

RESEARCH ARTICLE

The Effect of Branch Diameter on Primate Gait Sequence Pattern

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Most mammals use lateral sequence gaits during quadrupedal locomotion, a pattern characterized by the touchdown of a forelimb directly following the ipsilateral hind limb in a given stride cycle. Primates, however, tend to use diagonal sequence (DS) gaits, whereby it is the touchdown of a *contralateral* forelimb that follows that of a given hind limb most closely in time. A number of scenarios have been offered to explain why primates favor DS gaits, most of them relating to the use of the arboreal habitat and, in particular, the exploitation of a narrow branch niche. This experimental study explores the potential explanation for the use of DS gaits by examining the relationship between branch diameter and gait patterns in 360 strides collected from six species of quadrupedal strepsirrhine primates on broad and narrow diameter supports. Gait sequence is quantified using *limb phase*, or the percentage of time during a stride cycle that a forelimb touchdown follows an ipsilateral hind limb touchdown. Although *Loris*, *Nycticebus* and *Eulemur rubriventer* individuals in this study did exhibit significantly lower locomotor velocities on narrower supports ($P < 0.01$ in all three species), analyses of covariance showed no significant differences in limb phase values between broad and narrow diameter supports. Hence, results indicate surprisingly little evidence to suggest that alterations in gait sequence pattern provide a specific advantage for negotiating narrow supports. *Am. J. Primatol.* 70:356–362, 2008. © 2007 Wiley-Liss, Inc.

Key words: arboreality; locomotion; limb phase; primates; quadrupedalism

INTRODUCTION

Primates are distinctive among mammals in that they are largely an arboreal radiation. Extant primates include a diversity of slow climbers, specialized leapers and species that use their limbs for suspension and brachiating locomotion. Most possess a suite of morphological features including a generalized limb structure with grasping cheiridia, enabled by a divergent pollex and hallux and the replacement of claws by nails [Le Gros Clark, 1971]. Taken together, such anatomical specializations are thought to facilitate life in the trees; indeed, for nearly a century it has been suggested that arboreality played a role in the evolution of the earliest primate ancestors [e.g., Le Gros Clark, 1971; Sargis, 2002; Smith, 1912; Wood Jones, 1916].

Nearly all primates include arboreal quadrupedalism in their locomotor repertoires [Hildebrand, 1967; Rose, 1973]. Using low stride frequencies, relatively low vertical substrate reaction forces on the forelimb, long stride lengths and broad limb excursions, most primates also employ a distinctive sequence of footfall patterns, the diagonal sequence (DS) gait [e.g., Alexander & Malooy, 1984; Demes et al., 1994; Larson, 1998; Larson et al., 2000, 2001; Vilensky & Larson, 1989]. Most scenarios have sought to link the use of DS gaits to maintaining balance in the arboreal habitat, particularly in the

terminal branch setting [Cartmill, 1972; Cartmill et al., 2002; Demes et al., 1994; Hildebrand, 1967; Lemelin et al., 2003; Muybridge, 1887; Prost & Sussman, 1969; Rollinson & Martin, 1981; Vilensky & Larson, 1989; Vilensky et al., 1994]. These arguments have been strengthened by the observation that certain non-primate mammals that habitually travel along narrow branches also use DS gaits, for example the phylogenetically distant opossum taxon, *Caluromys* [Lemelin et al., 2003; Schmitt & Lemelin, 2002].

Despite the number of studies documenting the use of DS gaits in primates, no environmental mechanism has yet been revealed that fully explains why primates tend to choose this particular footfall sequence pattern [Cartmill et al., 2002; Shapiro &

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Raichlen, 2005; Stevens, 2003; Vilensky & Larson, 1989]. Indirect support for the utility of DS gaits for maintaining balance in the arboreal setting has been suggested based on the use of lateral sequence (LS) gaits by callitrichids, primates that converge with non-primates in having claws and avoiding the terminal branch milieu [Hildebrand, 1967; Schmitt, 2003]. Yet observations of LS gaits have been made in other primates as well, including highly arboreal taxa such as lemurs, lorises and certain Old World monkeys, suggesting significant variability in interlimb coordination in the Primate Order [e.g., Dunbar & Badam, 2000; Prost & Sussman, 1969; Rollinson & Martin, 1981; Stevens, 2003, 2004; Vilensky & Larson, 1989; Vilensky & Moore, 1992; Vilensky et al., 1994].

