



Effects of limb mass distribution on the ontogeny of quadrupedalism in infant baboons (*Papio cynocephalus*) and implications for the evolution of primate quadrupedalism

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Abstract

Primate quadrupedal kinematics differ from those of other mammals. Several researchers have suggested that primate kinematics are adaptive for safe travel in an arboreal, small-branch niche. This study tests a compatible hypothesis that primate kinematics are related to their limb mass distribution patterns.

Primates have more distally concentrated limb mass than most other mammals due to their grasping hands and feet. Experimental studies have shown that increasing distal limb mass by adding weights to the limbs of humans and dogs influences kinematics. Adding weights to distal limb elements increases the natural period of a limb's oscillation, leading to relatively long swing and stride durations. It is therefore possible that primates' distal limb mass is responsible for some of their unique kinematics. This hypothesis was tested using a longitudinal ontogenetic sample of infant baboons (*Papio cynocephalus*). Because limb mass distribution changes with age in infant primates, this project examined how these changes influence locomotor kinematics within individuals.

The baboons in this sample showed a shift in their kinematics as their limb mass distributions changed during ontogeny. When their limb mass was most distally concentrated (at young ages), stride frequencies were relatively low, stride lengths were relatively long, and stance durations were relatively long compared to older ages when limb mass was more proximally concentrated. These results suggest that the evolution of primate quadrupedal kinematics was tied to the evolution of grasping hands and feet.

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Introduction

Primate quadrupedalism is kinematically unique among mammals (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990; Schmitt, 1998; Larson, 1998; Schmitt, 1999; Larson et al., 2000, 2001; Cartmill et al., 2002; Schmitt, 2003). At a given velocity, primates use relatively long strides and low stride frequencies, have relatively large limb angular excursions, and have relatively long stance durations compared to other mammalian quadrupeds (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990; Larson, 1998; Schmitt, 1999; Larson et al., 2000, 2001; Cartmill et al., 2002; Schmitt, 2003). Schmitt and Lemelin (2002) suggested that these traits are primitive for primates. Therefore, understanding the adaptive value of primate kinematics will provide insights into the selection pressures that may have acted during early primate evolution. The purpose of this study is to examine morphological correlates of primate kinematics in order to clarify these selection pressures. Specifically, this study tests the hypothesis that primate quadrupedal kinematics are associated with limb morphology.

Previous researchers have suggested that primate kinematics are adaptations for stable travel in an arboreal, small-branch environment (Demes et al., 1990; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Cartmill et al., 2002; Schmitt, 2003). In this environment, low stride frequencies reduce potentially dangerous branch oscillations (Demes et al., 1990). At a given velocity, low stride frequencies are associated with increased stride lengths, which, in turn, are created by increased limb angular excursions (Reynolds, 1987; Demes et al., 1990; Larson et al., 2000, 2001). Quadrupedal primates do, however, continue to use these unique kinematics when walking terrestrially (see Alexander and Maloiy, 1984, for a sample of primates using long strides and low stride frequencies when walking terrestrially). It is therefore plausible that other selection pressures are responsible for the evolution of primate quadrupedal kinematics. For example, Reynolds (1987) proposed that primates' long strides are a result of their relatively long limbs (see also Polk, 2004). However, after taking limb length into

account through the use of Alexander and Jayes' (1983) dynamic similarity methods, primate stride lengths remained longer than those of other mammals (Alexander and Maloiy, 1984). These results suggest that limb length alone does not completely explain differences in stride lengths between primates and other mammals.

Preuschoft and Günther (1994) and Raichlen (2004a) suggested that the unique kinematics in primates may be the result of relatively distally distributed limb muscle mass related to their grasping hands and feet. Relatively distal limb mass concentrations increase a limb's natural pendular period of oscillation (NPP; see also Myers and Steudel, 1997; Raichlen, 2004a). Since the NPP is the time it takes the limb to swing through a single complete pendular oscillation, any increases in NPP should increase an individual's swing phase duration (time between limb lift-off and touchdown) and therefore increase that individual's stride duration (time between two successive limb touchdowns; see Holt et al., 1991; Myers and Steudel, 1997). Large NPPs should therefore lead to low stride frequencies because stride frequency is the reciprocal of stride duration. Since velocity is the product of stride frequency and stride length, low stride frequencies are associated with relatively long strides at a given velocity.

Relatively long swing durations may also lead to relatively long stance durations. In walking gaits, stance duration decreases with increasing velocity (see Alexander and Jayes, 1983; Demes et al., 1990) until it is equal to swing duration. At this velocity, stance duration is 50% of stride duration (stride duration = stance duration + swing duration) and the individual begins to run (Alexander and Jayes, 1983). If an increase in swing duration is not met by an increase in stance duration, then as stance duration decreases with increasing velocity, it will be equal to swing duration at a lower velocity. The individual will therefore begin running at a lower velocity. An early transition to a run may increase energy expenditures in mammalian quadrupeds (see Hoyt and Taylor, 1981), implying that relatively long stance durations may be an energetically efficient response to relatively long swing durations.

Primate limb mass distributions may also affect limb angular excursions, which is suggested by the work of Reynolds (1987), who demonstrated that relatively long stance durations may be responsible for large limb angular excursions. Relatively distal limb mass concentrations may therefore have large impacts on primate quadrupedal kinematics.

Experimental studies support the link between temporal kinematics and limb mass distribution. When limb mass distributions of humans and dogs were altered by adding mass to distal elements (increasing the limb's NPP), swing durations and stride durations increased significantly (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel, 1990; Mattes et al., 2000). These results, however, have not yet been verified in a more natural context.

This study explicitly tests the hypothesis that primate kinematic characteristics are related to their limb mass distribution patterns using an ontogenetic sample of infant baboons (*Papio cynocephalus*). The infant baboon sample offers a “natural experiment” because their limb mass distributions change with age (see Raichlen, 2004b). Infant baboons have relatively more distal limb mass concentrations at young ages, needed for strong grasping of their mothers' hair during travel. Limb mass distributions shift proximally with age as the infants begin independent locomotion (hindlimb centers of mass changed from 45% to 39% of limb length as infant baboons aged from one to nine months; see Raichlen, 2004b). Therefore, it is possible to examine how infant baboon locomotor kinematics change as limb mass becomes more proximally concentrated.

