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Locomotor mechanics of the slender loris (*Loris tardigradus*)[☆]

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Abstract

The quadrupedal walking gaits of most primates can be distinguished from those of most other mammals by the presence of diagonal-sequence (DS) footfall patterns and higher peak vertical forces on the hindlimbs compared to the forelimbs. The walking gait of the woolly opossum (*Caluromys philander*), a highly arboreal marsupial, is also characterized by diagonal-sequence footfalls and relatively low peak forelimb forces. Among primates, three species—*Callithrix*, *Nycticebus*, and *Loris*—have been reported to frequently use lateral-sequence (LS) gaits and experience relatively higher peak vertical forces on the forelimbs. These patterns among primates and other mammals suggest a strong association between footfall patterns and force distribution on the limbs. However, current data for lorises are limited and the frequency of DS vs. LS walking gaits in *Loris* is still ambiguous. To test the hypothesis that patterns of footfalls and force distribution on the limbs are functionally linked, kinematic and kinetic data were collected simultaneously for three adult slender lorises (*Loris tardigradus*) walking on a 1.25 cm horizontal pole. All subjects in this study consistently used diagonal-sequence walking gaits and always had higher peak vertical forces on their forelimbs relative to their hindlimbs. These results call into question the hypothesis that a functional link exists between the presence of diagonal-sequence walking gaits and relatively higher peak vertical forces on the hindlimbs. In addition, this study tested models that explain patterns of force distribution based on limb protraction angle or limb compliance. None of the *Loris* subjects examined showed kinematic patterns that would support current models proposing that weight distribution can be adjusted by actively shifting weight posteriorly or by changing limb stiffness. These data reveal the complexity of adaptations to arboreal locomotion in primates and indicate that diagonal-sequence walking gaits and relatively low forelimb forces could have evolved independently.

Keywords: Locomotion; Kinematics; Kinetics; Force; Gait; Lorises; Primates

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Introduction

Three locomotor features distinguish the quadrupedal walking gaits of most primates from those of most other mammals (Vilensky, 1989; Larson, 1998; Schmitt, 1998, 1999, 2003a,b,c; Larson et al., 2000, 2001; Cartmill et al., 2002; Schmitt and Lemelin, 2002; Lemelin et al., 2003) (Fig. 1). First, during walking, quadrupedal primates rely primarily on diagonal-sequence (DS) footfall patterns (i.e., each hind footfall is followed by a contralateral fore footfall), whereas most other quadrupedal mammals use primarily lateral-sequence (LS) gaits (i.e., each hind footfall is followed by an ipsilateral fore footfall) (Muybridge, 1887; Magne de la Croix, 1936; Hildebrand, 1967, 1985; Tomita, 1967; Rollinson and Martin, 1981; Vilensky and Larson, 1989; Meldrum, 1991; Dunbar and Badam, 2000; Cartmill et al., 2002; Lemelin et al., 2003). Second, quadrupedal primates exhibit a more protracted position of the arm at forelimb touchdown (Fig. 1) (Schmitt, 1995, 1998, 1999; Larson et al., 2000, 2001). Finally, most quadrupedal primates experience higher peak vertical forces on the hindlimbs relative to the forelimbs, resulting in a relatively lower forelimb to hindlimb (FL/HL) peak vertical force ratio (Kimura et al., 1979; Kimura, 1985, 1992; Reynolds, 1985b; Demes et al., 1994; Schmitt and Lemelin, 2002). Most other quadrupedal mammals are characterized by a relatively higher FL/HL peak vertical force ratios (Kimura et al., 1979; Kimura, 1985, 1992; Reynolds, 1985b; Demes et al., 1994; Schmitt and Lemelin, 2002). The mechanism by which this unusual pattern of force distribution is achieved on the limbs of primates remains unclear. Reynolds (1985a) proposed that primates actively shift weight posteriorly by recruiting hindlimb retractors when the hindlimb is highly protracted. Schmitt (1999), in contrast, suggested that peak forces are lowered on the forelimb by increasing limb compliance through joint yield and increased contact time, a finding supported by recent studies (Schmitt and Hanna, 2004; Larney and Larson, in press).