Exploring the contexts in which different gait sequence patterns are used may show whether primates select particular footfall sequences to cope with biomechanical challenges associated with the arboreal environment. Although the fine branch niche is often implicated for the use of DS gaits, few experimental data have been collected specifically to test the notion that this gait sequence pattern offers greater stability for making and maintaining contact with narrow arboreal supports. If DS gaits convey a mechanical advantage associated with mediolateral stability in the terminal branch setting, one may expect to observe significant alterations in interlimb timing in animals traveling atop broad and narrow supports.

METHODS

Data collection for this study was legally conducted in the United States with permission from the Stony Brook University and the Duke University Institutional Animal Care and Use Committees, and in adherence with the American Society of Primatologists principles of ethical treatment of non-human primates. The study subjects included members of six strepsirrhine primate species housed at the Duke University Primate Center. Notably, experimental animals had regular access to naturalistic supports

in their enclosures. Owing to subject availability for rarer species, the study sample was limited to one adult male and female per species. Subjects examined herein represent three families (cheirogaleids, lemurids and lorises), selected to consider adaptations for arboreality in a sample of arboreal quadrupeds ranging in body size and proportions, with well-documented morphologies and positional behaviors [e.g., Dagosto, 1995; Ganzhorn, 1985; Hamrick, 1996; Jouffroy & Lessertisseur, 1978; Jungers, 1985; Overdorff, 1996; Shapiro et al., 2001; Sussman, 1977; Ward & Sussman, 1979].

Cheirogaleids (*Cheirogaleus medius* and *Mirza coquereli*) are generalized arboreal quadrupeds with the relatively shortest limbs of all primates, and have been suggested to closely resemble the ancestral primate morphotype [Cartmill, 1972; Covert, 1995; Fleagle, 1988; Gebo, 1987; Godinot, 1990; Martin, 1972]. Lemurids (*Eulemur fulvus* and *Eulemur rubriventer*) are adept arborealists, some of which spend nearly all of their time moving through the continuous canopy [e.g., Sussman, 1977]. Lorises (*Nycticebus coucang* and *Loris tardigradus*) are a derived group, with the relatively longest limbs of all primates and specializations for deliberate walking and agile climbing [Curtis, 1995; Ishida et al., 1983; Jouffroy et al., 1983; Nekaris & Stevens, 2007; Runestad, 1997].

Simulated branches were constructed from 2.44-m sections of polyvinyl chloride pipes, coated with a non-slip surface and oriented horizontally. To examine effects of support diameter in animals of differing body proportions, substrates were scaled to the cube root of subjects' body mass (Table I). This provides a refinement on previous definitions of narrow and broad branch diameter, although in all cases, it was possible for the subjects' cheiridia to grasp around narrow branches, whereas on broader branches, the hands and feet were able to comfortably rest along the upper surface of the horizontal support. *E. fulvus* subjects were also filmed moving on the narrowest (1.25 cm) support to ensure that narrow branch responses were accurately captured by the branch diameter categories in the largest taxa.

TABLE I. Branch Diameter Categories Used in this Study

Category	Body mass (M) (in kg)	Species	Narrow diameter ~cube root (M) × 2.5 (cm)	Broad diameter ~cube root (M) × 10 (cm)
1	0.16–0.27	<i>Loris tardigradus</i> <i>Cheirogaleus medius</i>	1.25	5
2	0.31–0.33	<i>Mirza coquereli</i>	1.88	7.5
3	1.0–1.2	<i>Nycticebus coucang</i>	2.5	10
4	1.9–2.3	<i>Eulemur fulvus</i> <i>Eulemur rubriventer</i>	3.13	12.5

Subjects were placed into one of four body size categories and substrate diameters were scaled to the cube root of body mass. Narrow diameter supports were approximately 2.5 times the cube root of body mass (in centimeters), whereas broad diameter supports were approximately ten times the cube root of body mass.

Animals were acclimated to these substrates in their naturalistic enclosures before data collection to minimize the impact of the experimental setting on their performance. Using standard two-dimensional kinematic techniques, cameras were positioned to provide lateral and fore-aft views of the subjects, and synchronized with a special effects generator. Frame rates were optimized to catch rapid movements by splitting the fields, and shutter speeds were set to reduce motion blur. Video clips were imported into Peak Motus (version 7.1) and 15 symmetrical strides per individual per substrate were collected, with the total number of individual ($n = 12$) and support ($n = 2$) combinations yielding 360 strides. A full description of the experimental setup may be found in Stevens [2003].

