

Stability, Limb Coordination and Substrate Type: The Ecorelevance of Gait Sequence Pattern in Primates

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ABSTRACT The coordination of limb movements during mammalian locomotion has been well documented in the literature. Most mammals use lateral sequence (LS) gaits, in which a forelimb follows an ipsilateral hind limb during the stride cycle. Primates, however, tend to utilize diagonal sequence (DS) gaits, whereby a contralateral forelimb follows a given hind limb during the stride cycle. 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 terminal branch niche. Yet to date, there is surprisingly little evidence to support the advantage of DS gaits for negotiating different aspects of the terminal branch environment. Nonetheless, it is apparent that primates possess unique morphologies and a higher than typically recognized degree of flexibility in gait sequence pattern, both of which likely offer advantages for moving upon discontinuous and unstable terminal branches. This paper reviews potential explanations for the use of DS gaits in primates and considers mechanisms by which gait sequence may be altered during different types of arboreal challenges. *J. Exp. Zool.* 305A:953–963, 2006. © 2006 Wiley-Liss, Inc.

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The coordination of limb movements during locomotion has long been a topic of interest among biologists. Early efforts by the Marquis of Newcastle in the 1650s (cited in Muybridge, 1887) categorized equine footfall patterns using the terms walk, trot, amble and gallop. Descriptions of gait in the 18th and 19th centuries often relied on the sounds produced by rhythmic footfall patterns, useful for describing when each foot initiates contact with the ground, but not for when each foot is raised. It was not until the advent of rapid photographic methodologies that workers were able to more accurately document the entire gait cycle (e.g., Muybridge, 1887). Such advances eventually led to the development of the motion picture, making possible the modern study of kinematics.

Through the years, myriad graphical representations have been created to describe footfall patterns in reference to body support (Smith, '12; Prost, '65; Hildebrand, '66, '67, '76, '77, '85; Sukhanov, '74; Cartmill et al., 2002), and considerable efforts have focused on analyzing gait

sequence patterns utilized by different animals during locomotion (e.g., Muybridge, 1887; Magne de la Croix, '29; Gray, '44; Hildebrand, '65, '66, '70; Prost and Sussman, '69; Sukhanov, '74; Vilensky and Larson, '89; Meldrum, '91; Demes et al., '94; Vilensky et al., '94; Reilly and Delancey, '97; Cartmill et al., 2002; Schmitt and Lemelin, 2002; Reilly and Biknevicius, 2003). Hildebrand's ('66) classification has become a common method for describing gait and support patterns during the stride cycle (but see papers in this volume by Biknevicius and Reilly and by Biewener for gait terminology based on kinetic and potential energy fluctuations). In Hildebrand's approach, variables

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are summarized in 2D scatter plots with hind limb duty factor (stance duration/stride duration) on the *x*-axis, and limb phase (the duration of time between hind limb touchdown and touchdown of the ipsilateral forelimb, expressed as a percentage of the stride cycle) on the *y*-axis. Limb phase describes the *gait sequence* of a given stride. Symmetrical gaits are divided into two main categories, lateral sequence (LS) and diagonal sequence (DS). In LS gaits, touchdown of a hind limb is directly followed by that of an *ipsilateral* forelimb during the stride cycle (Left Hind–Left Fore–Right Hind–Right Fore). In contrast, DS gaits are characterized by the touchdown of a *contralateral* forelimb directly following that of a given hind limb during the stride cycle (Left Hind–Right Fore–Right Hind–Left Fore). Hence LS strides exhibit lower limb phase values than DS strides. Intermediate between these are gait sequence patterns in which a forelimb and hind limb strike in near synchrony. In the trot, it is the contralateral limbs that strike closely together in time, whereas the pace is characterized by ipsilateral limb synchronization.

An understanding of the ordered patterning of footfalls can lend insight into different aspects of locomotor biology. Tetrapods tend to cluster into different regions of gait space, presumably reflecting the combined influence of phylogeny and function upon their locomotor tendencies (Hildebrand, '66, Figure 17). Whereas the vast majority of tetrapods employ LS and trotting patterns during continuous symmetrical locomotion (Hildebrand, '65, '66; Sukhanov, '74; Vilensky and Larson, '89; Reilly and Delancey, '97; Cartmill et al., 2002; Reilly and Biknevicius, 2003), DS gaits are utilized by far fewer taxa, most notably members of the Order Primates (Hildebrand, '66, '67; Prost and Sussman, '69; Vilensky and Larson, '89; Meldrum, '91; Demes et al., '94; Vilensky et al., '94; Cartmill et al., 2002; Schmitt and Lemelin, 2002; Stevens, 2003; Shapiro and Raichlen, 2005). This paper considers why primates may be different from other tetrapods in this regard.

