# Notes and Comments

## Understanding the Adaptive Value of Diagonal-Sequence Gaits in Primates: A Comment on Shapiro and Raichlen, 2005

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In a recent article in this journal, Shapiro and Raichlen (2005) took issue with our hypothesis (Cartmill et al., 2002, 2007; Lemelin et al., 2003) that primates adopt their distinctive diagonal-sequence, diagonal-couplet (DSDC)[1] gaits to ensure that they are securely balanced over a protracted hindfoot when their forefoot comes down on an untested support. Shapiro and Raichlen (2005) suggest that lateral-sequence, lateral-couplet (LSLC) gaits provide equal or greater stability at the point of forelimb touchdown, and that stability at forelimb touchdown, therefore, cannot be invoked as a selective advantage of DSDC walking gaits in primates.

To support their contention that LSLC gaits are more stable at forelimb touchdown, Shapiro and Raichlen (2005) videotaped two infant baboons walking on a laboratory floor, and measured their footfall timing and limb excursion angles. Their data show that these animals, like other infant cercopithecoids observed by Rollinson and Martin (1981) and Nakano (1996), used a variety of different walking gaits. One infant used mainly (83%) DSDC walks of the usual primate sort, but also a few LSLC walks like those of a camel (7%), and some lateral-sequence, diagonal-couplets (LSDC) walks like those of a horse (8%). The other infant showed a decided preference for camel-type walking (62%) and practically never walked like a typical monkey. Shapiro and Raichlen compared the phase relationships between the fore and hind pairs of limbs ("gait number" or "diagonality") with the angle of hindlimb protraction in their data, and discovered the following facts, on which they based their rejoinder to our hypothesis:

- *Fact 1*. Hindlimb protraction at the moment of forefoot touchdown was not maximized by the intermediate phase values seen in DSDC or LSLC walking.
- *Fact 2*. Rather, hindlimb protraction peaked when the fore and hindlimb cycles were either exactly in-phase (the pace) or exactly 180° out-of-phase (the trot).
- *Fact 3*. At forefoot touchdown, the hindlimb was just as protracted in many of the infants' LSLC walks as in typical DSDC walks.
- *Fact 4*. In a DSDC (primate-type) walking gait, the animal is standing precariously on two ipsilateral feet placed close together at the moment when the opposite forefoot comes down.
- *Fact 5*. When the forefoot comes down in LSLC walks, the animal is standing on two diagonally opposite feet, which probably makes it more stable at that moment than in DSDC walks.

From these observations, Shapiro and Raichlen (2005; p. 212) conclude that "... stability at the moment of forelimb touchdown was unlikely to be a particularly important selective factor in the evolution of DSDC walking in primates," that "LSLC gait is possibly a better choice at that moment in time, and might in fact be ... frequently used by primates in their natural environments," and that the function (if any) of DSDC walking in primates remains to be discovered.

We affirm the facts adduced by Shapiro and Raichlen. But as we see it, their conclusions do not follow from those facts. Their observations confirm, rather than refute, the importance of stability at the moment of forelimb touchdown in determining the walking gaits of primates.

Facts 1–4 are true by definition. The hindlimb has to be at its most protracted at the moment when it touches down; therefore, hindlimb protraction at the moment of fore footfall will be maximal when a hind and forefoot touch down simultaneously. Such a gait is either a trot or a pace, by definition (Fact 2). If the hindfoot strikes down slightly earlier than the forefoot (a DSDC walk if contralateral, LSLC if ipsilateral), it will necessarily have moved into a more retracted position when the forefoot descends (Fact 1). The difference between a monkey-type DSDC walk and a camel-type LSLC walk reflects a 180° phase shift between the fore and the hind-

