadrupedal walking are mathematical predictions of theoretical optima. Cartmill et al. (2002) provided convincing data that primates approach these predicted values when using DSDC, strengthening the argument that DSDC gaits were selected for in primates to maximize support polygons during walking. However, the second explanation for DSDC walking (position of the hindlimb under the center of the body when the contralateral forelimb touches down on an untested support) is open to the suggestion that a comparison of a primate to a horse confounds the question of limb positioning. That is, the positioning of the limbs relative to the trunk is not solely a question of the timing of limb movements (i.e., diagonal vs. lateral sequence or couplets), but is also affected by the angular excursions of the limbs, limb joint flexibility, and relative limb length. Indeed, a cursorial mammal (such as a horse) differs dramatically from primates in the extent to which its forelimbs and hindlimbs protract at touchdown (Larson et al., 2000, 2001).

In order to isolate the effects of footfall sequence/timing from those of limb excursion angles or joint flexibility, one should compare limb positioning at forelimb touchdown in primates (using DSDC walking) to that of other *noncursorial* (i.e., more primate-like) mammals walking in lateral sequence. An even better control would be to compare limb positioning across different walking gaits *within* primates. However, due to the relative rarity of LS walks in adult primates, such comparisons have not been carried out empirically (but for a hypothetical depiction of a primate walking in a lateral sequence, lateral couplets gait, see Cartmill et al., in press).

Primate infants, on the other hand, use a wider range of gaits than adult primates typically do (Hildebrand, 1967; Rose, 1977; Rollinson and Martin, 1981; Hurov, 1982; Vilensky and Gankiewicz, 1989; Nakano, 1996; Dunbar and Badam, 1998). Thus, they provide us with the opportunity to compare more directly the difference in limb positioning during LS and DS gaits *within* primates. This allows us to test empirically the hypothesis of Cartmill et al. (2002) that DSDC walking evolved in primates (and certain marsupials) because it is the most stable gait when reaching out to an untested arboreal support. The goal of this study was to evaluate the position of the hindlimbs during LS and DS gaits (using both types of couplets) in primate infants, at the critical moment when a forelimb touches down, representing the hypothetical case when it would land on an untested support.

MATERIALS AND METHODS

Kinematic data during quadrupedal walking were collected for two *Papio cynocephalus* infants, one female and one male, approximately every 2 weeks as the animals aged from 2.4 to 7.2 months (female) and 2.6 to 7.5 months (male). Table 1 lists sample

¹The gait number (their "diagonality") reported for the horse in Cartmill et al. (2002) is 25. According to their modified Hildebrand plot, 25 is a lateral sequence gait in single foot, i.e., on the borderline between lateral sequence/diagonal couplets and lateral sequence/lateral couplets.

TABLE 1. Sample sizes and frequencies of walking strides for each gait type¹

Age in months	N	PACE	LSLC	LSSF	LSDC	Trot	DSDC	DSSF	DSLCL
Subject 1. <i>P. cynocephalus</i> (F)									
2.4	9	0	0	0	9	0	0	0	0
2.6	5	0	0	0	5	0	0	0	0
3.1	5	0	0	0	5	0	0	0	0
3.3	1	0	0	0	1	0	0	0	0
4.0	4	0	1	0	3	0	0	0	0
4.5	9	0	9	0	0	0	0	0	0
5.6	1	0	1	0	0	0	0	0	0
5.8	13	0	12	0	1	0	0	0	0
6.3	8	0	8	0	0	0	0	0	0
6.8	6	0	3	0	2	0	1	0	0
7.2	15	0	13	1	1	0	0	0	0
Total number	76	0	47	1	27	0	1	0	0
Total Frequency		0	62	1	36	0	1	0	0
Subject 2. <i>P. cynocephalus</i> (M)									
2.6	4	0	0	0	4	0	0	0	0
3.3	11	0	0	0	0	1	8	1	1
3.6	8	0	0	0	0	0	8	0	0
4.3	7	0	0	0	4	0	3	0	0
4.7	19	0	4	2	2	0	11	0	0
5.9	35	0	1	0	1	0	33	0	0
6.1	34	0	2	0	2	1	29	0	0
6.6	28	0	1	0	2	0	25	0	0
7.0	35	0	4	0	0	0	31	0	0
7.5	26	0	2	0	1	0	23	0	0
Total number	207	0	14	2	16	2	171	1	1
Total frequency		0	7	1	8	1	83	0	0
Total observed	283	0	61	3	43	2	172	1	1
Total: kinematic analysis	84	0	25	1	8	0	50	0	0

LSLC, lateral sequence, lateral couplets; LSSF, lateral sequence, single foot; DSDC, diagonal sequence, diagonal couplets; DSSF, diagonal sequence, single foot; DSLCL, diagonal sequence, lateral couplets. See Hildebrand (1966).