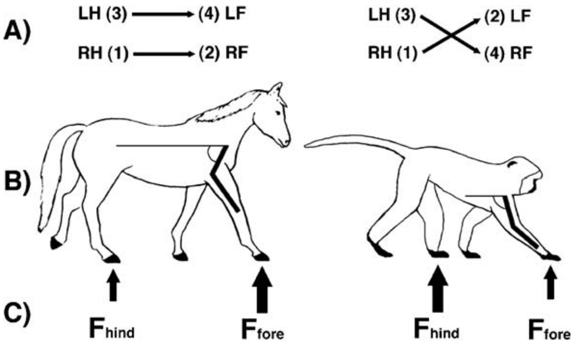

Fig. 1. Locomotor differences that distinguish primates from most other mammals. As a group, most primates commonly use diagonal-sequence (DS) walking gaits (A), have a more protracted humerus at touchdown of the forelimb (B), and have higher peak vertical forces on their hindlimbs compared to the forelimbs (C). Most other mammals (like the horse seen on the left) show a different pattern (see text for more details) (from Schmitt and Lemelin, 2002).

Diagonal-sequence walking gaits, increased arm protraction, and relatively lower forelimb forces are often seen as a functional suite of features that provides an important advantage for moving and foraging on thin and flexible branches (Rollinson and Martin, 1981; Larson, 1998; Schmitt, 1998, 1999; Larson et al., 2000, 2001; Cartmill et al., 2002). This viewpoint is supported by the recent finding that the woolly opossum (*Caluromys philander*)—a marsupial that spends most of its time foraging on terminal branches—is also characterized by all three of the locomotor features typical of most primates (Schmitt and Lemelin, 2002; Lemelin et al., 2003). Similarly, Schmitt (2003b) reported that the common marmoset (*Callithrix jacchus*)—a clawed primate that spends much of its time clinging on large tree trunks—is characterized by lateral-sequence walking gaits, more retracted arm positioning at forelimb touchdown, and relatively higher peak vertical forces on the forelimbs.

Available data for primates, woolly opossums, and other mammals support a link between these kinematic and kinetic features. However, it remains unclear if any or all of these locomotor features must co-occur. Schmitt (2003b) cautioned that any adaptive explanation that focuses on these locomotor features individually may be moot if a single feature provides no specific advantage for fine-branch locomotion, but instead exists simply as by-product of another characteristic of that animal's gait.

As summarized above, current evidence does suggest the existence of a strong association in mammals between lateral-sequence walking gaits and relatively higher peak vertical forces on the forelimbs and vice versa. Demes et al. (1990: 186-187) were explicit in arguing that "the occurrence of lateral sequence gaits in primates should correlate with a higher percentage of weight supported by the forelimbs."

Lorises represent an opportunity to test the strength of the association between LS gaits and relatively high forelimb peak forces. Slow and slender lorises (*Nycticebus* and *Loris*) have been reported to use LS walking gaits more frequently (Hildebrand, 1967; Tomita, 1967, Tomita 1973 cited in Dykyj, 1980; Jouffroy, 1989), both DS and LS walking gaits in equal proportions (Glassman and Wells, 1984; Jouffroy and Petter, 1990), or only DS walking gaits (Demes et al., 1990; Ishida et al., 1990). Force platform data clearly indicate relatively higher peak vertical forces on the forelimbs of *Nycticebus* (Ishida et al., 1990) and in *Loris* (Nieschalk, 1991), although data for the latter species are limited and can only be found in an unpublished dissertation. Ishida et al. (1990) observed DS walking gaits and relatively higher peak vertical forces on the forelimbs in their *Nycticebus* subjects.

Lorises also offer the opportunity to study in more detail the mechanism by which locomotor forces are mitigated on the forelimbs of primates. In other words, why are primates so unusual in having such lower FL/HL peak vertical force ratios? If lorises are characterized by a higher FL/HL peak vertical force ratio as previously reported, then concomitant patterns of limb protraction predicted by Reynolds (1985a) model or joint yield and contact time predicted by Schmitt (1999) should be found.

Materials and methods

We took advantage of the availability of slender lorises (*Loris tardigradus*) housed at the Duke University Primate Center to quantify locomotor kinematics and kinetics in these rare primates. Three adult *L. tardigradus* were included in this study: one adult male (215 g) and two adult females (177 g and 178 g). Video and force platform data were recorded simultaneously. The following variables were examined: (1) footfall pattern, (2) contact time, (3) peak vertical force for both forelimb (FL) and hindlimb (HL), (4) forelimb and hindlimb protraction angles, and (5) forelimb and hindlimb yield. Only walks with no aerial phase of either forelimbs or hindlimbs were considered for analysis. A single step—with no obvious acceleration or deceleration—was collected per locomotor bout (travel down the trackway) in order to preserve as much independence as possible between steps. Using these criteria, 34 walking steps were selected for analysis (12 FL steps and 22 HL steps).