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[1]Diagonal-couplet gaits are those in which, the contralateral hindfoot and forefoot move more or less synchronously. In diagonal-sequence gaits, the contact of the hindfoot is followed by that of the contralateral (opposite side) forefoot; in lateral-sequence gaits, this order is reversed. Diagonal couplets are common in most mammals, but diagonal-sequence gaits are found commonly only in primates, arboreal marsupials, and a few other mammals (Hildebrand, 1967, 1985; Vilensky and Larson, 1989; Cartmill et al., 2002, 2007; Lemelin et al., 2003). Although lateral-sequence gaits are common among nonprimate mammals, lateral couplets are relatively rare; LSDC gaits are more common (Hildebrand, 1967, 1985; Vilensky and Larson, 1989; Cartmill et al., 2002, 2007).
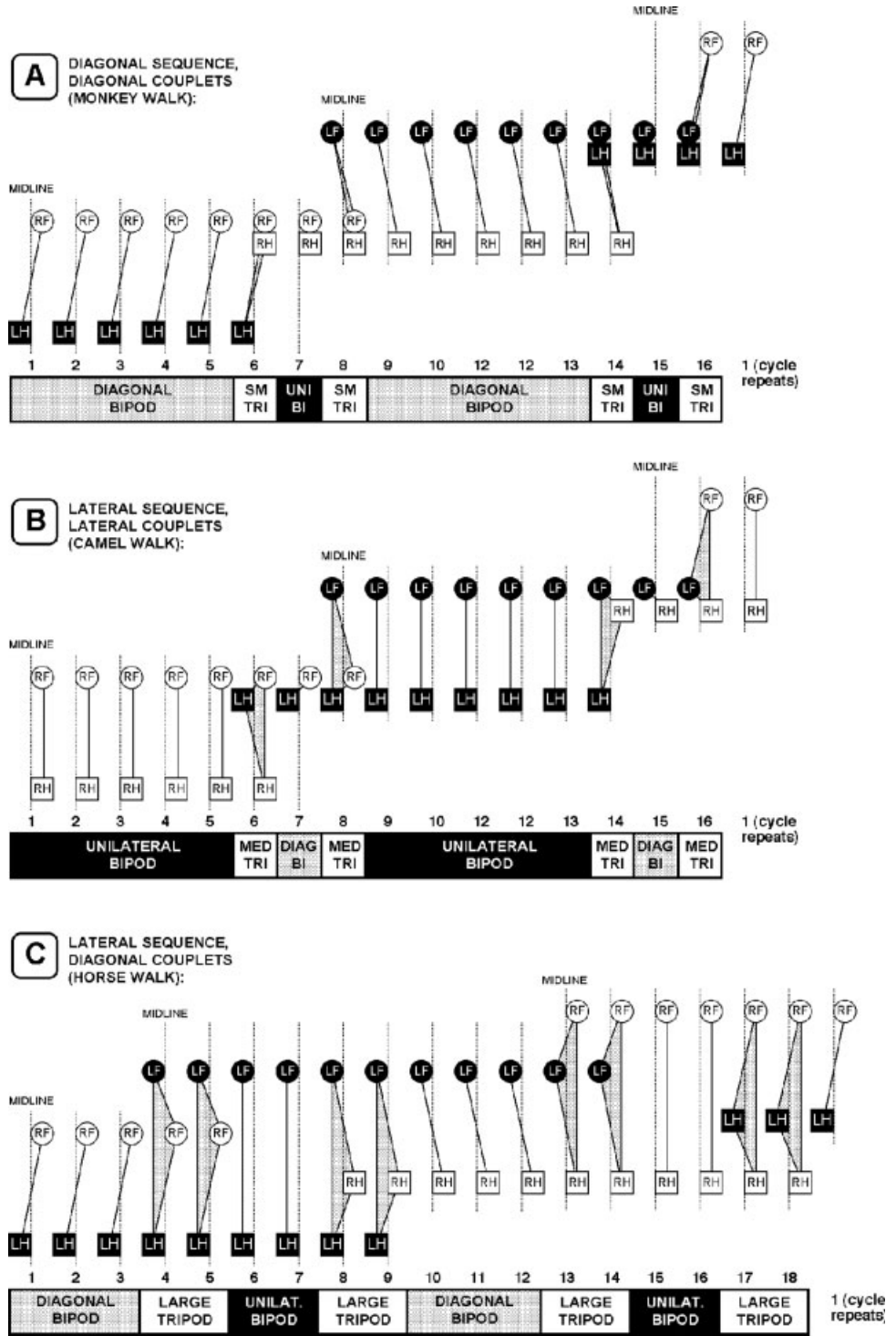
Fig. 1. Schematic diagram illustrating limb contact positions during a complete stride, as though seen from above. Open circles represent the right forelimb (RF). Filled circles represent the left forelimb (LF). Open squares represent the right hindlimb (RH). Filled squares represent the left hindlimb (LH). The dotted line indicates midline of body and line of travel. Lines connecting the limb contact points indicate size and shape of the support polygon. The bar chart below each stride diagram shows the relative amounts of time spent in bipedal (both unilateral and bilateral) and tripedal contact combinations for each of three footfall patterns: (A) diagonal-sequence diagonal couplets, (B) lateral-sequence lateral couplets, (C) lateral-sequence diagonal couplets.

