

Limb proportions and the ontogeny of quadrupedal walking in infant baboons (*Papio cynocephalus*)

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Abstract

Much of the diversity in preferred walking gait (footfall sequence, interlimb timing) observed among mammals can be understood as a biomechanical response to variation in body shape, in conjunction with efforts to maintain stability. Primates, unlike most other mammals, exhibit a preference for diagonal sequence, diagonal couplets (DSDC) walking gait, but there remains no clear consensus on this gait's possible biomechanical or adaptive advantages. This study examines primate gait from an ontogenetic perspective, and tests the hypothesis that ontogenetic gait transitions are influenced by changes in body shape. Support for this hypothesis could provide insight on the biomechanics and evolution of DSDC gait preferences in adult primates. Data on limb proportions, footfall sequence and interlimb timing were collected at 2-week intervals for four infant baboons (*Papio cynocephalus*) as they aged from 1 to 9 months. Despite some variation among individuals, DSDC walking was the most frequently used gait throughout the developmental period, but it was nearly always used in combination with lateral sequence walking. An important transition occurred at *c.* 5 months, when limb couplets used in lateral sequence walking shifted from diagonal to lateral, and the frequency of DSDC walking increased. The couplets shift within lateral sequence walking coincided with a relative increase in hind limb length, and was most likely attributable to the avoidance of ipsilateral limb interference. Limb proportions thus appear to have a functional influence on lateral sequence walking, but do not explain the consistent use of DSDC walking during the sampled developmental period.

Introduction

The diversity of quadrupedal walking gaits utilized by mammals has been well documented and quantified, due in large part to Muybridge's (1887, 1957) early photography of animal locomotion and Hildebrand's extensive quantitative analyses of tetrapod footfall sequences and interlimb timing (Hildebrand, 1966, 1967, 1968, 1976, 1980). Quantitative approaches to gait have facilitated broad, interspecific comparisons of gait types utilized by mammals (see Cartmill, Lemelin & Schmitt, 2002 for a recent view), and have allowed us to ask the compelling question 'Why do mammals differ in the walking gaits that they prefer?' This question is of particular interest to the study of primate adaptation and evolution, because primates prefer diagonal sequence, diagonal couplets (DSDC) walking, a relatively unusual gait among mammals (Hildebrand, 1967, 1976).

Hildebrand (1966, 1976) described walking gaits by quantifying footfall sequence and interlimb timing (couplets) in relation to speed. For example, in a lateral sequence walk, a foot touches the ground, followed by the same-side or ipsilateral hand. In a diagonal sequence walk, a foot

touches the ground, followed by the contralateral or opposite-side hand. Either sequence can be characterized by lateral or diagonal couplets. When couplets are lateral, the ipsilateral forelimb and hind limb swing and land close together in time. When couplets are diagonal, the movements of the contralateral forelimb and hind limb are related in time. The gaits most commonly utilized by mammals are lateral sequence, diagonal couplets (LSDC) and lateral sequence, lateral couplets (LSLC). DSDC walks are less common among mammals, and diagonal sequence, lateral couplets (DSLCL) walks are essentially never used. Mammals also utilize walking gaits in which ipsilateral (pace) or contralateral (trot) forelimbs and hind limbs land simultaneously, or in which all four limbs are equally spaced in time (single-foot, in lateral or diagonal sequence; Hildebrand, 1966, 1976).

Hildebrand (1980, p. 258; see also Gray, 1944) addressed the adaptive value of gait selection by noting that mammals and other tetrapods prefer walking gaits that maximize stability by '(1) maximizing support by four feet, (2) minimizing support by two feet' and '(3) selecting the combinations of two and three feet that are favorable to balance.'

Specifically, he noted that lateral sequence gaits provide larger, more stable tripods of support than do diagonal sequence gaits, and diagonal couplets provide more stable (contralateral) bipods of support compared with the ipsilateral bipods of support accompanying lateral couplets. On the basis of these factors, it is easy to see why stable, LSDC gaits (large tripods of support, with periods of support by contralateral bipods) are common, whereas unstable, DSLC gaits (small tripods of support, with periods of support by ipsilateral bipods) are avoided. In terms of overall stability, it is less obvious why some tetrapods prefer LSLC gaits (stable, large tripods combined with less stable ipsilateral bipods) or DSDC gaits (unstable small tripods combined with more stable contralateral bipods). However, this type of static stability may be critical only at very slow walking velocities. As velocity increases, dynamic stability (Full *et al.*, 2002) may permit any of these footfall sequences to be manageable. For example, the tendency to roll toward the unsupported size when using ipsilateral bipods of support (Hildebrand, 1980) may be minimized at all but the very slowest velocities. Gait preferences can also be understood, however, by considering factors other than overall stability, such as the influence of body shape.

The role of body shape in gait selection is well exemplified by the relationship between relative limb length and a preference for LSLC walking. The functional advantage of LSLC walking is best understood in terms of its avoidance of hind limb–forelimb interference. Because ipsilateral limbs swing and land nearly simultaneously in LSLC walking, there is little to no possibility that the hind limb will contact the ipsilateral forelimb, or that the hind limb's stride will be shortened (i.e. the forelimb is positioned well ahead of the hind limb). This is, of course, particularly true for the pace, in which ipsilateral limbs swing and land simultaneously (Blaszczyk & Loeb, 1993). In contrast, the potential for ipsilateral interlimb interference is higher for LSDC walking, and very high for DSDC walking. For this reason, LSLC gaits (and the related pace) are typical of mammals with long limbs (e.g. long-legged rodents, felids, canids, bovids, camelids, etc.), especially those with long legs relative to trunk width, because the feet can be placed underneath the midline of the body, minimizing the tendency to roll laterally (Hildebrand, 1976, 1980; see Janis, Theodor & Boisvert, 2002 on unique adaptations to lateral stability in pacing camelids). The relationship of limb length to the use of LSLC walking is also evident on an intraspecific level: LSLC walks (and the pace) are used more often by long-legged domesticated dogs than by short-legged ones (Hildebrand, 1968).

Adult primates are among only a small subset of mammals (kinkajous, giant armadillos, aardvarks and some arboreal marsupials) known to prefer DSDC walking (Hildebrand, 1976; Vilensky, 1989; Vilensky & Larson, 1989; White, 1990; Pridmore, 1994; Larson, 1998; Schmitt & Lemelin, 2002; Lemelin, Schmitt & Cartmill, 2003). DSDC walking is hampered by small support tripods and major interference between ipsilateral hind and forelimbs. Hilde-

brand (1980) noted that animals using DSDC walks have relatively large feet or a wide stance, mitigating the relatively unstable configuration of this gait (especially at slow velocities), while Prost (1969) noted that small support tripods cannot be formed on arboreal supports and so are of no consequence to DSDC walking in primates (see also Cartmill, Lemelin & Schmitt, in press). Nevertheless, any adaptive advantage provided by this gait has remained difficult to determine. In an effort to understand the evolution of DSDC walking in primates, researchers have addressed possible biomechanical and ecological advantages to this gait (Prost, 1965, 1969; Rollinson & Martin, 1981; Li, 2000; Cartmill *et al.*, 2002, in press; Lemelin *et al.*, 2003; Shapiro & Raichlen, 2005). DSDC walking has also been presented as a neurological by-product of adaptations directed at other limb functions (Vilensky & Larson, 1989; but see Vilensky, Moore & Libii, 1994), but there remains no consensus on why primates prefer this unusual type of gait.

One key to understanding primate quadrupedal gait lies in a consideration of locomotor ontogeny (Hurov, 1991). The limited number of studies available on locomotor ontogeny in primates has indicated that infant primate quadrupeds do not share with adults a clear preference for DSDC walking. Some studies show that the earliest quadrupedal walking gait is lateral sequence (Hildebrand, 1967; Hurov, 1982; Vilensky & Gankiewicz, 1989); others document early locomotion as a combination of lateral and diagonal sequence gaits (Rose, 1977; Rollinson & Martin, 1981; Nakano, 1996; Dunbar & Badam, 1998; Shapiro & Raichlen, 2005). As is the case for evolutionary explanations for primate gait, both biomechanical and neurological explanations have been offered to explain the developmental shift in primates to an adult-like preference for DSDC gait (Rollinson & Martin, 1981; Hurov, 1982; Vilensky, 1989; Vilensky & Gankiewicz, 1989; Nakano, 1996; Dunbar & Badam, 1998). Although these explanations are not mutually exclusive, biomechanical analyses of locomotor ontogeny have been de-emphasized, and investigations of ontogenetic changes in primate gait patterns have for the most part remained separate from those documenting developmental changes in body shape and size.