WHY DO PRIMATES USE DS GAITS?

Most primates possess a suite of anatomical specializations that include a generalized limb structure with grasping hands and feet, enabled by a divergent pollex and hallux and the replacement of claws by nails (Le Gros Clark, '71). In addition to a preference for DS gaits, it has been proposed that primates exhibit relatively lower

vertical substrate reaction forces on the forelimb, lower stride frequencies, longer stride lengths and broader limb excursions than do, for example, cursorial animals (Reynolds, '87; Demes et al., '94; Larson, '98; Schmitt, '99; Larson et al., 2000, 2001). Such specializations are thought to enable them to make a living in the trees, and for nearly a century it has been suggested that arboreality played a pivotal role in the evolution and subsequent diversification of the earliest primates (e.g., Smith, '12; Wood Jones, '16; Le Gros Clark, '71).

ARBOREALITY AND GAIT SEQUENCE PATTERN

Extant primates include a diversity of slow climbers, specialized leapers and species that use their limbs for suspension and brachiating locomotion. Yet the majority of primates include arboreal quadrupedalism as part of their locomotor repertoires (Hildebrand, '67; Rose, '73). Perhaps as a result, most of the scenarios formulated to explain why primates favor DS gaits relate to maintaining balance during locomotion in the arboreal habitat, and in particular, the exploitation of a terminal branch niche (Prost and Sussman, '69; Hildebrand, '67; Cartmill, '72; Grand, '72; Rollinson and Martin, '81; Grand '84; Vilensky and Larson, '89; Demes et al., '94; Vilensky et al., '94; Cartmill et al., 2002; Schmitt and Lemelin, 2002). Indirect support for the utility of DS gaits for maintaining balance in the arboreal setting has been suggested based on the use of LS gaits by callitrichids, primates that converge with non-primates in having claws and avoiding the fine branch milieu (Hildebrand, '67; Cartmill et al., 2002; Schmitt, 2003). Yet LS gaits have been observed in other primates as well, including highly arboreal taxa such as lemurs and lorises (Charles-Dominique, '77; Dykij, '80; Reynolds, '85; Stevens, 2003, 2004), other platyrhines (Hildebrand, '67; Prost and Sussman, '69; Rollinson and Martin, '81; Vilensky and Patrick, '85; Vilensky et al., '94) and certain catarrhines (Hildebrand, '67; Rollinson and Martin, '81), suggesting significant variability in interlimb coordination within the primate Order (e.g., Jungers and Anapol, '85; Vilensky and Larson, '89; Vilensky and Moore, '92; Shapiro et al., '97; Stevens, 2003, 2004).

Despite the number of studies positing a relationship between arboreality and the use of DS gaits, *no direct mechanism has yet been*

revealed to link the use of DS gaits with a specific aspect of the arboreal habitat (Vilensky and Larson, '89; Cartmill et al., 2002; Stevens, 2003; Shapiro and Raichlen, 2005). For example, it is widely believed that support on diagonal limbs may provide better stability in the face of mediolateral balance challenges on narrow branches. But it is important to underscore the distinction between gait sequences (the lateral or diagonal ordering of the footfalls) and support couplets (the support of the body by lateral or diagonal limbs). That is to say, diagonal limbs can support the body in two ways: the hind limb can touch down before the contralateral forelimb and both can maintain contact for a time, or a forelimb can touch down before a contralateral hind limb with both providing support. The former instance describes a DS-diagonal couplet (DC) step, whereas the latter characterizes a LS-DC step. Hence couplet pattern better describes body support, whereas gait sequence simply describes the order in which the limbs come into contact with a substrate in order to provide that support. Indeed, an examination of the relationship between branch diameter and gait sequence pattern in a sample of six primate species of differing body masses and limb proportions has shown that although primates typically employ DC support patterns, there is no evidence that primates employ a higher proportion of DS gaits when negotiating narrow branches (Stevens, 2003, in review).