The methods used to collect these data have been described elsewhere (Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2004) and will only be briefly summarized here. Data were recorded in the Animal Locomotion Laboratory located in the Department of Biological Anthropology and Anatomy at Duke University. Animals were videotaped while they walked freely on a raised horizontal pole. The pole was attached to a force platform that recorded vertical, fore-aft, and mediolateral components of force applied to the substrate. The pole (1.25-cm in diameter) was made of graphite and coated with a nonslip surface of sand and paint (Fig. 2). The pole consisted of two 1.2-m-long segments separated by 2-mm gaps on either side from a 5-cm long central segment attached to the force platform (Fig. 2).

Subjects were videotaped using two synchronized electronically shuttered (1/1000 s) video cameras (recording at 60 Hz) positioned lateral to the line of travel and at the end of the pathway collinear with the line of travel. Video and force platform data were collected synchronously using an event and video control unit and analog–digital converter made by Peak Performance Technologies, Inc., (Englewood CO, USA). Substrate reaction forces were filtered (Butterworth, 30 Hz) and angles and forces were calculated using Peak Motus® 2000 movement analysis software (Peak Performance Technologies, Inc.). We also recorded lateral video images using a Redlake Motion-Scope High-Speed camera (125 images/s)

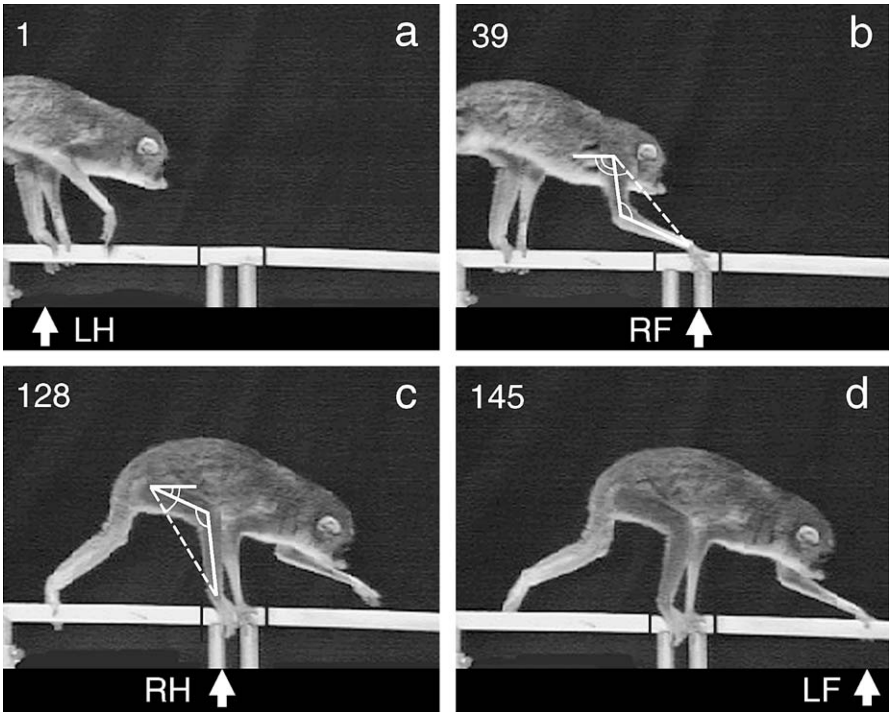

Fig. 2. Sequential high-speed images of *Loris tardigradus* walking on the instrumented pole. The images (a-d) show the timing of the footfall pattern in milliseconds (number in upper left corner). The footfall pattern is diagonal-sequence (LH: left hindfoot, RF: right forefoot, RH: right hindfoot, LF: left forefoot). Arm protraction and elbow angles were measured as indicated in (b) as the RF touches down. Total forelimb protraction angle was calculated as indicated by the dashed line in (b). Thigh protraction and knee angles were measured as indicated in (c) as the RH touches down. Total hindlimb protraction was calculated as indicated by the dashed line in (c).

in order to precisely identify contact time of the forelimb and hindlimb.

