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Gait Parameter Adjustments of Cotton-Top Tamarins (*Saguinus oedipus*, Callitrichidae) to Locomotion on Inclined Arboreal Substrates

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KEY WORDS diagonal sequence; lateral sequence; primate; gait variability; ambling gait

ABSTRACT The influence of different substrate inclinations on gaits and metric gait parameters (relative forelimb and hind limb protraction, relative forelimb, and hind limb retraction, stride length, stance, and swing phase duration) of cotton-top tamarin locomotion was studied using high-speed video films and evaluated by descriptive and analytical statistical methods. As previously shown, lateral sequence gaits predominantly occurred on descending arboreal substrates (branchlike pole with a smaller diameter than the animal's body). Gait sequence patterns display significant dependency on substrate inclination. Cotton-top tamarins utilize lower diagonality values the more the substrate declines. This tendency leads to a greater use of lateral sequence gaits on steeply declined substrates. Conversely, these primates display the tendency to utilize higher diagonality values the more the substrate inclines leading to the predominant occurrence of diagonal sequence (DS) gaits. Duty factor index, extent of relative protraction, and relative retraction of both limb pairs as well as the relation of forelimb stance phase duration to hind limb stance phase duration is also correlated to the inclination of the substrate. Stride length and swing phase duration display no significant dependence on inclination, but are determined by the speed of the moving animal. The relevant duty factor is approximately constant at all inclinations. Integrating our results with results of other authors we propose a hypothesis for the functional relevance of a utilization of lateral sequence gaits in downward locomotion and DS gaits in upward locomotion. Our data support the notion of a wide ranging behavioral plasticity as a general primate locomotor characteristic. Am J Phys Anthropol 135:13–26, 2008.

Arboreal locomotion on discontinuous and three-dimensional substrates, the evolution of prehensile extremities, the functional differentiation of forelimbs and hind limbs and the increase of forelimb mobility as well as the emergence of improved neural and visual control of the hands are discussed as important aspects of primate adaptation to a three-dimensional small branch habitat (see e.g., Cartmill, 1972, 1974; Kimura et al., 1979; Rollinson and Martin, 1981; Vilensky, 1989; Vilensky and Larson, 1989; Schmitt, 1999; Larson et al., 2000; Cartmill et al., 2002; Preuschoft, 2002; Schmitt and Lemelin, 2002; Schmitt, 2003). Arboreal primate locomotion differs from that of tree-shrews and most other quadrupedal mammals in several ways and is considered to be derived in the following features: utilization of diagonal couplets/diagonal sequence (DS) gaits (Hildebrand, 1967), the greater protraction of the forelimb (Larson, 1998; Larson et al., 2000) and the occurrence of higher peak substrate reaction forces in the hind limbs in relation to the forelimbs (Kimura et al., 1979; Reynolds, 1985a,b; Demes et al., 1994). Goldfinch and Molnar (1978) discovered the convergent use of DS gaits by an arboreal marsupial, the brush-tailed possum (*Trichosurus vulpecula*). Pridmore (1994) found DS gaits in another Marsupial (*Dromiciops australis*) whereas more recently Schmitt and Lemelin (2002) as well as Lemelin et al. (2003) reported all of the above characteristics of primate arboreal locomotion for the arboreal woolly opossum (*Caluromys philander*).

In a walking diagonal couplets gait (either diagonal or lateral in sequence) the overall time spent on only two feet is minimized (e.g., Gray, 1944; Rollinson and Martin, 1981), with diagonal bipedality maximized relative to unilateral bipedality (e.g., Cartmill et al., 2002). On arboreal substrates diagonal bipedality is more stable than unilateral bipedality because simultaneous swing phases of diagonal forelimbs and hind limbs reduce craniocaudal torsional moments, whereas diagonal limbs exert opposing mediolateral substrate reaction forces during stance phase and therefore help to stabilize trunk position above the substrate through lateral compensating motions (Hildebrand, 1976; Preuschoft, 2002). DS in combination with diagonal couplets have often been presumed to be advantageous on arboreal substrates and researchers have put forward different hypotheses that try to explain the occurrence of these gaits in arboreal quadruped primates and some arboreal marsupials. These explanations include biomechanical approaches

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such as the argument of Prost (1969), who postulates increased frictional forces during climbing in DS gaits which nullify other disadvantages of diagonal sequence gaits compared to lateral sequences (LS). Later, Rollinson and Martin (1981) postulated a diagonal sequence/diagonal couplets gait (DSDC) to be more stable when the center of body mass is located more posterior. Vilensky and Larson (1989) instead propose a neurological explanation in stating that the common DSDC gaits in primates are a simple byproduct of increased supraspinal control of locomotion, especially in the forelimbs. Recently, Cartmill et al. (2002, 2007) suggested an ecologically based theory, hypothesizing that the use of DSDC gaits in the small branched milieu is advantageous in that primates are better able to rely upon the grasping hind limb placed under the center of mass to draw back and recover when the forelimb is placed upon an unstable support. They postulate that this recovery would be more difficult in a lateral sequence diagonal couplet gait in which the forelimb touches down shortly before the contralateral hind limb (but see Shapiro and Raichlen, 2005, 2007). However, the functional relevance of LS gaits in primates has not been thoroughly investigated despite its being well documented in a variety of species (Hildebrand, 1967; Prost and Sussman, 1969; Dykyj, 1980; Rollinson and Martin, 1981; Vilensky and Larson, 1989; Vilensky et al., 1994; Shapiro and Raichlen, 2005, 2006; Stevens, 2006). It is important to note that wild primates have been observed to utilize LS gaits in the arboreal setting (Dunbar and Badam, 1998, 2000).

Primates derive from small, "shrew-sized", arboreal quadrupedal mammals (Cartmill, 1972; Gebo, 2004). Since tree-shrews lack grasping extremities and their locomotion differs dramatically from that of primates, small primates may be the most adequate models available for the investigation of the evolution of primate locomotor characteristics. Some members of the secondarily dwarfed callitrichid primates are among the smallest of all primates (Fleagle, 1998). All tamarins and marmosets are characterized by pointed nails (tegulae), except the great toe that bears a flat nail, as well as a nonopposable thumb. However, Hamrick (1998) showed that the grasping ability of the hands is not lowered by the tegulae and Napier (1967) as well as Rosenberger and Stafford (1994) point out that the thumb of callitrichids is "pseudo-opposable". Nevertheless the locomotor characteristics of callitrichids seem to be more ambiguous than those of other primates: Hildebrand (1967) described LS walks, DS walks and trots in three callitrichid genera. More recently Arms et al. (2002) reported DS walks and "pseudo-lateral" walks in cotton-top tamarins, but Schmitt (2003) observed only DS walks in red-handed tamarins (*Saguinus midas*). Cartmill et al. (2002) as well as Schmitt (2003) found locomotor characteristics in the common marmoset (*Callithrix jacchus*) that deviate substantially from most primates investigated so far. Schmitt (2003) attributed these findings to the preference of large vertical supports in marmosets instead of the small branch milieu that most arboreal quadruped primates prefer. Contrary to marmosets, tamarins are active arborealists that move and forage along thin branches and leap between terminal supports (Fleagle and Mittermeier, 1980; Garber, 1980; Garber and Leigh, 2001).

To investigate arboreal locomotion researchers use arboreal substrates (i.e., substrate diameter smaller than the diameter of the animal's trunk). These are, in some cases, even flexible. But in contrast to the number of studies of arboreal locomotion on horizontal substrates there has hitherto been a lack of studies conducted on the arboreal locomotion on inclined substrates and Preuschoft remarks fittingly: "Locomotion on inclined substrates was neglected in the literature" (2002; p 172). Regarding the fact that horizontal substrates are just one element of many in natural environments this trend may lead to an imbalanced representation of the three-dimensional habitat of arboreal animals. The use of differently inclined arboreal substrates (e.g., Stevens and Larson, 1999; Stevens, 2000, 2003, 2006; Arms et al., 2002; Krakauer et al., 2002) therefore yields a more differentiated insight into arboreal primate quadrupedalism.

In this article we investigate the influence of oblique arboreal substrates on metric gait parameters of symmetrical walking and running gaits of cotton-top tamarins and outline a functional explanation for the results.

MATERIALS AND METHODS

Subjects, experimental setup, and data analysis

Metric gait parameters were obtained from two adult male cotton-top tamarins (weighing 460 and 480 g respectively) moving at their preferred speeds along inclined branchlike substrates. The two 3-year-old animals were given to the Institut für Spezielle Zoologie of the Fr.-Schiller-Universität Jena, Germany by the German Primate Research Center, Göttingen, Germany. They did not show any peculiarities and were kept and nursed in adherence to the German animal welfare regulations. The experiments were registered by the Committee for Animal Research in the Freistaat Thüringen, Germany.

