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RESEARCH ARTICLE

Gait kinetics of above- and below-branch quadrupedal locomotion in lemurid primates

Michael C. Granatosky*, Cameron H. Tripp and Daniel Schmitt

ABSTRACT

For primates and other mammals moving on relatively thin branches, the ability to effectively adopt both above- and below-branch locomotion is seen as critical for successful arboreal locomotion, and has been considered an important step prior to the evolution of specialized suspensory locomotion within our Order. Yet, little information exists on the ways in which limb mechanics change when animals shift from above- to below-branch quadrupedal locomotion. This study tested the hypothesis that vertical force magnitude and distribution do not vary between locomotor modes, but that the propulsive and braking roles of the forelimb change when animals shift from above- to below-branch quadrupedal locomotion. We collected kinetic data on two lemur species (*Varecia variegata* and *Lemur catta*) walking above and below an instrumented arboreal runway. Values for peak vertical, braking and propulsive forces as well as horizontal impulses were collected for each limb. When walking below branch, both species demonstrated a significant shift in limb kinetics compared with above-branch movement. The forelimb became both the primary weight-bearing limb and propulsive organ, while the hindlimb reduced its weight-bearing role and became the primary braking limb. This shift in force distribution represents a shift toward mechanics associated with bimanual suspensory locomotion, a locomotor mode unusual to primates and central to human evolution. The ability to make this change is not accompanied by significant anatomical changes, and thus likely represents an underlying mechanical flexibility present in most primates.

KEY WORDS: Biomechanics, Brachiation, Evolution, Mechanical flexibility, Suspensory locomotion

INTRODUCTION

The ability to change locomotor modes by adjusting gait and/or posture is key to movement and foraging success in a complex three-dimensional arboreal environment (Blanchard and Crompton, 2011; Fleagle, 2013; Schmitt and Lemelin, 2002). One remarkable form of locomotor mode switching is the ability of an animal to drop below an arboreal support and adopt suspensory locomotion – any form of forward progression in which the body's center of mass (COM) lies below the point of contact (Stern and Oxnard, 1973). Suspensory locomotion has evolved in at least eight clades of extant mammals (Fujiwara et al., 2011), but primates are particularly adept at this form of locomotion (Table S1) and have an exceptional ability to quickly and seamlessly move between above- and below-branch locomotion when compared with other arboreal mammals. Currently, little information exists on how primates are

so readily able to adopt suspensory locomotion. In this study, we explored the kinetics of two closely related, yet behaviorally distinct primate species during above- and below-branch locomotion and tested specific hypotheses about the ways in which primates adjust their limb mechanics to below-branch movement.

While numerous studies have focused on the mechanics of highly specialized forms of suspensory locomotion such as brachiation and arm swinging (Chang et al., 2000; Michilsens et al., 2010, 2011; Swartz, 1989; Swartz et al., 1989; Turnquist et al., 1999), relatively few have explored the mechanics of below-branch quadrupedal locomotion (Ishida et al., 1990; Nyakatura, 2012; Nyakatura and Fischer, 2010; Nyakatura et al., 2010). Below-branch quadrupedal locomotion is a form of suspensory positional behavior that involves all four limbs, and superficially resembles the kinematics and timing of above-branch walking (Ishida et al., 1990; Jouffroy and Petter, 1990; Jouffroy and Stern, 1990; Nyakatura et al., 2010; Parsons and Taylor, 1977). It has been noted that there are a number of anatomical features shared between animals that commonly adopt below-branch quadrupedal locomotion and those that adopt specialized forms of suspensory locomotion such as brachiation and arm swinging (Cartmill and Milton, 1977; Mendel, 1979; Turnquist, 1975). This has led some authors (Cartmill and Milton, 1977; Mendel, 1979) to suggest that the ability to adopt below-branch quadrupedal locomotion may have been an important component during the transition from above-branch quadrupedal locomotion to specialized forms of suspensory locomotion that evolved independently in certain primate lineages. But no studies have explored the mechanical similarities and differences between below-branch quadrupedalism and bimanual suspensory locomotion. Understanding the mechanics of below-branch quadrupedal locomotion may help resolve debates about the evolution of arm swinging.

There are two general, not mutually exclusive, theories to explain why animals adopt suspensory positional behaviors. The first connects the use of suspensory behaviors to increased food acquisition (Grand, 1972). By being able to move below branches using suspensory behaviors, animals are thought to be able to more fully exploit all of the available resources. For example, suspensory primates can access fruit and leaves hanging below branches and increase foraging reach by hanging with one hand and reaching with the other. The second theory attributes a shift to below-branch movement to constraints of balancing on branches; as the body size to support diameter ratio increases, the ability to remain balanced above the support becomes more difficult (Cartmill, 1985; Napier, 1967). One solution is for arboreal animals to move below branches and adopt suspensory positional behaviors (Cartmill, 1985; Mendel, 1981; Napier, 1967). While these strategies may solve problems of balance and food acquisition, individuals moving from above- to below-branch quadrupedal locomotion experience a novel biomechanical environment and may need to adjust locomotor behavior in order

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List of symbols and abbreviations

COM	center of mass
$\mathbf{f}_{B,peak}$	peak braking force
$\mathbf{f}_{P,peak}$	peak propulsive force
$\mathbf{f}_{V,peak}$	peak vertical force
PI	propulsive impulse
BI	braking impulse
HI	horizontal impulse
%bw	percentage of body weight
%bws	percentage of body weight seconds

to effectively move below the support (Ishida et al., 1990; Jouffroy and Stern, 1990; Stern, 1975; Swartz et al., 1989).