limb pairs: that is, a camel walks like a monkey with its rear end mirror-imaged, so that left and right sides are swapped (Fig. 1A,B). Limb protraction angles are not affected by the mirror-imaging operation (Fact 3).

The necessity of balancing on a unilateral bipod at one point in the cycle (Fact 4) is only one of the intrinsic deficiencies of the DSDC gait (Cartmill et al., 2002, 2007). DSDC walking also suffers from the small size and brief duration of its triangles of support. A primate executing a

typical DSDC walk spends about two-thirds of its time standing on only two feet. It has three feet on the substrate during the remaining one-third of the cycle, but the resulting triangles of support are tiny, because two of the three feet are almost touching (Fig. 1A). By contrast, an animal walking with a horse-type LSDC gait (in which the hindfoot strikes down slightly later than the contralateral forefoot) spends about 45% of its time supported on three widely deployed feet, and most of the rest stand-

ing on two diagonally opposite feet (Fig. 1C). This is presumably why most terrestrial mammals adopt a LSDC walk. The overwhelming preference of primates for the DSDC walk, therefore, demands explanation.

The camel-type LSLC walk preferred by some juvenile primates produces slightly larger triangles of support than the typical DSDC walk (Fig. 1B). However, it constrains the animal to spend most of the gait cycle balanced on two ipsilateral feet. As Shapiro and Raichlen correctly point out, *"Throughout* the stride, LSLC can be considered to be less stable than DSDC, due to the former's more frequent periods of two-limbed support by ipsilateral forelimb–hindlimb pairs, associated with the tendency to roll to one side" (Shapiro and Raichlen, 2005;p. 212). Periods of two-limbed support predominate in both the LSLC and DSDC walks; but the LSLC animal spends two-thirds of its time swaying back and forth as it transfers its weight from two left feet to two right feet and back again, while the DSDC animal avoids this rolling by switching from one diagonal pair of feet to the other (Fig. 1A,B).

Despite the disadvantages of both these gaits, the two infant baboons reported by Shapiro and Raichlen preferred DSDC (monkey-type) and LSLC (camel-type) walks to the usual mammalian LSDC pattern. Presumably, these two gaits share some advantage that compensates for the disadvantages documented in Figure 1. One advantage that these two preferred gaits have in common is that they ensure that the body is supported by a protracted hindlimb placed roughly under the center of mass at the moment of forelimb touchdown. We suggest that this is why they were preferred. The data adduced by Shapiro and Raichlen, therefore, confirm the importance of stability at forelimb touchdown in primate locomotion.