Hypotheses

Infant baboon kinematics were examined during ontogeny to test the hypothesis that spatio-temporal kinematics are correlated with limb mass distribution. Changes in kinematics are expected to occur as limb mass becomes more proximally concentrated during ontogeny. First, swing durations should become relatively shorter during ontogeny as mass distribution becomes more proximally concentrated. Changes in other kinematic

variables should be associated with increased swing durations. Specifically, stance durations should decrease during ontogeny due to decreases in swing duration. Stride frequencies should increase during ontogeny due to the shorter swing and stance durations. Stride lengths should decrease during ontogeny due to the increase in stride frequencies. Finally, limb angular excursions should decrease during ontogeny due to decreases in stance durations.

Materials and methods

Four infant baboons (*Papio cynocephalus*) were obtained from the Southwest Foundation for Biomedical Research (SFBR) from a population rejected by their mothers and placed in the SFBR nursery. Infant baboons were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas Institutional Animal Care and Use Committee (IACUC) and the SFBR IACUC.

Limb inertial properties were calculated for each infant baboon at each age using methods developed by Crompton et al. (1996) and modified by Raichlen (2004a). Each body segment was modeled as a column with a circular cross-section. Model shapes were constructed using external circumference measurements taken at three locations on each limb segment. From these measurements, column models were constructed and segment inertial properties were calculated after Raichlen (2004a). Whole limb inertial properties, as well as limb natural pendular periods (NPP), were calculated from segment inertial properties. Natural pendular periods are the duration of time it takes the limb to swing through one complete oscillation if it were swinging as a pure pendulum and are calculated using the following equation:

$$\text{NPP} = \sqrt{\frac{I}{mg\text{CM}}} \quad (1)$$

where I is the limb's mass moment of inertia about a transverse axis through the proximal limb joint, m is the limb's mass, CM is the distance of the limb's center of mass from the proximal end, and

g is gravitational acceleration (9.8 ms^{-2}). This value represents a connection between the limb's inertial properties and kinematics during swing phase, and was therefore used to determine how inertial properties change with age in the infant baboons.

Three-dimensional kinematic data were obtained from each infant baboon at regular intervals during development (Table 1). Kinematic data were collected on each infant baboon two days before or after data were collected on limb inertial properties. Infant baboons were allowed to walk and run at freely chosen velocities through a lexan tunnel made up of three removable sections ($2 \times 3 \times 4$ feet each). Two or three sections were used depending on each infant baboon's body size at the time of data collection.

Table 1
Description of sample and number of strides analyzed at each age

Subject (SFBR ID)	Age (months)	Sex	n
Infant 1 (17194)	3.33	m	9
Infant 1 (17194)	4.27	m	10
Infant 1 (17194)	4.73	m	10
Infant 1 (17194)	5.87	m	16
Infant 1 (17194)	6.10	m	32
Infant 1 (17194)	7.50	m	26
Infant 2 (18573)	<3.0	f	21
Infant 2 (18573)	3.67	f	19
Infant 2 (18573)	4.67	f	38
Infant 2 (18573)	4.97	f	31
Infant 2 (18573)	5.53	f	18
Infant 2 (18573)	7.40	f	13
Infant 2 (18573)	8.10	f	22
Infant 3 (18572)	<4.7	f	5
Infant 3 (18572)	4.70	f	20
Infant 3 (18572)	5.00	f	11
Infant 3 (18572)	5.57	f	12
Infant 3 (18572)	6.23	f	23
Infant 3 (18572)	7.43	f	33
Infant 3 (18572)	8.13	f	29
Infant 3 (18572)	8.97	f	69
Infant 4 (17220)	2.60	f	11
Infant 4 (17220)	4.47	f	8
Infant 4 (17220)	7.23	f	21

Note: Subject describes the infant number that will be used in the text (its SFBR identification number is listed in parentheses); n is the number of accepted strides analyzed and included here for each sampled age.

At young ages, individuals were encouraged to walk and run the length of the tunnel using toys. As soon as they began eating solid foods (approximately three months of age), the infant baboons were encouraged to walk and run the length of the tunnel using food rewards. Prior to tunnel entry, spherical reflective markers (14 mm; Oxford Metrics, Inc.) were glued to the major joints of the forelimbs and hindlimbs of each infant baboon (hip, knee, ankle, shoulder, elbow, and knee). The placement of each marker was consistent with the segment definitions used for inertial property data collection (see Raichlen, 2004a).

Three-dimensional marker trajectories were captured for one side of the body during each locomotor trial using a 5 camera 60 Hz Vicon 250 data acquisition system (Oxford Metrics, Inc.). Camera placement was consistent for all data collection sessions. Although markers were placed on both sides of the body, cameras were placed in an arc on only one side of the tunnel in order to maximize the calibrated viewing volume and maximize the capabilities of the system to track the three-dimensional positions of the relatively small (14 mm) markers.

In addition to the Vicon system, video data of each trial were collected using a digital video camera (JVC-GRDVL9800E) at 60 frames per second. The video data were routed through a frame counter (manufactured by Oxford Metrics, Inc.) and transferred to Hi-8 analog tape. This transfer allowed the frame counter to be superimposed onto the image so that each kinematic trial could later be synchronized with Vicon-generated data.

Marker trajectories were reconstructed using Vicon Workstation[®] software. Kinematic data were processed using Vicon Bodybuilder[®] software. Gaps in marker trajectories of less than 10 frames (<0.17 s) were filled using the Vicon interpolation algorithm. Three-dimensional marker positions were then exported into Microsoft Excel[®] for the remainder of data processing.

A locomotor trial was accepted for use if the individual was not obviously accelerating or decelerating during the trial and if there was at least one visible stride before and after the stride of

interest. Data were collected for all walks, runs, and gallops, and all walks and runs (but not gallops) were also analyzed for symmetry. Symmetry is the time between a limb's touchdown and the next touchdown of the contralateral limb of the same girdle, expressed as a percentage of stride duration. In normal, steady-state walks and runs, this value should be 50 (see Hildebrand, 1966). In practice, symmetry values between 45 and 55 are viewed as acceptable for symmetrical walks and runs (see Cartmill et al., 2002; Shapiro and Raichlen, 2005). All walking and non-galloping running trials with symmetry values outside of this range were rejected.

Variables

Each stride's duration (seconds) was defined as the elapsed time between the touchdown of the hand or foot on the side facing the camera (ipsilateral) to the next touchdown of that hand or foot. Stride frequency (Hz) was calculated as the reciprocal of stride duration. Stance duration (seconds) was calculated as the elapsed time between limb touchdown and lift-off. Swing duration (seconds) was calculated as the elapsed time between limb lift-off and touchdown. Stride length (m) was calculated as the distance traveled by the ankle or wrist marker during a given stride. Velocity (m/s) was calculated as the quotient of stride length and stride duration.