Despite the importance of below-branch movement in primates and in several other specialized orders of mammals (i.e. sloths, bats, kinkajous), few studies (Fujiwara et al., 2011; Ishida et al., 1990; Jouffroy and Petter, 1990; Jouffroy and Stern, 1990; Mendel, 1981; Nyakatura, 2012; Nyakatura and Fischer, 2010; Nyakatura et al., 2010; Parsons and Taylor, 1977; Turnquist, 1975) have specifically focused on the mechanics of below-branch quadrupedal locomotion in mammals, and of those only one has measured substrate reaction forces (Ishida et al., 1990). Ishida et al. (1990) collected multiaxial force data from freely moving slow lorises (*Nycticebus coucang*) on an upright and inverted instrumented runway. From these data, Ishida et al. (1990) determined that (1) peak vertical force ($\mathbf{f}_{V,peak}$) magnitude and distribution between forelimbs and hindlimbs did not change between above- and below-branch quadrupedal locomotion; (2) during above-branch quadrupedal locomotion, animals exerted relatively greater peak propulsive ($\mathbf{f}_{P,peak}$) forces in the hindlimbs than in the forelimbs, and this pattern was reversed during below-branch quadrupedal locomotion; (3) during above-branch quadrupedal locomotion, animals exerted relatively lower peak braking ($\mathbf{f}_{B,peak}$) forces in the hindlimbs than in the forelimbs, and this pattern was reversed during below-branch quadrupedal locomotion; (4) during above-branch quadrupedal locomotion, the limb (forelimb or hindlimb) first applied a braking force to the substrate during the first portion of the support phase, followed by a propulsive force throughout the remainder of the support phase, and this pattern was reversed during below-branch quadrupedal locomotion; and (5) during above-branch quadrupedal locomotion, animals generated a net braking force [i.e. braking impulse (BI) > propulsive impulse (PI) = net negative horizontal impulse (HI)] in the forelimbs and a net propulsive force (i.e. net positive HI) in the hindlimbs, and this pattern was reversed during below-branch quadrupedal locomotion. Together, these findings indicate that movements during below-branch quadrupedal locomotion might be effectively modeled as a simple pendulum system (but see Nyakatura and Andrada, 2013), in which the forelimbs act as the primary propulsive limb, and the hindlimbs serve a minor braking role acting to decelerate the body's forward-moving COM.

While Ishida et al. (1990) laid the groundwork for interpretation of the kinetics of below-branch quadrupedal locomotion, their use of the slow loris may constrain the broad applicability of these data to understanding the mechanical behavior of more generalized primates. As a group, the lorisids have a highly derived postcranial anatomy specialized for slow and cautious quadrupedalism (Cartmill and Milton, 1977; Schmitt and Lemelin, 2004). Additionally, lorises exhibit a number of unusual gait patterns including the variable use of diagonal and lateral sequence gaits (Ishida et al., 1990; Schmitt and Lemelin, 2004). More pertinent to

the present study, during above-branch quadrupedal walking, lorises have a higher $\mathbf{f}_{V,peak}$ on their forelimb compared with the hindlimb (Ishida et al., 1990; Schmitt and Lemelin, 2004), a pattern common to non-primate mammals but not found in most other primates, which have the reverse pattern (Demes et al., 1994; Kimura et al., 1979; Reynolds, 1985a; Schmitt and Lemelin, 2002). This unusual $\mathbf{f}_{V,peak}$ ratio observed in most primates is thought to be a mechanism to reduce high substrate reaction forces on highly mobile and weak shoulder joints (Reynolds, 1985a). The combination of derived anatomy and specialized gait characteristics potentially makes the slow loris a poor model for understanding the mechanisms by which generalized primates manage to switch effectively from above- to below-branch quadrupedal locomotion.

The goal of this study was to examine limb-loading behavior of two quadrupedal primates, *Varecia variegata* Kerr 1792 (a committed arboreal quadruped that commonly adopts suspensory positional behaviors; Gebo, 1987; Meldrum et al., 1997) and *Lemur catta* Linnaeus 1758 (the most terrestrial of all the lemurs that moves mostly quadrupedally or by leaping, and that rarely adopts suspensory positional behaviors; Gebo, 1987) during above- and below-branch quadrupedal walking in order to determine patterns and mechanisms used by generalized primates when adopting suspensory locomotion. Based on data collected by Ishida et al. (1990) and studies on the kinetics of generalized primate locomotion (Chang et al., 2000; Demes et al., 1994; Franz et al., 2005; Kimura et al., 1979; Reynolds, 1985a,b; Schmitt and Lemelin, 2002), we developed the following predictions.

(1) The absolute magnitude of $\mathbf{f}_{V,peak}$ forces will not differ significantly between above- and below-branch quadrupedal locomotion and primates will display relatively greater $\mathbf{f}_{V,peak}$ in the hindlimbs compared with the forelimbs during movement in both orientations. This prediction is based on the assumption that weight distribution has no reason to change when orientation changes. This is largely because we have no definitive answer to what mechanism drives this difference in the first place (see Demes et al., 1994; Franz et al., 2005; Kimura et al., 1979; Raichlen et al., 2009; Reynolds, 1985a,b; Schmitt and Lemelin, 2002; Young, 2012). But the data here can serve to test some of those models if there is a change in $\mathbf{f}_{V,peak}$ patterns.

(2) During above-branch quadrupedal locomotion, the limb (forelimb or hindlimb) will first apply a braking force to the substrate as it touches down that will decelerate the animal's COM followed by a propulsive force prior to lift-off that will accelerate the animal's COM, and this pattern will be reversed during below-branch quadrupedal locomotion. This prediction is based on observations of force patterns during above-branch locomotion in many primates (Demes et al., 1994; Franz et al., 2005; Ishida et al., 1990; Kimura et al., 1979) and below-branch movement in lorises (Ishida et al., 1990) and arm-swinging primates (Chang et al., 2000). The remaining predictions below derive from the same studies.