Infant primates experience dramatic changes in body size and shape across a relatively short period of time, especially within the first year of life (Lumer & Schultz, 1941; Grand, 1977; Jungers & Fleagle, 1980; Turnquist & Wells, 1994; Ruff, 2003; Raichlen, 2005*b*). Therefore, it seems reasonable to propose that gait transitions throughout nonhuman primate locomotor development may be influenced by physical changes in body structure, such as limb proportions, limb mass distribution and/or the location of the body's center of mass. The influence of biomechanical factors on locomotor ontogeny has been supported by studies of other mammals (e.g. Carrier, 1983; Eilam, 1997; Hamrick, 1999; Muir, 2000; Lammers & German, 2002) and is also well recognized in the human developmental literature (e.g. Thelen, Fisher & Ridley-Johnson, 1984; Jensen *et al.*, 1994; Jensen & Bothner, 1998; Adolph, Vereijken & Shrout, 2003).

The purpose of this study was to document and quantify transitions in walking gait and limb proportions in a longitudinal sample of infant baboons (*Papio cynocephalus*) in order to test the hypothesis that limb proportions in primates influence gait transitions during ontogeny. (This study focuses on limb proportions as one component of our broader analysis assessing other biomechanical influences on gait, including body mass distribution.) A functional correspondence between changes in body shape and gait preferences during infant development could shed light on the morphological factors that might have contributed to the evolution of DSDC gait preferences in adult primates. While the development or evolution of complex motor behaviors (such as footfall sequence) is undoubtedly a result of the interaction between neurological and biomechanical mechanisms, determining how each factor may influence the emergence of a new behavior is essential for a complete understanding of locomotion.

Methods

All methodological procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Texas at Austin.

Kinematic data: footfall sequence and limb couplets

Kinematic data during quadrupedal walking were collected for four *P. cynocephalus* infants, three females and one male, *c.* every 2 weeks. Subjects were captive-reared, on loan from the Southwest Foundation for Biomedical Research (SFBR) in San Antonio, Texas. Subjects were not pulled from their mothers for this study. Rather, each had already been rejected by its mother and housed in a nursery at SFBR before transfer to the University of Texas at Austin Animal Resources Center. The age span varied slightly across subjects (Table 1), but the sample as a whole includes data collected between the ages of 2 and 9 months. Tables 1 and 2 list sample sizes of strides used in the analysis.

Subjects were filmed at 60 frames s^{-1} with a digital video camcorder (JVC GR-DVL9800). Subjects walked freely through a $2 \times 3 \times 10$ ft tunnel constructed of clear plastic (Lexan, GE Plastics, Pittsfield, Massachusetts, USA). The tunnel was used to encourage forward walking, but it should be noted that collection of kinematic data did not require the camera 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 hind limb on the same side of the body). Divisions between named gaits (e.g. DSDC, LSDC, etc.) are a slight modification of Hildebrand's divisions and follow that of Cartmill *et al.* (2002). Specifically, a gait number of 0 (or 100) corresponds to a pace, gait numbers 1–24 correspond to LSLC, gait number 25 corresponds to lateral

sequence, single-foot (LSSF), gait numbers 26–49 correspond to LSDC, gait number 50 is a trot, gait numbers 51–74 correspond to DSDC, gait number 75 corresponds to diagonal sequence, single-foot (DSSF) and gait numbers 76–99 correspond to DSLC. Only symmetrical walking gaits were included. Walking gaits were defined as those in which the hind limb duty factor (the percentage of a stride's duration that a hind limb is on the ground) was greater than or equal to 50 (Hildebrand, 1966). In a perfectly symmetrical walk, a hind limb contacts the ground at exactly 50% of the interval of time between footfalls of the contralateral hind limb (Hildebrand, 1966). Because perfect symmetry is rare, we accepted strides in which the symmetry value was between 45 and 55%.

Morphometric data

Limb proportions of each subject were measured during the same week as kinematic data were collected, on the same four subjects, *c.* every 2 weeks. Morphometric data span the ages of 0.7–9 months, beginning slightly earlier than locomotor data. The earlier starting point for morphometric data compared with gait data reflects the difficulty in obtaining consistent locomotion from infants younger than 2 months. Length measurements were taken with a cloth measuring tape.

Length measurements were used to calculate the following inter- and intralimb proportions: forelimb length = AL + FL (+HL), hind limb length = TL + LL (+FTL) and intermembral index (calculated with and without hands and feet) = (forelimb length/hind limb length) \times 100, where AL is arm length, FL is forearm length, HL is hand length, TL is thigh length, LL is leg length and FTL is foot length. See Table 3 for definitions of segment measurements. Relative limb and segment lengths were calculated by dividing the length of each limb and limb segment by the cube root of body mass.* Because body mass has a direct relationship with volume, it is proportional to the third power of linear dimensions. Therefore, expressing body mass as a cube root puts it into comparable units with linear measurements (Sneath & Sokal, 1973; Jungers, 1985; Vogel, 1988).

Statistical analysis

Raw gait numbers as well as frequencies of gait types (i.e. footfall sequence, limb couplets) were examined for their relationship with changes in age. Relationships among raw

*At each measurement session, subjects were weighed on a scale and body mass was recorded. In addition to weighing the subjects, lengths and circumferences of limbs and trunk in conjunction with head measurements were used to calculate the mass of each body segment using a geometric model (Raichlen, 2004a,b; see Crompton *et al.*, 1996). Body mass was then calculated as the sum of all segment masses. Because of technical problems with the scale on a few occasions, we chose to utilize modeled body masses in this study. For sessions during which we obtained both types of data, we found a close correlation between measured body mass and modeled body mass (see Raichlen, 2004a).

Table 1 Sample sizes (*n*) and counts (frequencies) of walking strides for each gait type