The data collected in this study did not permit an accurate calculation of limb angular excursions. Ankle and wrist markers are not sufficient for calculating limb retraction angles in digitigrade animals because the ankle and wrist are raised off of the ground at lift-off. Step lengths (distance traveled during stance duration) were used as a proxy for limb angular excursions because limb angular excursion and step length are directly related (Reynolds, 1987; Larson et al., 2001). Step length (m) was calculated as the distance traveled by the hip or shoulder marker during stance phase.

Forelimb vs. hindlimb

Most research into mammalian quadrupedal kinematics has focused on single limb kinematics

(e.g., Heglund et al., 1974). In this study, kinematic variables of interest were calculated for both the forelimb and the hindlimb on one side of the body for each stride. The values obtained for the forelimb and hindlimb for each variable were then compared at a given velocity to determine whether or not the infant baboons' kinematics could be generalized by a single limb analysis.

For the four major variables included in this analysis (stride length, stride frequency, stance duration, and swing duration), forelimbs and hindlimbs did not differ significantly in the infant baboons (Table 2). Because of this overall similarity in forelimb and hindlimb kinematics across all ages in the infant baboon sample, only the results for the hindlimb are presented.

Dimensionless numbers

In order to compare the infant baboons intra-individually and inter-individually as they aged, changes in size must be taken into account. Alexander and Jayes (1983) introduced the dynamic similarity hypothesis in order to compare

Table 2
Comparisons of forelimb and hindlimb kinematics variables

Variable	LSmean	95% CI	H ₀ :LSmean1 = LSmean2
Hindlimb stride frequency (s ⁻¹)	0.16	0.005	0.9991
Forelimb stride frequency (s ⁻¹)	0.16	0.005	
Hindlimb stride length (m)	-0.29	0.005	0.6825
Forelimb stride length (m)	-0.28	0.005	
Hindlimb stance duration (s)	-0.43	0.007	0.1391
Forelimb stance duration (s)	-0.42	0.007	
Hindlimb swing duration (s)	-0.51	0.006	0.1823
Forelimb swing duration (s)	-0.52	0.006	

Note: ANCOVA applied to forelimb and hindlimb values of the same variables with velocity as the covariate. H₀ is the probability that LSmean1 (the hindlimb LSmean) is equal to LSmean2 (forelimb LSmean).

kinematics in animals that differ in body size. Animals that are geometrically similar may use dynamically similar kinematics at the same dimensionless velocity. The Froude number ($\text{velocity}^2/(\text{gravity} \times \text{hip height})$) was used as the dimensionless velocity for their comparisons (see Alexander and Jayes, 1983). In this study, dimensionless velocity was calculated as the square root of the Froude number after Hof (1996; see also Aerts et al., 2000). Dynamic similarity is only possible when the subjects are geometrically similar (see Alexander and Jayes, 1983). For the infant baboons, hindlimb length (h , calculated as the sum of thigh, leg, and foot lengths) was used as the characteristic size variable since it increases isometrically with body size during infant baboon ontogeny (Table 3; see also Raichlen, 2004b). Stride frequencies were made dimensionless after Hof (1996; see also Zijlstra et al., 1996; Aerts et al., 2000):

$$dSF = \frac{SF}{\sqrt{\frac{g}{h}}} \quad (2)$$

Spatial variables (L : step length and stride length) were made dimensionless after Alexander and Jayes (1983; see also Hof, 1996; Aerts et al., 2000):

$$dL = \frac{L}{h} \quad (3)$$

All time variables (T : stance duration and swing duration) were made dimensionless after Hof (1996):

$$dT = \frac{T}{\sqrt{\frac{h}{g}}} \quad (4)$$

If age-related differences in infant baboon kinematics are due to differences in size alone (e.g.,

hindlimb length), then dimensionless kinematic variables will be equivalent at a given dimensionless velocity. If, however, limb mass distribution plays a role in age-related kinematic differences, dimensionless kinematic variables will differ at a given dimensionless velocity.

Grouping

Most ontogenetic studies of locomotion examine changes across age categories determined by either body size differences or broad behavioral changes (e.g., Vilensky et al., 1988; Dunbar and Badam, 1998; Irschick and Jayne, 2000; Wells and Turnquist, 2001). These categorizations are not as useful in this study, because, as described above, the purpose of this project was not simply an ontogenetic analysis; rather, it addressed specific questions about the impacts of ontogenetic changes in limb inertial properties on locomotion. Therefore, individuals must be grouped based on their limb inertial properties, and these groupings may or may not conform to arbitrary age classes. Additionally, limb flexion during swing phase affects the limb's NPP by changing the distance of each segment's center of mass from the shoulder or hip joint (see Myers and Steudel, 1997; Raichlen, 2004a). Because the NPP during swing phase is expected to influence kinematics, this change in limb NPP during locomotion must be taken into account when creating age groupings.

Since the limb NPP will change dynamically as the limb flexes during swing phase, NPPs were recalculated for each frame in each trial taking into account the change in limb segment positions, and the minimum NPP value during swing phase was found ($dNPP_{\min}$). The minimum NPP value represents the best approximation of the functionally relevant connection between limb inertial properties and swing phase kinematics. All ages where $dNPP_{\min}$ did not differ significantly were grouped together. The same amount of flexion has a proportionately greater impact on an individual with a more distal concentration of limb mass compared to an individual with a more proximal concentration of limb mass (Raichlen, 2004a). It is therefore expected that, even though the infant baboons' limb inertial properties change in

Table 3
Reduced major axis regression slope for hindlimb length vs. body mass in the infant baboon sample

Variable	n	slope	Lower CI	Upper CI	r
Hindlimb length	42	0.363	0.326	0.400	0.950

Note: Upper and lower CI are the 95% confidence limits for the slope of the reduced major axis regression line relating hindlimb length (m) and body mass (kg). A slope of 0.33 indicates isometry.

a regular way with age (see Raichlen, 2004b), individuals will not differ significantly in $dNPP_{\min}$ at all ages.

Statistical analysis

Because $dNPP_{\min}$ was correlated with dimensionless velocity for some ages for each individual, comparisons of $dNPP_{\min}$ across ages were carried out using ANCOVA with Tukey–Kramer post-hoc tests to correct for multiple comparisons and dimensionless velocity as the covariate. Least-squares means (LSmeans) and their 95% confidence limits were calculated to aid comparisons. Prior to performing an ANCOVA, data sets were checked for homogeneity of slopes (see Sokal and Rohlf, 1995). All ages for an individual that did not differ significantly in $dNPP_{\min}$ were grouped together. These groupings were then used for further analyses of the impacts of limb inertial properties on locomotor kinematics.