The cotton-top tamarins were trained to walk on a wooden pole (length: 1.5 m, diameter: 3 cm) inside an acrylic glass enclosure and were filmed with a Mikromak Camsys™ high-speed video camera system. The system yields short monochromic sequences (up to 2 s) of three simultaneously recording cameras which can be videotaped (VCR) in slow motion for further use. Video sequences were recorded at 500 frames/s. The cameras were positioned to capture the following views: lateral overview, lateral close-up and frontal position. Locomotion was enhanced with feeding rewards. To enable comparisons with inclined treadmill results for *Saimiri sciureus* (Cebidae, Primates) obtained by Vilensky et al. (1994), arboreal supports were set at the following inclinations: −28°, −16°, −8°, 0°, +8°, +16°, and +28°. Arms et al. (2002) demonstrated that cotton-top tamarins prefer horizontal and moderately inclined substrates (0°–10° inclination in 84% of the time); therefore the substrate inclinations chosen here seem appropriate. On each inclination at least 20 trials were recorded. In a single trial up to four strides could be analyzed, irregular trials (braking or accelerating) were discarded. A total of 332 strides were used to obtain metric gait parameters and statistically evaluated. One-hundred twenty three complete cycles were used for gait determination.

The taped video sequences were read into a PC using the video-card "Screen-Machine™ 1" and analyzed with the "Unimark™ 3.6" software. The software allows frame by frame examination of a trial and calculates distances between defined points. Therefore, the following landmarks on the animal's bodies were determined (Fig. 1): The distal end of each autopodium, the forehead and the

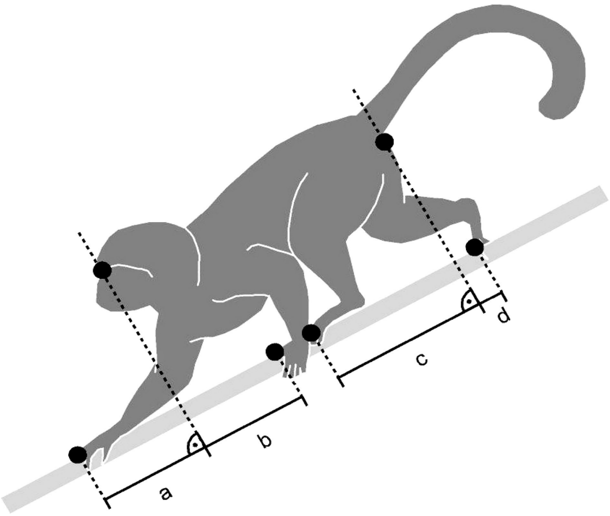

Fig. 1. Landmarks used for digitalization. (**a–d**) Distances obtained to assess variances in forelimb and hind limb protraction (instant of touch down) and forelimb and hind limb retraction (instant of lift off).

base of tail at the instant of touch down ("hard contact") and lift off of an extremity.

To assess the variation of subjective identification of landmarks, the analysis of a randomly chosen sequence was repeated on 10 different days. The maximum digitizing error was less than 2 mm for the y-coordinate of the forehead landmark. All other landmarks were identified with higher accuracy. Similarly the variation of intra-observer identification of the exact frame of touch down and lift off was estimated. Here, the maximum deviation was just three frames (equivalent to 6/1,000 s).

With the acquired data metric gait parameters were calculated: Footfall sequences, velocity, stance phase duration, swing phase duration, stride length (definitions follow Demes et al. 1990). Stride frequency (strides per time unit) correlates inversely to stride duration, which is determined by the addition of stance phase duration and swing phase duration of a given limb. Gait parameter analysis followed Hildebrand (1966, 1967, 1976, 1980) and others (e.g. Cartmill et al., 2002). The student's t-test after Gossett for unrelated samples was used to test the equality of two sample variances (significant when $P < 0.01$), whereas Pearson's product-moment correlation coefficient (r) was calculated to establish an estimated association (or independence) of two samples distributed as bivariate normal variables. Spearman (r_s) rank correlation coefficients were computed to test the association of a normally distributed bivariate variable (e.g., stance phase duration) and ordinal scaled categories (different inclinations).

Gait determinants

Hildebrand (1966, 1967, 1976, 1980) introduced a method to classify any symmetric gait independent of an animal's size or speed. It makes symmetric gaits of different mammalian taxa highly comparable and was recently reviewed by Cartmill et al. (2002). Hildebrand's formula comprises two characteristic dimensions, the percentage of the stride interval the footfall of a forefoot lags behind the strike of the ipsilateral hind foot (also limb phase, termed diagonality (D) by Cartmill et al., 2002) and the percentage of stride interval that each foot is on the ground (also relative stance phase duration or duty factor; S). Whereas diagonality reflects the spatial temporal coordination of the four limbs during locomotion, the duty factor provides information about the speed. We adopt here Cartmill et al.'s terminology, but concede slight deviations to the strict value of these authors for the trot because two limbs will never swing perfectly in phase in a natural environment.

In a trot diagonality is ~0.5 ($0.45 < D < 0.55$ following Schmitt et al., 2006). With D two major states can be distinguished: In a lateral sequence (LS; $D < 0.5$) the footfall pattern is as follows: right hind (rh), right front (rf), left hind (lh), left front (lf). In a diagonal sequence (DS; $D > 0.5$) the footfall pattern is: rh, lf, lh, rf. If a LS gait resembles a trot ($0.31 < D < 0.45$), that is swing and stance phase of diagonal limbs are closely related, the gait is classified as a lateral sequence/diagonal couplets gait (LSDC). If a DS gait resembles a trot ($0.55 < D < 0.69$), the gait is classified as a diagonal sequence/diagonal couplets gait (DSDC). In single foot gaits (either in lateral or diagonal sequence) no limbs are swinging closely temporally related; rather all swing and stance phases are approximately evenly spaced in time.

If S is less than 50% (or 0.5) the gait is classified as a run, that is there are not always at least two feet on the ground and an aerial phase is adopted. A gait is classified as a walk, if the duty factor is more than 50%. Cartmill et al. (2002) incorporated the fact that forelimb duty factor (S_f) and hind limb duty factor (S_h) rarely have the exact same value. Therefore, they introduced the duty factor index ($100\ S_h/S_f$), that is "average hind limb duty factor over a given gait cycle expressed as a percentage of average forelimb duty factor" (Cartmill et al., 2002; p 410). A duty factor index of more than 100 depicts a higher S_h than S_f. Conversely, a duty factor index of less than 100 indicates a smaller S_h than S_f. Sometimes forelimb and hind limb pairs exhibit different S values, such that one pair is effectively walking ($S > 0.5$) while the other is running ($S < 0.5$). These cases are termed half-runs following Cartmill et al. (2002). Furthermore, Cartmill et al. (2002) formulated a support-polygon model to predict diagonality in walking gaits that maximizes overall stability for a given duty factor. According to the model the duty factor leading to maximum stability for LS is S_f, whereas it is S_h for diagonal sequence gaits. Therefore, the authors termed S_f the relevant duty factor for LS gaits and S_h the relevant duty factor for DS gaits. In running symmetrical gaits primates are rarely reported to trot, but instead utilize an ambling gait that maintains contact between the substrate and at least one foot at all times (Schmitt et al., 2006). Here, we follow these authors in their definition of an amble: symmetrical gaits with a duty factor of less than 0.5 in at least one limb and diagonality between 0.55 and 0.95, or 0.05 and 0.45. In ambling gaits the relevant duty factor is S_f according to the support-polygon model (cf. Schmitt et al., 2006).

RESULTS

Walking gaits on sloped substrates

All recorded trials showed a diagonal coupling of extremities (diagonal couplets, $0.31 < D < 0.69$). However, the two experimental animals displayed different footfall sequences in relation to substrate inclination.

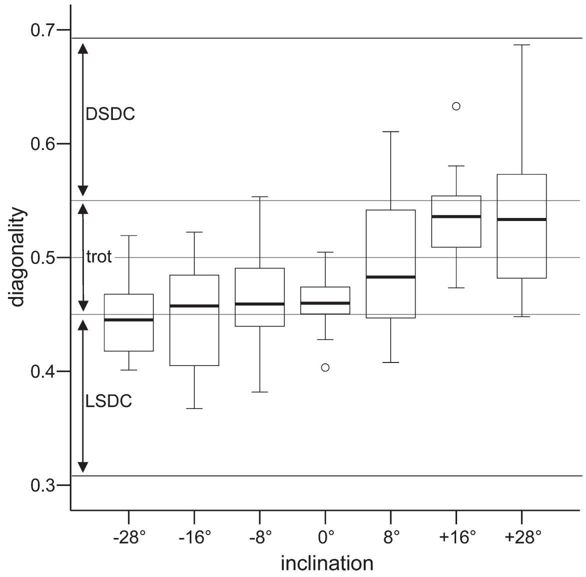

Fig. 2. Box- and whisker-plots of diagonality for separate inclinations. Boxes represent 50% of data, the line within the box represents the median and each whisker corresponds to 25% of the data. Circles represent outliers and asterisks depict extreme outliers.