Video sequences were used to identify footfall sequence and contact time (s) for each limb beginning with the contact of the right hindfoot. Arm angle was measured as the angle of the humerus relative to a horizontal line passing through the shoulder joint (Fig. 2). Thigh angle was measured as the acute angle of the femur relative to a horizontal line passing through the hip joint (Fig. 2). Elbow and knee angles were measured as the acute angle between the proximal and distal limb segments (Fig. 2). Total forelimb/hindlimb protraction was measured as the angle between a line running from the shoulder/hip to the point of contact of the hand/foot with the pole and a horizontal line passing through the shoulder or hip (Fig. 2). Elbow and knee yields, a measure of limb compliance during walking, were measured as the difference between elbow/knee angle at touchdown and the same angle at midsupport. All angles were measured in degrees (°). Force platform output was in Newtons (N). Peak vertical force (V_{pk}) values for both forelimb and hindlimb were converted into percentages of body weight (% BW) of each corresponding animal.

As we have done previously, limb angular data were collected relative to a horizontal line (Schmitt, 1998, 1999, 2003a,b,c; Schmitt and Lemelin, 2002). However, because we collected the acute thigh and hindlimb angle and the obtuse arm and forelimb angle, these values were not directly comparable to each other (Fig. 2). To correct this, we simply calculated the obtuse angle for the thigh and hindlimb by subtracting the original value from 180°. These are the values given in Table 2.

Larson et al. (2000, 2001) calculated angular values relative to a vertical line passing through the joint center. In order to compare our forelimb and hindlimb angular values to those of Larson et al. (2000, 2001), we added 90° to all of their angular values. Then we subtracted their hip and hindlimb angle values from 180°. These values are given in Table 2. Elbow and knee angles and yield needed no conversion for comparison with previous studies (Larney and Larson, in press).

Speed (m/s) and contact time were recorded for all steps and association between speed and other variables was examined using a nonparametric Spearman *rho* correlation. A nonparametric Mann–Whitney *U*-test was used for all pairwise comparisons.

Results

Table 1 summarizes the data for speed, contact time, and peak vertical force of both forelimb and hindlimb. All three subjects examined in this study consistently used DS walking gaits for all steps examined (Fig. 2). Subjects walked at an average speed of 0.73 m/s (Table 1). These speed values are slightly lower than those reported for *Loris* by Demes et al. (1990) and higher than those of Ishida et al. (1990) for *Nycticebus*. In this study, peak vertical forces (V_{pk}) on both forelimb and hindlimb were not correlated with speed. The absence of correlation between speed and V_{pk} is probably due to our small sample size or because slender lorises tend to increase speed by increasing stride length rather than stride frequency (Demes et al., 1990). Other studies with a larger speed range have shown that speed and peak forces on the limbs are correlated in primates (Demes et al., 1994).

Table 1
Speed, contact time, and peak vertical force (V_{pk}) for the forelimb (FL) and hindlimb (HL) of *Loris tardigradus* during quadrupedal walking[a]

	Speed (m/s)	Contact time (s)	V_{pk} (N)	V_{pk} (% BW)
FL (N = 12)	0.735 (0.21)	0.317 (0.22)	1.547 (0.11)	88.2 (4.4)
HL (N = 22)	0.736 (0.23)	0.280 (0.14)	1.278 (0.18)	71.5 (11.0)

[a] Mean and one standard deviation (in parentheses).

On average and at equivalent speeds, FL V_{pk} was consistently and significantly higher than HL V_{pk} in slender lorises ($P < 0.05$) (Fig. 3; Table 1). Forelimb and hindlimb V_{pk} values, expressed as a percentage of body weight, were somewhat higher than those reported for *Nycticebus* (Ishida et al., 1990). This difference is probably due to the higher speeds adopted by our animal subjects. Contact times between the forelimb and hindlimb were not significantly different. However, forelimb contact time was on average slightly higher than hindlimb contact time (0.317 s vs. 0.28 s) (Table 1). These contact times are consistent with the findings of previous studies, although slightly higher forelimb contact times were reported in both *Loris* and *Nycticebus* (Demes et al., 1990; Ishida et al., 1990).