Vilensky and Larson ('89) observed that many hypotheses related to balance in the arboreal setting assume the need for static stability at particular instants, rather than exploring the dynamic stability that typically characterizes locomotion. For example, it has been suggested that DS gaits permit better support of the body at the precise time that a forelimb touches down on a compliant arboreal support (Cartmill et al., 2002). Yet this would not explain why so many primates persist in using DS gaits on the ground, whereas naturalistic observations have actually documented a switch to LS gaits in the terminal branches (Dunbar and Badam, 2000). In fact, Shapiro and Raichlen (2005) have pointed out that, at least on the ground, LS gaits with ipsilateral couplets can offer similar if not greater body support as DS gaits with contralateral limb support at the instant of forelimb touchdown, particularly in non-cursorial animals with broad limb excursions. So it is perhaps not surprising that there is little evidence that DS gaits provide primates with

greater stability on flexible supports. Indeed, a sample of over 200 arboreal strides does not reveal a consistent increase in the frequency of DS gaits on unstable branches across a sample of primate species varying in body sizes and limb proportions (Stevens, 2003).

MASS DISTRIBUTION AND GAIT SEQUENCE PATTERN

Some have sought to link DS gaits with a more posteriorly placed center of mass (COM) in primates (e.g., Rollinson and Martin, '81). Kimura et al. ('79) suggested that primates may exhibit lower forelimb/hind limb force ratios than do other animals, perhaps because they also use forelimbs for foraging. But Demes et al. ('94), found little to suggest that quadrupedal primates employ relatively higher hind limb forces, suggesting that the patterns observed by Kimura et al. ('79) may have been driven by the suspensory taxa in their sample.

Some evidence does, however, point to a relationship between gait sequence pattern and mass distribution in quadrupeds. For example, numerous studies have observed a consistent shift to LS gaits in primates moving on declines (e.g., Hildebrand, '67; Rollinson and Martin, '81; Vilensky et al., '94; Stevens, 2003). And the use of LS gaits in young primates observed by Hildebrand ('67) and more recently by Shapiro and Raichlen (2005) may relate to ontogenetic changes in whole-body mass distribution, if for example the proportionally larger head acts to shift the COM anteriorly, as posited by Rollinson and Martin ('81). Also, work by Tomita ('67) and later Lee et al. (2004), has demonstrated a relationship between limb phase and mass distribution in canines experimentally loaded with weighted backpacks that altered the fore-aft position of the COM. Vilensky and Larson ('89) have pointed out that in the primate taxa for which mass distribution information has been documented, the anatomical COM is actually *not* located significantly more caudad than in animals such as cats that habitually use LS gaits, and that the position of the COM changes with every movement an animal makes. Schmitt and Lemelin (2004) further reject a relationship between weight distribution and primate gait sequence pattern, arguing that DS gaits are decoupled from lower forelimb/hind limb force ratios in the slender loris on horizontal supports. Moreover, anatomical COM observed in standing animals may not always equate with

substrate reaction forces in the dynamic setting. Indeed, Reynolds ('85) has suggested that some primates may employ a *behavioral* posterior weight shift strategy, a notion also promoted by Krakauer et al. (2002) to reduce forelimb forces on declines. As mentioned above, however, most primates shift to a higher percentage of trots and LS gaits on declined substrates (e.g., Stevens, 2003), suggesting that the interplay between gravity and gait sequence pattern requires further clarification. Both explanations could be accommodated, for example, should a posterior weight shift occur on declines, insufficient to shift the COM rearward enough to result in DS gaits, yet sufficient to spare forelimbs from unnecessarily high impact forces.

Shapiro and Raichlen (2002) have suggested that gait sequence in primates may actually reflect mass distribution, not in fore-aft position of whole-body COM, but rather in greater mass of distal limb segments as a result of musculature associated with the grasping cheiridia. As pointed out by Preuschoft et al. ('96), increased mass in distal limb segments may contribute to the longer swing phase durations and lower stride frequencies observed in primates relative to many other mammals (Reynolds, '87). Demonstrating that the limbs of primates exhibit a lower natural pendular period than do, for example, those of canids, Raichlen (2004) noted that the resulting longer swing phase durations might contribute to differences in the timing of limb touchdown events. Indeed, increases in swing phase and stride durations have been obtained by experimentally increasing mass in human and canid limbs (Skinner and Barrack, '90; Steudel, '90). Yet the tremendous range in interlimb proportions across primates and other mammals suggests that limb mass distributions may not seamlessly explain the use of DS gaits. If limb masses were the primary factor driving gait sequence pattern, interspecific differences in limb lengths and proportions would be expected to have a more systematic effect upon relative stride lengths, stride frequencies and thus gait sequence patterns in primates of different proportions. Moreover mass distribution, alone, cannot account for the *variability* in gait sequence pattern observed within primate individuals (e.g., Hildebrand, '67; Stevens, 2003). An extreme example is illustrated in Figure 1, demonstrating the locomotor plasticity exhibited by a single slender loris on a broad range of arboreal supports. If primates are disposed to utilize DS gaits due to greater distal limb segment masses,

what explains their frequent use of LS and trotting gaits?