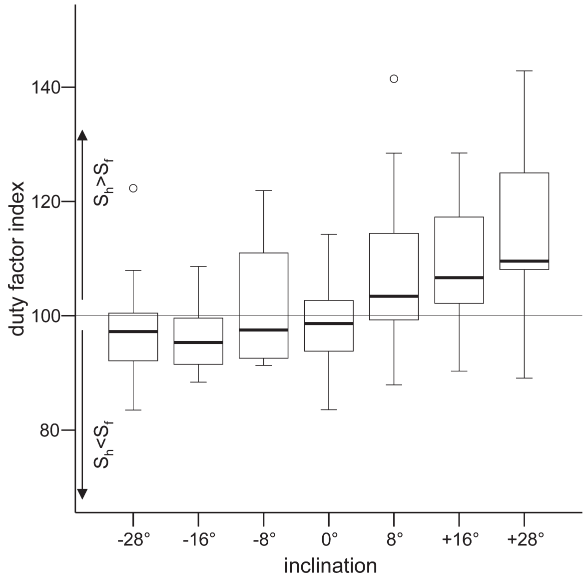

Fig. 3. Box-and-whisker-plots of the duty factor index for separate inclinations.

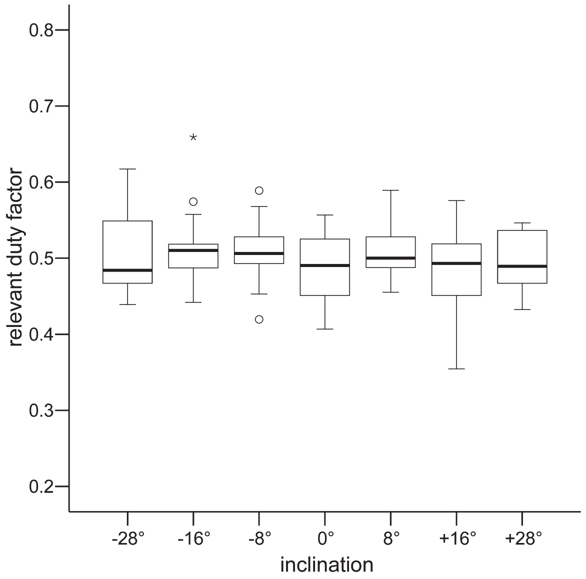

Fig. 4. Box-and-whisker-plots of the relevant duty factor for separate inclinations. Following Cartmill et al. (2002) the relevant duty factor is S_f for LSDC gaits and S_h for DSDC gaits.

LSDC, trot, and DSDC walking gaits occurred. The walking trot was the most common gait ($D \sim 0.5$). On declines LSDC gaits occurred frequently (76.1% of all recorded LSDC gaits), whereas they were rare on inclines (16.9%). Conversely, DSDC gaits appeared more commonly on inclines (94.3% of all DSDC gaits) and were almost completely absent upon declined substrates (5.7%). The values for diagonality scatter between 0.37 and 0.69, but the distribution is influenced by inclination. On declines diagonality had smaller values than on inclines (Fig. 2). This is statistically reflected in the correlation coefficient although there is a considerable dispersion about the means and the values overlap to some extent. The positive correlation is significant at the 0.01 level ($r_s = 0.556$).

The duty factor index also appears to be related to substrate inclination in cotton-top tamarins. On steep declines the duty factor index tends to be below 100, indicating that hind limb duty factors are smaller than forelimb duty factors. On steeply inclined substrates the duty factor index tends to be above 100, that is hind limb duty factors are greater than forelimb duty factors. This correlation is also statistically significant at the 0.01 level ($r_s = 0.48$). The values scatter between 83.5 and 142.9 (Fig. 3).

As an effect of a combined adjustment of diagonality as well as duty factor index to inclination the relevant duty factor remains approximately constant if substrate inclination is changed. This is due to the fact that the relevant duty factor is hind limb duty factor in DS and forelimb duty factor in LS gaits. The correlation coefficient between substrate inclination and relevant duty factor does not indicate any correlation ($r_s = -0.126$). The mean value is 0.501 (approximately at the walk/run transition) with a standard deviation of 0.05 (Fig. 4).

Running gaits on sloped substrates

Two types of half-runs can be differentiated. Either the forelimbs or the hind limbs can adopt the aerial phase. A total of 36 half-runs occurred in the 123 complete cycles available. Eleven of 16 half-runs with a forelimb aerial phase occurred on declined substrates; vice versa 16 of 20 recorded half-runs with a hind limb aerial phase occurred on inclined substrates. This appears connected to the inclination dependent duty factor index.

Running gaits with suspensions in both, forelimbs and hind limbs, occurred in 41.7% (51 of 123) of the complete cycles available for gait determination. Running trots as well as lateral and diagonal sequence ambles occurred. Values for diagonality range from 0.41 to 0.69 and seem to be substrate inclination related. On steep declines lateral sequence ambles were more frequent than on other

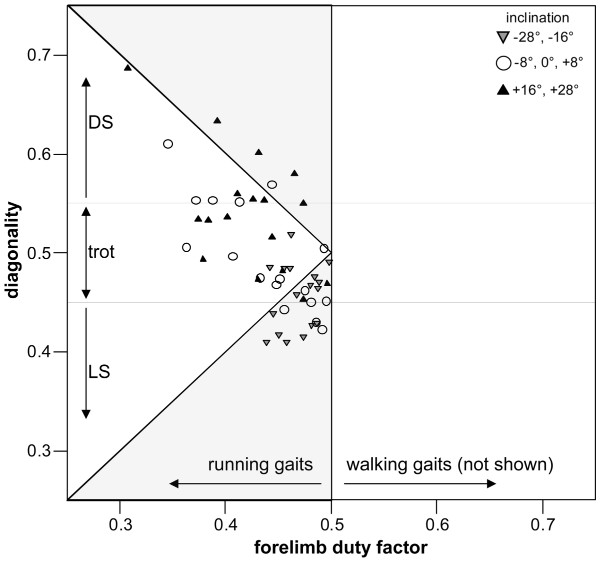

Fig. 5. Forelimb duty factor (S_f) plotted against diagonality for running gaits. The y-axis reference lines frame the trot area. Above the trot area animals amble in diagonal sequence when running. Below the trot area animals amble in lateral sequence when running. Runs plotted inside the gray area do not have a whole body areal phase following Schmitt et al. (2006). Note: No lateral sequence ambles occurred on steep inclines (+28°; +16°) whereas no diagonal sequence ambles occurred on steep declines (−28°; −16°). The running trot was the most common running gait.

inclinations, whereas on moderate inclinations and horizontal substrates the running trot was the most frequently utilized gait. On steep inclinations the diagonal sequence amble was predominantly observed (Fig. 5).

Metric gait parameters

The spatio-temporal gait parameters stance phase duration, swing phase duration, stride length, and velocity as well as their variation according to a change in substrate inclination were analyzed for forelimbs and hind limbs. Because of variability in metric gait parameters, significant differences were apparent only between extremely inclined and extremely declined branches (+28° and −28° respectively), hence comparisons below are limited to these support inclinations (Table 1).

Stance phase duration. For the different inclinations of our study the mean forelimb and hind limb stance phase durations vary unevenly in both animals (cf. Fig. 6 and Table 1). Thus, a consistent substrate inclination dependent influence can not be assumed for cotton-top tamarins for both, forelimbs and hind limbs. But, hind limb stance phase duration in relation to forelimb stance phase duration is linked to substrate inclination (Fig. 6). In both experimental subjects mean forelimb stance phase durations were longer than mean hind limb stance phase durations on declines (except on the −8° decline in Animal B). Conversely, on inclines hind limb stance phase durations were longer than mean forelimb stance phase durations. This corresponds to the substrate inclination dependent shift of the duty factor index.