¹ The gait number (their “diagonality”) reported for the horse in Cartmill et al. (2002) is 25. According to their modified Hildebrand plot, 25 is a lateral sequence gait in single foot, i.e., on the borderline between lateral sequence/diagonal couplets and lateral sequence/lateral couplets.

sizes of strides used in the analysis. Data were collected using a 3D Vicon Motion System with five infrared cameras (Vicon 250, Oxford Metric Systems) in conjunction with synchronized video (JVC GR-DVL9800) filmed at 60 frames per second. Subjects walked freely through a $2 \times 3 \times 10$ foot tunnel constructed of Lexan to encourage straight walking (but it should be noted that neither the angular data calculated by the Vicon system nor the gait data required cameras to be perpendicular to the subject’s line of movement). Footfall sequence and couplets were calculated from the video sequences, using the methods of Hildebrand (1966, 1976). In this study, we use the term “gait number” to indicate the Y-axis of a traditional Hildebrand diagram (i.e., the percentage of a stride that the touchdown of a forelimb follows that of the hindlimb on the same side of the body). Divisions between named gaits (e.g., DSDC, LSDC) are a slight modification of the divisions of Hildebrand (1966, 1976) and follow those of Cartmill et al. (2002). Only symmetrical walking gaits were included. Walking gaits were defined as those in which the hindlimb duty factor was greater than or equal to 50 (Hildebrand, 1966). In a perfectly symmetrical walk, a hindlimb contacts the ground at exactly 50% of the interval of time between footfalls of the contralateral hindlimb (Hildebrand, 1966). Because perfect symmetry is rare, we ac-

cepted strides in which the symmetry value was between 45 and 55%.

Reflective markers were placed on the hip, knee, ankle, shoulder, elbow, and wrist of each subject. Not all markers were used in this study. In order to compare hindlimb positioning across different gait numbers, the Vicon Motion System was used to calculate hindlimb protraction/retraction angles and ankle position at the moment of forelimb touchdown for each gait type. The five Vicon cameras were placed on one side of the tunnel in order to maximize the viewing volume. As a result, hindlimb angular data and ankle position for any given stride were calculated for a hindlimb on one side of the body. Hindlimb angle was calculated as the angle formed between a line connecting the hip and ankle markers relative to a vertical line through the hip marker. Hip and ankle marker locations exhibit minimal skin movement (see also Goslow et al., 1973) and are therefore reliable areas for kinematic study (Schamhardt et al., 1993). Positive angles indicate that the hip-ankle segment is protracted relative to the vertical, and negative angles indicate retraction of the hip-ankle segment (Fig. 1).

Markers could not be placed on the feet of the animals without being disturbed. Therefore, in order to evaluate how far beneath the body the foot is placed, we calculated the position of the ankle rela-

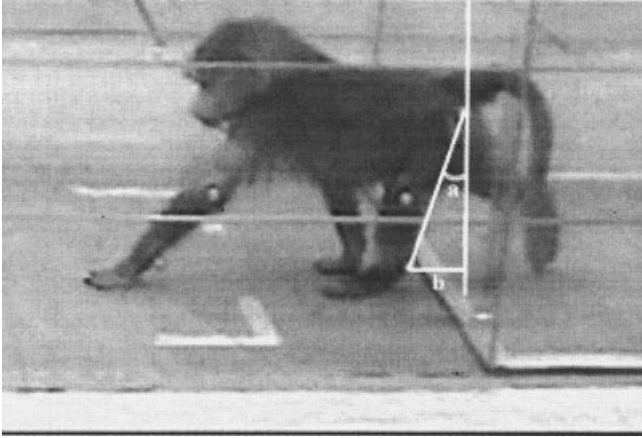


Fig. 1. Kinematic measurements. a, hindlimb angle in degrees, measured as angle formed between a line connecting hip and ankle markers and a vertical line through hip marker; b, ankle position, relative to a vertical line through hip marker. See text for further explanation.

tive to a vertical line through the hip joint (Fig. 1). Ankle position is reported as a percentage of trunk length. Trunk length was calculated as the average distance between the shoulder and hip markers throughout each stride. Although there tends to be more skin movement at the shoulder joint compared to the hip or ankle, calculating average distance minimizes potential error, and is preferable to estimating the location of the shoulder joint without a marker. For ankle position, a value of 0% indicates that the ankle is positioned directly below (in line with) the hip joint, negative values indicate that the ankle is positioned behind (caudal to) a vertical line through the hip joint, and positive values indicate that the ankle is positioned in front of (cranial to) a vertical line through the hip joint. A value of 50% indicates that the ankle lies directly below the midpoint of the trunk (an assumed approximation of the body's center of mass; see Cartmill et al., 2002). It should be noted that ankle position underestimates the actual position of the foot relative to the hip. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Texas at Austin.

RESULTS

Footfall sequence and couplets ("gait number")

Each of the two subjects used a variety of gait types during the developmental period, and they differed dramatically from each other in overall frequency of gait category (Table 1). Ninety-nine percent of all walking gaits observed in the female subject were lateral sequence, and 98% of those were either LSLC (62%) or LSDC (36%). The male subject used predominantly diagonal sequence, diagonal couplets walking (83% of all strides observed). For the purposes of this study, data from the two subjects were combined in order to compare hindlimb positioning across gaits. Functional explanations for

differences in gait preferences, across developmental stages and between the two subjects will be discussed in a separate publication (Shapiro and Raichlen, unpublished data). Of the total number of strides used to calculate gait number from the video analysis (283 for both subjects, combined), 84 were available for the calculation of hindlimb angle and ankle position. The reason for the discrepancy is that while gait number can be calculated easily from a frame-by-frame analysis of the videotape, hindlimb angle and ankle position were calculated using the Vicon 3D positional data of the markers. Because the position of individual markers is not always captured by the Vicon cameras, the data collected for hindlimb angle and ankle position represent a subset of the total number of strides. Nevertheless, a sufficient sample was available for a comparison of hindlimb positioning across the most commonly used gait types, LSLC ($n = 25$), LSDC ($n = 8$), and DSDC ($n = 50$) (Table 1).