A "SYNTHETIC" APPROACH: INTERACTIONS AMONG KINEMATIC VARIABLES

A partial answer may be that the effects of limb mass may be combined with different kinematic responses to arboreal challenges. Modification in the degree of limb joint flexion throughout swing phase effectively changes the length of a swinging pendular limb, altering the duration of the swing phase and affecting the initiation of the subsequent limb touchdown (Raichlen, 2004). Likely differences in the line of gravity on oblique supports disrupt normal pendular mechanics on inclines, and may act to accelerate the limbs during swing phase on declines. Differential mass and flexion of forelimbs and hind limbs (Raichlen, 2004), in combination with differential muscular effort during limb protraction (e.g., Jungers and Stern, '83; Whittlesey et al., 2000) may then contribute to produce the gait sequence patterns observed in various locomotor contexts, such that gait sequence pattern may not *itself* convey an adaptive advantage, but may instead result from a kinematic constraint.

Importantly, stride cycles are comprised not simply of swinging pendular limbs, but also of interchanging intervals of body *support*. Not surprisingly, animals with grasping cheiridia often employ alterations in absolute and/or relative stance phase durations to maintain contact with narrow, oblique and flexible supports (Stevens, 2000, 2001, 2003, 2004). On inclined supports, primates must use their hands and feet to generate greater propulsive forces to overcome gravity, whereas on declines, greater breaking forces may be applied to resist acceleration (Lammers et al., 2003). Unstable supports may favor longer relative contact times in order to minimize branch disturbances (Demes et al., '90). The use of grasping hands and feet for braking, propulsion and mediolateral stability in animals of different body shapes may be reflected in alterations in limb flexion patterns. Taken together, this "kinematic integration" takes into account the many variables that can play a role in explaining the variability observed in primate gait sequence patterns. Just as duty factor can change by altering either stance or swing phase durations (e.g., Stevens, 2003, 2004), so too can gait sequence pattern change by altering relative

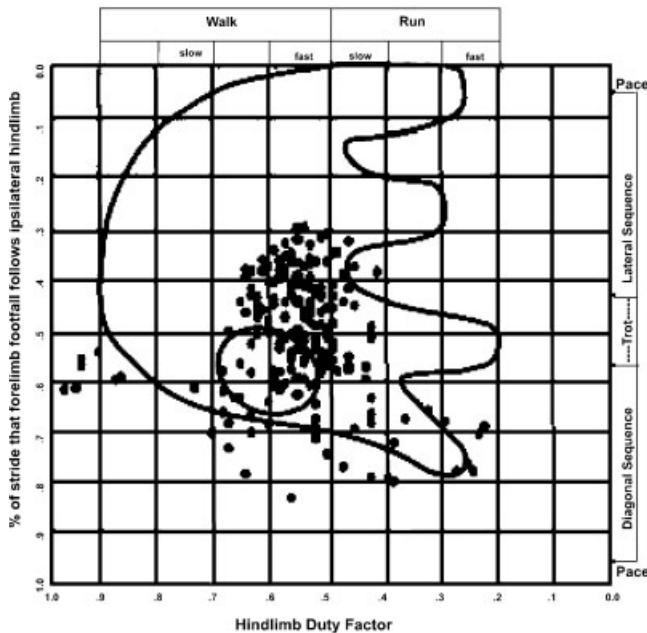


Fig. 1. Hildebrand plot of gait sequence patterns demonstrating locomotor variability in a single slender loris individual on arboreal branches. See text for explanation of the Hildebrand plot and gait definitions. Note the broad range of gait sequences exhibited in the slender loris, including the frequent use of trotting and lateral sequence gaits ($n = 210$ strides representing 15 strides on each of 14 support types ranging in size, orientation and stability). Most gait patterns actually plot outside the region typically used to describe primate locomotion (smaller oval) in Hildebrand's studies. Large outlined region denotes gait space typically used by all vertebrates. Experimental setting detailed in Stevens (2003).

support durations in either the forelimbs or the hind limbs (e.g., Cartmill et al., 2002). Yet how and in what context primates alter these gait parameters is less well understood. The subtle interplay among forelimb and hind limb stance and swing phase durations is not captured by traditional Hildebrand plots, hence a closer examination of footfall patterns is in order.