Age (months)	<i>n</i>	Pace	LSLC	LSSF	LSDC	Trot	DSDC	DSSF	DSLCL
<i>Infant 1 (ID 17194), Papio cynocephalus (M)</i>									
2.6	4	0 (0)	0 (0)	0 (0)	4 (100)	0 (0)	0 (0)	0 (0)	0 (0)
3.3	11	0 (0)	0 (0)	0 (0)	0 (0)	1 (9)	8 (73)	1 (9)	1 (9)
3.6	8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	8 (100)	0 (0)	0 (0)
4.3	7	0 (0)	0 (0)	0 (0)	4 (57)	0 (0)	3 (43)	0 (0)	0 (0)
4.7	19	0 (0)	4 (21)	2 (11)	2 (11)	0 (0)	11 (58)	0 (0)	0 (0)
5.9	35	0 (0)	1 (3)	0 (0)	1 (3)	0 (0)	33 (94)	0 (0)	0 (0)
6.1	34	0 (0)	2 (6)	0 (0)	2 (6)	1 (3)	29 (85)	0 (0)	0 (0)
6.6	28	0 (0)	1 (4)	0 (0)	2 (7)	0 (0)	25 (89)	0 (0)	0 (0)
7.0	35	0 (0)	4 (11)	0 (0)	0 (0)	0 (0)	31 (89)	0 (0)	0 (0)
7.5	26	0 (0)	2 (8)	0 (0)	1 (4)	0 (0)	23 (88)	0 (0)	0 (0)
Total number	207	0	14	2	16	2	171	1	1
Total frequency		0	7	1	8	1	83	0	0
<i>Infant 2 (ID 18573), P. cynocephalus (F)</i>									
2.0	22	0 (0)	0 (0)	0 (0)	5 (23)	0 (0)	16 (73)	0 (0)	1 (5)
2.8	19	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	17 (89)	0 (0)	1 (5)
3.7	15	0 (0)	0 (0)	0 (0)	4 (27)	0 (0)	11 (73)	0 (0)	0 (0)
4.1	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)
4.7	16	0 (0)	0 (0)	0 (0)	0 (0)	1 (6)	14 (88)	0 (0)	1 (6)
5.0	23	0 (0)	2 (9)	0 (0)	1 (4)	0 (0)	20 (87)	0 (0)	0 (0)
5.5	5	0 (0)	1 (20)	0 (0)	0 (0)	0 (0)	4 (80)	0 (0)	0 (0)
6.9	3	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (100)	0 (0)	0 (0)
7.4	12	0 (0)	1 (8)	0 (0)	0 (0)	0 (0)	11 (92)	0 (0)	0 (0)
8.1	14	0 (0)	1 (7)	0 (0)	0 (0)	0 (0)	13 (93)	0 (0)	0 (0)
8.9	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)
Total number	133	0	5	0	11	1	113	0	3
Total frequency		0	4	0	8	1	85	0	2
<i>Infant 3 (ID 18572), P. cynocephalus (F)</i>									
2.9	2	0 (0)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)
3.7	1	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
4.2	2	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)
4.7	11	0 (0)	1 (9)	2 (18)	6 (55)	0 (0)	1 (9)	1 (9)	0 (0)
5	10	0 (0)	2 (20)	0 (0)	2 (20)	0 (0)	6 (60)	0 (0)	0 (0)
5.6	10	0 (0)	4 (40)	0 (0)	3 (30)	0 (0)	3 (30)	0 (0)	0 (0)
6.2	21	0 (0)	6 (29)	0 (0)	1 (5)	0 (0)	14 (67)	0 (0)	0 (0)
7.4	32	0 (0)	5 (16)	0 (0)	1 (3)	0 (0)	26 (81)	0 (0)	0 (0)
8.1	31	0 (0)	10 (32)	0 (0)	0 (0)	0 (0)	21 (68)	0 (0)	0 (0)
9.0	52	0 (0)	11 (21)	0 (0)	0 (0)	0 (0)	41 (79)	0 (0)	0 (0)
Total number	172	0	40	2	17	0	112	1	0
Total frequency		0	23	1	10	0	65	1	0
<i>Infant 4 (ID 17220), P. cynocephalus (F)</i>									
2.4	9	0 (0)	0 (0)	0 (0)	9 (100)	0 (0)	0 (0)	0 (0)	0 (0)
2.6	5	0 (0)	0 (0)	0 (0)	5 (100)	0 (0)	0 (0)	0 (0)	0 (0)
3.1	5	0 (0)	0 (0)	0 (0)	5 (100)	0 (0)	0 (0)	0 (0)	0 (0)
3.3	1	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
4.0	4	0 (0)	1 (25)	0 (0)	3 (75)	0 (0)	0 (0)	0 (0)	0 (0)
4.5	9	0 (0)	9 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
5.6	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
5.8	13	0 (0)	12 (92)	0 (0)	1 (8)	0 (0)	0 (0)	0 (0)	0 (0)
6.3	8	0 (0)	8 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6.8	6	0 (0)	3 (50)	0 (0)	2 (33)	0 (0)	1 (17)	0 (0)	0 (0)
7.2	15	0 (0)	13 (87)	1 (7)	1 (7)	0 (0)	0 (0)	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

DSLCL, diagonal sequence, lateral couplets; DSDC, diagonal sequence, diagonal couplets; LSDC, lateral sequence, diagonal couplets; LSLC, lateral sequence, lateral couplets; LSSF, lateral sequence, single-foot; DSSF, diagonal sequence, single-foot.

Table 2 Sample sizes (*n*) and counts (frequencies) of walking strides for each gait type for all *Papio cynocephalus* infants combined

Age	<i>n</i>	Pace	LSLC	LSSF	LSDC	Trot	DSDC	DSSF	DSLC
All months (2–9)	588	0 (0)	106 (18)	5 (1)	71 (12)	3 (1)	397 (68)	2 (<1)	4 (1)
Less than 5 months	172	0 (0)	16 (9)	4 (2)	53 (31)	2 (1)	91 (53)	2 (1)	4 (2)
5–9 months	416	0 (0)	90 (22)	1 (<1)	18 (4)	1 (<1)	306 (74)	0 (0)	0 (0)

DSLC, diagonal sequence, lateral couplets; DSDC, diagonal sequence, diagonal couplets; LSDC, lateral sequence, diagonal couplets; LSLC, lateral sequence, lateral couplets; LSSF, lateral sequence, single-foot; DSSF, diagonal sequence, single-foot.

Table 3 Measurements of limb segments

Segment	Proximal point	Distal point
Arm	Between the acromion process of the scapula and the greater tubercle of the humerus	Most proximal edge of the radial head
Forearm	Most proximal edge of the radial head	Styloid process of the radius
Hand	Styloid process of the distal radius	End of the longest digit
Thigh	Greater trochanter	Caudal edge of the lateral condyle of the femur
Leg	Proximal edge of the lateral tibial condyle	Lateral malleolus of the fibula
Foot	Posterior edge of the calcaneus	Tip of the longest digit

gait numbers, age and duty factor were tested using the nonparametric Kendall's coefficient of rank correlation and analysis of covariance (ANCOVA). Differences in the relative frequencies of gait types were tested using a *G*-test of independence with the Williams correction (Sokal & Rohlf, 1995). Significance level was set to 0.05.

Age trends with respect to limb proportions were examined using nonparametric, locally weighted regression (Loess). Loess is a multivariate smoothing technique that fits a low-degree polynomial to a subset of the data, giving more weight to points close to each other than to outliers (Cleveland, 1979; Cleveland & Devlin, 1988; Hen *et al.*, 2004). Loess is similar to a moving average, but is much more robust with respect to outliers, and therefore useful for growth data that are irregularly spaced and subject to interindividual variation (Moses, Gale & Altmann, 1992; Leigh, 1996; Koppe, Swindler & Lee, 1999; Ruff, 2003). For all Loess regressions, the polynomial degree was 1, the smoothing parameter (bandwidth) was 0.5 and the weight function was tricube (Cleveland, 1979). The *G*-test and ANCOVA were calculated using Biomstat 3.30 (Exeter Software). Kendall's rank correlations were calculated using XLSTAT 7.5 (Addinsoft) and Loess was calculated with SAS (Version 8.2).

Results

Gait frequencies

The results of the gait analysis indicated variability in foot-fall sequence and limb couplets across ages within subjects

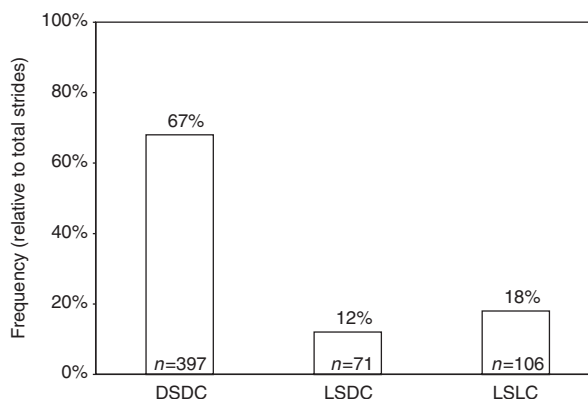


Figure 1 Frequency of gait types used relative to all walking strides (*n*=588) observed across all age categories, by all infant *Papio cynocephalus* subjects (*n*=4). DSDC, diagonal sequence, diagonal couplets; LSDC, lateral sequence, diagonal couplets; LSLC, lateral sequence, lateral couplets. Gait types not shown represent 3% of the total strides observed (see Table 2).

as well as across subjects. Before addressing variation among individual subjects, it is informative to examine the data across all infants (Figs 1–3, Table 2).