Hindlimb angle and ankle position

Because gait types are defined on the basis of the timing of the limbs relative to one another, the hindlimb of interest for calculating angle and ankle position differs depending on the gait considered. The hindlimb of interest is that which, at the moment of a given forelimb touchdown, is in contact with the substrate and relatively most protracted (i.e., closer to the midline of the trunk). This is the hindlimb that will provide the most stability if the forelimb lands on an unstable support. In diagonal sequence gaits, the hindlimb of interest is *contralateral* to the forelimb that has just touched down (Fig. 2A). In lateral sequence gaits, the hindlimb of interest is *ipsilateral* to the forelimb (Fig. 2B,C). Note that the relatively most protracted hindlimb in contact with the substrate can in actuality be *retracted*, depending on the gait number and duty factor (Fig. 2C).

Figure 3 illustrates the angles for the relevant hindlimbs across the three types of gaits sampled; LSLC, LSDC, and DSDC. Within both LS and DS gaits, there is a significant negative correlation between hindlimb angle and gait number, such that lower gait numbers *within* LS or DS gaits are accompanied by a more protracted hindlimb at forelimb touchdown (LS, Kendall's $\tau = -0.57$, $P \leq 0.01$, $n = 34$; DS, Kendall's $\tau = -0.57$, $P \leq 0.05$, $n = 50$). More specifically, as an LS gait approaches a pace (i.e., as the gait number approaches zero, and the gait type moves from LSDC to LSLC), the (ipsilateral) hindlimb moves from retraction to protraction at the moment of forelimb touchdown. A similar (though weaker) pattern is evident within DS gaits. As DS gait numbers approach the trot (gait number 50), the (contralateral) hindlimb becomes more highly protracted at the moment of forelimb touchdown. At a pace (gait number zero; not sampled here), ipsilateral fore- and hindlimbs land simultaneously. This interlimb timing necessarily causes

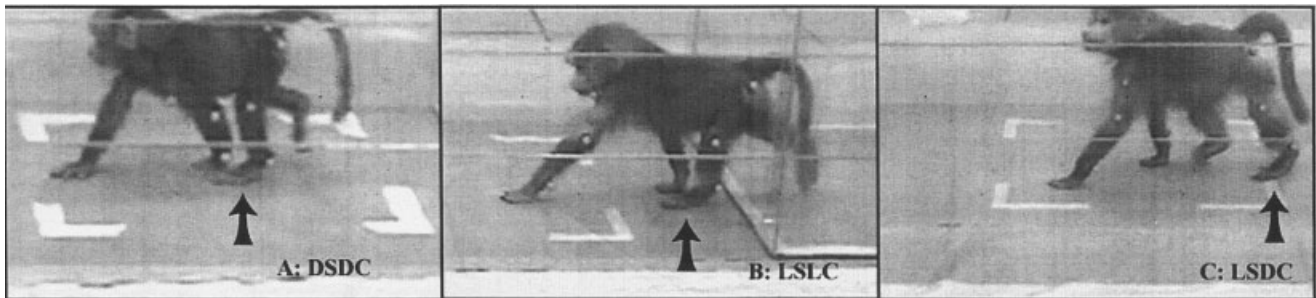


Fig. 2. Limb positions at moment of forelimb touchdown in three walking gaits. **A:** Diagonal sequence, diagonal couplets (gait number 70, hindlimb duty factor 62). **B:** Lateral sequence, lateral couplets (gait number 20, hindlimb duty factor 66). **C:** Lateral sequence, diagonal couplets (gait number 32, hindlimb duty factor 72). Arrows point to hindlimb from which kinematic measurements were calculated. Note that forelimb and hindlimb beneath trunk are ipsilateral pairs in DSDC (A) and contralateral pairs in LSLC (B), whereas hindlimb in contact with substrate does not lie beneath trunk in LSDC (C).