(3) During above-branch quadrupedal locomotion, both species will exert relatively greater $\mathbf{f}_{P,peak}$ and lower $\mathbf{f}_{B,peak}$ in the hindlimbs compared with the forelimbs, and this pattern will be reversed during below-branch quadrupedal locomotion.

(4) During above-branch quadrupedal locomotion, both species will generate a net negative HI in the forelimbs and a net positive HI in the hindlimbs, and this pattern will reverse during below-branch quadrupedal locomotion.

(5) Despite differences in the relative amount of arboreal locomotion present in the locomotor repertoires of *V. variegata*

and *L. catta*, both animals will display similar kinetic patterns when switching between above- and below-branch quadrupedal locomotion.

MATERIALS AND METHODS

Kinetic gait data were collected from *V. variegata* and *L. catta* at the Duke Lemur Center (Durham, NC, USA) following the protocols approved by the Duke Lemur Center (DLC Research Project no. MO-10-11-3) and Duke's Institutional Animal Care and Use Committee (IACUC protocol no. A270-11-10). All animals were adults and were clear of any pathologies or gait abnormalities (Table 1). The methods used here have been described extensively elsewhere (Schmitt, 2003; Schmitt and Lemelin, 2002), and will only be summarized below.

Forelimb and hindlimb forces were collected while animals walked above and below an instrumented runway measuring 3.66 m in length and 3.10 cm in diameter (Fig. S1). The instrumented portion of the runway consisted of two Kistler force plates (model 9317B) that have been used in previous studies (Bishop et al., 2008). A small section of dowel was secured on one end of each force plate measuring the same diameter as the rest of the runway and large enough to accommodate an entire hand or foot (∼10 cm). These instrumented sections were mounted in the middle of the runway flush with, but separated by a small gap from, the rest of the runway. Force plate output was sampled at 12,000 Hz, and imported, summed and processed using BioWare™ v5.1 software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB. From these data, six variables were calculated for each limb: (1) $\mathbf{f}_{V,peak}$, (2) $\mathbf{f}_{P,peak}$, (3) $\mathbf{f}_{B,peak}$, (4) PI, (5) BI and (6) HI. The HI provides a means for differentiating the overall braking or propulsive role of the limb during particular locomotor behaviors (Demes et al., 1994) and was measured as the area under the force–time curve in the horizontal component of the substrate reaction force. The overall HI for each limb was calculated by subtracting the BI from the PI; positive values indicate a net propulsive limb while negative values indicate a net braking limb (Demes et al., 1994; Ishida et al., 1990; Kimura et al., 1979).

Prior to all trials, animals were weighed and forces for each day of trials were normalized to the weight recorded for that day. The animals were videotaped during trials within a clear plastic enclosure from a lateral view

using a GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA, USA) modified with a Back-Bone Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON, Canada), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera (Fig. S2). All videos were recorded at 120 fields s^{-1}. For each step, the subject's velocity was calculated by digitizing a point on the subject's head and determining the time necessary to cross a known distance marked on the runway. Only walking steps (i.e. duty factor over 50%) in which the animal was traveling in a straight path and not accelerating or decelerating (i.e. steady-state locomotion) were selected for analysis. Steady-state locomotion was determined by calculating the instantaneous velocity between subsequent video frames throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride. Only strides in which no change in velocity was detected were used for subsequent analyses. Additionally, only steps with single-limb contacts on the plate or those steps in which the forelimb and hindlimb forces were clearly differentiated were analyzed.

In order to make statistical comparisons between subjects of differing body masses, $\mathbf{f}_{V,peak}$, $\mathbf{f}_{P,peak}$ and $\mathbf{f}_{B,peak}$ are given as a percentage of body weight (%bw) and PI, BI and HI as a percentage of body weight seconds (bws). We used a Shapiro–Wilk and Levene's test to determine normality and equal variance within the data (Sokal and Rohlf, 2012). Prior to any statistical comparisons, body weight-normalized $\mathbf{f}_{V,peak}$, $\mathbf{f}_{P,peak}$ and $\mathbf{f}_{B,peak}$, and PI, BI and HI for above- and below-branch walking were compared with velocity and duty factor using a regression analysis to determine whether our variables of interest were influenced by variation in speed or duty factor within the sample. The magnitude of substrate reaction forces is thought to be influenced by speed (Demes et al., 1994) or duty factor (Alexander, 1984). In order to account for the effect of speed or duty factor, all data were examined using a non-parametric ANCOVA with velocity or duty factor as the covariate to compare across limbs (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with velocity, we used a Kruskal–Wallis test, a non-parametric ANOVA, to determine whether there were statistically significant differences across limbs. We analyzed each species separately, and only qualitative comparisons were made between species in order to confirm broad kinetic patterns. All *P*-values were Bonferroni adjusted to account for type I error resulting from multiple

Table 1. Animal subjects used in the study, and the number of steps analyzed for each individual

Species	Sex	Body mass (kg)	Date of birth (dd/mm/yyyy)	Orientation	Limb	No. of steps analyzed
Varecia variegata						
1	Male	3.3	24/05/2010	Above	Forelimb	12
					Hindlimb	10
				Below	Forelimb	24
					Hindlimb	20
2	Female	3.76	17/04/2005	Above	Forelimb	12
					Hindlimb	15
				Below	Forelimb	18
					Hindlimb	12
3	Female	3.7	31/05/2001	Above	Forelimb	21
					Hindlimb	13
				Below	Forelimb	3
					Hindlimb	2
Lemur catta						
1	Male	2.58	03/05/2010	Above	Forelimb	9
					Hindlimb	7
				Below	Forelimb	25
					Hindlimb	15
2	Female	2.1	16/05/2011	Above	Forelimb	9
					Hindlimb	8
				Below	Forelimb	18
					Hindlimb	16
3	Female	2.34	09/04/2012	Above	Forelimb	7
					Hindlimb	9
				Below	Forelimb	9
					Hindlimb	9

comparisons. All statistical tests were conducted using JMP Pro v11 (SAS Institute Inc., Cary, NC, USA).