Table 2 summarizes kinematic data for all three loris subjects. Both forelimbs and hindlimbs landed on the pole in a protracted position. Still, the average protraction angle (larger values indicate greater protraction) of the thigh at the hip joint was significantly higher ($P < 0.01$) than that of the arm at the shoulder joint (Table 2). Total protraction of the forelimb and hindlimb were not significantly different, mainly because the knee joint was more flexed at touchdown than the elbow joint. The same was true for total excursion of the forelimb and hindlimb (Table 2). Elbow yield was significantly higher compared to knee yield (36.3° vs. 8.4°) ($P < 0.01$).

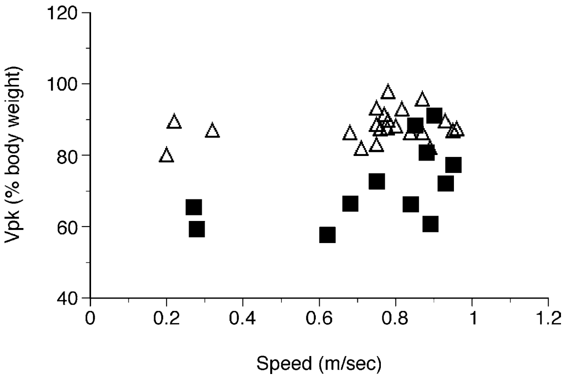

Fig. 3. Bivariate plot of speed (m/s) against peak vertical force (V_{pk}) expressed as a percentage of body weight in *Loris tardigradus*. Open triangles indicate forelimb V_{pk} values and solid squares hindlimb V_{pk} values.

Table 2
Kinematic variables of the forelimb and hindlimb during quadrupedal walking in *Loris tardigradus*, lorisids, and primates. All kinematic variables are angular values in degrees (°) and measured at limb touchdown[a]

Kinematic variable	This study	Lorisids[b,c,d]	*Loris*[e]	*Nycticebus*[e]	Primates[b,c,d]
Arm protraction	108.7 (9.7)	124.6	—	—	118
Thigh protraction	170.2 (3.2)	143	—	—	136.7
Elbow angle	128 (10.3)	135.4	—	—	144.5
Knee angle	109.6 (7.4)	108.4	—	—	140.0
Total forelimb protraction	139.1 (3.3)	129.6	—	—	124.7
Total hindlimb protraction	133.3 (6.0)	115	—	—	113.8
Forelimb excursion	90.9 (5.0)	83.9	100	92	72.1
Hindlimb excursion	89.3 (11.4)	70	81	77	63.4
Elbow yield	36.3 (12.7)	33.6	—	—	22.6
Knee yield	8.4 (3.7)	7.1	—	—	22.0

[a] Mean and one standard deviation (in parentheses). Limb angle mean values from Larson et al. (2000, 2001) and Larney and Larson (in press) have been modified to make them comparable to our values. In those studies, limb angles were taken relative to a vertical line. All limb angles were recalculated relative to a horizontal line (see Fig. 2). Thigh and total hindlimb protraction angles were also recalculated to make them comparable to arm and total forelimb protraction angles (see text for further details). For all protraction angles, higher values indicate greater protraction.

[b] Larson et al. (2000).

[c] Larson et al. (2001).

[d] Larney and Larson (in press).

[e] Demes et al. (1990).

Our kinematic data for *Loris tardigradus* were consistent with those reported by Demes et al. (1990) for *Loris* and those reported by Larson et al. (2000, 2001) and Larney and Larson (in press) for lorisids (see Table 2). Still, there were some slight differences. Our average arm protraction value was lower than that reported by Larson et al. (2000) for primates (all species pooled) and lorisids (four species pooled). Moreover, our average thigh protraction value was higher than that reported by Larson et al. (2001) for primates (all species pooled) and lorisids (four species pooled). Consequently, total limb protraction and excursion were also different from these pooled samples. No data for *Loris* alone is provided in Larson et al. (2000, 2001).

Discussion

The primary goal of this study was to test the hypothesis that specific patterns of footfalls and peak vertical forces on the limbs must co-occur. We predicted, based on previous studies (Demes et al., 1990; Schmitt and Lemelin, 2002; Schmitt, 2003b), that LS walking gaits and relatively higher peak vertical forces on the forelimbs would occur together and the reverse force pattern would be found with DS walking gaits.