All infants combined

When all walking strides were combined for all infants at all ages (*n* = 588), the most frequently utilized gait was DSDC (67%). The only other two gait types utilized in appreciable frequencies were LSDC (12%) and LSLC (18%) (Fig. 1). This result confirms that infant primates (and even adult primates; see Vilensky & Larson, 1989) do not rely exclusively on one type of walking gait. However, calculating total frequencies without regard to age masks a very prominent pattern in the variation of gait type. That is, when data for all walking strides among all subjects are plotted against age (Fig. 2), it becomes evident that age makes a difference with respect to gait-type frequencies. Table 4 lists the correlation coefficients for age against gait number. For all gait numbers combined, there is a small, but significant correlation with age. When only trots and diagonal sequence gait numbers (50–99) are considered, gait number is not significantly correlated with age. More notably, when only lateral sequence gait numbers (1–49) are considered, gait number is well correlated (negatively) with age ($\tau = -0.39$; $P \leq 0.01$). In other words, although DSDC walking was utilized throughout the developmental

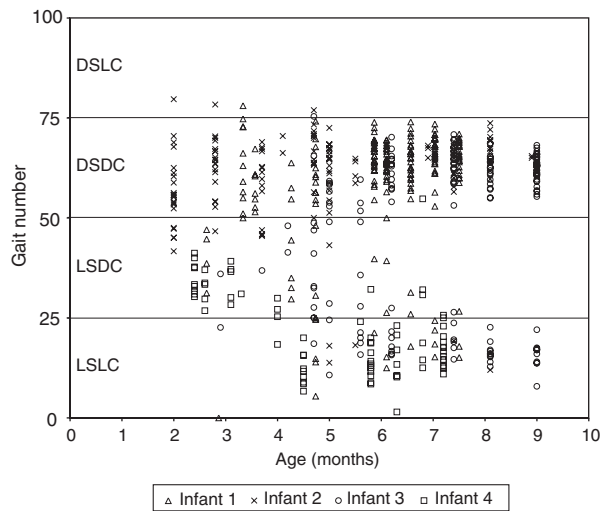


Figure 2 Gait number for all strides plotted against age, for all infant *Papio cynocephalus* subjects. DSLC, diagonal sequence, lateral couplets; DSDC, diagonal sequence, diagonal couplets; LSDC, lateral sequence, diagonal couplets; LSLC, lateral sequence, lateral couplets.

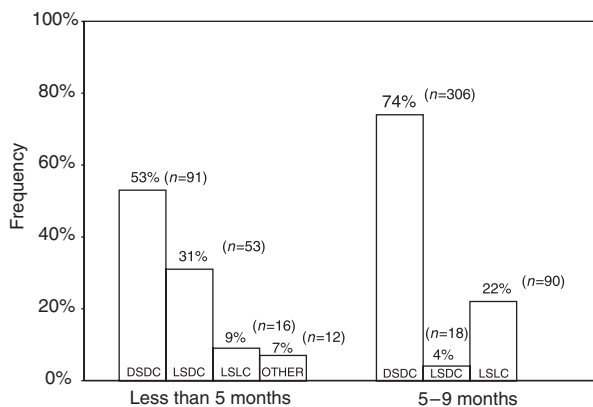


Figure 3 Frequency of gait types used by all infant *Papio cynocephalus* subjects, in two age categories. Frequencies were calculated by dividing the total number of strides for each gait type by the total number of strides observed in each age category ($n = 172$ for less than 5 months; $n = 416$ for 5-9 months). Abbreviations as in Fig. 1.

period explored in this study (by three out of four infants; see below), the developmental timing of the two types of lateral sequence gaits (LSDC, LSLC) differed markedly.

Before 5 months, approximately half (53%) of all strides used by all infants were DSDC. Of the remaining strides, LSDC was the most preferred (31%). LSLC was used very infrequently before 5 months (9% of all strides), as were other gaits (7%) (Fig. 3). At or after 5 months, most (74%) strides used were DSDC. Of the remaining strides, the preferences for LSDC and LSLC were reversed compared with earlier ages. That is, of the non-DSDC strides used at 5 months or older, 22% were LSLC and only 4% were LSDC (Fig. 3). Age has a significant influence on the frequency of gait type used [$G(\text{Williams}) = 80.9, P \leq 0.001$].

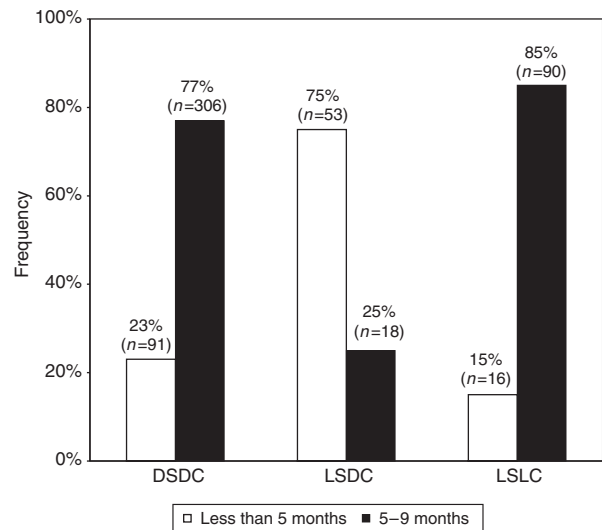


Figure 4 Frequency of each gait type relative to age category, all infant *Papio cynocephalus* subjects combined. Frequencies were calculated by dividing the total number of strides for each gait type in each age category by the total number of strides observed for that gait type: DSDC ($n = 397$), LSDC ($n = 71$), LSLC ($n = 106$). For example, of all DSDC gaits used across the sample ($n = 397$), 77% of those ($n = 306$) were used between 5 and 9 months of age. Abbreviations as in Fig. 1.

In other words, the infants as a group utilized a substantial amount of DSDC gaits throughout the developmental period, especially at or after 5 months, when 77% of all DSDC gaits were used (Fig. 4). Of great interest, though, is the change in style of lateral sequence walking with age. *Within* lateral sequence gaits, lateral couplets were utilized more frequently than diagonal couplets at and after 5 months of age. More specifically, 75% of all instances of LSDC gait were documented *before* 5 months of age, whereas 85% of all instances of LSLC gait appeared at 5 months of age or *later* (Fig. 4).

Individual infants

The relative gait frequencies and patterns of gait transitions with age that describe all infants combined are not characteristic of each individual infant when considered separately (Table 1). However, the patterns specific to each infant do not contradict the overall trend described above: specifically, the shift within lateral sequence from diagonal couplets to lateral couplets at or after 5 months. Infants 1 and 2 (Fig. 5a, b) exhibit a pattern similar to that summarized for all infants: DSDC throughout much of the developmental window, with LSDC shifting to a preference for LSLC after *c.* 5 months, although these two infants used lateral sequence gaits fairly infrequently on the whole. Infant 3 (Fig. 5c) also exhibits the shift from LSDC to LSLC near the 5-month mark, but has a delayed use of DSDC compared with infants 1 and 2. (It is possible that the lack of DSDC strides before 5 months may be a reflection of the relatively small sample of strides for infant 3 at those young

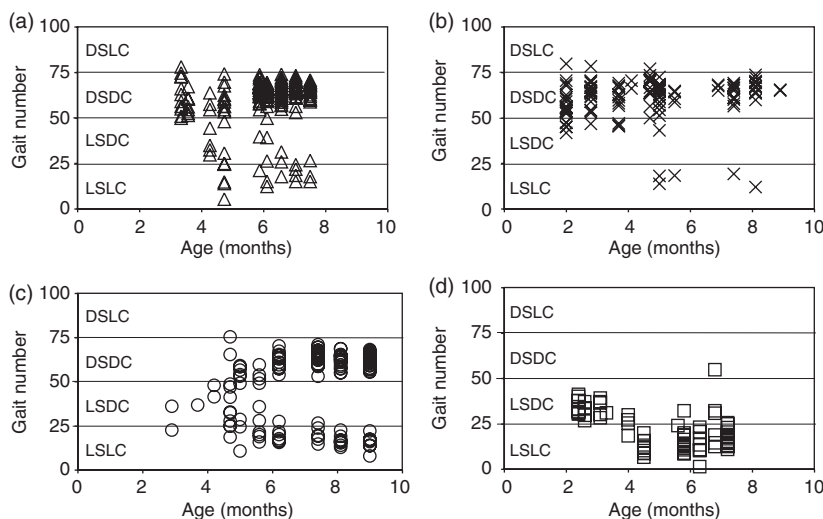


Figure 5 Gait number plotted against age for (a) infant 1, (b) infant 2, (c) infant 3 and (d) infant 4. See also Table 1. Abbreviations as in Fig. 2.

ages.) Infant 4 essentially never utilized diagonal sequence gait (Table 1, Fig. 5d), but its shift from predominantly LSDC to LSLC after 5 months is consistent with the combined sample pattern. In short, although there is variability among infants in their gait preferences and age-related changes, and although the pattern for infant 4 is essentially a portion of the total pattern described for the group as a whole, no infant shows a pattern that reverses or contradicts the basic finding. That is, within lateral sequence, no infant shows a preference for lateral couplets before 5 months or a preference for diagonal couplets after 5 months.