RESULTS

In total, 303 single limb forces were collected and analyzed. Table 2 summarizes the number of steps collected per limb for each orientation, and data for velocity, duty factor, $f_{V,peak}$, $f_{P,peak}$, $f_{B,peak}$, PI, BI and HI. All data displayed a non-normal distribution and unequal variances; therefore, non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between $f_{V,peak}$ and velocity. No significant relationship between velocity and $f_{P,peak}$, $f_{B,peak}$ and HI was detected. No significant relationship was observed between duty factor and any of the variables of interest.

Both species displayed significantly different ($P \leq 0.001$) $f_{V,peak}$ between the forelimb and hindlimb during both above- and below-branch quadrupedal locomotion. Consistent with other data on the kinetics of primate walking (Demes et al., 1994; Kimura et al., 1979; Reynolds, 1985a), forelimb $f_{V,peak}$ was significantly ($P \leq 0.001$) lower than hindlimb $f_{V,peak}$ during above-branch quadrupedal locomotion. The opposite limb-loading pattern was observed during below-branch quadrupedal locomotion, in which forelimb $f_{V,peak}$ was significantly ($P \leq 0.001$) greater than hindlimb $f_{V,peak}$ (Figs 1–3).

During above-branch quadrupedal locomotion, a consistent limb-loading pattern was observed, in which as the limb (forelimb or hindlimb) touched down, it first applied a braking force to the substrate followed by a propulsive force prior to lift-off. This pattern is the norm for quadrupedal locomotion as it acts to decelerate and accelerate the COM during a stride (Demes et al., 1994; Kimura et al., 1979). In contrast, during below-branch quadrupedal locomotion, we observed that as the limb (forelimb or hindlimb) touched down, it first applied a propulsive force to the substrate followed by a braking force prior to lift-off. This pattern was consistent for both species (Figs 1, 2).

In addition, both species displayed significantly different ($P \leq 0.001$) $f_{P,peak}$ between the forelimbs and hindlimbs during above- and below-branch quadrupedal locomotion. Forelimb $f_{P,peak}$ was significantly ($P \leq 0.001$) lower than hindlimb $f_{P,peak}$ during above-branch quadrupedal locomotion, suggesting that the hindlimbs play a greater role in propulsion. The opposite limb-loading pattern was observed during below-branch quadrupedal locomotion, in which forelimb $f_{P,peak}$ was significantly ($P \leq 0.001$) greater than hindlimb $f_{P,peak}$ (Fig. 4). No significant differences were observed in $f_{B,peak}$ between the forelimbs and hindlimbs or between above- and below-branch quadrupedal walking, with the exception that *V. variegata* displayed significantly greater $f_{B,peak}$ in the forelimbs than the hindlimbs during above-branch quadrupedal locomotion (Fig. 5).
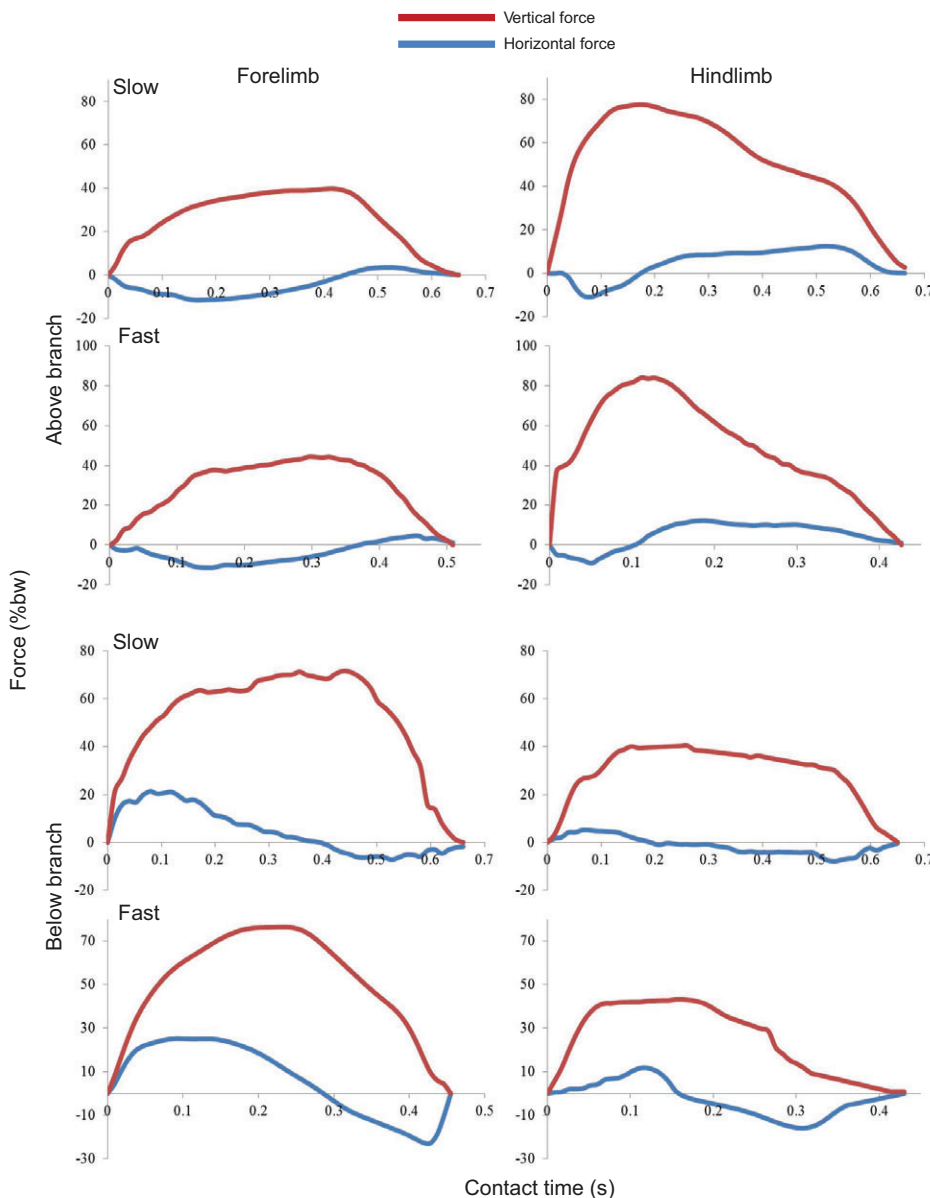
During above-branch quadrupedal walking, both species displayed a negative net HI in the forelimbs and a positive net HI in the hindlimbs, meaning that the forelimbs were net braking whereas the hindlimbs were net propulsive, a pattern consistent with previous studies (Demes et al., 1994; Ishida et al., 1990; Kimura et al., 1979). This pattern was reversed during below-branch quadrupedal locomotion, in which our animals displayed a positive net HI in the forelimbs and negative net HI in the hindlimbs (Fig. 6). Although no significant differences were observed between the propulsive magnitude of the hindlimb during above-branch quadrupedal locomotion and the forelimb during below-branch quadrupedal locomotion, and vice versa in respect to the braking