To explore how alterations in the timing and duration of support and swing phase can result in different gait sequence patterns, it is useful to begin with a simple running trot, whereby contralateral footfalls occur simultaneously and are separated by aerial phases (Fig. 2a). By extending the stance phase of each limb in the same exact way, it is possible to eliminate aerial phases, resulting in a walking trot. This is equally true whether the stance phase is lengthened at the end (Fig. 2b), at the beginning (Fig. 2c) or both (Fig. 2d).

But when forelimb and hind limb stance phases change independently, *different gait sequence patterns* can result. Relative to the trot, LS gaits can result from either relatively earlier forelimb touchdowns (Fig. 2e), or relatively later hind limb touchdowns (Fig. 2f). Conversely, DS gaits can result either from relatively earlier hind limb touchdowns (Fig. 2g) or relatively later forelimb touchdowns (Fig. 2h). This distinction between forelimb and hind limb timing may not seem particularly relevant, yet it has been suggested that one feature of primate locomotion is that forelimbs touchdown in a more protracted position than they do, for example, in cursorial mammals (e.g., Larson, '98; Larson et al., 2000, 2001). As such, it could be tempting to suggest that the DS gait patterns observed in large primates relative to most other mammals may result from a relatively more protracted forelimb posture at the beginning of a stride cycle, requiring a slight delay in the forelimb touchdown event. If primates exhibit more protracted forelimbs than do other mammals both in the trees and on the ground, this explanation could account for why many primates tend to use DS gaits on both arboreal and terrestrial supports. Another arboreal mammal, the woolly opossum, utilizes protracted forelimb postures on both arboreal and terrestrial substrates (Schmitt and Lemelin, 2002) and also exhibits DS gait patterns. Yet a protracted *forelimb* posture at touchdown may not be sufficient to ensure DS gaits, if *hind limbs*, too are also protracted at touchdown, as has been observed by Larson et al. (2001). A successful evaluation of the importance of limb protraction for gait sequence pattern will require the synthesis of support parameters with differences in forelimb and hind limb mass, angular kinematics and muscular activity. This is particularly true given that Fischer et al. (2002) have argued that whereas primates may exhibit more protracted limb postures than do cursorial mammals, this comparison may actually reflect specializations of the *cursorial* taxa as limb kinematics of small primates resemble those of small mammals that use LS gaits (e.g., Schmidt, 2005).

Turning to the mechanisms that primates exhibit for interchanging among gait sequence patterns, it is convenient to begin with a DS stride (Fig. 2i). Here, too, gait shifts can result from differences in relative contact time. In this case, an increase in duty factor can be accomplished by grasping the branch relatively longer, but if relative stance phase durations are increased