Shapiro and Raichlen (2005) give the impression that primates are more variable than they actually are in terms of gait preferences. Many studies, including our own survey of 19 primate species (Cartmill et al., 2002), have demonstrated that adult primates overwhelmingly adopt DSDC walking gaits (Hildebrand, 1967, 1985; Vilensky and Larson, 1989). The only well-documented exceptions are *Nycticebus*, which walks like a chameleon, using slow gaits approximating a walking trot (Demes et al. 1990; Cartmill et al., 2004), and *Callithrix*, which uses LSDC walking gaits like those of a horse (Cartmill et al., 2002; Schmitt, 2003). Although juvenile cercopithecines frequently use camel-like LSLC walking gaits, they do not do so consistently, and they shift to typical primate DSDC gaits as they mature (Hildebrand, 1967; Rollinson and Martin, 1981). Shapiro and Raichlen suggest that the camel-style LSLC gait produces more stability than the DSDC gait at forelimb touchdown, because the animal is supported at that moment by two diagonally opposite feet (Fact 5). However, this supposed advantage is essentially irrelevant for an arboreal animal walking on a branch, for two reasons: (1) the period of such support is extremely brief, and (2) the diagonally opposite supporting feet are immediately adjacent to each other on the support and afford little or no improvement over the ipsilateral DSDC bipod in the size of the resulting triangle of support (Fig. 1A,B). The fact that LSLC walking gaits are not characteristic of any adult arboreal mammal suggests that the supposed advantage of the LSLC walk is outweighed by the disadvantage of side-to-side rolling. As we have shown quantitatively (Cartmill et al., 2002, 2007), DSDC gaits represent the only footfall pattern that can serve simultane-
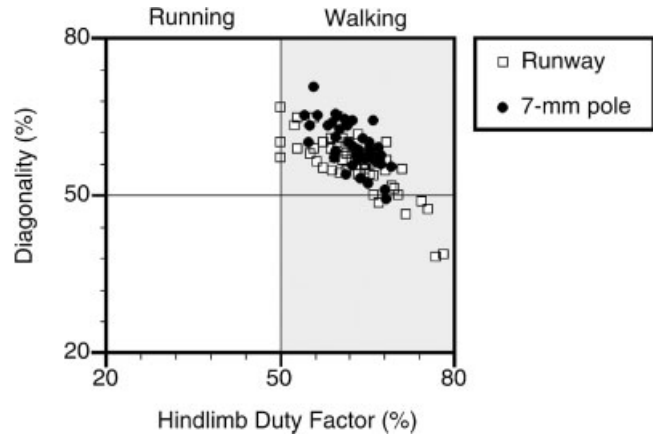


**Fig. 2.** Bivariate plot of symmetrical gaits in the woolly opossum (*Caluromys philander*). Open squares represent gait cycles on runway; solid circles represent cycles on 7-mm pole. *X*-axis, hindlimb duty factor (i.e., the stance period of the hindfoot as a percent of the gait cycle); *Y*-axis, diagonality (i.e., the percent of the cycle period by which the hind footfall precedes the fore footfall on the same side). Lower right shaded area represents lateral-sequence (LS) walking gaits; upper right shaded area, diagonal-sequence (DS) walking gaits. (Adapted from Lemelin et al., 2003).

ously: (1) to maximize security at forelimb touchdown and (2) to minimize periods of bipedal support by two feet on the same side.

Why, then, do camels and juvenile cercopithecines use LSLC gaits? Hildebrand (1968, 1980) proposed that long-limbed animals adopt LC gaits, in which ipsilateral limbs move in near-synchrony, to keep from hitting their front feet with their ipsilateral back feet. Shapiro and Raichlen (2005) suggest that the transient preference for LSLC gaits in juvenile primates may serve to reduce such limb interference during a temporary relative growth spurt in the limbs, while still affording the benefit of support on a protracted hindlimb at fore footfall. If the implied correlation with relative limb length is real, this explanation may hold, at least for walking on a flat surface. But the supposed benefit would be minimized on narrow arboreal supports, where all foot placement is nearly collinear and an animal can easily step on one forefoot with either hindfoot.