Table 2. Summary statistics for the kinetic variables analyzed in this study

Species	Orientation	Velocity (m s⁻¹)	Duty factor	Limb	N	$f_{V,peak}$ (%bw)	$f_{P,peak}$ (%bw)	$f_{B,peak}$ (%bw)	PI (%bws)	BI (%bws)	HI (%bws)
Varecia variegata	Above	0.81±0.17	0.57±0.04	Forelimb	45	57.38±7.30	5.74±2.36	19.52±5.57	0.46±0.56	−3.12±0.91	−2.66±0.91
			0.59±0.05	Hindlimb	38	77.68±8.85	11.60±4.83	11.60±4.83	2.82±0.94	−0.69±0.60	2.13±1.17
	Below	0.61±0.08	0.57±0.07	Forelimb	45	83.71±9.87	21.77±8.78	13.55±6.33	4.23±1.87	−1.87±1.09	2.35±2.12
			0.59±0.05	Hindlimb	34	66.82±11.14	9.36±4.67	11.01±5.20	0.89±0.65	−2.21±1.36	−1.32±1.44
Lemur catta	Above	0.57±0.15	0.59±0.04	Forelimb	25	45.19±5.11	4.66±2.38	10.88±4.42	0.62±0.52	−3.09±1.10	−2.47±1.08
			0.65±0.03	Hindlimb	24	80.26±9.97	11.00±3.31	7.55±2.77	4.22±1.87	−0.78±1.40	2.62±1.36
	Below	0.54±0.13	0.64±0.08	Forelimb	52	71.26±9.93	23.51±8.17	14.77±6.62	4.12±1.73	−1.63±1.04	2.49±2.20
			0.65±0.05	Hindlimb	40	41.37±7.43	10.63±4.96	12.82±6.97	0.95±0.82	−2.22±1.46	−1.27±1.46