Effects of walking speed

In order to assess whether or not differences in walking speed could account for variation in gait number with age (particularly, the shift from LSDC to LSLC), we tested whether or not duty factor (which is inversely related to speed; see Hildebrand, 1976; Vilensky, Gankiewicz & Townsend, 1988) was correlated with gait number or age. There is a slight, but significant positive correlation of duty factor with gait number when LS gaits and DS gaits are considered together or separately (Table 4). Nevertheless, Fig. 6 shows clearly that there is much overlap of gait number at all duty factors sampled.

Duty factor showed a slight, but significant negative correlation with age for LS but not DS gaits, indicating that older animals tended to walk slightly faster, but only during LS gaits. Combined with the slight positive correlation of duty factor with gait number within LS gaits (walking faster is associated with a tendency toward lateral couplets), these results imply that speed might have had a slight influence on the correlation of age and gait number within LS walking (Table 4). However, given the extensive overlap in duty factors used across the ages sampled, we conclude that walking speed alone cannot account for the dramatic shift from LSDC to LSLC walking observed in our sample. In

Table 4 Kendall's coefficient of rank correlation (τ): all infants combined

	All gaits	LS only	DS only
Age versus gait number	0.07*	-0.39*	0.04 NS
Duty factor versus gait number	0.10*	0.13*	0.18*
Duty factor versus age	-0.09*	-0.17*	-0.05 NS

*Significant at $P \leq 0.01$.

NS, not significant at the 0.05 level.

LS, lateral sequence; DS, diagonal sequence.

fact, an analysis of covariance indicates that age has a significant effect on gait number within LS gait, even after variation in duty factor is taken into account ($F = 9.84$, d.f. = 30, $P \leq 0.05$).

Intermembral index, limb and segment lengths

All infants combined

When all infant data were combined, the intermembral index showed an interesting pattern of variation with age (Fig. 7). In the combined sample, the intermembral index first exhibited a decrease and then a less pronounced increase during the observed developmental period. The pattern is similar whether or not hands and feet are included in the calculation. The intermembral index decreased to its lowest value between 5 and 6 months of age. The decrease in intermembral index between 1 and 5–6 months was driven by an increase in relative hind limb length and a decrease in relative forelimb length, with the hind limb becoming much longer in relative length than the forelimb between 5 and 6 months (Fig. 8). The decrease in relative forelimb length between 1 and 5–6 months is due mainly to a relative decrease in length of the hand (Fig. 9). Although the thigh and leg both increase in relative length between 1 and

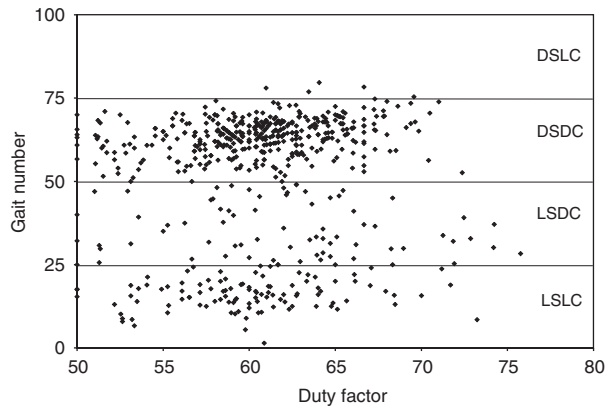


Figure 6 Gait number plotted against duty factor for all strides ($n=588$), all infant *Papio cynocephalus* subjects ($n=4$).

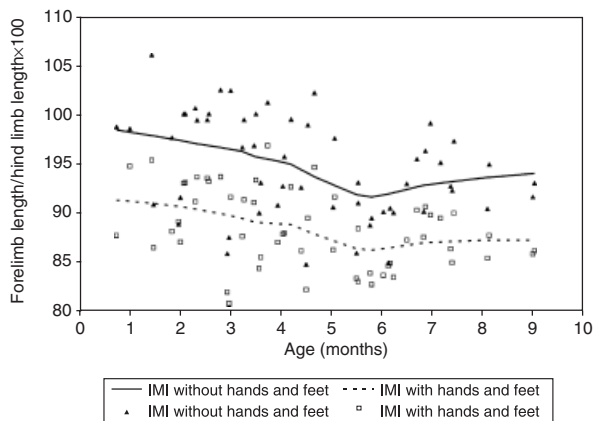


Figure 7 Intermembral index, calculated with and without hands and feet, plotted against age for all infant *Papio cynocephalus* subjects. Data are fitted with Loess.

3 months (while the relative foot length decreases), the dramatic increase in relative hind limb length as age approaches 5 months is driven by a prominent increase in relative thigh length at this time (Fig. 10).

Individual infants

Figure 11 illustrates the variation in ontogenetic changes in limb proportions (intermembral index) when individual infants are plotted separately. Infants 1 and 4 show the clearest resemblance to the pattern of all infants combined, with the drop in intermembral index in infant 1 slightly delayed compared with that of infant 4. As infant 1 is the only male in the sample, this difference might reflect sexual dimorphism in growth rates, but given the young ages sampled here, interindividual variation is a more likely explanation (e.g. Coelho, 1985; Setchell *et al.*, 2001; Bolter & Zihlman, 2003). A larger sample would be needed to draw any conclusions in this regard. The pattern for infant 2 generally resembles that for infants 1 and 4, with an overall

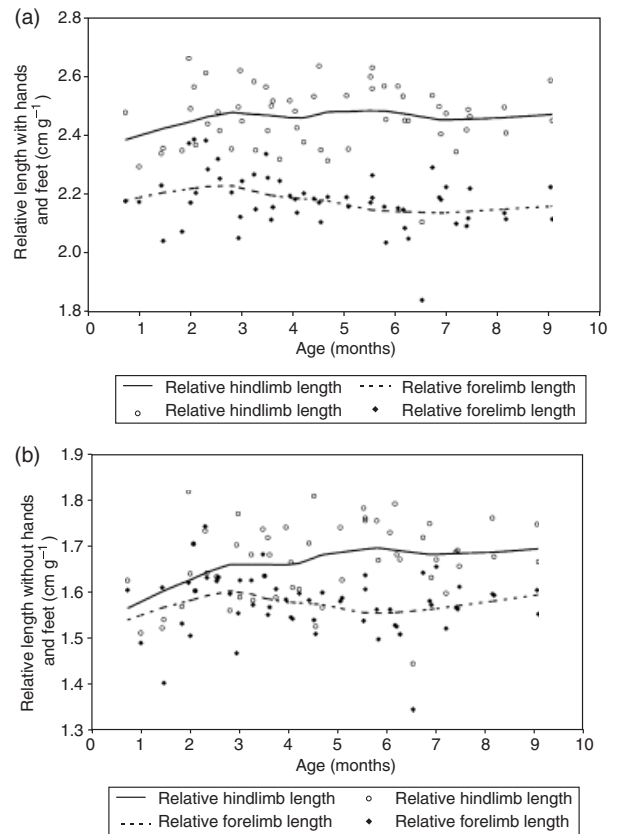


Figure 8 Relative hind limb and forelimb length plotted against age for all infant *Papio cynocephalus* subjects. Data are fitted with Loess. Relative limb length values were calculated (a) with hands and feet and (b) without hands and feet.

drop in intermembral index between 1 and 5 months, but the data for infant 2 fluctuate more erratically than those of infants 1 and 4. Infant 3, like the others, exhibits a drop in intermembral index near the 5-month mark. However, unlike the other infants, infant 3 exhibited an *increase* rather than a decrease in intermembral index between *c.* 2 and 5 months. The discrepancy between infant 3 and the other three infants is difficult to interpret in the context of this small sample size. Infant 3's values for intermembral index might be a function of measurement error, or may represent a true biological difference. Either way, the uniqueness of infant 3 in this regard is not substantial enough to influence the overall trend present when all infants are combined (Fig. 7).