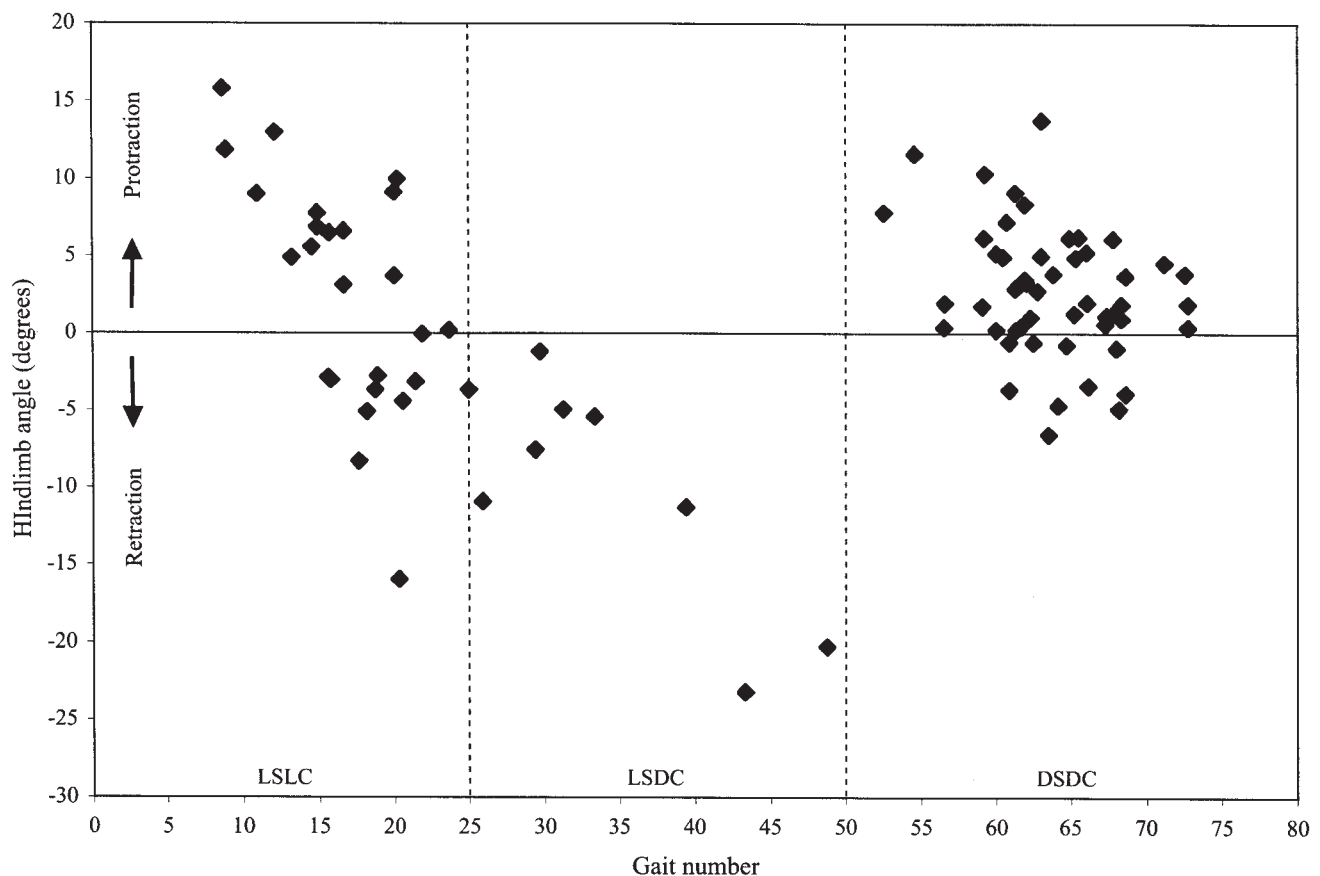


Fig. 3. Hindlimb angle vs. gait number. Positive angles indicate a protracted hindlimb-ankle segment; negative angles indicate a retracted hindlimb-ankle segment. Within both lateral and diagonal sequence walks, hindlimb angle is significantly negatively correlated with gait number (LS, Kendall's $\tau = -0.57$, $P \leq 0.01$, $n = 34$; DS, Kendall's $\tau = -0.17$, $P \leq 0.05$, $n = 50$). See text for further explanation.

the hindlimb to be at its most protracted when the forelimb makes contact. Similarly, in a trot, contralateral fore- and hindlimbs land simultaneously, so the hindlimb is at its most protracted at forelimb touchdown.

Figure 3 gives the impression that DS gaits are accompanied by less frequent hindlimb retraction than are LS gaits. However, with the exception of one stride, DSLC gaits were not used by the sub-

jects² (nor by other tetrapods; Hildebrand, 1976, 1980). As a result, the LS hindlimb angle values span a greater range of gait numbers (9–49) than do the DS hindlimb angle values (53–73). In

²The absence of DSLC gaits in the sample likely contributes, at least in part, to the weaker correlation between gait number and hindlimb angle within DS compared to LS gaits.