Video clips were analyzed frame by frame, and gait variables were collected by digitizing limb touchdown and lift off events. Gait terminology discussed herein follows Hildebrand [1966]. Limb phase, also referred to as “gait number” [Shapiro & Raichlen, 2005] and “diagonality” [Cartmill et al., 2002], was defined as the percentage of time relative to a stride duration that touchdown of a forelimb followed touchdown of an ipsilateral hind limb (Table II). Strides in which limb phases exceeded 0.56 were identified as DS gaits, whereas strides exhibiting limb phases below 0.44 were recorded as LS gaits. Strides with limb phase values between 0.44 and 0.56 were recorded as functional trots (T), with nearly simultaneous contralateral forelimb and hind limb contact.

Gait sequence or limb phase was also examined as a continuous variable, and as this variable did not typically follow a normal distribution, data were rank-transformed before analysis. Original variates

were replaced with the ranks, and ties were broken by assigning mean ranks to tied cases [SPSS version 13.0, 1997]. Rank transformations permit two-way analysis of variance without loss of power in data sets that are not normally distributed [Conover & Iman, 1981].

No attempt was made to constrain speeds in this study, as any observed differences may themselves constitute a response to branch type. It is also possible that relationships may exist between limb phase and velocity, with animals altering the sequence of limb contact at different speeds. To explore substrate-related differences in limb phase while taking into account differences in speed, means were analyzed using an analysis of covariance [ANCOVA; Sokal & Rohlf, 1981] with velocity (meters per second) as the covariate. ANCOVAs compare kinematic variables collected on two substrates at the mean velocity observed on both substrates. When no significant relationships with velocity were observed, data were analyzed using analyses of variance for substrates of differing diameters.

RESULTS

Gait sequence, mean limb phase and velocity values on broad and narrow supports are reported for each species in Table II. Data analyzed at the level of the individual yielded strikingly similar patterns. The majority of species (four of six) examined in this study exhibited lower locomotor velocities on narrower supports (Fig. 1), although these differences reached significance in only three species, *Loris*, *Nycticebus* and *E. rubriventer* ($P < 0.01$ for all three).

TABLE II. Comparisons of Gait Sequence, Limb Phase, Duty Factor and Velocity on Broad and Narrow Diameter Horizontal Supports for Entire Sample

	<i>n</i>	#LS	#T	#DS	Limb phase		Velocity (m/sec)	
					Mean	SD	Mean	SD
Broad diameter								
<i>Loris tardigradus</i>	30	0	15	15	0.56	0.04	0.36	0.12
<i>Nycticebus coucang</i>	30	0	10	20	0.59	0.07	0.54	0.16
<i>Eulemur fulvus</i>	30	0	0	30	0.67	0.02	0.72	0.15
<i>Eulemur rubriventer</i>	30	0	0	30	0.67	0.03	0.68	0.08
<i>Mirza coquereli</i>	30	0	8	22	0.59	0.06	0.81	0.31
<i>Cheirogaleus major</i>	30	0	6	24	0.60	0.06	0.78	0.28
Narrow diameter								
<i>Loris tardigradus</i>	30	0	10	20	0.58	0.04	0.18	0.09
<i>Nycticebus coucang</i>	30	2	14	14	0.54	0.07	0.28	0.09
<i>Eulemur fulvus</i>	30	0	0	30	0.66	0.03	0.76	0.14
<i>Eulemur rubriventer</i>	30	0	1	29	0.66	0.04	0.53	0.06
<i>Mirza coquereli</i>	30	0	0	30	0.63	0.09	0.82	0.30
<i>Cheirogaleus major</i>	30	0	10	20	0.58	0.06	0.67	0.26

Limb phase is percentage of stride cycle that a forelimb touchdown follows touchdown of an ipsilateral hind limb. LS, lateral sequence; T, trot; DS, diagonal sequence.

Mean limb phase values of most taxa considered in this study tended to be similar, or even slightly lower on narrower supports (Fig. 2). Partitioning limb phase values into discrete gait sequence categories showed that lemurids used almost exclusively DS gaits regardless of branch diameter, with *E. rubriventer* exhibiting only a single stride with a limb phase value below 0.56 (Table II). Lorisids and cheirogaleids used a mixture of DS and trotting gaits on study supports, the proportion of DS gaits increasing on narrower branches in *Loris* and *Mirza*, and decreasing on narrower branches in *Cheirogaleus* and *Nycticebus*. *Nycticebus* occasionally used LS gaits on the narrower branches (Table II).

For each species, mean limb phase values were remarkably similar on broad and narrow supports; even among the strides within a given gait sequence category, limb phase was not appreciably higher on the narrower supports (Table III). Yet a closer examination shows that discrete gait sequence categories do not reflect significant responses to support diameter when the limb phase is exam-

ined as a continuous variable for any of the study species except *Nycticebus* ($P < 0.05$). ANCOVAs show that even those differences can be explained by the aforementioned substrate-related differences in velocity alone.