Discussion

The results of this study indicate that before the age of 5 months (and as early as 2 months), infant baboons are capable of walking in DSDC gait, the gait preferred by adult primates. The use of this gait continued throughout the sampled developmental time period (up to 9 months). The study also revealed variability among individuals. Some infants used DSDC walking more frequently than others,

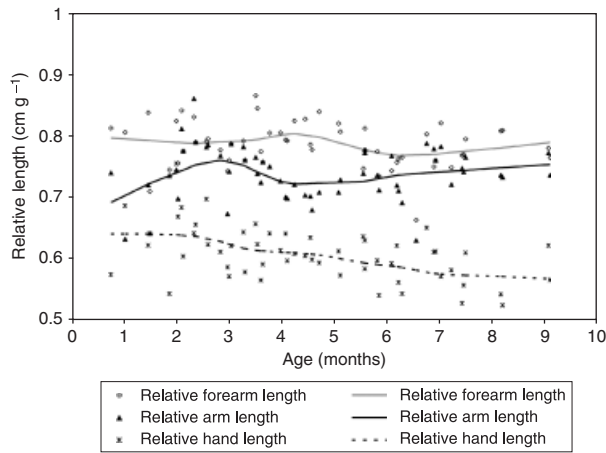


Figure 9 Relative forelimb segment lengths plotted against age for all infant *Papio cynocephalus* subjects. Data are fitted with Loess.

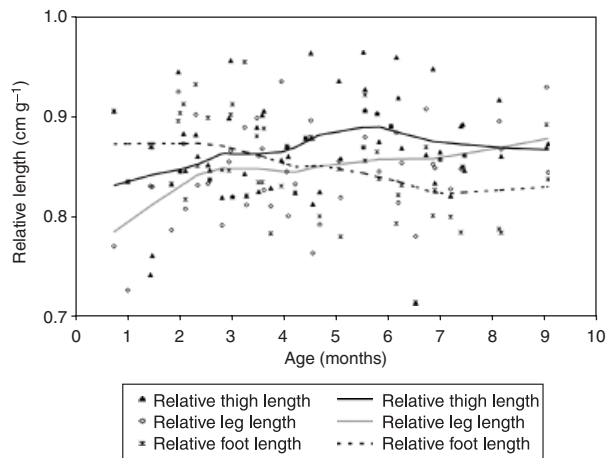


Figure 10 Relative hind limb segment lengths plotted against age for all infant *Papio cynocephalus* subjects. Data are fitted with Loess.

and one essentially never used DSDC walks. Yet, when DSDC walking was used, it was almost always used in combination with LS gaits, and when LS gaits were used, all infants showed a preference for diagonal couplets before 5 months and lateral couplets after 5 months. The combined use of DS and LS walking in this developmental time period is consistent with data reported for macaques (Hildebrand, 1967; Nakano, 1996) and vervets (Hurov, 1982; Vilensky & Gankiewicz, 1989).

Data reported on primates at ages younger than 2 months are less consistent. Some studies report the predominant use of LS walking, with DS walking rare or nonexistent (Hildebrand, 1967; Hurov, 1982; Vilensky & Gankiewicz, 1989), while at least one study reports the opposite (Nakano, 1996). Inconsistency of gait data collected at ages less than 2 months is likely related to the fact that muscle strength and postural control mechanisms are not well developed at this time (e.g. Vilensky & Gankiewicz, 1989) and sample sizes for walking strides are often small. We could not coax consis-

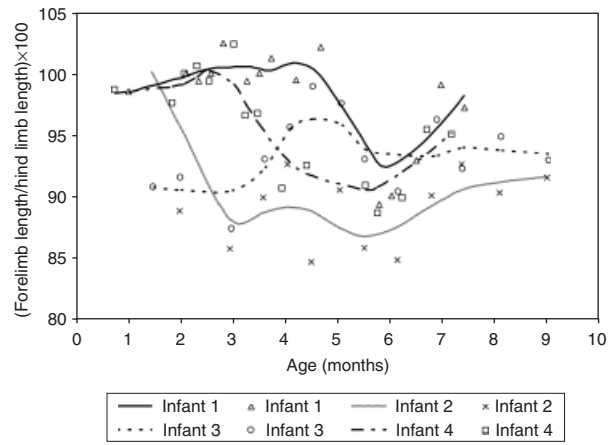


Figure 11 Intermembral index calculated without hands and feet, plotted against age for each subject. Data are fitted with Loess. Intermembral index calculated with hands and feet (not shown) shows similar trends.

tent locomotion from our subjects when they were younger than 2 months, an age at which, in the wild, infant baboons spend most of their time clinging to their mother (Altmann, 1980). Therefore, although our study cannot address ‘initial’ locomotion in baboons, we can address the factors that might contribute to locomotor transitions after 2 months.

In our four subjects, the marked shift from the use of LSDC walking gait to LSLC walking gait at *c.* 5 months coincides with a relative lengthening of the hind limbs and a concomitant decrease of the intermembral index. This is true for all infants, despite infant 3’s unique transitions in intermembral index before 4 months or infant 4’s absence of DSDC walking. In other words, in *all* infants, intermembral index decreases near the time when LSLC becomes preferred over LSDC. Further research with an expanded sample size is likely to confirm the basic patterns common to our four subjects.

Developmental studies of other taxa show some parallels to these results. For example, kittens begin their locomotor development walking in lateral sequence diagonal couplets, but shift to LSLC (or the pace) at 8 weeks, when their hind limbs reach a peak in relative length (Peters, 1983). The data on kittens are a compelling argument for the effects of body shape and mechanical constraints on gait; 8-week-old kittens are as neurologically mature as adults, but utilize gaits closer to the pace than adults (Peters, 1983).

No other study of nonhuman primates has directly addressed the possible influence of limb proportions on gait choice during development, but, intriguingly, separate studies on the ontogeny of gait (Nakano, 1996) and body proportions (Turnquist & Wells, 1994) in infant macaques point to an association between limb proportions and walking gait preference. Specifically, Nakano’s (1996) infant macaques utilized DSDC walking combined with other gaits throughout the developmental period tested (1–39 weeks). LSLC walks, however, were not observed until *c.* 6.5 months (although gaits were not sampled at 4 or 5 months) and were

still being used at almost 10 months. In a separate study, Turnquist & Wells (1994) found that the intermembral index of infant macaques decreased between 2.4 and 4.8 months, and was still relatively low at 7.2 months. Therefore, the onset of LSLC walking at 6.5 months in infant macaques appears to correspond fairly closely with a time period in which their hind limbs become longer relative to their fore limbs.

In accordance with Peters' (1983) study of kittens and Hildebrand's (1966, 1976, 1980) intra- and interspecific comparisons of tetrapods, one explanation for the baboons' shift within lateral sequence walks from diagonal to lateral couplets close to *c.* 5 months could be the avoidance of limb interference brought about by the lengthening of the hind limb relative to the forelimb at this time period. In other words, relatively long hind limbs can be viewed as a morphological *constraint* that leads to a temporary preference for LSLC walking, a gait rarely reported to be utilized by adult primates (Vilensky & Patrick, 1985).

After its onset close to 5 months, we did not observe a disappearance of LSLC walking in the developmental period studied (up to 9 months). Even though the intermembral index increased somewhat between 5 and 9 months (Fig. 7), the hind limb remained longer relative to the forelimb in this time frame compared with the first five postnatal months (Fig. 8). Given the continued use of LSLC between 5 and 9 months, it is likely that the hind limb continued to be long enough during this time to cause potential interference with the forelimb.

The fact that the correspondence of LSLC walking with relative hind limb lengthening in baboons resembles ontogenetic data for macaques provided independently by Nakano (1996) on gait and Turnquist and Wells on limb proportions (1994) suggests a common ontogenetic trajectory among primates worthy of further investigation. In their natural habitat, infant baboons and macaques begin to become more independent from their mothers between 4 and 6 months of age (Altmann, 1980; Turnquist & Wells, 1994). Therefore, it is not surprising to find morphological changes coinciding with changes in gait during this critical developmental time period. The timing of these changes in our subjects indicates that, despite premature separation from their mothers, their locomotor development does not appear to have been adversely affected in any obvious way. A follow-up study on the same four individuals will address limb proportions and gait preferences at older ages (2–3 years). We expect more adult-like proportions and gait usage by this age (Ruff, 2003).