For each locomotor variable, a similar approach was used. First, Pearson product-moment correlations were performed between each variable and dimensionless velocity. If the correlation was not significant, then locomotor variables were compared between different groups using single-factor ANOVA with Tukey–Kramer post-hoc tests to correct for multiple comparisons. If correlations were significant, ANCOVA was performed with Tukey–Kramer post-hoc tests to accommodate multiple tests. If an ANCOVA was used, LSmeans and their 95% confidence limits were calculated to aid comparisons. All statistical

Table 4

Results of ANCOVA comparing dimensionless hindlimb NPPs in Infant 1 at all sampled ages

Age	4.27	4.73	5.98	6.10	7.50	LSmean	95% CI
3.33	0.78	0.93	<0.0001	<0.0001	<0.0001	5.01	0.07
4.27	—	0.86	<0.0001	<0.0001	<0.0001	4.95	0.06
4.73	—	—	<0.0001	<0.0001	<0.0001	4.97	0.06
5.98	—	—	—	0.70	0.95	4.75	0.03
6.10	—	—	—	—	0.63	4.77	0.05
7.50	—	—	—	—	—	4.73	0.04

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval (CI). Values in boldface are significant.

tests were performed using SAS version 8.0 (SAS Institute, Inc., 2003).

Results

Groupings

Infant baboons did not show significant differences in $dNPP_{\min}$ at all ages (Tables 4–7). Infants 1–3 fell into two age groups based on limb inertial properties calculated during swing phase. At young ages, these infant baboons had large $dNPP_{\min}$ s and then shifted to smaller $dNPP_{\min}$ s at older ages. The transition occurred after five months of age in Infants 1 and 3, and after four months in Infant 2. Infant 2 did show some significant differences within these two age groups, but these differences were small and consistent with the overall trend of each age group.

Table 5

Results of ANCOVA comparing dimensionless hindlimb NPPs in Infant 2 at all sampled ages

Age	2.83	3.67	4.67	4.97	5.53	7.40	8.10	LSmean	95% CI
2.03	0.61	0.08	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	5.20	0.09
2.83	—	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	5.30	0.07
3.67	—	—	<0.0001	<0.0001	0.01	0.01	<0.0001	5.02	0.08
4.67	—	—	—	0.89	0.45	0.81	0.93	4.68	0.06
4.97	—	—	—	—	0.05	0.95	0.89	4.63	0.06
5.53	—	—	—	—	—	0.36	0.06	4.77	0.07
7.40	—	—	—	—	—	—	0.11	4.48	0.25
8.10	—	—	—	—	—	—	—	4.62	0.07

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval (CI). Values in boldface are significant.

Table 6
Results of ANCOVA comparing dimensionless hindlimb NPPs in Infant 3 at all sampled ages

Age	4.17	4.70	5.00	5.57	6.23	7.43	8.13	8.97	LSmean	95% CI
3.70	0.66	0.48	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	5.13	0.010
4.17	—	0.88	0.005	0.01	<0.0001	0.00	0.01	0.001	4.75	0.010
4.70	—	—	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	4.79	0.010
5.00	—	—	—	0.92	0.96	0.76	0.90	0.82	4.47	0.010
5.57	—	—	—	—	0.68	0.83	0.58	0.53	4.45	0.010
6.23	—	—	—	—	—	0.72	0.98	0.36	4.48	0.005
7.43	—	—	—	—	—	—	0.76	0.64	4.47	0.004
8.13	—	—	—	—	—	—	—	0.78	4.41	0.010
8.97	—	—	—	—	—	—	—	—	4.44	0.003

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval (CI). Values in boldface are significant.

Note that the values of $dNPP_{min}$ for Infant 4 do not differ significantly among the three sampled age ranges (Table 7). The results for Infant 4 should be treated with caution, however, as sample sizes are much lower for this individual compared to Infants 1–3 (see Table 1). Regardless of the low sample sizes, the fact that Infant 4's $dNPP_{min}$ s did not differ significantly over the three sampled ages allows Infant 4 to act as a control for the effects of neurological ontogeny on kinematics. If Infant 4 experienced the same changes in kinematics as Infants 1–3 despite her similar inertial properties, then support for a connection between limb mass distribution and kinematics would be weakened considerably.

For the kinematic analyses that follow, there were two groups for Infants 1–3. Group 1 included all of the youngest ages that do not differ significantly in $dNPP_{min}$, and Group 2 included all of the oldest ages that do not differ significantly in $dNPP_{min}$. For Infant 4, three groups were assigned, one for each sampled age.

Dimensionless swing and stance durations

Infants with relatively distal limb mass (Group 1) were hypothesized to use relatively long swing durations, and these long swing durations were expected to lead to relatively long stance durations. In Infants 1–3, dimensionless swing durations were significantly longer when limb mass was most distally concentrated (Group 1; Table 8). Infant 4, who did not have significant between-group differences in her

limb inertial properties, did not have significantly different dimensionless swing durations in any of her groups (Table 9). When Infants 1–3 were combined, Group 1 individuals had significantly longer dimensionless swing durations than Group 2 individuals (Fig. 1; Table 10). These results support the hypothesized relationship between $dNPP_{min}$ and swing duration.

Two of the three infant baboons had significantly longer stance durations at ages when limb mass was most distal (Infants 2 and 3; Table 8). Dimensionless stance durations did not differ significantly with age in Infants 1 and 4 (Tables 8 and 9). Group 1 for the combined sample of Infants 1–3 had significantly larger dimensionless stance durations than Group 2 (Fig. 2; Table 10). These results only partially support the hypothesis that long dimensionless swing durations lead to long dimensionless stance durations.

Table 7
Results of ANCOVA comparing dimensionless hindlimb NPPs in Infant 4 at all sampled ages

Age	4.47	7.23	LSmean	95% CI
2.60	1.00	0.32	4.14	0.10
4.47	—	0.38	4.14	0.11
7.23	—	—	4.05	0.07

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval (CI). Values in boldface are significant.