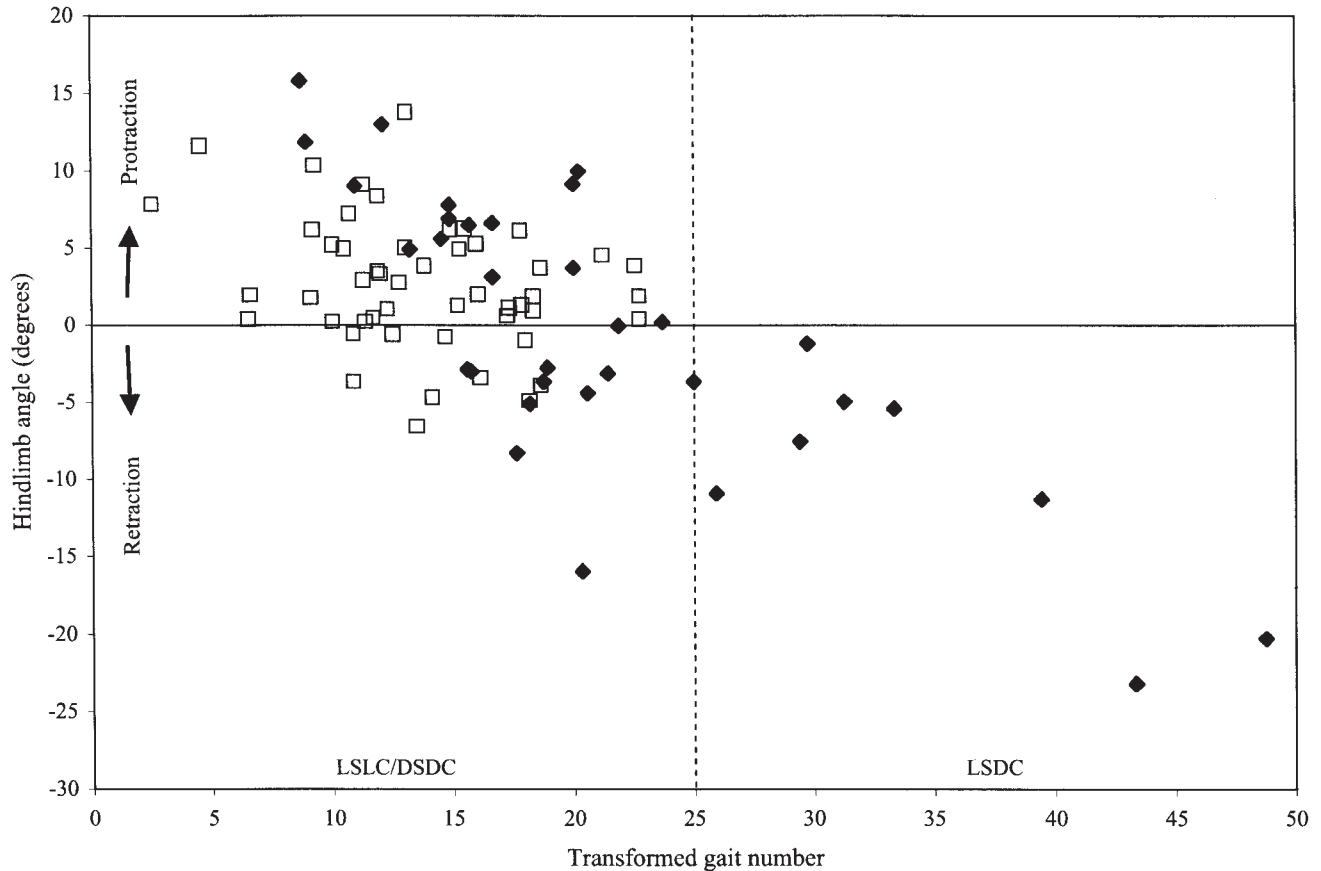


Fig. 4. Hindlimb angle vs. transformed gait number. Solid diamonds represent lateral sequence walking (with either lateral or diagonal couplets). Open squares represent diagonal sequence, diagonal couplets walking. Compare to Figure 3. Note overlap between LS and DS hindlimb angle values in their common range of transformed gait numbers. See text for further explanation.

order to compare values across gaits more directly, each gait number was transformed to express its distance from either a pace (LS gaits) or a trot (DS gaits), which are the points of transition from which LS and DS gait numbers increase, respectively (Fig. 4). Zero (the gait number for a pace, in which ipsilateral fore- and hindlimbs move in synchrony) was subtracted from all gait numbers within LS. Fifty (the gait number for a trot, in which contralateral fore- and hindlimbs move in synchrony) was subtracted from all gait numbers within DS. As a result, DSDC and LSLC transformed gait numbers lie below 25, and LSDC gait numbers lie above 25 (DSL/C gaits, if they were used, would lie above 25 as well). The transformed gait numbers reflect the movement of the hindlimb relative to its most protracted position (pace for LS gaits, trot for DS gaits).

The slopes of the two gait types are not parallel, so an analysis of covariance could not be performed to compare hindlimb angle values. However, hindlimb angle values exhibit substantial overlap in the range of transformed gait numbers common to both LS and DS gaits, i.e., between 0–25 (which includes both LSLC and DSDC) (Fig. 4). The slight elevation of LSLC values above those of DSDC is intriguing (since it suggests more pronounced protraction in

LSLC at similar gait numbers), but larger sample sizes are needed to assess its potential significance. More importantly, these results highlight the similarity between DSDC and LSLC walking with respect to hindlimb position at the moment of forelimb touchdown, and demonstrate that the benefits of hindlimb protraction at the moment of forelimb touchdown are not exclusive to DSDC walking, but also occur in LSLC gait (see also Cartmill et al., in press). By comparison, as the gait number increases toward 25 (the transition to LSDC), the hindlimb in contact with the substrate becomes less consistently protracted, and is then predominantly retracted in LSDC walking.

Our data on ankle position relative to the hip joint are consistent with the hindlimb angle data. At the moment of forelimb touchdown in both DSDC and LSLC walking, the (relevant) ankle approaches a position below the midpoint of the trunk at lower values of the gait number (Fig. 5). The ankle itself does not reach the 50% value (directly under the trunk's midpoint), but it is likely that the foot does. Therefore, as shown by hindlimb angle values, DSDC and LSLC walking are very similar with respect to the position of the ankle at the moment of forelimb touchdown.