DISCUSSION

The locomotor behavior of the six strepsirrhine species considered herein did not provide clear support for the notion that DS gaits convey an advantage for moving on fine branch supports as there were no significant differences in limb phase values between broad and narrow supports. This is interesting in light of the findings of Lemelin et al. [2003] that showed higher limb phase values in opossums walking on narrow diameter supports. Although this certainly does not rule out the possibility that DS gaits have functional advantages on arboreal supports in general, mediolateral balance on narrow supports alone does not seem to be the driving factor behind gait selection for the

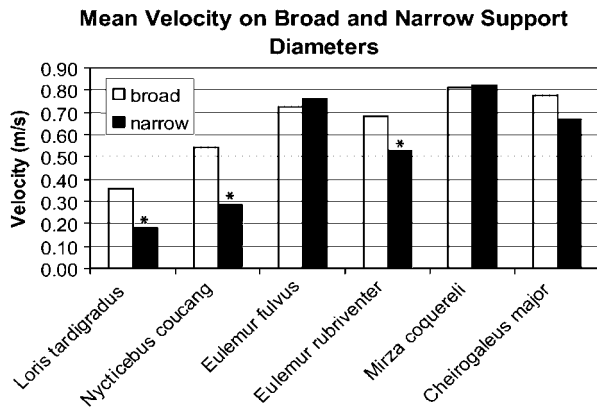


Fig. 1. Mean velocities on broad and narrow supports ($n = 360$ for 30 strides per species per support type). A trend for lower velocity locomotion was observed on narrower branches, but differences were significant only in three species (*Loris tardigradus*, *Nycticebus coucang* and *Eulemur rubriventer*).

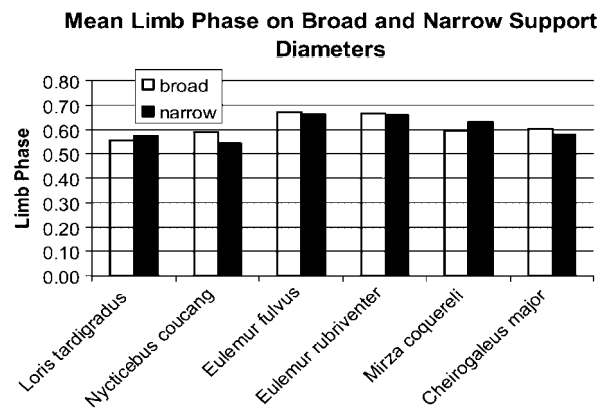


Fig. 2. Mean limb phase on broad and narrow support diameters ($n = 360$ for 30 strides per species per support type). No significant differences were observed in mean limb phase between broad and narrow supports once differences in velocity were taken into account.

TABLE III. Average Limb Phase by Gait Sequence Category on Broad and Narrow Diameter Horizontal Supports

	DS		T		LS	
	Broad	Narrow	Broad	Narrow	Broad	Narrow
<i>Eulemur fulvus</i>	0.67	0.66	NA	NA	NA	NA
<i>Eulemur rubriventer</i>	0.67	0.66	NA	NA	NA	NA
<i>Mirza coquereli</i>	0.62	0.61	0.53	NA	NA	NA
<i>Cheirogaleus medius</i>	0.62	0.62	0.53	0.51	NA	NA
<i>Loris tardigradus</i>	0.59	0.60	0.52	0.54	NA	NA
<i>Nycticebus coucang</i>	0.62	0.60	0.52	0.49	NA	0.38

DS, diagonal sequence; T, trot; LS, lateral sequence; NA, not observed.

animals examined here. This is perhaps not surprising as it has long been acknowledged that either DS or LS gaits can be used in combination with diagonal limb couplet support patterns [e.g., Hildebrand, 1966, 1976, 1985; Muybridge, 1887]. Although few LS gaits were observed in this sample, this support pattern is equally true of trots, which are defined by near simultaneous contact by diagonal limb couplets. The diagonal couplet support enables primates to surmount mediolateral balance challenges associated with decreased support width in part by allowing the grasping cheiridia to maintain contact with the branch, exerting forces to counter tendencies to roll in either direction [e.g., Vilensky et al., 1994]. Indeed, use of narrow-diameter branches has been linked with increases in absolute and relative contact times in some species [e.g., Stevens, 2003, 2004]. Thus, it seems only natural that animals possessing adaptations for grasping respond to mediolateral balance challenges by increasing the relative time their hands and feet are in contact with the support.