Swing phase duration. Mean forelimb swing phase durations on steep declines were shorter than on level substrates in both animals (significantly in Animal A,

TABLE 1. Fore- and hind limb gait parameters on −28° (d), 0° (h), and +28° (i) substrate inclination for both animals

		−28°				0°				+28°				Differences	
		Forelimb		Hind limb		Forelimb		Hind limb		Forelimb		Hind limb			
Gait parameter	Animal	Mean	s. d.	Mean	s. d.	Mean	s. d.	Mean	s. d.	Mean	s. d.	Mean	s. d.	Forelimb	Hind limb
Stance phase duration	A	0.180	0.023	0.170	0.023	0.166	0.027	0.175	0.021	0.148	0.042	0.184	0.052	$d > h > i$	$d < h < i$
	B	0.179	0.053	0.179	0.030	0.193	0.037	0.193	0.024	0.135	0.024	0.186	0.033	$d < \boldsymbol{h > i}$	$d < h > i$
Swing phase duration	A	0.157	0.012	0.162	0.012	0.169	0.008	0.178	0.012	0.166	0.022	0.170	0.023	$\boldsymbol{d < h} > i$	$\boldsymbol{d < h} > i$
	B	0.170	0.015	0.188	0.024	0.189	0.027	0.218	0.015	0.205	0.050	0.177	0.030	$d < h < i$	$\boldsymbol{d < h > i}$
Stride length	A	30.930	2.370	31.271	2.625	33.763	1.713	33.460	1.565	32.548	3.275	33.186	2.840	$\boldsymbol{d < h} > i$	$\boldsymbol{d < h} > i$
	B	36.024	2.252	34.372	1.950	31.107	2.190	30.375	1.163	40.419	4.869	37.473	5.906	$\boldsymbol{d > h < i}$	$d > h < i$

Significant relative substrate differences at the 0.01 level in bold.

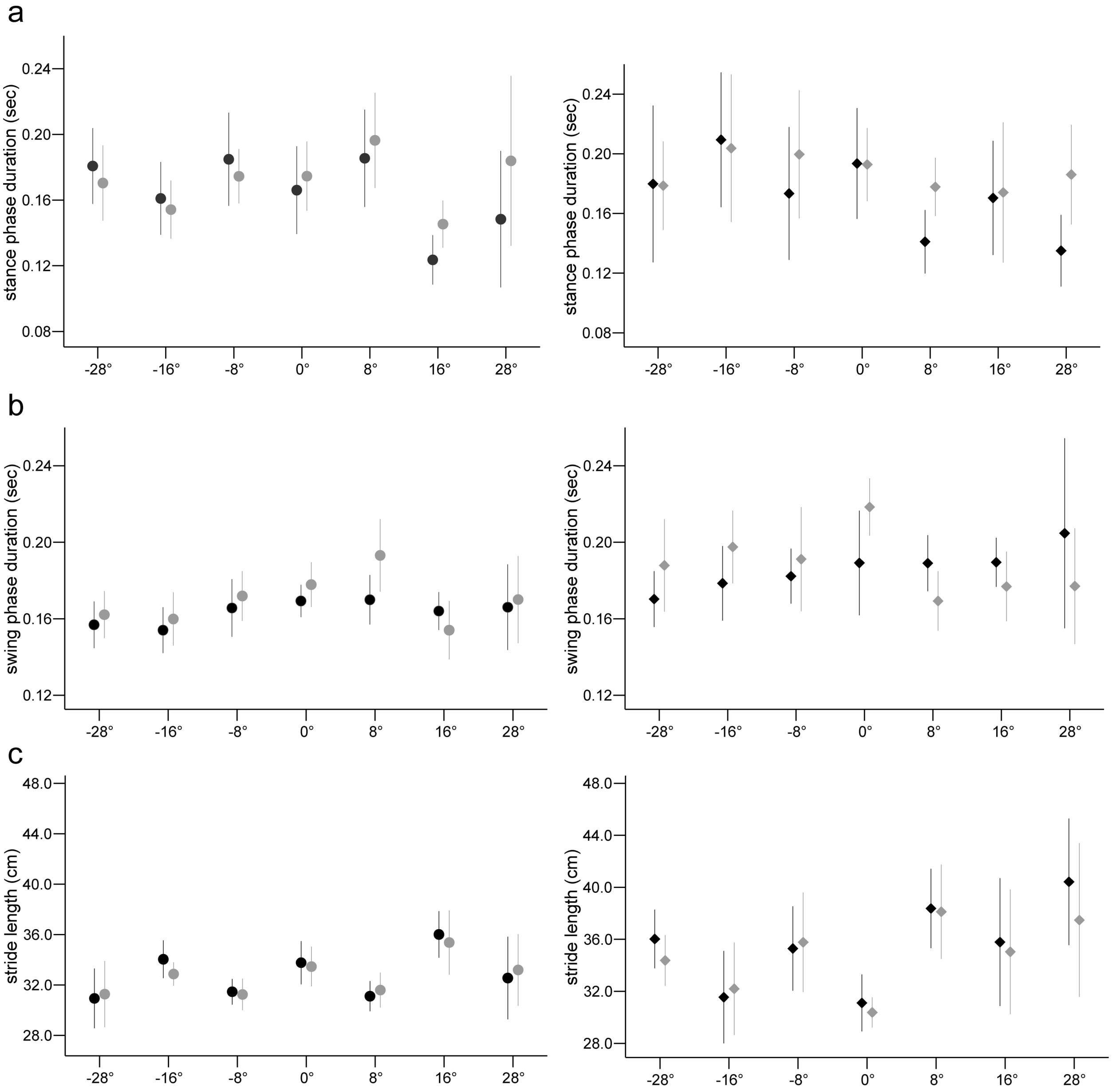

Fig. 6. Error bars for analyzed metric gait parameters for separate inclinations, animals and limb pairs. Arithmetic mean +/− standard deviation. Circles: Animal A, rhombs: Animal B; black: forelimb; gray: hind limb.

Table 1), but did not display a consistent trend in both subjects on inclined substrates. Mean hind limb swing phase durations on steep declines were significantly shorter than on level substrates for both animals (Table 1), and also shorter on inclines compared to the horizontal substrate (significant in Animal B). Mean hind limb swing phase durations seem to increase from steep declines to the level substrate (or moderate ascent in the case of Animal A) and then drop to a lower level on inclined substrates (cf. Fig. 6). Therefore, a consistent trend for the influence of variable substrate inclinations is difficult to formulate. But, in analogy to stance phase durations, the relation of hind limb swing phase duration to forelimb swing phase duration seems to be connected to substrate inclination (Fig. 6). Whereas mean hind limb swing phase durations are longer than mean forelimb swing phase durations on all declines, they are shorter on all inclines (except +8° and +28° in Animal A). This also corresponds to the substrate inclination dependent shift of the duty factor index.

Stride length. Values of mean stride length are very uneven in both animals and both limb pairs (Fig. 6). Thus, no dependency on inclination can be assumed. Also, comparing hind- and forelimb stride durations does not reveal any trend. In Animal A forelimb stride lengths were shorter than hind limb stride lengths on steep declines as well as on steep inclines. Vice versa, in Animal B forelimb stride durations were longer than hind limb stride durations on both, steep declines and steep inclines.

Velocity related aspects. Velocity ranged from 0.52 m/s to 1.48 m/s and was not correlated with substrate inclination ($r_s = 0.148$). Gait parameters exhibited sub-