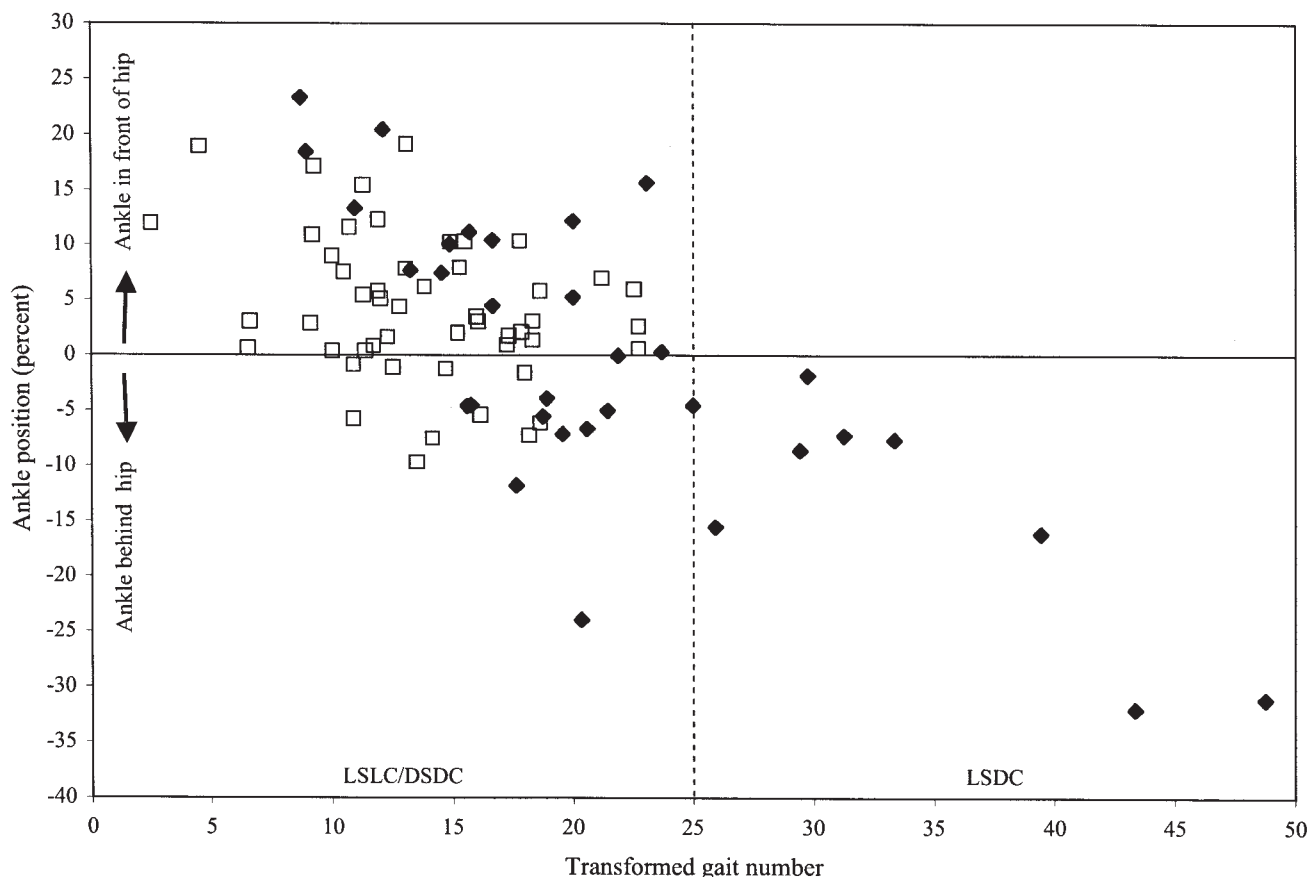


Fig. 5. Ankle position (as percentage of trunk length) vs. transformed gait number. Positive values indicate that ankle lies in front of a vertical line through hip joint; negative values indicate that ankle lies behind a vertical line through hip joint. Fifty percent would indicate that the ankle lies directly beneath the midpoint of trunk. Symbols as in Figure 4. Within both lateral and diagonal sequence walks, ankle position is significantly negatively correlated with gait number (LS, Kendall's $\tau = -0.55$, $P \leq 0.01$, $n = 34$; DS, Kendall's $\tau = -0.18$, $P \leq 0.05$, $n = 50$). See text for further explanation.

It is unlikely that variation in walking speed affected our conclusions. Hindlimb duty factor (the percentage of a stride's duration that a hindlimb is on the ground) is inversely related to speed (e.g., Hildebrand, 1976; Vilensky et al., 1988). We found no correlation between duty factor (i.e., speed) and either hindlimb angle (LS, Kendall's $\tau = 0.06$, $P > 0.10$, $n = 34$; DS, Kendall's $\tau = -0.03$, $P > 0.10$, $n = 50$) or ankle position (LS, Kendall's $\tau = 0.07$, $P > 0.10$, $n = 34$; DS, Kendall's $\tau = -0.03$, $P > 0.10$, $n = 50$) within LS or DS gaits.

Figure 2 illustrates the positioning of the limbs at the moment of forelimb touchdown in LSLC, LSDC, and DSDC gaits. It is clear that in both LSLC and DSDC walking, a hindlimb is well under the body when a forelimb touches down. In fact, both types of gaits are accompanied by a hindlimb *as well as* a forelimb under the body. There is one important difference, however. In LSLC, the (retracted) forelimb positioned under the body is *contralateral* to the protracted hindlimb. In DSDC, the (retracted) forelimb positioned under the body is *ipsilateral* to the protracted hindlimb. The functional implications of this difference are discussed below.

DISCUSSION

The lateral sequence walking gaits sampled here are not unique to primates, but are utilized by non-primate mammals and other tetrapods (Hildebrand, 1966, 1976). DSDC walking is rare among mammals, but along with primates, is used by giant armadillos, kinkajous, aardvarks, and some marsupials (Hildebrand, 1976; White, 1990; Pridmore, 1994; Schmitt and Lemelin, 2002; Lemelin et al., 2003). By definition, interlimb timing in primates is essentially identical to that of other mammals at a given gait number and duty factor (Hildebrand, 1966). For example, a camel utilizing LSLC walking would, like infant baboons, have its ipsilateral hindlimb relatively more protracted at forelimb touchdown than its contralateral hindlimb. But interlimb timing is distinct from limb angular excursion. Due to the enhanced limb angular excursions characteristic of primates (Larson et al., 2001), it cannot be assumed that a camel's (or any other cursorial mammal's) hindlimb would be protracted enough to land under its trunk when its forelimb contacts the ground during LSLC walking. Therefore, this study

highlights the important contribution that joint flexibility and limb angular excursion make to the walking style of primates.