The preceding observation underlines the fact that theories about arboreal locomotion need to be studied using arboreal-type supports. Shapiro and Raichlen (2005) considered only animals walking on the ground and ignored contradictory data from studies of arboreal locomotion. Lemelin et al. (2003) found that woolly opossums (*Caluromys philander*), which are prosimian-like in ecology, behavior, grasping morphology and abilities, and locomotor mechanics (Rasmussen, 1990; Lemelin, 1999; Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2007), show the sort of gait flexibility that Shapiro and Raichlen (2005) report for their two juvenile baboons—but only when walking on a flat runway. On that surface, our *Caluromys* used gaits with diagonalities ranging from 38 (diagonalities below 50 are LS) to 67 (diagonalities above 50 are DS). But on a 7-mm diameter pole, almost all gaits clustered in the adult-primate DSDC range (Fig. 2). This is the reverse of what would be expected if Shapiro and Raichlen were right to think that LSLC gaits improve stability in walking on thin supports.

Why do woolly opossums increase their average diagonality in moving from a flat surface to a thin pole? As we noted, increasing the diagonality of a DC walk above 50 (i.e., above that seen in a walking trot) gives the hindfoot enough time to secure a firm foothold on the support before the opposite fore footfall (Lemelin et al., 2003; Cartmill et al., 2007). We believe that DSDC gaits were evolved in both primates and arboreal marsupials for the same functional reasons: to minimize periods of bipedal support on ipsilateral limbs, while at the same time allowing the descending forelimb to test each new support when the grasping hindlimb is protracted underneath the center of mass. Only DSDC gaits afford these advantages.

In summary, Shapiro and Raichlen (2005) make interesting observations about locomotor behavior in juvenile primates. However, rather than contradicting our conclusions, their data corroborate our analysis of the adaptive advantages of DSDC gaits in primates and other arboreal mammals.

## ACKNOWLEDGMENTS

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# A Response to Cartmill et al.: Primate Gaits and Arboreal Stability

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Primates' preference for diagonal sequence, diagonal couplets (DSDC) walking gaits has presented anthropologists with a conundrum for decades. To date, few explanations for this unusual gait preference have been adequately tested. Cartmill et al. (2002) suggested a hypothesis consistent with the well-established notion that primate locomotion is adaptive for a small branch niche. They hypothesized that primates prefer DSDC gait during arboreal locomotion because DSDC gait places a hind limb securely under the body on a tested support at the moment a forelimb touches down on an untested support.

We tested their hypothesis using a sample of infant baboons, which allowed us to examine limb positioning at forelimb touchdown in primates using a wide array of gaits (infant primates use a wider variety of footfall patterns than do adults). Our kinematic analysis of several walking gaits in infant baboons (Shapiro and Raichlen,

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2005) demonstrated that like DSDC walking, lateral sequence, lateral couplets (LSLC) walking ensures that if a forelimb contacts a potentially unstable branch, there is a protracted hind limb positioned underneath the body to provide stability. Further, we highlighted the difference between these two gaits at the moment of forelimb touchdown (i.e., the proposed selection pressure). While in both gait types, there is a hind limb and forelimb positioned underneath the body at the moment of forelimb touchdown, the stabilizing limb pairs are ipsilateral in DSDC, but contralateral in LSLC.

From these results, we drew three basic conclusions. First, we concluded that with regard to this particular moment in time (the landing of a forelimb on an unstable branch), DSDC gait does not provide an exclusive advantage over LSLC gait. Second, we proposed that because of the contralateral limb pairs placed under the body, LSLC might provide even more stability than DSDC gait at that moment in time. In other words, when a forelimb lands on an unstable substrate, DSDC gait is sufficient, perhaps not the most efficient, and certainly not necessary for stabilizing the body. Third, because it is not the only gait that can provide a stabilizing function in this context, and might not even be the most advantageous gait at the moment in question, we suggested that this "moment" of a primate's arboreal stride may not have been a particularly important selective factor in the evolution of DSDC walking (contra Cartmill et al., 2002). In other words, the fact that DSDC gait provides stability at forelimb touchdown does not necessarily mean that this was why it was selected for in the first place.