What remains to be explained is the utilization of DSDC walking throughout the developmental period by three of four infants, despite changes in relative limb lengths. Like LSDC walks, DSDC walks provide the stability of support by contralateral, rather than ipsilateral, limbs during the stride. However, compared with LSDC, ipsilateral limb interference is much more problematic in DSDC walks, the walking gait preferred by adult primates and used in high frequencies by three of our four infants. Because of the sequencing of limb movements in DSDC walking, ipsilateral

limb interference is unavoidable except by moving a hind limb around the inside or outside of a forelimb, or shortening the hind limb's stride (Hildebrand, 1967). Therefore, one would expect hind limb lengthening to be associated with a *reduction* in the frequency of DSDC walking. This was not the case for the infant baboons studied here, nor for infant macaques (Nakano, 1996); DSDC walking continues to be utilized in both taxa even as the intermembral index decreases. This result is less readily interpretable than the increase in the use of LSLC as hind limbs lengthen. Interestingly, though, there is a parallel among domestic dogs. When walking in lateral sequence, lateral couplets are used essentially only by long-legged dogs, whereas dogs with either long or short legs use walking trots or diagonal sequence gaits, gaits with the problem of limb interference (Hildebrand, 1968). To avoid limb interference, long-legged dogs (like primates) pass their hind limbs to the inside or outside of the ipsilateral forelimb.

We conclude, therefore, that infant baboons opt to utilize one of two types of walking at the time of hind limb lengthening. If using lateral sequence walking during this time, infant baboons can avoid interference (and maintain hind limb stride length) by changing to lateral couplets, but when using diagonal sequence walking, interference (or stride length shortening) is avoided by navigating hind limbs to the inside or outside of ipsilateral forelimbs.[†] Such overstriding, if combined with the trunk turned at an angle to the direction of travel, might also serve to mitigate the effects of small support tripods in DSDC walking, especially on a flat substrate (Cartmill *et al.*, in press). Nevertheless, our data show that the disappearance of LSDC followed by the appearance of LSLC (i.e. a shift in couplets within lateral sequence gait) could be related to changes in limb proportions, but the utilization of DSDC throughout the developmental period appears to be independent of these changes.

Although DSDC walking was utilized in higher frequencies than any other gait throughout the 2–9-month period (by three of the infants), we also documented an increase in the relative frequency of DSDC walking at or after 5 months (when 77% of all DSDC strides occurred). This result hints at the possibility that changes in aspects of infant baboon morphology other than limb proportions might be relevant at this important developmental transition, associated with a more prominent advantage for DSDC walking. Turnquist & Wells (1994) reported that in infant macaques, increases in hind limb length within the first year are accompanied by a striking increase in hind limb mass, a proximal shift in limb center of mass and a caudal shift in trunk center of mass (see also Grand, 1977). These changes were shown to be correlated with locomotor activities and substrate use (Wells & Turnquist, 2001; see Dunbar, 1994), but footfall sequences were not reported. We have found similar changes in mass distribution in our infant baboon sample (Raichlen,

[†]Theoretically, diagonal sequence, lateral couplets would avoid interference but our infants used this gait only four times out of 588 strides, and it is an unstable gait avoided by tetrapods in general (Hildebrand, 1976, 1980).

2004a, 2005a,b). Thus, we are currently investigating whether such changes could explain why at ages older than 5 months, DSDC and LSLC appear to be preferred over LSDC walking.

If biomechanical factors influence gait choices during ontogeny, it is likely that adult primates utilize walking gaits that are biomechanically advantageous as well. Notwithstanding hypotheses that have been put forth to explain the biomechanical advantages of DSDC walking in primates, the frequency of other types of walking gaits used by primates has not been thoroughly explored. Vilensky & Larson's (1989) compilation of data from numerous studies suggests a tantalizing flexibility to gait choice among primates, including lateral sequence walks. However, most studies documenting primate gait are lab based, and the types of couplets used during lateral sequence walking are not always reported. Although primates do appear to have a clear preference for DSDC walking, we know next to nothing about the variability of walking gaits utilized by primates in their natural habitats. There is some evidence that primates vary footfall sequence and/or couplets in association with changes in substrate orientation or size (e.g. Prost & Sussman, 1969; Vilensky *et al.*, 1994; Dunbar & Badam, 2000), supporting the general hypothesis that biomechanical constraints influence gait choice. Creativity in the lab (e.g. Stevens, 2003) is a good beginning toward testing hypotheses regarding gaits and substrate use, but detailed field-based analyses of gait are also needed to address this issue adequately.

Conclusions

This study suggests that changes in limb proportions influence ontogenetic transitions in walking gait among infant baboons, particularly with respect to the type of couplets used during lateral sequence gait. The association between a time period of hind limb lengthening and increased frequency of LSLC walking in infant baboons is concordant with ontogenetic trends observed in other infant primates (e.g. macaques) and nonprimate mammals (e.g. kittens), as well as with the frequent use of LSLC walking in long-limbed adult mammals. Avoidance of ipsilateral limb interference is the most likely biomechanical explanation for the use of LSLC gait in both infants and adults.

Our data also reveal that between 2 and 9 months, infant baboons do not show a linear transition from one gait type to another, but utilize combinations of gaits at different time periods. It is likely that infant primates, like adults, prefer gaits that are biomechanically advantageous or that mitigate morphological constraints. We did not find an association between limb proportions and DSDC walking in infant baboons, but our results do not preclude an association between other aspects of body structure and this relatively uncommon form of walking.

This study has confirmed the utility of an ontogenetic perspective for understanding the biomechanics of gait. Further research comparing ontogenetic transitions in morphology and gait in baboons is currently underway in order

to test hypotheses regarding DSDC walking. Similar research on a broader comparative sample of primates is needed in order to explore interspecific variation in growth trajectories of morphology and gait.

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References

- Adolph, K.E., Vereijken, B. & Shrout, P.E. (2003). What changes in infant walking and why. *Child Dev.* **74**, 475–497.
- Altmann, J. (1980). *Baboon mothers and infants*. Cambridge: Harvard University Press.
- Blaszczak, J. & Loeb, G.E. (1993). Why cats pace on the treadmill. *Physiol. Behav.* **53**, 501–507.
- Bolter, D.R. & Zihlman, A.L. (2003). Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in old world monkeys, apes and humans. *J. Zool. (Lond.)* **260**, 99–110.
- Carrier, D. (1983). Postnatal ontogeny of the musculoskeletal system in the black-tailed jack rabbit (*Lepus californicus*). *J. Zool. (Lond.)* **201**, 27–55.
- 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 *Primate origins: Adaptations and evolution*. Ravosa, M. & Dagosto, M. (Eds). Berlin: Springer.
- Cleveland, W.S. (1979). Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* **74**, 829–836.
- Cleveland, W.S. & Devlin, S.J. (1988). Locally weighted regression: an approach to regression analysis by local fitting. *J. Am. Stat. Assoc.* **83**, 596–610.