This is clearly not the case in the slender loris (*Loris tardigradus*). In this study, all subjects used DS walking gaits exclusively. This is contrary to the observation that lorisids frequently use LS walking gaits (Hildebrand, 1967; Dykyj, 1980) and confirms similar findings from other studies (Glassman and Wells, 1984; Demes et al., 1990; Ishida et al., 1990). In the slender loris, diagonal-sequence footfall patterns are associated with a mean peak vertical force ratio (V_{pk} FL/V_{pk} HL) of 1.39. This mean force value is well above the primate average of 0.79 and is identical to the average of 1.39 found in nonprimate mammals (based on values published in Demes et al., 1994). Our force data are also consistent with previous data reported by Nieschalk (1991) for *Loris* and by Ishida et al. (1990) for *Nycticebus*.

This peculiar force ratio observed in *Loris* cannot be explained simply by an overall lowering of peak vertical forces on the limbs that is more pronounced on the hindlimbs compared to the forelimbs. Indeed, although the ratio of forelimb to hindlimb forces is different in *Loris* compared to other primates, the absolute peak vertical forces (as percentages of body weight) we recorded on individual forelimbs and hindlimbs of the slender loris are not substantially different from those found in other primates and woolly opossums (Kimura et al., 1979; Kimura, 1985, 1992; Reynolds, 1985b; Ishida et al., 1990; Demes et al., 1994; Schmitt, 1998, 1999, 2003b,c; Schmitt and Lemelin, 2002).

Our kinematic and kinetic data on the slender loris do not support the notion that a specific footfall pattern is necessarily associated with a specific pattern of force distribution on the limbs. In other words, DS walking gaits and lower FL/HL peak vertical force ratios are not necessarily correlated, even if this is the case for most primates and woolly opossums. Nevertheless, it should be emphasized that a lack of association in one primate taxon does not preclude the hypothesis that DS walking gaits and relatively lower forelimb V_{pk} represent important mechanical adaptations for locomotion on thin branches. Instead, data on slender lorises suggest that the three locomotor features typical of primate quadrupedal walking could have originated independently rather than as a suite in the earliest primates.

It is quite clear that the locomotor mechanics of *Loris tardigradus* are different from that of other primates. It is not unusual for some primates to have nearly equal forelimb and hindlimb peak vertical forces when walking on the ground [i.e., *Macaca fuscata* (Kimura et al., 1979); *Papio anubis* (Kimura et al., 1979; Schmitt and Hanna, 2004); *Erythrocebus patas* (Reynolds, 1985b; Polk, 2001, 2002; Schmitt and Hanna, 2004); *Chlorocebus aethiops* (Polk, 2001, 2002)]. However, lorises are highly unusual among primates in having such a high FL/HL peak vertical force ratio. The only other primate known to exhibit such a high force ratio on the limbs is the common marmoset (*Callithrix jacchus*), which, unlike slender lorises, relies mostly on lateral-sequence walking gaits and spends more of its time on large tree trunks (Schmitt, 2003b).

In order to better understand the unusual locomotor mechanics of *Loris tardigradus*, we also examined the mechanism by which peak vertical forces are moderated and distributed on the limbs. Two biomechanical models have been advanced to explain how primates maintain relatively higher peak vertical forces on their hindlimbs. The first model, proposed by Reynolds (1985a,b, 1987), suggests that primates actively shift weight posteriorly on their relatively protracted hindlimbs using powerful muscular retractors of the hindlimb. This model argues that low FL/HL V_{pk} ratios are associated with high degrees of hindlimb protraction (Reynolds, 1985a,b, 1987). The second model, proposed by Schmitt (1998, 1999) and recently tested by Larney and Larson (in press) for a large mammal sample, argues that primates change vertical stiffness of their limbs by increasing limb yield, contact time, and angular excursion. In this case, lower FL/HL V_{pk} ratios will be associated with higher degrees of forelimb joint yield and longer forelimb contact times. These models are not mutually exclusive and both provide important mechanisms by which locomotor forces on the limbs can be moderated.

In the case of the slender loris, the expectations of the posterior weight-shift and compliance models are reversed. If the posterior weight-shift model is correct, then the hindlimb of *Loris* should be much less protracted compared to that other primates. As the results in Table 2 indicate, total hindlimb protraction (larger values indicate greater protraction) is not significantly less than that of the forelimb in *Loris*, nor is total hindlimb protraction of *Loris* (133.3°) lower than that of other primates (113.8°) (Demes et al., 1990; Larson et al., 2001).