Cartmill et al. agree with our analysis of limb positioning, as well as with the fact that DSDC gait is not unique in providing a stabilizing hind limb underneath the body at the moment of forelimb touchdown. Their disagreement lies with our second and third conclusions. We believe there is sufficient evidence, from both the lab and the field, to maintain that our original conclusions remain valid. Below, we respond to the critiques offered by Cartmill and colleagues.

First, Cartmill et al. note that our infants preferred DSDC and LSLC over LSDC (lateral sequence, diagonal couplets), and suggest the preference for these two gaits can be explained by the fact that DSDC and LSLC share the stabilizing advantage at forelimb touchdown discussed above. Because of this, they suggest that our "observations confirm, rather than refute, the importance of stability at the moment of forelimb touchdown in determining the walking gaits of primates." This summary of our data obscures our discussion of the fact that LSLC was not preferred over LSDC until the baboons were approximately 5 months of age or older. We attributed the use of LSLC gaits to the developmentally timed increase in relative limb length and the need to avoid ipsilateral limb interference during LS gaits. A full treatment of this issue in an expanded sample can be found in Shapiro and Raichlen (2006).

Later in their comment, Cartmill et al. consider our hypothesis regarding the relationships among LSLC gait, changes in limb length and avoidance of limb interference, but discount its relevance to the argument at hand because "the supposed benefit would be minimized on narrow arboreal supports, where all foot placement is collinear and an animal can easily step on one forefoot with either hind foot." Whether or not LSLC walking confers benefits related to limb interference on arboreal substrates

may be a moot point, as we were not proposing that primates should have evolved LSLC over DSDC walking on arboreal substrates because of this potential advantage. We were simply attempting to explain a developmental transition to LSLC walking in functional terms. It is already well known that due to the timing of limb movements, DSDC walking produces a potential interference problem between ipsilateral fore and hind limbs, even on the ground (Hildebrand, 1967). Therefore, if narrow substrates confer an interference problem with all types of gaits, then, as Cartmill et al. indicate, interference can be taken out the equation when trying to identify an adaptive advantage to DSDC walking in primate evolution.

Cartmill et al. take issue with our suggestion that LSLC might be more stable than DSDC at forelimb touchdown. Our suggestion was based on the fact that at this moment in time, a primate would be supported by diagonally opposite fore and hind limbs in LSLC, compared with same side fore and hind limbs in DSDC. Although Cartmill et al. agree with us in regard to limb positioning, they discount the relevance of this difference for an arboreal animal for two reasons. First, they note that this period of diagonally opposite limb support is "extremely brief," as shown by their Figure 1B/8. Second, they note that the diagonally opposite supporting hand and foot are "immediately adjacent to each other on the support and afford little or no improvement over the ipsilateral DSDC bipod in the size of the resulting triangle of support." Without information on the diagonality values or duty factors used to construct their Figure 1, we cannot directly comment on the relative time periods of two or three-limbed support illustrated across the three types of gaits.

However, using the values supplied in their Figure 1, we agree that the period of support by contralateral fore and hind limbs (at the moment of forelimb touchdown) during LSLC is brief, as is the comparable moment in time during DSDC (8 in Fig. 1A). If the brevity of this time period makes the relevance of contra vs. ipsilateral supporting limbs irrelevant, then we would ask why this moment in time (reaching out to an unstable branch) is considered so critical to the evolution of DSDC gait (see Cartmill et al., 2002, and this volume). On the other hand, if this moment is truly important, then certainly (all else being equal regarding a hind limb protracted under the body), we maintain that diagonally opposite limbs add further stability to this moment. Stability would be improved by a larger triangle of support during LSLC at this moment (the triangle in Fig. 1B/8 appears to be larger compared with that in Fig 1A/8, despite Cartmill et al.'s description of this difference as offering "little to no improvement."