- Coelho, A.M.J. (1985). Baboon dimorphism: growth in weight, length and adiposity from birth to 8 years of age. In *Nonhuman primate models for human growth and development*: 125–159. Watts, E.S. (Ed.). New York: Alan R. Liss, Inc.
- Crompton, R.H., Li, Y., Alexander, R.M., Wang, W. & Gunther, M.M. (1996). Segment inertial properties of primates: new techniques for laboratory and field studies of locomotion. *Am. J. Phys. Anthropol.* **99**, 547–570.
- Dunbar, D.C. (1994). The influence of segmental movements and design on whole body rotations during the airborne phase of primate leaps. *Z. Morphol. Anthropol.* **80**, 109–124.
- Dunbar, D.C. & Badam, G.L. (1998). Development of posture and locomotion in free-ranging primates. *Neurosci. Biobehav. Rev.* **22**, 541–546.
- Dunbar, D.C. & Badam, G.L. (2000). Locomotion and posture during terminal branch feeding. *Int. J. Primatol.* **21**, 649–669.
- Eilam, D. (1997). Postnatal development of body architecture and gait in several rodent species. *J. Exp. Biol.* **200**, 1339–1350.
- Full, R.J., Kubow, T., Schmitt, J., Holmes, P. & Koditschek, D. (2002). Quantifying dynamic stability and maneuverability in legged locomotion. *Integ. Comp. Biol.* **42**, 149–157.
- Grand, T. (1977). Body weight: its relation to tissue compositions, segment distribution, and motor function. II. Development of *macaca mulatta*. *Am. J. Phys. Anthropol.* **47**, 241–248.
- Gray, J. (1944). Studies in the mechanics of the tetrapod skeleton. *J. Exp. Biol.* **20**, 88–116.
- Hamrick, M. (1999). Development of epiphyseal structure and function in *Didelphis virginiana* (Marsupialia, Didelphidae). *J. Morphol.* **239**, 283–296.
- Hen, I., Sakov, A., Kafkafi, N., Golani, I. & Benjamini, Y. (2004). The dynamics of spatial behavior: how can robust smoothing techniques help? *J. Neurosci. Methods* **133**, 161–172.
- Hildebrand, M. (1966). Analysis of symmetrical gaits of tetrapods. *Folia Biotheoret.* **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 *Neural control of locomotion*: 203–236. Herman, R.M., Grillner, S., Stein, P.S.G. & Stuart, D.C. (Eds). New York: Plenum Press.
- Hildebrand, M. (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255–267.
- Hurov, J.R. (1982). Diagonal walking in captive infant vervet monkeys. *Am. J. Primatol.* **2**, 211–213.
- Hurov, J.R. (1991). Rethinking primate locomotion: what can we learn from development. *J. Mot. Behav.* **23**, 211–218.
- Janis, C.M., Theodor, J.M. & Boisvert, B. (2002). Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *J. Vert. Paleontol.* **22**, 110–121.
- Jensen, J.L. & Bothner, K. (1998). Infant motor development: the biomechanics of change. In *Pediatric anaerobic performance*: 23–43. Van Praagh, E. (Ed.) Champaign: Human Kinetics.
- Jensen, J.L., Ulrich, B.D., Thelen, E., Schneider, K. & Zernicke, R.F. (1994). Adaptive dynamics of the leg movement patterns of human infants: I. The effects of posture on spontaneous kicking. *J. Mot. Behav.* **26**, 303–312.
- Jungers, W.L. (1985). Body size and scaling of limb proportions in primates. In *Size and scaling in primate biology*: 345–381. Jungers, W.L. (Ed.) New York: Plenum Press.
- Jungers, W.L. & Fleagle, J.G. (1980). Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. *Am. J. Phys. Anthropol.* **53**, 471–478.
- Koppe, T., Swindler, D.R. & Lee, S.H. (1999). A longitudinal study of the growth pattern of the maxillary sinus in the pig-tailed macaque (*Macaca nemestrina*). *Folia Primatol.* **70**, 301–312.
- Lammers, A.R. & German, R.Z. (2002). Ontogenetic allometry in the locomotor skeleton of specialized half-bounding mammals. *J. Zool. (Lond.)* **258**, 48–495.
- Larson, S.G. (1998). Unique aspects of quadrupedal locomotion in nonhuman primates. In *Primate locomotion: recent advances*: 157–173. Strasser, E. & Fleagle, J. (Eds). New York: Plenum Press.
- Leigh, S.R. (1996). Evolution of human growth spurts. *Am. J. Phys. Anthropol.* **101**, 455–474.
- 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.
- Li, Y. (2000). Arboreal primates and the origin of diagonal gait. *Acta Anthropol. Sinica* **19** (Suppl.), 83–89.
- Lumer, H. & Schultz, A.H. (1941). Relative growth of the limb segments and tail in macaques. *Hum. Biol.* **13**, 283–305.
- Moses, L.E., Gale, L.C. & Altmann, J. (1992). Methods for analysis of unbalanced longitudinal growth data. *Am. J. Primatol.* **28**, 49–59.
- Muir, G. (2000). Early ontogeny of locomotor behavior: a comparison between altricial and precocial animals. *Brain Res. Bull.* **53**, 719–726.
- Muybridge, E. (1887). *Animal locomotion: an electro-photographic investigation of consecutive phases of animal movements, 1872–1885: plates*. Philadelphia: University of Pennsylvania.
- Muybridge, E. (1957). *Animals in motion*. New York: Dover Publications Inc.

- Nakano, Y. (1996). Footfall patterns in the early development of the quadrupedal walking of Japanese macaques. *Folia Primatol.* **66**, 113–125.
- Peters, S.E. (1983). Postnatal development of gait behavior and functional allometry in the domestic cat (*Felis catus*). *J. Zool. (Lond.)* **199**, 461–486.
- Pridmore, P.A. (1994). Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). *Aust. J. Zool.* **42**, 679–699.
- Prost, J.H. (1965). The methodology of gait analysis and the gaits of monkeys. *Am. J. Phys. Anthropol.* **23**, 215–240.
- Prost, J.H. (1969). A replication study on monkey gaits. *Am. J. Phys. Anthropol.* **30**, 203–208.
- Prost, J.H. & Sussman, R.W. (1969). Monkey locomotion on inclined surfaces. *Am. J. Phys. Anthropol.* **31**, 53–58.
- Raichlen, D. (2004a). *The relationship between limb muscle mass distribution and the mechanics and energetics of quadrupedalism in infant baboons (Papio cynocephalus)*. PhD thesis, University of Texas at Austin.
- Raichlen, D. (2004b). Convergence of forelimb and hind limb natural pendular periods in baboons (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism. *J. Hum. Evol.* **46**, 719–738.
- Raichlen, D.A. (2005a). Effects of limb mass distribution on the ontogeny of quadrupedalism in infant baboons (*Papio cynocephalus*) and implications for the evolution of primate quadrupedalism. *J. Hum. Evol.* **49**, 415–431.
- Raichlen, D.A. (2005b). Ontogeny of limb mass distribution in *Papio cynocephalus*. *J. Hum. Evol.* **49**, 452–467.
- Rollinson, J. & Martin, R.D. (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.
- Ruff, C. (2003). Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *J. Hum. Evol.* **45**, 317–349.
- Schmitt, D. & Lemelin, P. (2002). Origins of primate locomotion: gait mechanics of the woolly opossum. *Am. J. Phys. Anthropol.* **118**, 231–238.
- Setchell, J.M., Lee, P.C., Wickings, E.J. & Dixson, A.F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *Am. J. Phys. Anthropol.* **115**, 349–360.
- Shapiro, L.J. & Raichlen, D. (2005). Lateral sequence walking in infant *Papio cynocephalus*: implications for the evolution of diagonal sequence walking in primates. *Am. J. Phys. Anthropol.* **126**, 205–213.
- Sneath, P. & Sokal, R. (1973). *Numerical taxonomy*. San Francisco: W.H. Freeman.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry: the principles and practice of statistics in biological research*. 3rd edn. New York: W. H. Freeman.
- Stevens, N. (2003). How does branch stability affect prosimian arboreal quadrupedalism? *Am. J. Phys. Anthropol.* **36** (Suppl.), 200–201.
- Thelen, E., Fisher, D.M. & Ridley-Johnson, R. (1984). The relationship between physical growth and a newborn reflex. *Infant Behav. Dev.* **7**, 479–493.
- Turnquist, J.E. & Wells, J.P. (1994). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *J. Hum. Evol.* **26**, 487–499.
- Vilensky, J.A. (1989). Primate quadrupedalism: how and why does it differ from that of typical quadrupeds? *Brain Beh. Evol.* **34**, 357–364.
- Vilensky, J.A. & Gankiewicz, E. (1989). Early development of locomotor behavior in vervet monkeys. *Am. J. Primatol.* **17**, 11–25.
- Vilensky, J.A., 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, J.A. & Larson, S.G. (1989). Primate locomotion: utilization and control of symmetrical gaits. *Annu. Rev. Anthropol.* **18**, 17–35.
- Vilensky, J.A., Moore, A.M. & Libii, J.N. (1994). Squirrel monkey locomotion on an inclined treadmill: implications for the evolution of gaits. *J. Hum. Evol.* **26**, 375–386.
- Vilensky, J.A. & Patrick, M.C. (1985). Gait characteristics of two squirrel monkeys, with emphasis on relations with speed and neural control. *Am. J. Phys. Anthropol.* **68**, 429–444.
- Vogel, S. (1988). *Life's devices: the physical world of animals and plants*. Princeton: Princeton University Press.
- Wells, J.P. & Turnquist, J.E. (2001). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. *Am. J. Phys. Anthropol.* **115**, 80–94.
- White, T.D. (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.