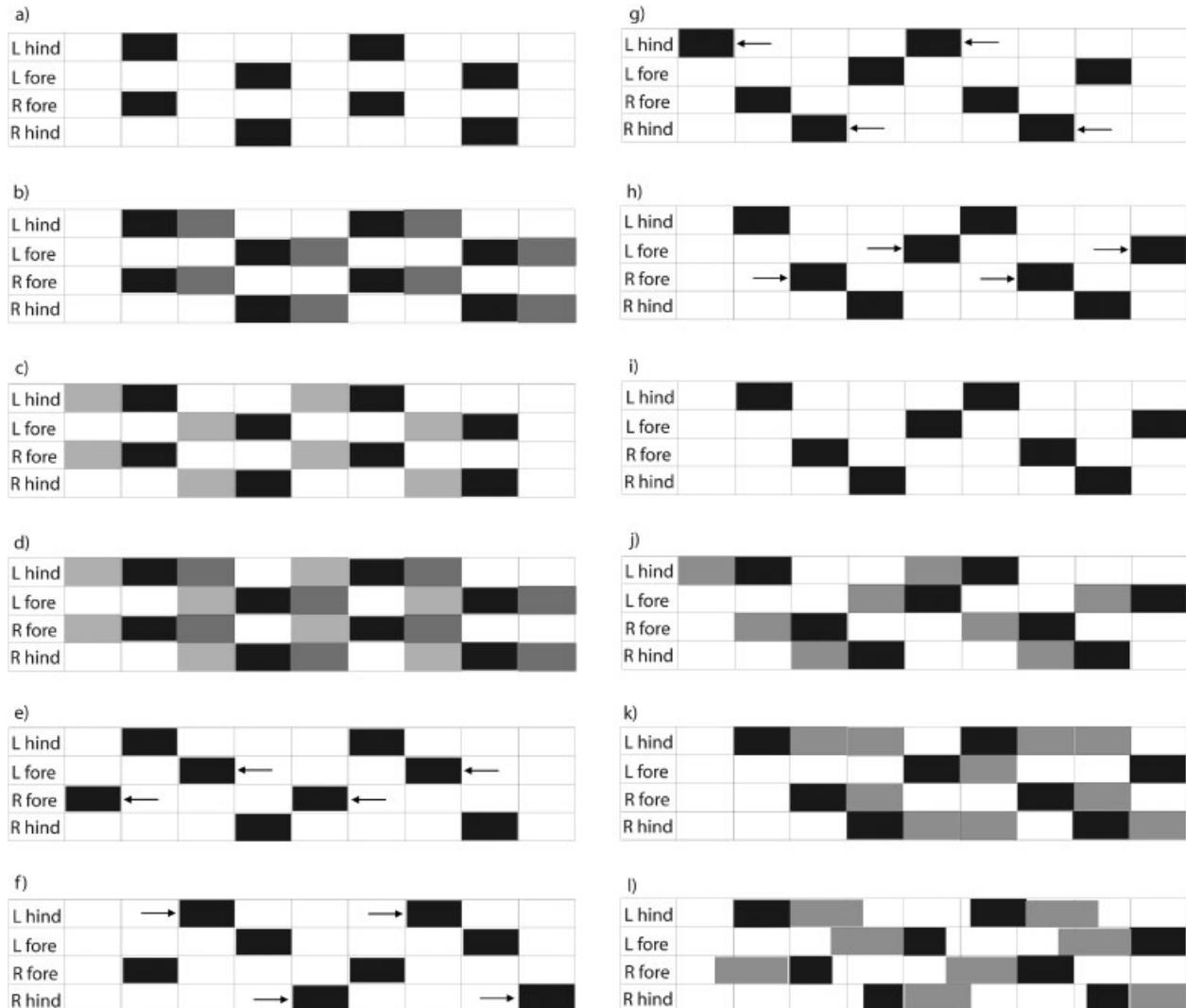


Fig. 2. Support diagram demonstrating how advanced or delayed forelimb and hindlimb touchdown and lift off events (denoted by arrows) can result in transformations in gait sequence pattern. Extended contact times are denoted with lighter shading.

by equal amounts in all limbs by initiating stance phases sooner, there is no net effect upon the *sequence* in which the limbs come into contact with the support (Fig. 2j). Similarly, increasing the duration of contact only at the end of stance phase, even by different amounts, need not affect the sequence in which limbs *come into contact* with the support (Fig. 2k). But it is also possible to employ a mixed strategy, maintaining longer contacts with the support by lifting off later with some limbs and touching down sooner with others (Fig. 2l). An example of this phenomenon has been described for a slender loris walking along fixed and moving supports (Stevens, 2003). On moving branches, forelimb contact times were often

increased by touching down relatively sooner than on a fixed support (Fig. 3). Hind limb duty factors also increased on moving supports, but via later lift-off events, often resulting in an LS gait pattern on swaying and twisting supports. Alterations in the stance and swing phase durations of the limbs were observed not only in gait sequence, but perhaps more importantly in support pattern, including the number and geometry of limbs in contact at any point during the stride (e.g., Hildebrand, '67; Rollinson, '75; Meldrum, '91; Cartmill et al., 2002). In this case, the observed switch from DS steps on fixed supports to LS steps on some of the moving supports may actually reflect a mixed strategy of increasing relative