Table 8
Between group ANCOVAs for dimensionless kinematic variables in Infants 1–3

Dimensionless variable	Group	n	r	p-value	LSmean	95% CI	H ₀ :LSmean1 = LSmean2
Swing duration	Infant 1 Group 1	29	0.84	<0.01	0.283	0.022	<0.0001
	Infant 1 Group 2	74	0.78	<0.01	0.201	0.014	
	Infant 2 Group 1	40	0.79	<0.01	0.261	0.02	<0.0001
	Infant 2 Group 2	122	0.71	<0.01	0.202	0.011	
	Infant 3 Group 1	25	0.72	<0.01	0.299	0.026	<0.0001
	Infant 3 Group 2	177	0.40	<0.01	0.226	0.009	
Stance duration	Infant 1 Group 1	29	0.97	<0.01	0.297	0.019	0.909
	Infant 1 Group 2	74	0.98	<0.01	0.298	0.011	
	Infant 2 Group 1	40	0.97	<0.01	0.349	0.016	0.002
	Infant 2 Group 2	122	0.96	<0.01	0.252	0.009	
	Infant 3 Group 1	25	0.98	<0.01	0.415	0.022	<0.0001
	Infant 3 Group 2	177	0.97	<0.01	0.326	0.007	
Stride frequency	Infant 1 Group 1	29	0.99	<0.01	−0.61	0.011	<0.0001
	Infant 1 Group 2	74	0.98	<0.01	−0.561	0.007	
	Infant 2 Group 1	40	0.97	<0.01	−0.606	0.012	<0.0001
	Infant 2 Group 2	122	0.96	<0.01	−0.54	0.007	
	Infant 3 Group 1	25	0.98	<0.01	−0.662	0.016	<0.0001
	Infant 3 Group 2	177	0.95	<0.01	−0.591	0.005	
Stride length	Infant 1 Group 1	29	0.96	<0.01	0.244	0.012	<0.0001
	Infant 1 Group 2	74	0.86	<0.01	0.19	0.007	
	Infant 2 Group 1	40	0.88	<0.01	0.299	0.013	<0.0001
	Infant 2 Group 2	122	0.87	<0.01	0.234	0.007	
	Infant 3 Group 1	25	0.93	<0.01	0.303	0.017	<0.0001
	Infant 3 Group 2	177	0.89	<0.01	0.231	0.005	
Step length	Infant 1 Group 1	29	0.00002	ns	−0.114	0.015	0.446
	Infant 1 Group 2	74	0.016	ns	−0.107	0.009	
	Infant 2 Group 1	40	0.052	ns	−0.074	0.016	<0.0001
	Infant 2 Group 2	122	0.00041	ns	−0.088	0.009	
	Infant 3 Group 1	25	0.045	ns	−0.009	0.026	<0.0001
	Infant 3 Group 2	177	0.00003	ns	−0.024	0.01	

Note: Correlation coefficients (r) and their p-values (ns is non-significant at alpha = 0.05) are given for correlations between each variable and dimensionless velocity. H₀ is the probability that LSmeans do not differ between groups. In addition, since dimensionless step lengths were not correlated with velocity, ANOVAs were used to test for differences between groups.

Relationship between dimensionless stride frequency and age

Stride frequencies were hypothesized to increase with age in the infant baboons due to the relative decrease in swing durations. Infants 1–3 used lower dimensionless stride frequencies at a given dimensionless velocity when their limb mass was most

distally distributed (Group 1; Table 8). Infant 3's ANCOVA results are only presented for walking dimensionless velocities because this was the only region where slopes for the relationship between dimensionless stride frequency and dimensionless velocity were parallel in the two groups. Infant 4 did not show significant between-group differences in dimensionless stride frequencies (Table 9).

Table 9
Between group ANCOVAs for dimensionless kinematic variables in Infant 4

Dimensionless variables	Group	2	3	LSmean	95% CI	n	r	p-value
Swing duration	1	0.798	0.096	0.266	0.068	11	0.77	<0.01
	2	—	0.513	0.299	0.082	8	0.56	ns
	3	—	—	0.35	0.041	21	0.70	<0.01
Stance duration	1	0.997	0.831	0.497	0.067	11	0.96	<0.01
	2	—	0.827	0.493	0.08	8	0.87	<0.01
	3	—	—	0.519	0.04	21	0.89	<0.01
Stride frequency	1	0.959	0.176	-0.699	0.045	11	0.96	<0.01
	2	—	0.425	-0.708	0.055	8	0.84	<0.01
	3	—	—	-0.746	0.027	21	0.92	<0.01
Stride length	1	0.941	0.213	0.191	0.042	11	0.69	ns
	2	—	0.495	0.201	0.05	8	0.46	ns
	3	—	—	0.233	0.026	21	0.76	<0.01
Step length	1	0.977	0.070	-0.065	0.039	11	0.09	ns
	2	—	0.061	-0.072	0.047	8	0.636	ns
	3	—	—	-0.050	0.023	21	0.043	ns

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed are LSmeans for each group, and their 95% confidence intervals (CI). Correlation coefficients (r) and their p-values (ns is non-significant at $\alpha = 0.05$) are given for correlations between each variable and dimensionless velocity. In addition, since dimensionless step lengths were not correlated with velocity, ANOVA was used to test for differences between groups.

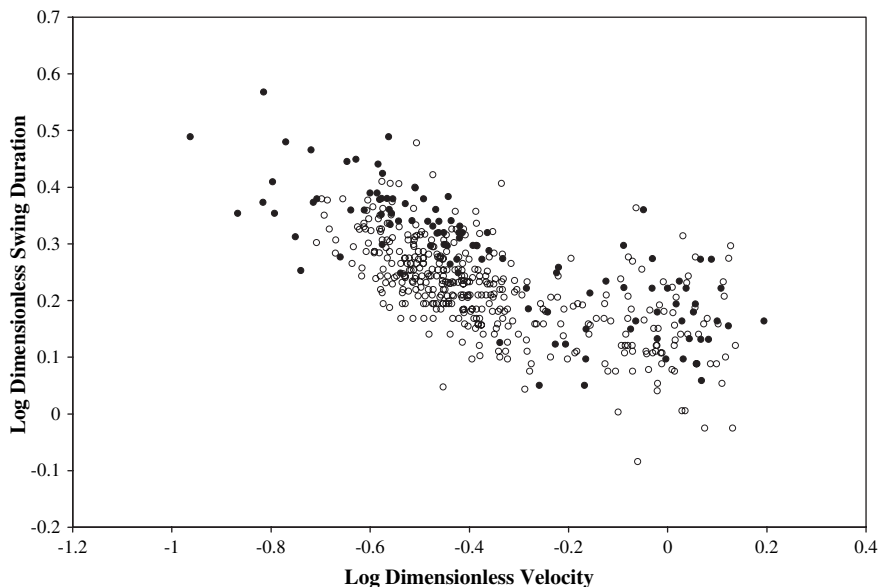


Fig. 1. Dimensionless swing durations over the range of dimensionless velocities for the combined sample of infant baboons. Group 1 individuals (relatively distal limb mass concentrations) are closed circles; Group 2 individuals (relatively proximal limb mass concentrations) are open circles.