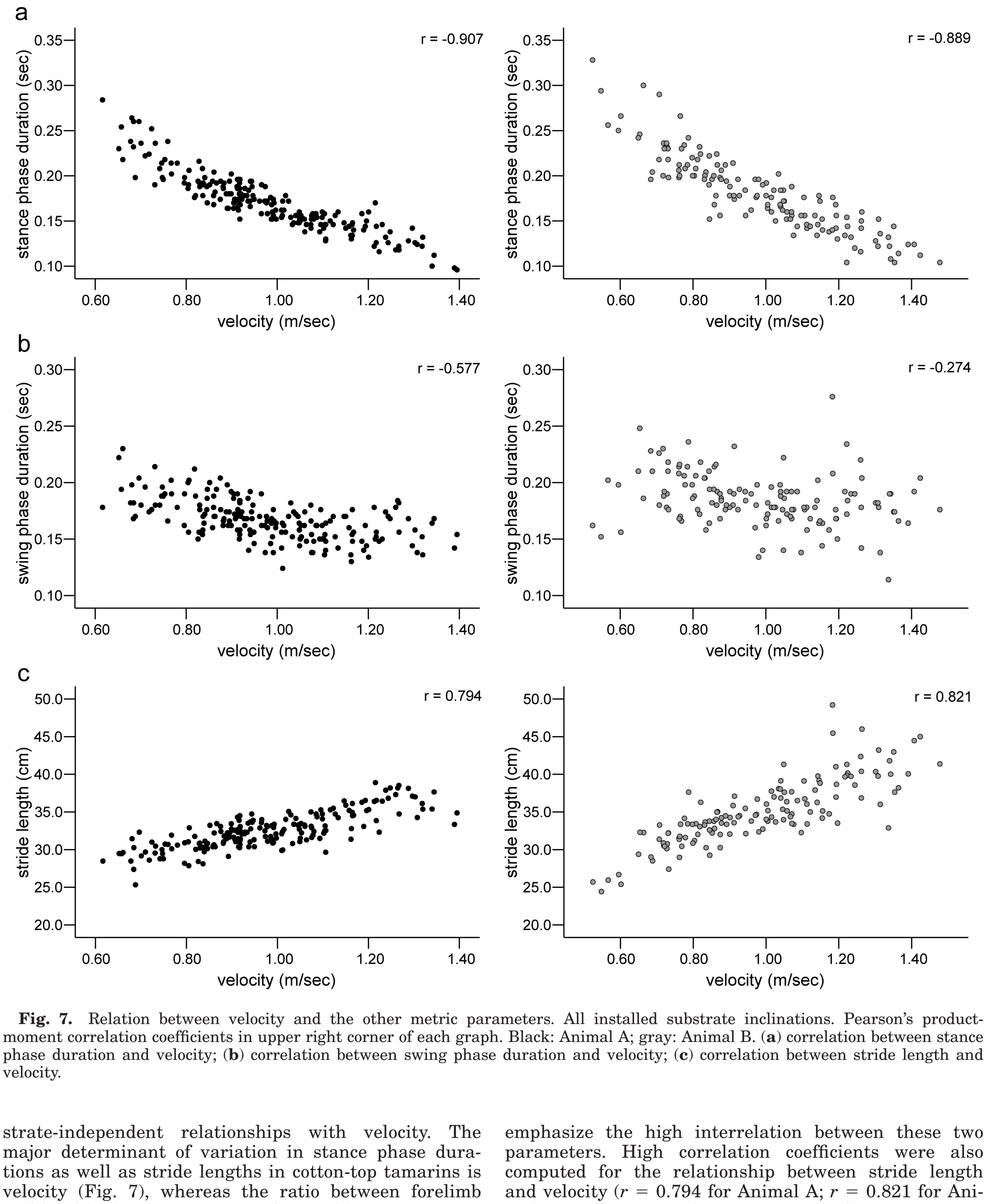

Fig. 7. Relation between velocity and the other metric parameters. All installed substrate inclinations. Pearson's product-moment correlation coefficients in upper right corner of each graph. Black: Animal A; gray: Animal B. (**a**) correlation between stance phase duration and velocity; (**b**) correlation between swing phase duration and velocity; (**c**) correlation between stride length and velocity.

strate-independent relationships with velocity. The major determinant of variation in stance phase durations as well as stride lengths in cotton-top tamarins is velocity (Fig. 7), whereas the ratio between forelimb and hind limb parameters is influenced by substrate inclination. There are three possible strategies to increase the speed of symmetrical quadrupedal locomotion. Either stride frequency, stride length or both have to be increased. High negative correlation coefficients of $r = -0.907$ (Animal A) and $r = -0.889$ (Animal B) for the correlation between velocity and stance phase duration emphasize the high interrelation between these two parameters. High correlation coefficients were also computed for the relationship between stride length and velocity ($r = 0.794$ for Animal A; $r = 0.821$ for Animal B). Hence, in order to increase velocity cotton-top tamarins reduce stance phase duration (resulting in increased frequency) and elongate stride length. Correlation coefficients between swing phase duration and velocity indicate a less close relationship between these two parameters ($r = -0.577$ for Animal A; $r = -0.274$ for Animal B).

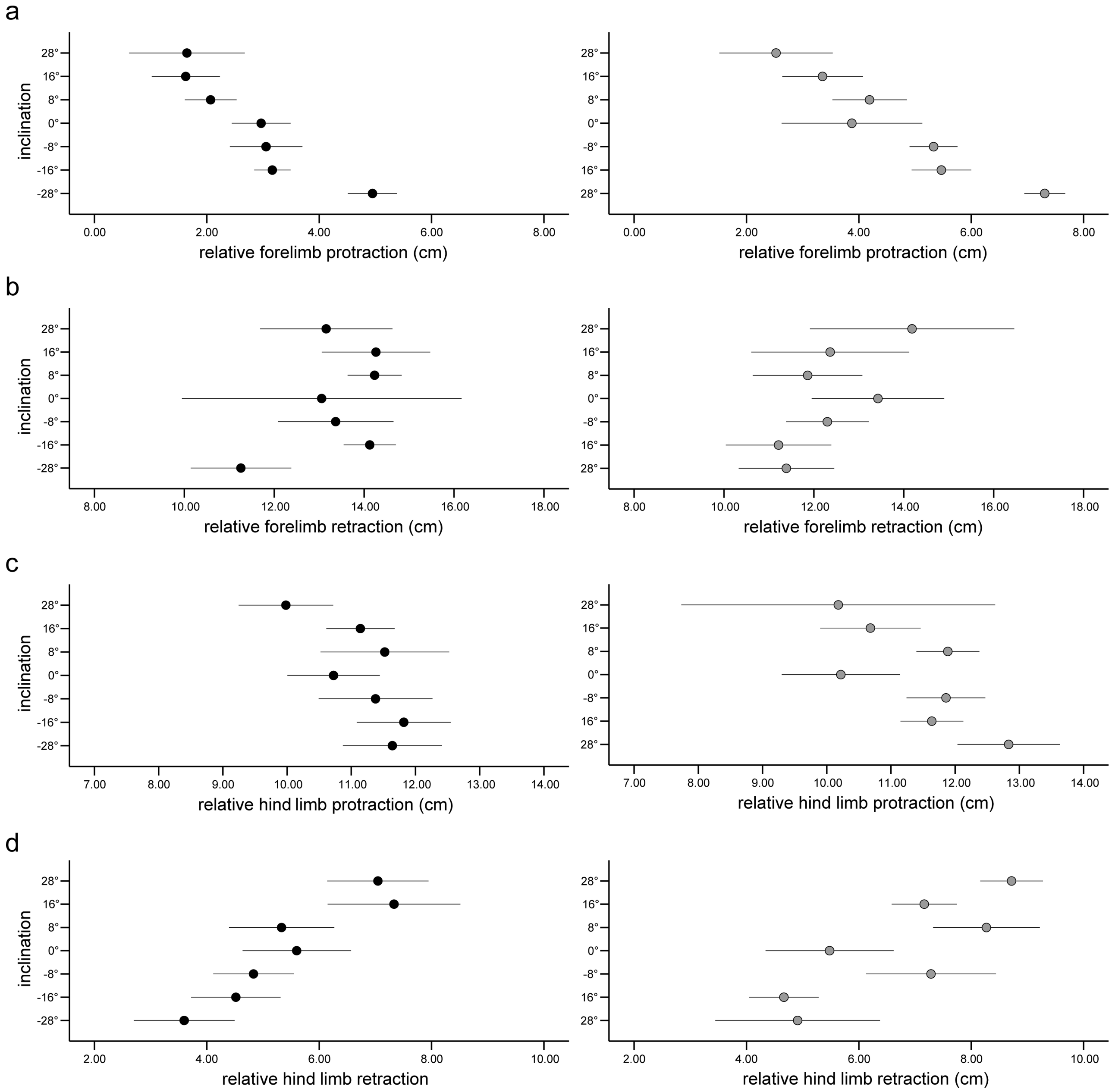

Fig. 8. Protraction, retraction and influence of substrate inclination. Arithmetic mean +/− standard deviation. Black: Animal A; gray: Animal B. (**a**): relative forelimb protraction; (**b**): relative forelimb retraction; (**c**): relative hind limb protraction; (**d**) relative hind limb retraction.

Protraction and retraction of forelimbs and hind limbs

Distances from the distal end of a forelimb autopodium to the intersection point of the perpendicular from the forehead landmark to the substrate were obtained for the instant of touch down and lift off (Fig. 1, distance a and b). The resulting distances are termed here relative forelimb protraction and relative forelimb retraction (for instant of touch down and lift off, respectively). To obtain relative hind limb protraction and relative hind limb retraction the distance from the distal end of a hind limb autopodium to the intersection point of the perpendicular from the tail base landmark to the substrate was measured in the same manner (Fig. 1, distances c and d).

Relative forelimb protraction and relative forelimb retraction. Both animals display a relative forelimb protraction of more than 5 cm on substrates with a steep decline (−28°) at the instant of touch down (Fig. 8a). On steep inclines (+28°) it is reduced to about 2 cm and the extremity touches ground just in front of the head. Correlation coefficients point out the close negative relationship between relative forelimb protraction and substrate inclination: $r_s = -0.793$ (Animal A) and $r_s = -0.877$ (Animal B).

In accordance with a substrate inclination dependent shift of relative forelimb protraction, a lower average relative forelimb retraction is obtained for extreme declines (−28°) than for extremely inclined substrates (+28°; Fig. 8b). Relative forelimb retraction and substrate inclination are not correlated as closely as are relative forelimb protraction and substrate inclination. The correlation coefficients for both animals are well below the level of a high correlation (r_s = 0.293 and r_s = 0.456 for animals 1 and 2 respectively) and hence a close relationship can not be assumed.

Relative hind limb protraction and relative hind limb retraction. In contrast to conditions in the forelimbs, relative hind limb protraction does not display a clear substrate inclination dependent shift as correlation coefficients for the negative relationship between relative hind limb protraction and substrate inclination are not statistically significant: $r_s = -0.389$ for Animal A and $r_s = -0.568$ for Animal B (Fig. 8c).