Similarly, if an increase in limb yield (i.e., compliance) is necessary for maintaining lower FL/HL V_{pk} ratios, then higher knee yield and hindlimb contact time should be expected in the slender loris. This prediction is also not supported. As noted by Larney and Larson (in press) and confirmed here, *Loris* is characterized by high degrees of elbow yield. However, our study and that of Larney and Larson (in press) show that knee yield is trivial compared to elbow yield. Moreover, hindlimb contact time is not significantly higher compared to forelimb contact time, nor is hindlimb angular excursion significantly greater than forelimb angular excursion (Table 2).

Clearly, biomechanical models proposed by Reynolds (1985a,b, 1987) and Schmitt (1995, 1998, 1999) cannot account for the unusual force ratio observed in the limbs of slender lorises. Moreover, it is possible that both models may not apply across the board for all primates.

The unusual weight distribution pattern observed on the limbs of *Loris tardigradus* during quadrupedal walking might be explained by differences in the placement of the center of gravity compared to other primates. Recently, Lemelin and Schmitt (2004) found that a caudal shift in the center of mass associated with seasonal accumulation of fat in the tail region of *Cheirogaleus medius* accentuates V_{pk} on the hindlimbs. Because of its very reduced tail and relatively slight hindquarters, it is possible that the slender loris may have a center of gravity positioned more anteriorly. However, Vilensky and Larson (1989) presented some evidence that the center of mass is not positioned more posteriorly in primates compared to other mammals. In addition, some macaques with reduced tails and chimpanzees with no external tail and massive forequarters all have lower FL/HL V_{pk} ratios compared to lorises, suggesting that primates actively regulate weight distribution (Schmitt, 2003b). Therefore, differences in the position of the center of gravity cannot explain the force distribution pattern found in primates.

Why, then, are the locomotor mechanics of the slender loris so different from that of most other primates? It is generally argued that reduced forelimb peak vertical forces are associated with a functional differentiation of the forelimbs and hindlimbs in primates (Kimura et al., 1979; Reynolds, 1985a,b; Schmitt, 1995, 1998, 1999, 2003a,b,c; Larson, 1998; Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2004; Schmitt and Hanna, 2004). Under this paradigm, reduction of peak forces is seen as facilitating the evolution of the forelimbs for manipulation and grasping, while the hindlimbs retained a primary role for weight-bearing functions. Lorises may represent an exception to this paradigm, probably because of their highly derived locomotor behavior and postcranial anatomy. When moving, lorises are characterized by slow and cautious quadrupedalism (Walker, 1979). As part of these peculiar locomotor adaptations, lorises have manual and pedal ray proportions that are more similar to one another than those of other prosimians (Lemelin, 1996). In other words, the hands and feet of lorises show far less morphological differentiation compared to other prosimians (see also Jouffroy and Lessertisseur, 1979). This lack of morphological differentiation is also found in the cross-sectional geometry of the long bones of lorises (Demes and Jungers, 1989, 1993; Runestad, 1997). The humerus and femur of *Nycticebus* and *Loris* show similar degrees of cortical thickness (i.e., *K*-values), unlike those of most other prosimian primates that show greater differentiation (Demes and Jungers, 1989, 1993). Thus, lorises may have no need to “spare” one limb over the other. Like marmosets (Schmitt, 2003b), lorises may simply not actively shift weight posteriorly or change limb stiffness in the manner of other primates.

Summary

It has often been argued that the diagonal-sequence (DS) walking gaits of primates are associated with lower peak vertical forces on the forelimbs relative to the hindlimbs (Demes et al., 1990; Schmitt and Lemelin, 2002; Schmitt, 2003b). The kinematic and kinetic data presented here show that that is not the case in the slender loris (*Loris tardigradus*). All three subjects examined in this study consistently used DS walking gaits, but were characterized by higher peak vertical forces on their forelimbs relative to their hindlimbs. The lack of a functional link between DS walking gaits and relatively lower peak vertical forces on the forelimbs of the slender loris—unlike other primates—suggests that these locomotor features could have evolved independently in ancestral primates and their adaptive value for fine-branch locomotion may be evaluated separately. In addition, the unusual kinetic pattern observed in *Loris* cannot be explained by current biomechanical models of forelimb force reduction (i.e., active weight shifting and limb compliance). Unlike other primates, it appears that *Loris tardigradus* does not actively reduce forelimb peak vertical forces, probably because of the lack of functional differentiation between forelimbs and hindlimbs.

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