Table 10

LSmeans and 95% CIs for between group comparisons of dimensionless kinematic variables in combined sample (Infants 1–3)

Dimensionless variable	LSmean1	CI	LSmean2	CI	H ₀ :LSmean1 = LSmean2
Swing duration	0.284	0.012	0.220	0.006	<0.0001
Stance duration	0.358	0.012	0.312	0.006	<0.0001
Stride frequency	-0.632	0.008	-0.580	0.004	<0.0001
Stride length	0.277	0.008	0.223	0.004	<0.0001
Step length	-0.034	0.014	-0.062	0.007	0.001

Note: LSmean1 is the least squares mean for Group 1 for each variable after dimensionless velocity has been taken into account. LSmean2 is the least squares mean for Group 2 for each variable after dimensionless velocity has been taken into account. H₀ is the probability that LSmean1 is equal to LSmean2. In addition, since dimensionless step lengths were not correlated with velocity, ANOVA was used to test for differences between groups.

The infant baboons that did group by hindlimb NPP (Infants 1–3) were combined so that all Group 1 individuals were compared to all Group 2 individuals. Dimensionless stride frequencies were significantly lower in the combined Group 1 individuals compared to the combined Group 2 individuals (Fig. 3; Table 10). These results support the hypothesized relationship between limb mass distribution and temporal kinematics.

Dimensionless stride length

The results for dimensionless stride lengths closely follow the expectation that long dimensionless stride frequencies will lead to long dimensionless stride lengths. In all three individuals that were divided into two age groups, dimensionless stride lengths were longer in Group 1 compared to Group 2 after dimensionless velocity had been taken into account (Table 8). In Infant 4, dimensionless stride

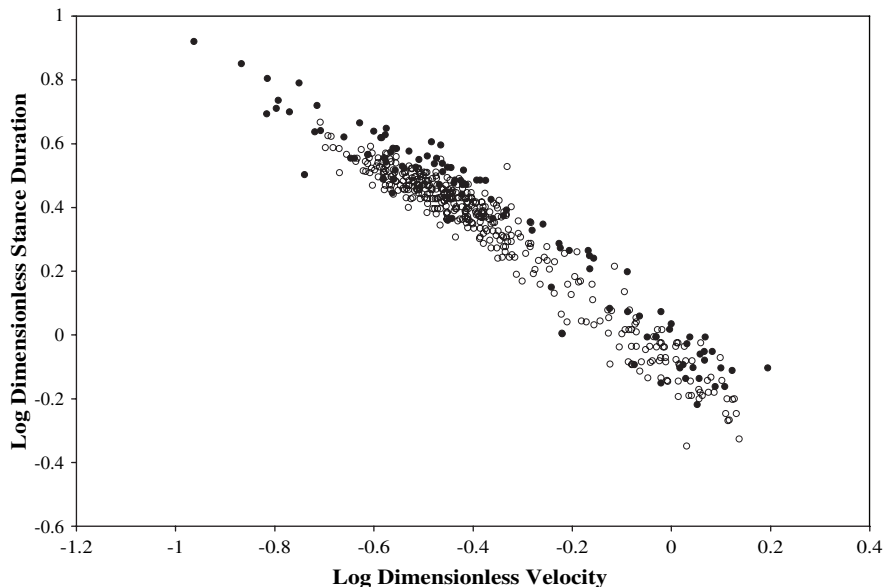


Fig. 2. Dimensionless stance durations over the range of dimensionless velocities for the combined sample of infant baboons. Group 1 individuals (relatively distal limb mass concentrations) are closed circles; Group 2 individuals (relatively proximal limb mass concentrations) are open circles.

lengths did not differ among the different age categories after dimensionless velocity had been taken into account (Table 9). When Infants 1–3 were grouped together, Group 1 individuals had significantly longer dimensionless stride lengths compared to Group 2 individuals (Fig. 4; Table 10).

Step length

It was hypothesized that dimensionless step length differences would be related to dimensionless stance duration differences in the infant baboon sample. Infants 2 and 3, who showed significant differences in dimensionless stance durations that were correlated with age related changes in limb inertial properties, also showed significant between-group differences in dimensionless step length (Table 8). Infants 1 and 4 did not show between-group differences in dimensionless step length (Tables 8 and 9), and also did not have significant between-group differences in dimensionless stance durations. When Infants 1–3 were grouped together, Group 1 individuals used significantly longer

dimensionless step lengths compared with Group 2 individuals (Table 10). These results imply partial support for increased angular excursions in infant baboons with relatively distal limb mass since angular excursion and step length are directly related (see Reynolds, 1987; Larson et al., 2001).

Comparison with other mammals

Because of their relatively distal limb mass concentrations, infant baboons should use lower stride frequencies than other mammalian quadrupeds, including adult primates. Additionally, infant baboons should use longer dimensionless stride lengths at a given dimensionless velocity than other mammalian quadrupeds. Unfortunately, stride frequencies over a range of dimensionless velocities are not available for quadrupedal mammals in general. Therefore, only stride lengths can be compared between the infant baboons and other mammals. Dimensionless stride lengths for the infant baboons were compared with those of non-primate and primate quadrupeds

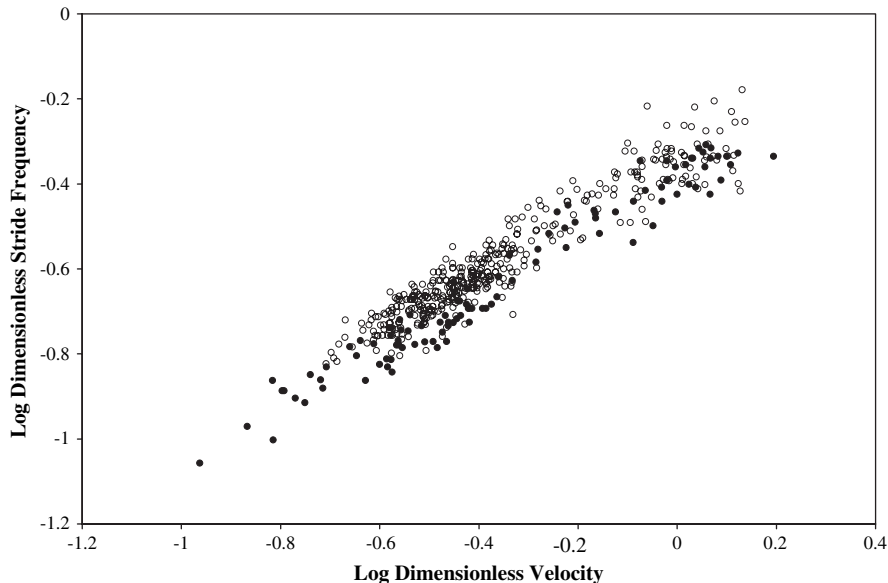


Fig. 3. Dimensionless stride frequencies over the range of dimensionless velocities for the combined sample of infant baboons. Group 1 individuals (relatively distal limb mass concentrations) are closed circles; Group 2 individuals (relatively proximal limb mass concentrations) are open circles.