More important than support triangles perhaps is that grasping with diagonally opposite hands and feet would create an opposing torque about the long axis of the support, minimizing lateral deviations of the body's center of mass (Schmidt, 2005). This would be even more critical just before forelimb touchdown, providing maximum stability in case the forelimb touches down on an unstable support. This benefit would not be available at this moment during DSDC walking, where ipsilateral fore and hind limbs serve as support when the forelimb touches down. Therefore, although we agree with Cartmill et al. that this moment in time may be very brief, if this moment is important enough to propose that it was critical in the evolution of primate gait, it is important enough to consider pros and cons of all aspects of the moment.

We agree whole-heartedly with Cartmill et al.'s suggestion that data from arboreal supports are essential to understanding the adaptive value of DS gait, and we hope we did not give the impression that we (intentionally) "ignored contradictory data from studies of arboreal locomotion". Cartmill et al. specifically highlight Lemelin et al.'s (2003) important data comparing arboreal to terrestrial locomotion in *Caluromys* (woolly opossum). It is certainly compelling that *Caluromys* increased its average diagonality when moving from a flat surface to a thin pole, and essentially only used DSDC walking on the pole. However, both our lab study and that of Lemelin et al. (2003) were under the handicap of artificial substrates. As we discussed at some length in Shapiro and Raichlen (2005), at least some evidence from more natural habitats directly contradicts Cartmill et al.'s association of DSDC gaits with stability on small or unstable branches. Dunbar and Badam (2000) demonstrated that juvenile macaques preferred LS, not DS gaits on the (narrow) distal ends of longitudinal branches, and preferred DS walking on the proximal ends of branches or on lateral stems, both of which are characterized by relatively large (and thus more stable) diameters. These observations, in conjunction with the fact that DSDC walking is not consistently preferred by primates when substrates are manipulated in the lab to be unstable (Stevens, 2003, 2006), lead us to reiterate that further research on gait in natural habitats is likely to reveal more gait flexibility among primates than has been documented in the lab.

Additionally, we agree that Lemelin et al.'s (2003) study of gait in *Caluromys* is noteworthy in demonstrating that pole walking is associated with higher diagonality values than walking on a flat runway, even when duty factor is held constant through analysis of covariance. In other words, at any given duty factor (which is inversely related to speed), *Caluromys* used higher diagonality values on the pole than on the runway (see Cartmill et al.'s Figure 2). However, given the negative correlation between duty factor and diagonality on the pole and runway, combined with the wider range of duty factors sampled on the runway, it would be interesting to know if *Caluromys* would have used LS gaits on the pole if very slow speeds (i.e. large duty factors) were elicited. (In fact, there is one slow pole stride that looks to have an LSDC diagonality value). If this were the case, then it is important to realize that increased diagonality on the pole would accompany LS, as well as DS gaits, complicating the argument surrounding increased diagonality, DS gaits, and stability.

Cartmill et al. conclude by stating "We believe that DSDC gaits were evolved in both primates and arboreal marsupials for the same functional reasons: to minimize periods of bipedal support on ipsilateral limbs, while at the same time allowing the descending forelimb to test each new support when the grasping hind limb is protracted underneath the center of mass. Only DSDC gaits afford these advantages." As we discussed in our 2005 paper, DSDC gait is not unique with regard to the first function (LSDC also minimizes periods of ipsilateral bipedal support; see Cartmill et al., 2002), nor is it unique with regard to the second, as we have discussed at length above. We agree with Cartmill et al. that DSDC is the only gait providing both of these functional advantages, but our 2005 paper set out to test their hypothesis as originally stated (Cartmill et al., 2002); that DSDC gait was selected for in the context of stability at forelimb touchdown. We maintain that this specific moment in the stride does not provide a particularly compelling explanation for the evolution of DSDC gait in primates, but we cannot rule out the possibility that DSDC gait evolved for its combination of advantages. We strongly believe that the answer lies in further study of primate gait. This can be accomplished in the lab with artificial substrates that more closely resemble the complexity of natural habitats, as well as in the field.

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