The interrelationship between relative hind limb retraction and substrate inclination is much clearer (Fig. 8d). Stronger correlation coefficients are obtained between these parameters for both animals (r_s = 0.725 for Animal A; r_s = 0.681 for Animal B).

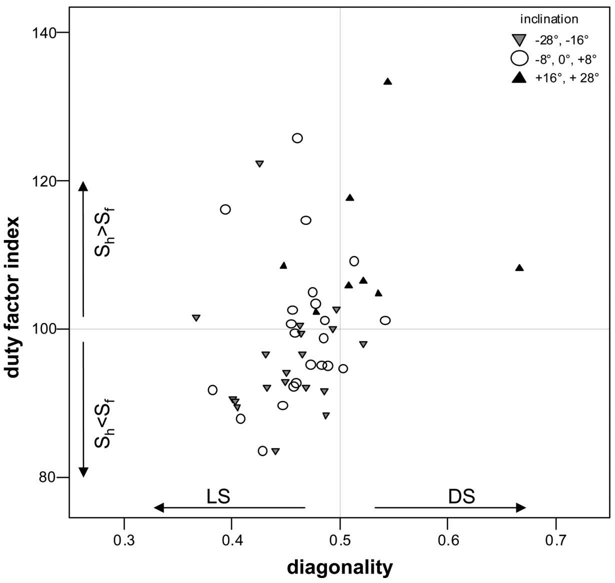

Fig. 9. Duty factor index plotted against diagonality for all walking gaits. The duty factor index reference line indicates the idealized $S_h = S_f$ case. Note that most diagonal sequence walks have a duty factor index above 100 and occurred upon inclined substrates.

DISCUSSION

Gaits and gait parameters of primates on sloped substrates

Whereas diagonality in cotton-top tamarins increased the more the substrate inclined, it decreased the more the substrate declined. This tendency led to increased use of LS gaits on descending substrates. The first indication for a substrate inclination dependent shift in diagonality that led to a conversion of gaits was given by Prost and Sussmann (1969). They stated that *Saimiri sciureus* (squirrel monkeys) utilized LS more frequently on horizontal and moderately ascending substrates, whereas on steep inclines diagonal sequences dominated. Likewise, Rollinson and Martin (1981) reported LS gaits during locomotion of different catarrhine primates (*Cercocebus albigena*, *Cercocebus galeritus*, *Cercocebus torquatus* (all Papionini), *Cercopithecus nictitans*, *Cercopithecus pogonias*, *Cercopithecus cephus*, *Cercopithecus neglectus*, *Miopithecus talapoin* (all Cercopithecini)) on descending substrates. Vilensky et al. (1994) were the first to confirm these observations quantitatively in their investigation on squirrel monkeys moving on differently inclined flat treadmills. Our results are in agreement with these observations, and with the pattern observed for six species of strepsirhine primates (cf. Stevens, 2003). Hildebrand (1967) specified LSDC, trot, and DSDC gaits for three genera of callitrichids on nearly horizontal substrates (no exact inclinations and species given) and attributed the observed LS to an inadequate quality of underlying video material and proposed a greater variability of locomotion for relatively small animals on uneven substrates. For cotton-top tamarins Arms et al. (2002) reported a "pseudo-lateral" gait, which is characterized by a lateral sequence in combination with diagonal couplets (equivalent to a LSDC gait). Unfortunately these authors did not further differentiate diagonal couplet gaits, hence no information about the frequency or the situation in which "pseudo-lateral" gaits occurred is given. Vilensky et al. (1994) do not include the raw data on gait sequence patterns for all treadmill inclinations, reporting only the gaits used with highest frequency. The footfall patterns presented in their study do not indicate a clear dependency of diagonality on substrate inclination. However, in agreement with the results of the present study squirrel monkeys displayed a preference for DS gaits on steep inclines (+28°). But, in contrast to cotton-top tamarins, squirrel monkeys preferred LS gaits on all other inclinations. In addition to the LSDC gait also utilized by cotton-top tamarins, squirrel monkeys displayed even LSSF gaits (cf. Vilensky et al., 1994). Following Hildebrand's classification, a LSSF gait requires a diagonality that does not exceed 0.31 ($0.19 < d < 0.31$). The lowest acquired value for cotton-top tamarins in our analysis was 0.37 (Animal B, −16°). The relatively low diagonality in squirrel monkeys observed in the study of Vilensky et al. (1994) may also be influenced by the locomotion on flat treadmills since these primates did not show any LS in a later study of level arboreal locomotion from Schmidt (2005b).

Cartmill et al. (2002) derived the duty factor index for a wide sample of primate species (19 species; 20 individuals) moving at preferred speeds on either flat ground or horizontal bars. The only callitrichid species (the common marmoset) tested in their data set diverged from the other primates in that its duty factor index did not correlate with diagonality in walking gaits (Cartmill et al., 2002). A high duty factor index, that is $S_h > S_f$, corresponded to higher values of diagonality in all of the "noncallitrichid" primates tested by these authors. The common marmoset instead showed low diagonalities (mostly LS) that seemed to be independent of the duty factor index. In our study cotton-top tamarins also displayed a relatively low diagonality (especially on declined substrates), but, in contrast to the common marmoset, a slight correlation between duty factor index and diagonality can be computed for walking gaits (r = 0.334; significant at the 0.05 level; Fig. 9). Cotton-top tamarins obviously display intermediate characteristics

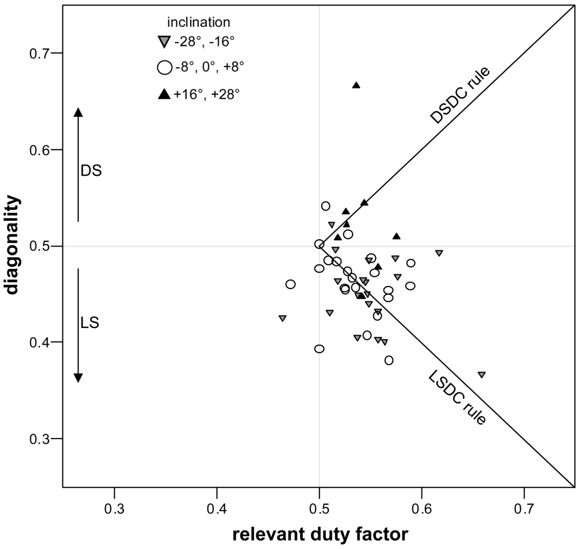

Fig. 10. Modified Hildebrand diagram for walking gaits. Half-runs with average duty factor of more than 0.5 were scored as walks. Note that most DSDC walks approximate the DSDC rule and most LSDC walks cluster near the line predicted for the LSDC rule after Cartmill et al. (2002).

that are similar to those of common marmosets, but resemble more the "noncallitrichid" data of Cartmill et al. (2002).

Furthermore, Cartmill et al. (2002) formulated a set of rules, namely the DSDC rule, the LSDC rule and the LSLC rule, with which they predicted that in diagonal couplets gaits the values for diagonality and for the relavant duty factor would converge. The values for all "noncallitrichid" primates in the authors' data set clustered around the predicted line of the "DSDC rule" in accordance with the model. But again, the values of the common marmoset diverged substantially from those of all other analyzed primates. Our results for cotton-top tamarins indicate a more differentiated picture: These primates followed the "DSDC rule" when utilizing a DSDC gait and followed the "LSDC rule" when utilizing a LSDC gait. Hence, cotton-top tamarins are able to switch from obeying one rule to the other if substrate inclination changes and therefore approximate the most stable mathematically calculated gait. According to Cartmill et al. (2002) and Schmitt (2003) the unusual gait characteristics of the common marmoset reflect some behavioral adaptations of marmosets (e.g., arboreal activity mainly on secure branches, vertical clinging on trunks). In analogy, the resemblance of tamarins, which are agile arborealists that often move along thin branches, to other "noncallitrichid" primates can thus be proposed to be linked to behavioral habits (Fig. 10).