contact times in all of the limbs at different times (Fig. 3). By exploring the percentage of time that the body is supported by 1, 2, 3 and 4 limbs, it becomes apparent that changes in duty factor and gait sequence patterns result in a higher proportion of strides with support by more limbs at a time on supports that challenge stability. Furthermore, the percentage of the 2-footed support time spent on diagonal limbs increases from around 85% on a fixed branch, to 100% on moving supports (Fig. 3). A more detailed examination demonstrates that gait sequence pattern on these supports is often subtly asymmetric, with each limb spending a slightly different amount of time on the substrate. Although most studies of primate locomotion to date have concentrated on the use of symmetrical gaits, it is likely that many primates employ subtle differences in support coordination far more often than has been discussed previously (e.g., the “amble”: Cartmill, 2003; Hanna et al., 2003; Schmitt et al., 2003, 2006). By concentrating solely on symmetrical gait patterns, researchers may in essence be ignoring valuable data regarding strategies used by pri-

mates to maintain stability and improve maneuverability.

These basic observations are significant in that gait sequence patterns are typically regarded as a static property of animal locomotion, with different clades assigned to specific gait sequence categories (e.g., most tetrapods generally use LS gaits, primates generally use DS gaits). Yet as recognized by Hildebrand as early as 1967, gait is far more dynamic, and responds differently to balance challenges in different species and even among individuals of a single species (e.g., Stevens, 2003). It could be argued that rather than a *static* characteristic of locomotion, gait sequence patterns in fact represent an *emergent* property of locomotion, dependent on the timing and duration of individual footfalls, which in turn can be related to contact time, limb mass and the angular movements of different limb segments through space. As exemplified by Figure 1, it is possible to “move” an individual all around “Hildebrand space” by introducing variability in substrate parameters, thereby underscoring the flexibility inherent in primate gait patterns. Yet

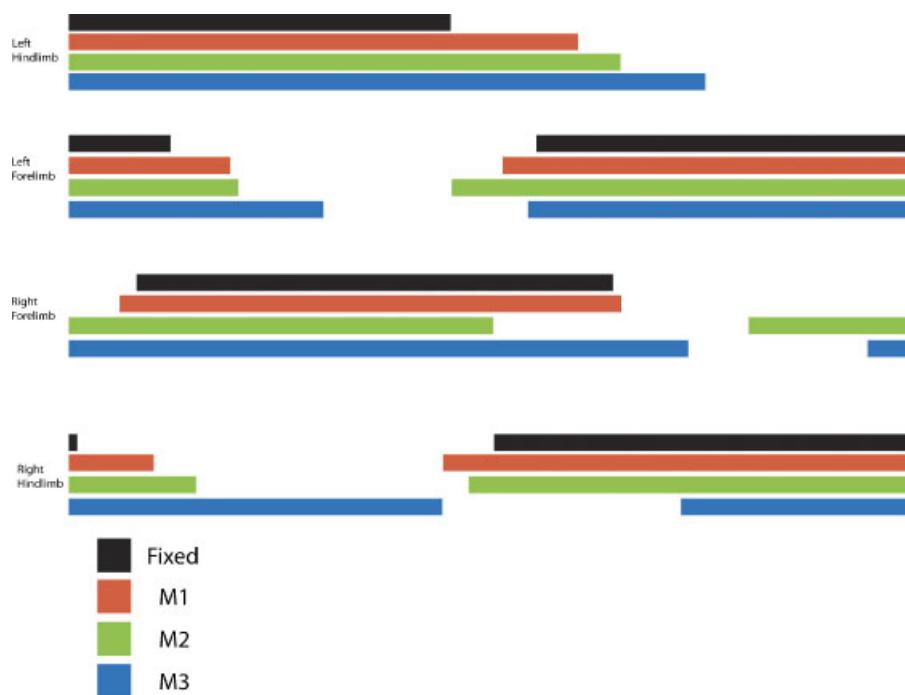


Fig. 3. Support diagram comparing slender loris (*Loris tardigradus*) footfalls on fixed and moving supports. Bars indicate a typical footfall pattern for each support type. Supports were all 1.25 cm in diameter, differing only in stability. Fixed supports were immobile during the experiments, whereas M1–3 represent different types of branch movements. M1 supports were displaced in the sagittal plane, M2 supports were displaced mediolaterally and M3 supports were rotated clockwise and counterclockwise in half-turn increments. The experimental setting is further detailed in Stevens (2003). Note that stance phase durations are dramatically higher on moving supports, and that differentially altering stance phases can result in a shift from DS to LS gait patterns.

responses to individual aspects of the arboreal environment are highly variable, both inter- and intra-specifically (e.g., Stevens, 2003). What might ultimately account for this enhanced ability among primates to vary limb configuration and timing?