Our results clearly illustrate that when a primate's forelimb contacts the substrate, *both* DSDC and LSLC walking gaits are accompanied by similar angular movements of the (relevant) hindlimb, with the ankle positioned at a comparable location relative to the midpoint of the trunk. In this respect, DSDC walking does not appear to confer a unique advantage over LSLC walking in primates, weakening support for the suggestion that DSDC gaits evolved specifically (in lieu of other gaits, such as LSLC) to provide stability on narrow branches during forelimb touchdown (Cartmill et al., 2002, in press). In fact, a closer look at LSLC walking reveals a possible advantage over DSDC walking with respect to stability. When a forelimb lands on a potentially unstable substrate, the forelimb-hindlimb pair positioned under the trunk in an LSLC walk consists of *contralateral* (diagonal) pairs, whereas the forelimb-hindlimb pair positioned under the trunk in a DSDC walk consists of *ipsilateral* (lateral) pairs. Therefore, because two-limbed support from opposite sides of the body provides more stability than two-limbed support from the same side of the body (Hildebrand, 1980), it seems that LSLC would provide *more* stability than DSDC if a forelimb landed on an unstable branch, not less (cf., Cartmill et al., in press). Specifically, if a substrate tested by a forelimb were unstable, a primate walking in LSLC would not only have its hindlimb protracted to lie well under the center of its trunk to stabilize the body, but the opposite side forelimb would be retracted under the body as well, forming a stable base of support.

In light of this observation, it is intriguing to note other lines of evidence from both the field and laboratory pointing to the possible advantage of LSLC over DSDC walking on small branches. For example, a field study by Dunbar and Badam (2000) demonstrated that juvenile macaques prefer LS, not DS gaits on distal ends of longitudinal branches. In their Figure 2F, the macaque's limb positioning appears to be consistent with LSLC walking on such a branch (although it was only briefly using two-limbed support in the sequence illustrated; Dunbar, personal communication). In contrast, DS gaits were preferred by macaques on the proximal end of longitudinal branches, where diameter was relatively *large*, or on appropriately spaced lateral stems which provide a wide base of support. Relatedly, Stevens (2003, and personal communication) tested gait preferences in several prosimians, utilizing a variety of substrates in a laboratory setting. She found much variability in gait types across species and substrates, and did not find a consistent preference for DSDC walking on small or unstable substrates. Clearly, DS gaits are not the only answer to small branch challenges.

Of course, the advantages of LSLC walking discussed here apply only to a particular moment in time, i.e., the moment a forelimb lands on an unstable substrate. *Throughout* the stride, LSLC can be considered to be less stable than DSDC, due to the former's more frequent periods of two-limbed support by ipsilateral forelimb-hindlimb pairs, associated with the tendency to roll to one side (Hildebrand, 1980; Vilensky et al., 1994; Cartmill et al., 2002). Despite these disadvantages, LSLC walking avoids same-side limb interference (because ipsilateral limbs swing nearly synchronously), and is thus the gait of choice for mammals with elongated limbs, such as camels (Hildebrand, 1968, 1980). Relatedly, LSLC has been shown to be used at developmental stages during which limbs temporarily elongate relative to body size (Peters, 1983). This appears to be the reason why our infant female increased the frequency of LSLC walking over LSDC walking at 4.5 months of age (Table 1 and Shapiro and Raichlen, unpublished data), and most likely explains similar results reported for macaques (Nakano, 1996; Turnquist and Wells, 1994). On the other hand, raccoons and coatis both use LSLC walking, but the former have elongated limbs (McClernan, 1992) and larger hindlimb angular excursions (Larson et al., 2001) compared to the latter. Further research on the relative contributions of limb length and limb excursion to gait choice should provide much-needed insight into the function and evolution of mammalian footfall sequence.

CONCLUSIONS

We conclude that stability at the moment of forelimb touchdown was unlikely to be a particularly important selective factor in the evolution of DSDC walking in primates, because LSLC gait is possibly a better choice at that moment in time, and might in fact be more frequently used by primates in their natural environment than is currently known. Field studies that quantify footfall sequence are rare. Further research in this area is certainly necessary to test these hypotheses.

It is difficult to attempt to single out a particular selection factor for the evolution of DSDC walking in primates. DSDC walking may be more advantageous than LSLC walking throughout the stride, but no more so than LSDC walking (which also avoids ipsilateral two-limbed support), and does not appear to confer a unique advantage at critical moments on unstable, presumably small branches. Our results do not preclude the possibility that the small branch niche was an important component in the evolution of primate walking style (especially given the use of DSDC in arboreal marsupials in similar environments). Rather, we highlight the fact that an exclusive functional explanation for DSDC walking in such an environment remains to be determined. Obviously, the evolution of gait in primates remains a complex issue, one that can only be sorted out with further research in both the laboratory and field

settings. We have only begun to explore the gait flexibility of which primates are capable (Vilensky and Larson, 1989) in the laboratory, and we have even less documentation of this flexibility in a complex, natural environment. While it remains intriguing that primates' preference for DSDC gait is rare among other mammals, it will be equally useful to document the contexts in which primates use other forms of walking.