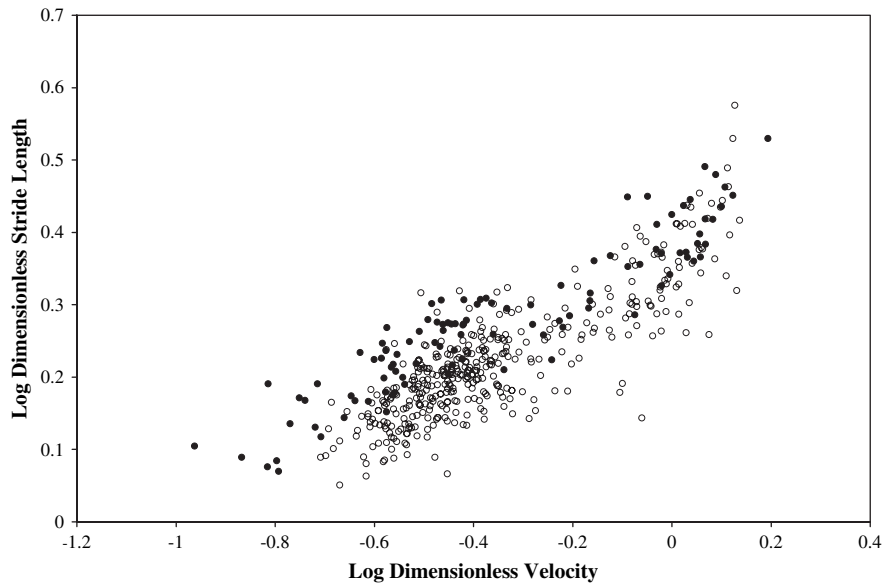


Fig. 4. Dimensionless stride lengths over the range of dimensionless velocities for the combined sample of infant baboons. Group 1 individuals (relatively distal limb mass concentrations) are closed circles; Group 2 individuals (relatively proximal limb mass concentrations) are open circles.

(data from Alexander and Jayes, 1983; Alexander and Maloij, 1984). At low dimensionless velocities, the infant baboons used longer dimensionless stride lengths than adult primates, non-cursorial non-primates, and cursorial non-primates (Fig. 5). At higher dimensionless velocities, the infant baboons appear to converge on the dimensionless stride lengths of the primate sample and even fall into the range of non-primate, non-cursorial mammals.

Discussion

The results of this study support the hypothesis that limb mass distribution patterns have a significant impact on locomotor kinematics. Although changes in kinematics with increasingly proximal limb mass concentrations are slight, they are consistent with predictions made from the hypothesized relationship between limb mass distribution and locomotor kinematics. When the infant baboons had more distal limb mass concentrations, their dimensionless stride frequencies were lower and their dimensionless stride lengths were

longer compared to older ages, when their limb mass was more proximally concentrated.

Importantly, Infant 4 serves as a control against an argument that these changes could be related to ontogenetic changes in neuromuscular control mechanisms. Infant 4 did not show any change in functional limb inertial properties and did not undergo any change in kinematics. If the kinematic changes in Infants 1–3 were simply a result of ontogenetic changes in neuromuscular control, then these same changes should have occurred in Infant 4 despite the lack of age-related changes in $dNPP_{\min}$.

The data from this sample of infant baboons provide a convincing explanation for the influence of limb mass distribution on locomotor variables. In an individual who has relatively distal limb mass concentrations, that distal limb mass will lead to relatively long swing durations. Relatively long swing durations may necessitate relatively long stance durations. In combination, the increased swing and stance durations lead to relatively low stride frequencies, long strides, and in some cases long steps, and likely large limb angular excursions.

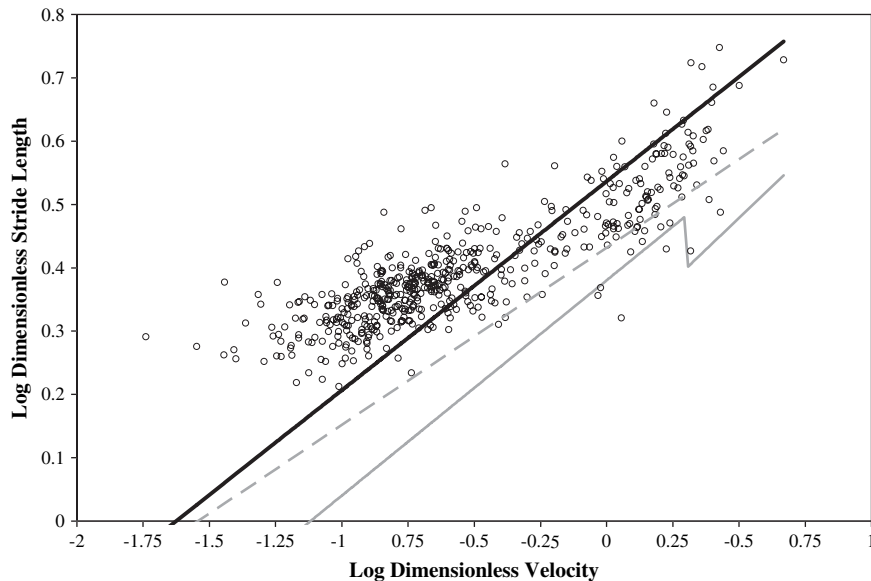


Fig. 5. Dimensionless stride lengths over the range of dimensionless velocities for the combined infant baboon sample compared to adult primates and non-primates. Adult primate data (solid black line) are from Alexander and Maloiy (1984); adult non-primate non-cursorial (dashed gray line) and cursorial mammal (solid gray line) data are from Alexander and Jayes (1983).