Both loris species and *E. rubriventer* in this study significantly reduced travel velocities on narrower supports. It is likely that alterations in velocity may assist in maintaining balance on narrow branches. Although the lemurids used almost exclusively DS gaits regardless of support diameter, lorises and cheirogaleids tended to use trots more frequently. *Loris tardigradus* and *M. coquereli* trotted more frequently on broader supports, and their overall limb phase values were slightly higher on narrower branches. In contrast, a higher narrow-branch frequency of non-DS gaits in *N. coucang* and *C. medius* likely contributed to the lower limb phase values observed overall for those taxa on narrow branches. Despite these slight differences in velocity and limb phase, there were no significant responses in gait sequence pattern that could be attributed solely to substrate diameter in any of the species examined in this study. So although most primates tend to employ a higher percentage of DS gaits than do their non-primate relatives, it does not seem to be exclusively related to moving along horizontal linear narrow supports.

Clearly other biomechanical challenges associated with arboreality may contribute to the use of DS gaits, and their examination can provide additional windows into locomotor patterns in primates [Grand, 1972, 1984; Lammers et al., 2003; Stevens, 2000, 2001, 2003; Stevens et al., 2001]. For example, gait sequence pattern does seem to vary with support orientation. DS gaits are common on inclined branches, whereas a higher frequency of LS gaits have been reported on declined supports [e.g., Hildebrand, 1967; Rollinson & Martin, 1981; Stevens, 2003; Vilensky et al., 1994]. The reasons for this are not clear, but possible explanations include differences in relative stance and swing phase durations or the effects of a shift in body

posture to make contact with and avoid sliding and toppling on oblique supports [e.g., Stevens, 2006]. The effects of branch stability on gait sequence pattern also deserve consideration, as maintaining balance during movement through the arboreal canopy is often complicated by the use of branches that sway in response to an animal's movements [e.g., Stevens, 2003, 2006]. It is important to recognize that the terminal branch setting can offer a broad array of different supports to grasp, and animals often distribute their weight across multiple supports, carefully selecting hand and foot placements among numerous pliable supports extending in different directions [Grand, 1972, 1984]. Cartmill et al. [2002] suggested that DS gaits relate to increased stability in this setting, whereby the grasping foot is in firm contact with the support before a hand places weight on an untested support. Yet Shapiro and Raichlen [2005] have shown that in lateral sequence lateral couplets gaits, a hind limb is also positioned under the body at the instant of forelimb touchdown. It seems more likely that *if* DS gaits are more common in the terminal branch setting, this could result from a lag in the forelimb making contact, as it searches out a suitable substrate. But this is also somewhat unsatisfactory, as it does not explain the persistence of DS gaits in primates moving on other substrate types, notably the ground. In any case, animals often negotiate fine branch habitats during foraging, taking a few steps at a time and stopping to feed by bringing the mouth to the food item or using the hands to bring food items to the mouth [e.g., Grand, 1972]. As such, steady speed locomotion in this setting may not be ecologically relevant for a great many species that nonetheless habitually use DS gaits.

Yet coordination of interlimb timing requires greater independence of forelimb and hind limb movements. In particular, flexibility in gait sequence patterns among primates provides a particularly interesting venue for further research. As suggested by Vilensky and Larson [1989], the use of DS gaits may relate to evolutionary changes that released the tight neurological control between forelimb and hind limb movements. Hence, primates may use DS gaits simply because it is possible for them to do so, with neither gait offering a particular balance advantage on horizontal supports. Such reasoning is supported by the fact that subjects readily switch between DS and LS gaits treadmills [e.g., Vilensky & Moore, 1992], and on different arboreal supports [Stevens, 2006]. A phylogenetic pattern within primates is also possible, as LS gaits have been reported more frequently in strepsirrhines and platyrrhines than in Old World monkeys [but see Rollinson and Martin [1981] for mention of a mangabey using LS gaits—interestingly that animal had a damaged spine]. Furthermore, the observation of LS lateral couplet gaits in juvenile primates in captivity [Hildebrand,

1967; Nakano, 1996; Rollinson & Martin, 1981; Shapiro & Raichlen, 2005] and in the wild [Dunbar & Badam, 2000] suggests promise of further exploration of ontogenetic variability in gait patterns.

Finally, it is important to recognize that although many studies have focused on gait sequence pattern during continuous symmetrical quadrupedal locomotion in primates, such studies have only touched on the types of arboreal movements that characterize the Order. Asymmetric gaits, vertical and horizontal leaping and suspension and arm swinging behaviors (with and without the use of a prehensile tail) comprise additional components of the diverse toolkit that primates have developed to cope with arboreal challenges over the course of tens of millions of years of evolutionary history.

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