Hildebrand (1967) rarely observed running symmetrical gaits in the locomotion of the 26 primate genera he investigated. The author therefore postulates that instead of utilizing symmetrical running gaits primates immediately switch to asymmetrical gaits like gallop or bound. Deviating from Hildebrand's postulation Kimura (1992) observed running trots for *Macaca mulatta* (Papionini). Furthermore, modern high speed video locomotion analysis with high temporal resolution facilitates the identification of short aerial phases (i.e., running gaits) even for animals with high stride frequencies. With respect to Hildebrand's observation that primates rarely utilize running trots Schmitt et al. (2006) recently analyzed intermediate-speed running gaits (between walk and gallop) of 12 primate species including two callitrichid representatives, the common marmoset and *Saguinus fuscicollis* (the saddleback tamarin). The tested primates almost exclusively adopted a DS ambling gait when running in a symmetrical gait, an intermediate-speed gait with no whole-body aerial phase that minimizes vertical oscillations of the center of mass (Schmitt et al., 2006). The authors therefore argue that the utilization of ambling running gaits is preferable in arboreal mammals. However, the common marmoset was the only primate tested that did not prefer the DS amble and instead displayed running trots more often. Additionally, the common marmoset as well as the saddleback tamarins more frequently utilized canters compared to "noncallitrichids" in Schmitt et al.'s (2006) study. The canter is an asymmetrical running gait resembling an amble (no whole-body aerial phase, at least one foot in contact with the substrate at all times). Our data for symmetrical running gaits contribute to the perception that gaits in callitrichids are more variable than in other primates. On level arboreal substrates cotton-top tamarins utilized mainly running trots. This is conflicting the results for saddleback tamarins that never displayed a running trot in Schmitt et al.'s (2006) study. It gets even more complicated when different inclinations are considered, since the effect of substrate inclination on diagonality leads to the utilization of DS ambles on inclines and LS ambles on declines in cotton-top tamarins (Fig. 5).

Vilensky et al. (1994) documented an increase of all metric gait parameters (stride duration, cycle duration, and swing phase duration of both limbs) in squirrel monkeys except stance phase duration from −28° to 0° on the treadmill, whereas in ascents the parameters remained relatively constant. In agreement with these results, our data for cotton-top tamarins do not reflect a relationship between stance phase duration and substrate inclination and exhibit an increase of forelimb and hind limb swing phase durations from the −28° inclination to horizontal substrates. In contrast to squirrel monkeys however, cotton-top-tamarins in this study exhibited relatively constant stride duration on branches of differing inclination. Also in contrast to squirrel monkeys, forelimb-hind limb stance phase ratios are higher on declines and lower on inclines in cotton-top tamarins (as reflected by the duty factor index). Following the recent argumentation of Stevens (2006) these relative alterations in forelimb and hind limb stance phase durations can result in different gait sequence patterns. Squirrel monkeys displayed longer hind limb stance phase durations than forelimb stance phase durations for all treadmill inclinations (Vilensky et al., 1994). As in lemurids and cheirogaleids (Stevens, 2003), swing phase durations of cotton-top tamarins tend to be shorter in the forelimbs on declines, and were additionally longer on inclines. The decrease in swing duration on negatively tilted substrates observed in squirrel monkeys is attributed by Vilensky et al. (1994) to gravity accelerating protraction of the limb.

Metric gait parameters seem to be closely tied to velocity. In primates, as in all mammals, an increase of velocity is mainly achieved by a reduction of stance phase duration and an extension of stride length, whereas the swing phase duration remains constant (see e.g., Vilensky and Gankiewicz, 1986 for *Cercopithecus aethiops*;

Kimura, 1992 for *Pan troglodytes*, *Macaca mulatta*, *Cebus apella*, and *Lemur catta*). A reduction of stance phase duration is often linked to an adoption of an aerial phase. This strategy is also predominantly utilized by cotton-top tamarins. Demes et al. (1990) documented a reduction of swing phase duration that correlated with an increase of velocity in *Loris* and *Nycticebus* (both Lorisidae). This was also observed by Vilensky and Patrick (1985) for squirrel monkeys and Schmidt and Fischer (2000) for *Eulemur fulvus* (brown lemur; Lemuridae). At least to some extent this is also true for cotton-top tamarins. Demes et al. (1990) argue that lorises actively move limbs forward during swing phase and are therefore able to increase velocity without shortening support phases, and thus not necessarily leading to higher reaction forces that would cause fine branches to swing and alarm prey. This explanation is apparently not applicable to cotton-top tamarins, since the reduction of stance phase duration strongly correlates with velocity and whole-body aerial phases occurred frequently in running trots making higher substrate reaction forces probable.

The position of forelimbs and hind limbs at the instant of touch down (here relative protraction) and lift off (here relative retraction) is shifted anteriorly on descending substrates and shifted posteriorly on ascending substrates in cotton-top tamarins. The extent of the shift correlates to substrate inclination. Vilensky et al. (1994) as well as Stevens (2000) found larger angular excursions of the hip and shoulder joints on declines and inclines for squirrel monkeys and *Cheirogaleus* sp. (fat-tailed lemurs), respectively. And Stevens and Larson (1999) earlier reported larger angular excursions of these joints in *Aotus* sp. (night monkeys) on inclined branches and smaller excursions on declined branches. However, these results are not directly comparable to ours. On the basis of our experience with small mammal motion analysis, we contend that a reliable description of proximal limb joint motion can only be obtained through cineradiography (cf. Fischer et al., 2002; Schmidt, 2005a) and is therefore not aimed at in this study. Data for protraction and retraction on inclined substrates is given by Lammers et al. (2006) for the gray short-tailed opossum (*Monodelphis domestica*), a small terrestrial marsupial. The gray short-tailed opossum displayed increased forelimb and hind limb protraction on both declines and inclines, when compared to level substrates. Retraction of forelimbs and hind limbs in the gray short-tailed opossum was less on declines than on level and inclined substrates. Thus, the inclination related shift in protraction and retraction we found in cotton-top tamarins is not congruent with the locomotion of the gray short-tailed opossum. Our results are more profound for relative forelimb protraction and relative hind limb retraction than for relative forelimb retraction and relative hind limb protraction.

Positions of forelimb lift off and hind limb touch down in a diagonal couplets walking gait on an arboreal substrate may be influenced by interference of ipsilateral limbs. These interferences come to bear because at the instant of hind limb touch down the ipsilateral forelimb is still in stance phase. "Overstriding" of ipsilateral limbs as described for terrestrial primates (Hildebrand, 1967) was not observed in cotton-top tamarins on the arboreal substrate and seems to be generally problematic on thin branches. Therefore, the more uniform and less variable lift off position of forelimbs and touch down position of hind limbs should be a result of the diagonal couplet gait pattern in combination with slender supports. Our own observations on brushed-tailed possums, that also exhibited diagonal couplets gaits when walking on inclined arboreal substrates, reveal similar adjustments.

Lateral versus diagonal sequence gaits in primates

Most primates usually utilize DS gaits when moving on horizontal arboreal substrates. Although exceptions from this gait pattern are often reported (e.g. Hildebrand, 1967; Prost and Sussman, 1969; Dykyj, 1980; Rollinson and Martin, 1981; Vilensky and Larson, 1989 for a broad overview; Dunbar and Badam 1998, 2000; Schmitt, 2003; Shapiro and Raichlen, 2005, 2006; Stevens, 2006), possible functional advantages of DS gaits are almost exclusively discussed whereas LS are regarded as representing the primitive state for primate locomotion on thin arboreal supports (cf. Schmitt, 2003). From a phylogenetic perspective, the ability to utilize diagonal sequence gaits is most parsimoniously considered primitive for the primate order. Hence an examination of the utility of LS gaits may be more informative from a functional perspective.

Many different approaches to an explanation of the typical DS gaits in primates have been taken (see discussion later), but as Stevens puts it, "no direct mechanism has yet been revealed to link the use of DS gaits with a specific aspect of the arboreal habitat" (2006, p 954) and the author proposed a synthetic approach to account for the variability observed in primate gait sequence pattern.

Gray (1944) introduced a biomechanical model that proposed LS gaits to be more stable than DS gaits at slow speeds. Incorporating Gray's model into his own considerations Prost (1969) suggested that the advantage of DS gaits lies in a reduction of yawing and rolling torques during climbing and therefore nullifies the postulated advantages of LS gaits. Consequently primates adopted DS gaits. Gray's model is based on a 'static stability concept' and is today regarded as inappropriate to describe mammalian locomotion, which is considered to be best described by a "dynamic stability concept" (cf. Vilensky and Larson, 1989; Cartmill et al., 2002).

Early studies of weight distribution found, that most primates support more weight on their hind- than on their forelimbs, whereas most other mammals carry more weight on their forelimbs. From today's standpoint it can be stated that in most primates higher peak vertical substrate reaction forces are measured in the hind limbs than in the forelimbs (Kimura et al., 1979; Kimura, 1992; Demes et al., 1994; Schmitt and Lemelin, 2002), but if this is a result of actively shifting weight posteriorly as suggested by Reynolds (1985a,b) or an effect of a suite of other adaptations in arboreal locomotion ("compliant walk") as presumed by Schmitt (1999), has yet to be determined (cf. Schmitt and Hanna, 2004). Rollinson and Martin (1981) proposed that differences in weight support were responsible for DS gaits in primates. The authors obtained further evidence by documenting LS gaits on declined substrates (discussed earlier) and observing LS gaits in gray-cheeked mangabey infants (*Cercocebus albigena*) that have relatively larger heads for their body size than adults do. They argue that both scenarios lead to an anteriorly shifted center of gravity. Contradicting this view, Vilensky and Larson (1989) pointed out the fact that primates that support relatively more of their weight on their hind limbs do not exhibit LS gaits less frequently. Additionally these authors argue that, if Rollinson and Martin's hypothesis was right, nonprimates should utilize DS gaits as often as primates utilize LS gaits, which is not the case.