Comparisons with other mammals

Infant baboons have relatively more distal limb mass concentrations than other adult primates during much of their development, and have more distal limb mass concentrations than those of non-primate cursorial and non-cursorial quadrupeds (see Raichlen, 2004b). The results from this study show that the infant baboons also use longer dimensionless stride lengths compared to both adult primate and non-primate quadrupeds over most of their velocity range. This result is consistent with their more distal limb mass concentrations (see Raichlen, 2004b).

Studies testing the dynamic similarity hypothesis in mammalian quadrupeds also support a relationship between limb mass distribution and kinematics (see Alexander and Jayes, 1983; Alexander and Maloiy, 1984). If individuals depart from dynamic similarity in stride lengths, then individuals that use long dimensionless stride lengths should be those animals with the most distal limb mass concentrations. Non-cursorial quadrupeds appear to have more distal limb mass than cursors (Myers and

Studel, 1997), and they use longer dimensionless strides at all dimensionless velocities compared to more cursorial quadrupeds (Alexander and Jayes, 1983). Additionally, as mentioned above, adult primates have more distal limb mass concentrations than other mammals (Preuschoft and Günther, 1994; Raichlen, 2004a), and use longer dimensionless strides than both non-cursorial and cursorial quadrupedal mammals (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990).

Although these broad comparisons support the hypothesized relationship between limb mass distribution and kinematics, deviations from these trends may also be informative. For example, the two data points for the domestic cats in Figure 3 of Alexander and Jayes (1983) show extremely long strides compared to the other cursorial mammals. In fact, both points lie above the regression line for non-cursorial quadrupeds (see Fig. 3 of Alexander and Jayes, 1983). This departure from dynamic similarity within the cursorial group provides further support for the results from the infant baboon sample. Cats have limb mass distributions that resemble those of non-cursorial quadrupeds

more than cursors (Taylor et al., 1974). Their long dimensionless strides compared to other more cursorial mammals are therefore consistent with their relatively distal limb mass concentrations.

In Alexander and Maloiy's (1984) examination of dynamic similarity in primate quadrupeds, the two points for *Papio* fall well below the regression line describing the relationship between dimensionless stride length and Froude number for primates in general (see their Fig. 2). Again, these deviations from within group dynamic similarity may be consistent with the results of this study. *Papio* has the most proximal limb mass concentrations of the primates that have been analyzed (Raichlen, 2004a).

So, this comparative evidence, along with the results from the present ontogenetic "natural experiment" strongly suggest that spatiotemporal kinematics must, in part, be driven by limb mass distribution patterns. This suggestion has important implications for the evolution of primate quadrupedalism.

Implications for the evolution of primate quadrupedalism

Several researchers have suggested that the unique quadrupedal kinematics of primates evolved to facilitate locomotion in an arboreal, small-branch niche (Demes et al., 1990; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Schmitt, 2003). For example, large limb angular excursions in primates would increase stride length and facilitate lower stride frequencies at a given velocity, thereby reducing potentially dangerous branch oscillations. Increased stance durations are part of Schmitt's (1999) compliant gait model of primate walking. Increased stance durations would both help to reduce branch sway by decreasing stride frequency, and help reduce substrate reaction forces to alleviate problems associated with the crouched postures used by arboreal primates.

If the results from the infant baboon sample are expanded to primates in general, then the increased distal limb mass concentrations of primates may, in part, lead to their long strides, low stride frequencies, long contact times, and large limb angular excursions. The conclusions of this

study are compatible with the small-branch niche hypothesis. In fact, this analysis provides a plausible explanation for how all these features of gait may have evolved as a related functional complex within the small-branch niche. Early primates that invaded this niche would have first developed clawless grasping hands and feet (Cartmill, 1972). The features of gait that would be advantageous in this niche would have been a by-product of this original adaptation. Importantly, because most extant primates have retained clawless grasping hands and feet for climbing or food manipulation, and therefore relatively distal limb mass concentrations compared to non-primates, the results from this study help explain why primates use these kinematic characteristics even when they no longer occupy a small-branch niche.

These results do not preclude changes in kinematics that vary with substrate use, often used as a test of the small-branch niche hypothesis (see Schmitt, 2003). Schmitt (2003) showed that several cercopithecoids increased forelimb protraction angles on arboreal compared to terrestrial substrates. Increased protraction would likely be the result of increases in stance durations (increases in stance duration cause increases in step length, which must be brought about by larger limb angular excursions). The results from this study suggest that relatively long stance durations may be a response to increases in swing durations.

There is reason to expect increased swing durations on arboreal substrates. When walking on a branch, a primate may maintain a relatively more extended knee and elbow during swing phase compared to terrestrial walking because its hands and feet no longer need to clear the substrate (see Schmitt et al., 1994, for an example of vervet monkeys passing their hands below the substrate during arboreal quadrupedalism). This more extended knee and elbow would increase each limbs' NPP relative to terrestrial locomotion (see Myers and Steudel, 1997; Raichlen, 2004a), and therefore increase swing duration.

The connection between limb mass distribution and primate kinematics does not preclude non-primates from converging on primate locomotor characteristics. Other mammals have been shown to share many of the primate kinematic characteristics

described above (see Schmitt and Lemelin, 2002). Larson et al. (2000, 2001) showed that the woolly opossum (*Caluromys philander*) walks with large limb angular excursions, similar to those of primates (see also Schmitt and Lemelin, 2002). *Caluromys* also possesses grasping hands and feet (Lemelin, 1996, 1999), and Grand (1983) showed that *Caluromys* does, in fact, have relatively distal limb mass concentrations. Although no data are available showing relatively long strides and low stride frequencies in this taxon, if their large limb angular excursions are an indicator of these kinematic characteristics, then they may also be the by-product of adaptations for grasping extremities.

Conclusion

The stride lengths and stride frequencies of infant baboons are dependent on their limb mass distribution patterns. As infant baboons age, and their limb mass becomes more proximally concentrated, they use significantly higher dimensionless stride frequencies and significantly shorter dimensionless strides. Changes in stride lengths and stride frequencies that occur with limb mass distribution changes are brought about by changes in both swing and stance durations.

The relationship between limb mass distribution and locomotor kinematics may have important implications for the evolution of primate quadrupedalism. Primates in general have more distal limb mass than do most other mammals, and this distal limb mass may explain their relatively long strides, low stride frequencies, increased stance durations, and large limb angular excursions compared to other mammalian quadrupeds. These uniquely primate kinematic traits likely evolved because of the evolution of grasping hands and feet in the earliest primates during their invasion of the small-branch niche.

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