$f_{V,peak}$, peak vertical force; $f_{P,peak}$, peak propulsive force; $f_{B,peak}$, peak braking force; PI, propulsive impulse; BI, braking impulse; HI, horizontal impulse; bw, body weight; bws, body weight seconds.
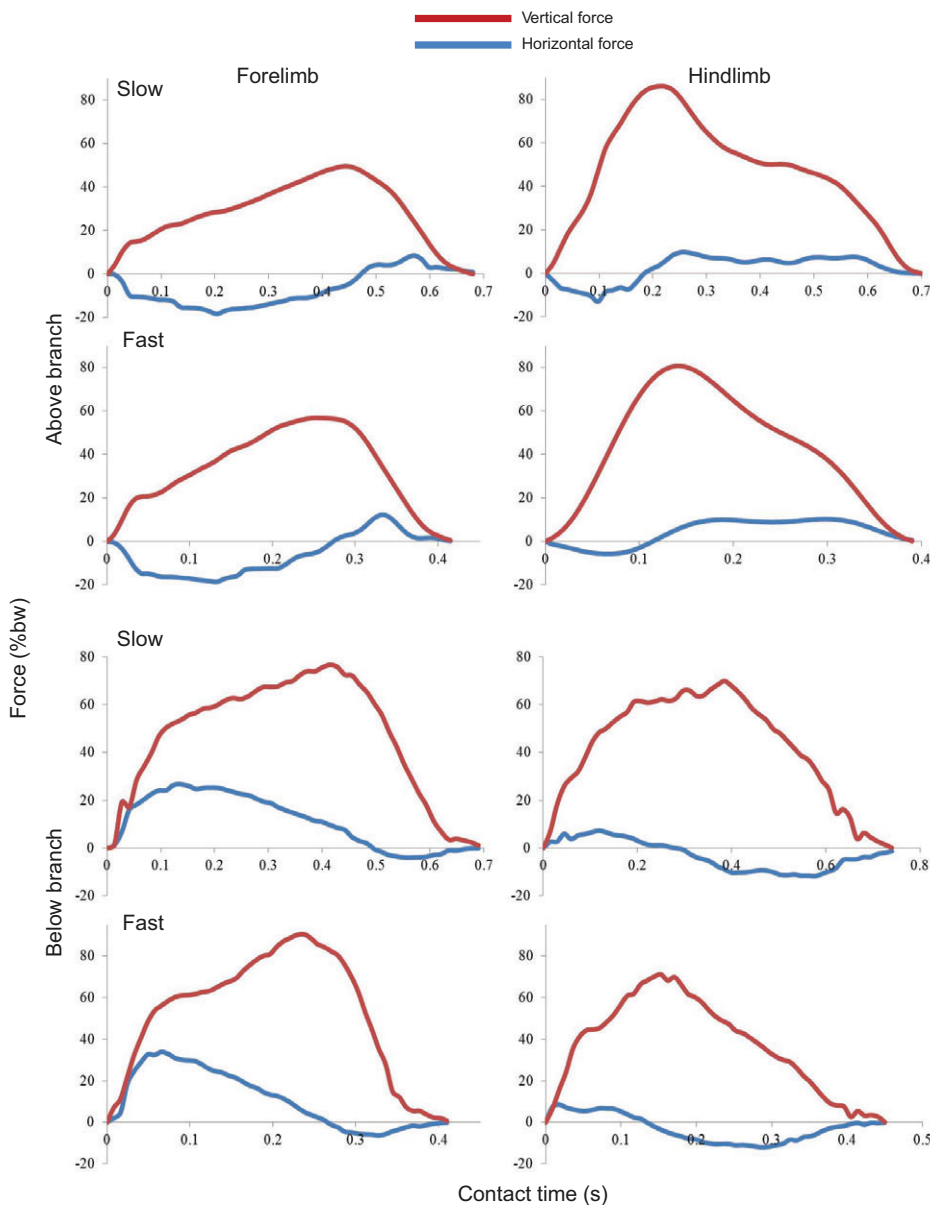
Fig. 1. Representative force traces for *Lemur catta* during above- and below-branch quadrupedal locomotion. All data are presented as a percentage of the animal's body weight (%bw) for the forelimb and hindlimb during slow and fast walking.

role, it should be noted that there did appear to be a generally greater input of net propulsive force during below-branch quadrupedal locomotion. This pattern is indicative of acceleration occurring throughout the stride. We attempted, as described in Materials and methods, to use only steady-state strides, but the presence of unbalanced propulsive forces in the forelimbs during below-branch quadrupedal locomotion would indicate that strides in which the animals were not moving at steady state are present within this study. Consequently, the reader should take note of this when interpreting the data.

An analysis of PI (Fig. 7) and BI (Fig. 8) separately for each limb showed that during above-branch quadrupedal walking, PI was significantly greater in the hindlimbs when compared with the forelimbs. The opposite pattern was observed during below-branch quadrupedal locomotion. With respect to BI, during above-branch quadrupedal locomotion, the forelimbs exerted significantly greater BI than the hindlimbs. In contrast, during below-branch quadrupedal locomotion, the hindlimbs tended to exert on average a relatively greater BI than the forelimbs, but this difference was not significant.

DISCUSSION

The primary goal of this study was to determine whether kinetic patterns used by two species of generalized arboreal primates remained the same or changed when individuals switched from above- to below-branch quadrupedal locomotion. During above-branch quadrupedal locomotion, the animals in this study showed kinetic patterns consistent with those reported for other primates (Demes et al., 1994; Franz et al., 2005; Kimura et al., 1979) including relatively higher hindlimb $f_{V,peak}$, and forelimbs that were net braking and hindlimbs that were net propulsive. Our data on above-branch quadrupedal locomotion in *V. variegata* and *L. catta* closely mirror the results of Franz et al. (2005), adding further evidence about the locomotor behavior of extant lemurids. Our data on below-branch quadrupedal locomotion were consistent with that of Ishida et al. (1990) but also deviated from the pattern they reported for lorises in key ways. In this sample of lemurs, $f_{B,peak}$ was always relatively greater in the forelimb and did not vary between above- and below-branch quadrupedal locomotion. Second, and more importantly, while our animals did exert greater $f_{V,peak}$ in the hindlimbs compared with the forelimbs during above-branch

Fig. 2. Representative force traces for *Varecia variegata* during above- and below-branch quadrupedal locomotion. All data are presented as a percentage of the animal's body weight (%bw) for the forelimb and hindlimb during slow and fast walking.

quadrupedal locomotion, both *V. variegata* and *L. catta* completely reversed this pattern during below-branch quadrupedal locomotion. It is likely that the lack of notable differences in $f_{V,peak}$ distribution patterns between above- and below-branch quadrupedal locomotion observed by Ishida et al. (1990) for *N. coucang* is a result of the unusual locomotor mechanics of the lorisids compared with other primates. We argue that lorisids did not shift the primary weight-bearing roles of the limbs during below-branch quadrupedal locomotion because these animals already demonstrate relatively higher $f_{V,peak}$ on the forelimbs during above-branch quadrupedal locomotion (Schmitt and Lemelin, 2004).