NEUROLOGICAL EXPLANATIONS FOR GAIT SEQUENCE PATTERN

Vilensky and Larson ('89) suggest that improved supraspinal control may explain primates' ability to utilize a broad range of gait patterns, linking such developments to the "emancipation of the forelimb" from a primarily weight-bearing function, to the role of a more finely tuned exploratory appendage that is equally useful in procuring food items and in negotiating a complex terminal branch milieu. Although it is really not clear exactly why this should result in DS gaits, a relationship with neurological control might find indirect support in Rollinson and Martin's ('81) observation of exclusively LS gaits in the single mangabey in their study colony that possessed a damaged vertebral column. And whereas central pattern generators have been proposed to generate movement independent of supraspinal input in non-primate mammals (e.g., Eidelberg et al., '80), the inability or extreme difficulty in catarrhine primates to reliably regain stepping and weight-bearing capability after spinal transection has been interpreted in support of a greater role of qualitatively different descending spinal input for locomotor function (Eidelberg et al., '81; Vilensky and O'Connor, '97).

A number of authors have examined the ontogeny of gait sequence pattern in primates (Hildebrand, '67; Rollinson and Martin, '81; Hurov, '82; Vilensky and Gankiewicz, '89; Nakano, '96; Dunbar and Badam, '98; Shapiro and Raichlen, 2005), most observing an increase in frequency of DS gaits as infant primates mature. Such a pattern might reflect not only changes in body proportions but also progressive neural development associated with the shift from dependent to habitually independent locomotion (e.g., Raichlen, 2005). Courtine et al. (2005) have demonstrated forelimb and hind limb muscular coordination in intact *Macaca* consistent with active supraspinal control of distal musculature during locomotion. This may relate less to overall balance and more to the need to "preshape" the hand prior to touchdown on irregularly shaped arboreal supports (Van Kan and McCurdy, 2001).

Hence from an integrative standpoint, DS gaits appear to ultimately be tied to neural aspects of the use of grasping cheiridia, which themselves are associated with heavier distal limb segments and permit a broad range of independently variable solutions to the challenges of the arboreal milieu. One paradox of simple arboreal balance hypotheses that have sought to account for DS gait patterns is that the very strepsirrhine primates that have been suggested to most closely resemble the primate ancestral bauplan (cheirogaleids) are typically the ones that exhibit the most variable gait sequence patterns, often choosing trots or even LS gait patterns on arboreal supports (e.g., Hildebrand, '67; Vilensky and Larson, '89; Stevens, 2003). Conversely, DS gaits are employed much more reliably by Old World monkeys, even in highly terrestrial species as they move about on the ground (e.g., Hildebrand, '67). Vilensky and O'Connor ('97) pointed out that supraspinal control appears greater in "higher" primates, perhaps explaining the more reliable use of DS gaits by catarrhines. Hence, at this time it seems that a neurological hypothesis (Vilensky and Larson, '89) may best explain why primates are *ultimately* able to utilize DS gaits. Nonetheless, the variability in gait sequence pattern observed in modern primates likely reflects a combination of more *proximate* factors relating to how primates currently use this flexibility to accommodate different aspects of the arboreal environment. Such a "kinematic integration" hypothesis would be supported if multiple factors were demonstrated to contribute to DS gaits, including body proportions, limb kinematics and active muscular recruitment in the face of a diversity of locomotor contexts.

FUTURE DIRECTIONS

Primates may ultimately exhibit exceptional locomotor behavioral plasticity as an outgrowth of possessing forelimbs are used not only in traveling, but also in complex manipulative activities related to foraging and feeding (e.g., Vilensky and Larson, '90; Lemelin, '96; Larson, '98). Although research in primate gait described herein has sampled a diverse range of taxa of differing body sizes and limb proportions, it only scratches the surface of the diversity of primate arborealists. Additional work is required to characterize arboreal kinematic variability in a wider range of primates, and also through the lens of ontogenetic differences in the acquisition of arboreal capabil-

ties among different species (e.g., Shapiro and Raichlen, 2005; Workman and Covert, 2005). Future studies must discern between proximate (substrate type), intermediate (body proportions at the developmental and/or species level) and ultimate (neural wiring at the level of the family and higher) that permit and promote the use of DS gaits by primates. It is only through the refinement of kinematic questions that we can begin to learn how and why primates move the way that they do.

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