Vilensky and Larson (1989) then hypothesized that the utilization of both DS and LS gaits, is more or less arbitrary and that stability is not a factor. Instead, the authors linked the evolutionary elaboration of the brain and unique patterns in forelimb control during locomotion in primates to the utilization of DS gaits. Vilensky and Larson (1989) suggested that as a side effect of these neural changes, intraspinal pathways that had favored LS gaits were no longer functional resulting in the observed preference of DS gaits in primates. The convergent evolutions of DS gaits in the woolly opossum (*C. philander*, Schmitt and Lemelin, 2002; Lemelin et al., 2003) as well as in the brush-tailed possum (*T. vulpecula*, Goldfinch and Molnar, 1978; Nyakatura et al., in press) in a fine branch niche render this approach less plausible. If DS gaits evolve convergently in fine branch niches in completely different taxa, a functional advantage acting as a selective factor is highly probable.

Shapiro and Raichlen (2002) suggest differences in limb-mass distribution in comparison to nonprimates as a result of increased muscle weight associated with grasping extremities to be involved with the utilization of DS gaits in primates. We agree with Stevens (2006) that these differences alone cannot explain the frequent use of LS and trotting gaits observed in many primate taxa.

With the support-polygon model Cartmill et al. (2002) demonstrated, that Vilensky and Larson (1989) might have been correct with their proposal that stability is not a factor in primate gait selection. They convincingly showed that LSDC and DSDC gaits are just as mathematically stable when the values for diagonality and for the relative duty factor converge. Therefore, Cartmill et al. (2002) propose an ecological based explanation for the preference of DS gaits in arboreal locomotion. In a DSDC gait at the instant of forelimb touch down, when weight is about to be transferred to a new and untested substrate, the diagonal hind limb is already in stance phase approximately under the animal's center of mass. Following Cartmill et al.'s (2002) hypothesis, in combination with grasping specializations of the hind extremities a DSDC gait enables primates to draw back or regain balance, if the new support breaks or bends precipitously and thus constitutes an adaptive advantage. However, the common appearance of LS gaits upon declined substrates in the study at hand somewhat contradicts that argumentation. Given that foraging in tamarins usually takes place in parts of the vegetation that are made up of small, flexible branches, it can be presumed that substrates often bend under the tamarins' weight and therefore form practically descending substrates leading to an increased utilization of LS gaits. It is also important to consider the enormous speed of locomotion of arboreal primates. It makes a "testing" of the substrate with a forefoot seem inconceivable. In addition Shapiro and Raichlen (2005, 2007) argue that stability at forelimb touchdown might not have been the exclusive selective factor for DSDC gaits and show that a lateral sequence/lateral couplet gait offers the same advantages in this instant of time. But only a DSDC gait combines different advantages that it shares with other gait patterns: Security at forelimb touchdown is given in LSLC and DSDC gaits (Cartmill et al., 2002, 2007; Shapiro and Raichlen, 2007), whereas a minimal period of ipsilateral bipedal support is given in LSDC and DSDC gaits (Cartmill et al., 2002). Although a combination of these advantages might be the best explanation for the selection for a DSDC gait pattern in an arboreal context this does not explain the variability of primate gaits becoming obvious with more data published (field: e.g., Dunbar and Badam, 1998, 2000; lab: e.g. Stevens, 2006).

Schmitt (2003) proposed a possible advantage of the LS gaits he observed in common marmosets to lie in an avoidance of interferences of ipsilateral feet (see discussion section later). He further argued that common marmosets actually are not adapted to the small branch milieu, but instead move on broad secure branches and therefore did not evolve a preference for DS gaits. This explanation is not conferrable to the common occurrence of LS gaits in cotton-top tamarins in our study, since these primates are active arborealists and displayed LS and DS gaits in relation to substrate inclination.

SUMMARY AND CONCLUSIONS

Our results show that gait utilization as well as some metric gait parameters are adjusted to different inclinations during locomotion along branchlike substrates in cotton-top tamarins. These adjustments to tilted substrates can be summarized as follows: During locomotion on declined branches, diagonality is lower, leading to increased frequency of LS gaits. On these supports, the duty factor index is typically below 100 with higher limb (especially forelimb) protraction and mean stance phase durations are longer in the forelimb than in the hind limb. Conversely, inclined substrates feature higher diagonality values, hence higher frequencies of DS gaits. The duty factor index is typically above 100, with longer mean stance phase durations in the hind limb than the forelimb, with posteriorly positioned limb excursions and greater limb (especially hind limb) retraction. Limb excursions in cotton-top tamarins tend to be more anteriorly positioned on declines and more posteriorly positioned on inclines, as in strepsirhines (Stevens, 2003). Results for the relevant duty factor, velocity, swing phase durations and stride length are not clearly related to substrate inclination.

Regarding the unresolved problems of the hypotheses for the occurrence of gaits in primates as shown above, we conclude with a different contention on gait utilization which is not mutually exclusive to these hypotheses but also incorporates both, LS and DS gaits, as well as our other results. We base our considerations on the observation that most primates, as other mammals, exhibit greater propulsive efforts with their hind limbs, whereas forelimbs have a greater retarding effect (Kimura et al., 1979; Demes et al., 1994) as well as on Cartmill et al.'s (2002) theoretical argument that LSDC and DSDC gaits are equally stable, if diagonality approximates the relevant duty factor. On inclined substrates additional propulsion is needed, whereas on declined substrates additional retarding effort is necessary (cf. Lammers et al., 2006). An increase of diagonality on inclined substrates results in a predominant occurrence of DSDC gaits in cotton-top tamarins. In these gaits hind limbs touch down shortly before contralateral forelimbs, that is at the instant of diagonal forelimb touch down a considerable share of the hind limbs' stance phase has already elapsed. Therefore, the hind foot is closer to the pivot of the extremity or may even already contribute to propulsion. We propose that a DS gait on inclined substrates thus constitutes an adaptive advantage to reduce the forelimbs' retarding role in the first part of stance phase, when the autopodium is still anterior to the extremities pivot. Also, on inclined substrates protraction is reduced (especially forelimbs). We argue that this adjustment additionally reduces the forelimb retarding role in the first part of stance phase. Conversely, the extension of retraction, may enable the limbs to contribute to propulsion for a greater share of stance phase (especially hind limbs). Accordingly, stance phase duration of forelimbs tends to be shorter than stance phase duration of hind limbs on inclines. This may also contribute to a reduction of the retarding role in the forelimbs and emphasize the enhanced importance of hind limbs for propulsion on inclined substrates. These changes of metric gait parameters on inclined substrates optimize conditions to generate propulsive effort and reflect the adjustments of locomotion against the action of gravity.

On declined substrates, diagonality is reduced, eventually leading to LS gaits in cotton-top tamarins. In a LSDC gait forelimbs touch down shortly before diagonal hind limbs. Rollinson and Martin (1981) state that in a LS gait the forefoot of a diagonal couplet lands first and provides a retardive "stop-jolt" prior to the contact of the hind foot. This is augmented by the fact that during the first part of forelimb stance phase in a LS gait, hind limbs do not contribute to propulsion because the autopodium is still in swing phase or at least clearly anterior the extremities pivot. On declined substrates increased protraction (especially of forelimbs) as well as the extension of stance phase duration of forelimbs in comparison to hind limbs emphasize the forelimb role and reduce the hind limbs' influence on propulsion. The retarding role of the forelimbs may also be increased by an anterior weight shift caused by the decline. Additionally, reduced retraction (especially of the hind limbs) counteracts propulsion. These changes of metric gait parameters on declines reflect the adjustments of locomotion to generate greater braking effort in order to maintain control of velocity to counter the acceleration because of gravity. In our opinion this argumentation serves as an explanation for an inclination related shift in diagonality. We expect to also observe a reduction of diagonality on declines and an increase of diagonality on inclines in other primates, although this need not necessarily result in a more frequent occurrence of LS gaits (e.g. shift from more single-foot DS gaits to trot-like DS gaits).

Our results support the notion that arboreal primate quadrupedalism may best be described by a characteristic behavioral locomotor plasticity (cf. Stevens, 2006). Arboreal substrates convey a wide spectrum of different supports (inclinations, substrate diameters, branch sway et cetera) to which adjustments are made during locomotion. Should the implications that our results suggest hold true for a larger sample of primates as previous observations by Prost and Sussman (1969) and Rollinson and Martin (1981) indicate and results from Vilensky et al. (1994) do not rule out, they constitute another aspect of quadrupedal arboreal locomotion that has to be kept in mind when reconstructing adaptations in early primate evolution.

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