The findings from this study provide insight into how primates may accommodate limb-loading patterns to mechanically adjust to a new biomechanical environment. The primary kinetic changes that occur when *V. variegata* and *L. catta* switch from above- to below-branch quadrupedal locomotion can be summarized in two statements: during below-branch quadrupedal locomotion (1) the forelimb becomes the primary propulsive element, while the hindlimb serves a braking role, and (2) the forelimb serves as the primary weight-bearing limb, while the hindlimb reduces its weight-bearing function. These patterns were similar for our two study species, and appear to not be affected by the relative amount of time each species utilizes suspensory locomotor behaviors during their normal locomotor repertoires.

One aspect of this study that has been particularly problematic is that during below-branch quadrupedal locomotion the net propulsive forces generated by the forelimbs far exceed the counteracting braking forces of hindlimbs – a pattern indicative of acceleration occurring throughout the stride. We attempted to eliminate accelerating and decelerating steps from the study, but it is obvious that our method for doing so did not eliminate changes in velocity within and across complete strides. This represents a systematic error and a potential limitation of the study, and the reader should be aware of this pattern during the interpretation of our results.

The altered pattern of braking and propulsive forces of the limbs during below-branch quadrupedal locomotion was not entirely unexpected, and may be explained in part by pendular mechanics
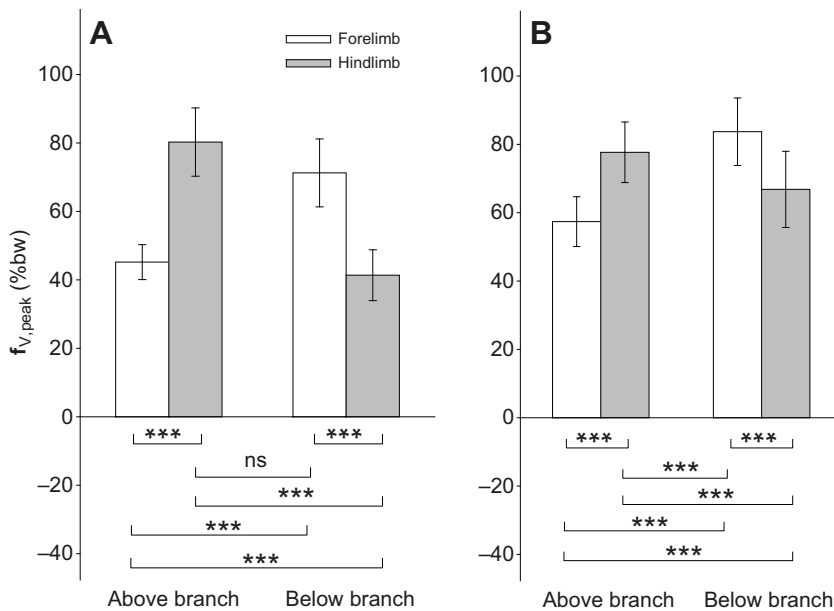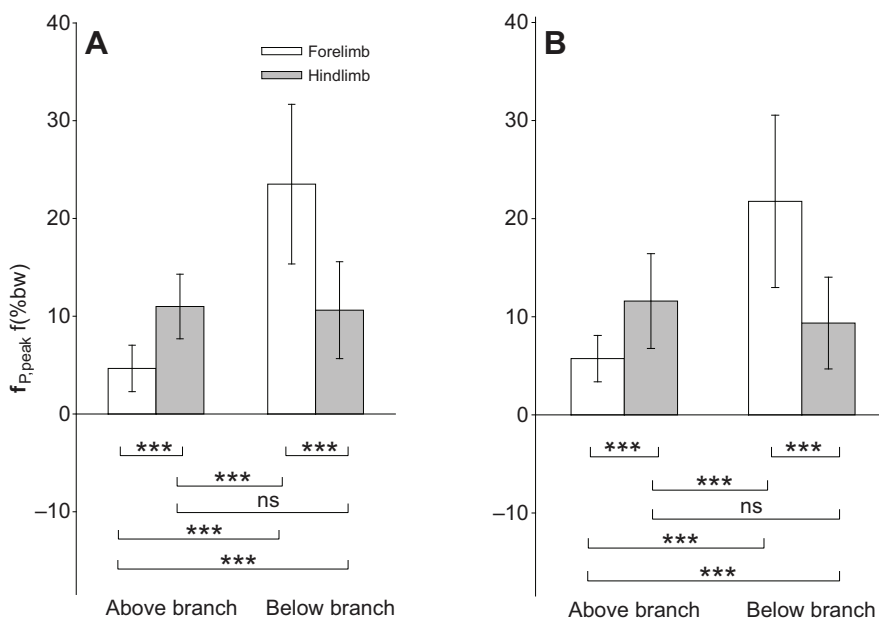
Fig. 3. Mean (±s.d.) peak vertical force (f$_{V,peak}$) in the forelimbs and hindlimbs. (A) *Lemur catta* (*N*=3 individuals and 141 steps). (B) *Varecia variegata* (*N*=3 individuals and 162 steps). All data are presented as a percentage of the animal's body weight (%bw). Asterisks indicate a significant difference (***P≤0.001). ns, no significant difference was observed.

(Chang et al., 2000). The pattern observed during below-branch quadrupedal locomotion may be similar, and animals may be governed by pendular mechanics (but see Nyakatura and Andrada, 2013), or some alternative mechanism related to control of body position and COM location below a support. This is an area of active exploration.