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LITERATURE CITED

- Alexander RM, Maloij GMO. 1984. Stride lengths and stride frequencies of primates. *J Zool Lond* 202:577–582.
- Cartmill M, Lemelin P, Schmitt D. 2002. Support polygons and symmetrical gaits in mammals. *Zool J Linn Soc* 136:401–420.
- Cartmill M, Lemelin P, Schmitt D. In press. Primate gaits and primate origins. In: Ravosa M, Dagosto M, editors. Primate origins and adaptations: a multidisciplinary perspective. New York: Plenum Press.
- Demes B, Larson SG, Stern JT Jr, Jungers WL, Biknevicius AR, Schmitt D. 1994. The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. *J Hum Evol* 26:353–374.
- Dunbar DC, Badam GL. 1998. Development of posture and locomotion in free-ranging primates. *Neurosci Biobehav Rev* 22: 541–546.
- Dunbar DC, Badam GL. 2000. Locomotion and posture during terminal branch feeding. *Int J Primatol* 21:649–669.
- Goslow GE, Reinking RM, Stuart D. 1973. The cat step cycle: hind limb joint angles and muscle lengths during unrestrained locomotion. *J Morphol* 141:1–42.
- Hildebrand M. 1966. Analysis of symmetrical gaits of tetrapods. *Folia Biotheor* 13:9–22.
- Hildebrand M. 1967. Symmetrical gaits of primates. *Am J Phys Anthropol* 26:119–130.
- Hildebrand M. 1968. Symmetrical gaits of dogs in relation to body build. *J Morphol* 124:353–360.
- Hildebrand M. 1976. Analysis of tetrapod gaits: general considerations and symmetrical gaits. In: Herman RM, Grillner S, Stein PSG, Stuart DC, editors. Neural control of locomotion. New York: Plenum Press. p 203–236.
- Hildebrand M. 1980. The adaptive significance of tetrapod gait selection. *Am Zool* 20:255–267.
- Hurov JR. 1982. Diagonal walking in captive infant vervet monkeys. *Am J Primatol* 2:211–213.
- Kimura T, Okada M, Ishida H. 1979. Kinesiological characteristics of primate walking: Its significance in human walking. In: Morbeck M, Preuschoft H, Gomberg N, editors. Environment, behavior and morphology: Dynamic interactions in primates. New York: Gustav Fisher. p 297–311.
- Larson SG. 1998. Unique aspects of quadrupedal locomotion in nonhuman primates. In: Strasser E, Fleagle J, editors. Primate locomotion: recent advances. New York: Plenum Press. p 157–173.
- Larson SG, Schmitt D, Lemelin P, Hamrick M. 2000. Uniqueness of primate forelimb posture during quadrupedal locomotion. *Am J Phys Anthropol* 112:87–101.
- Larson SG, Schmitt D, Lemelin P, Hamrick M. 2001. Limb excursion during quadrupedal walking: how do primates compare to other mammals? *J Zool Lond* 255:353–365.
- Lemelin P, Schmitt D, Cartmill M. 2003. Footfall patterns and interlimb co-ordination in opossums (family Didelphidae): evidence for the evolution of diagonal-sequence walking gaits in primates. *J Zool Lond* 260:423–429.
- McClearn D. 1992. Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. *J Mammal* 73:245–261.
- Nakano Y. 1996. Footfall patterns in the early development of the quadrupedal walking of Japanese macaques. *Folia Primatol (Basel)* 66:113–125.
- Peters SE. 1983. Postnatal development of gait behavior and functional allometry in the domestic cat (*Felis catus*). *J Zool Lond* 199:461–486.
- Pridmore PA. 1994. Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). *Aust J Zool* 42:679–699.
- Rollinson J, Martin RD. 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symp Zool Soc Lond* 48:377–427.
- Rose M. 1977. Positional behavior of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* 18:59–116.
- Schamhardt H, van den Bogert AJ, Hartman W. 1993. Measurement techniques in animal locomotion analysis. *Acta Anat (Basel)* 146:123–129.
- Schmitt D. 1998. Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In: Strasser E, Fleagle J, editors. Primate locomotion: recent advances. New York: Plenum Press. p 175–204.
- Schmitt D. 2003. Evolutionary implications of the unusual walking mechanics of the common marmoset (*C. jacchus*). *Am J Phys Anthropol* 122:28–37.
- Schmitt D, Lemelin P. 2002. Origins of primate locomotion: gait mechanics of the woolly opossum. *Am J Phys Anthropol* 118: 231–238.
- Stevens N. 2003. How does branch stability affect prosimian arboreal quadrupedalism? *Am J Phys Anthropol [Suppl]* 36: 200–201.
- Turnquist JE, Wells JP. 1994. Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): 1. Early postnatal ontogeny of the musculoskeletal system. *J Hum Evol* 26:487–499.
- Vilensky JA. 1989. Primate quadrupedalism: how and why does it differ from that of typical quadrupeds? *Brain Behav Evol* 34: 357–364.
- Vilensky JA, Gankiewicz E. 1989. Early development of locomotor behavior in vervet monkeys. *Am J Primatol* 17:11–25.
- Vilensky JA, Larson SG. 1989. Primate locomotion: utilization and control of symmetrical gaits. *Annu Rev Anthropol* 18:17–35.
- Vilensky JA, Gankiewicz E, Townsend D. 1988. Effects of size on vervet (*Cercopithecus aethiops*) gait parameters: a cross-sectional approach. *Am J Phys Anthropol* 76:463–480.
- Vilensky JA, Moore AM, Libii JN. 1994. Squirrel monkey locomotion on an inclined treadmill: implications for the evolution of gaits. *J Hum Evol* 26:375–386.
- White TD. 1990. Gait selection in the brush-tail possum (*Trichosurus vulpecula*), the northern quoll (*Dasyurus hallucatus*), and the Virginia opossum (*Didelphis virginiana*). *J Mammal* 71:79–84.