The altered role of the forelimbs as the primary weight-bearing limb during below-branch quadrupedal locomotion significantly deviates from the normal limb-loading pattern observed in primates (Demes et al., 1994; Franz et al., 2005; Kimura et al., 1979; Reynolds, 1985a; Schmitt and Lemelin, 2002). The standard limb-loading pattern observed in primates is thought to be an important mechanism to free the forelimbs from their normal weight-bearing role in locomotion, permitting the forelimbs to become highly manipulative and mobile grasping organs (Jones, 1916; Reynolds, 1985a; Schmitt and Lemelin, 2002). The mechanism for how this is

accomplished is still a matter of inquiry. There remains productive discussion as to whether this altered limb-loading pattern is an active process (Reynolds, 1985a,b, 1987; Schmitt, 1999), in which primates shift a cranially positioned COM caudally toward the hindlimbs, or a passive process, which is simply an unintentional byproduct of other aspects of normal primate locomotor patterns (Raichlen et al., 2009).

Primates, as a group, are characterized by a relatively greater amount of limb excursion during above-branch quadrupedal locomotion (Larson et al., 2000) that tends to place relatively protracted hindlimbs underneath the COM for longer periods of time than relatively retracted forelimbs (Raichlen et al., 2009). It has been argued that this pattern results in relatively greater hindlimb f$_{V,peak}$ simply because of the hindlimb's position in relation to the body's COM, though its importance was disputed by Larson and Demes (2011). It is unclear whether this mechanism, if it

Fig. 4. Mean (±s.d.) peak propulsive force (f$_{P,peak}$) in the forelimbs and hindlimbs. (A) *Lemur catta* (*N*=3 individuals and 141 steps). (B) *Varecia variegata* (*N*=3 individuals and 162 steps). All data are presented as a percentage of the animal's body weight (%bw). Asterisks indicate a significant difference (***P≤0.001). ns, no significant difference was observed.
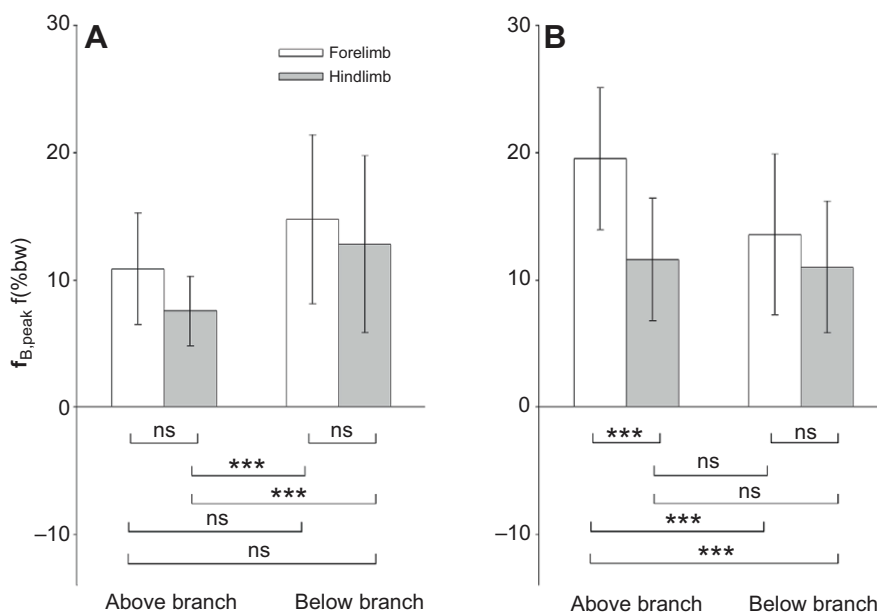
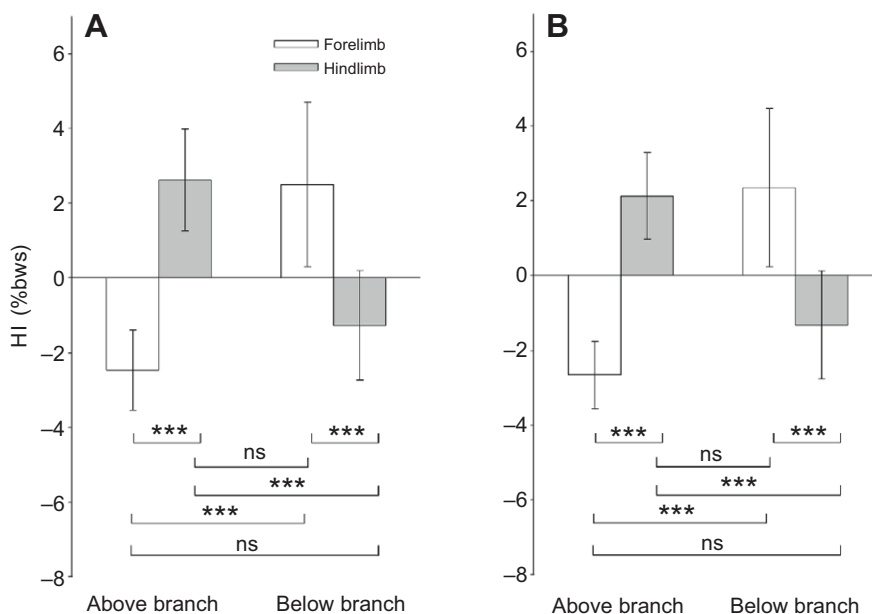**Fig. 5. Mean (±s.d.) braking peak force ($f_{B,peak}$) in the forelimbs and hindlimbs.** (A) *Lemur catta* (N=3 individuals and 141 steps). (B) *Varecia variegata* (N=3 individuals and 162 steps). All data are presented as a percentage of the animal's body weight (%bw). Asterisks indicate a significant difference (***$P \leq 0.001$). ns, no significant difference was observed.

is active during above-branch walking, is also at play during below-branch quadrupedal locomotion because the incorporation of kinematic data necessary to address this hypothesis was beyond the scope of this study.

In respect to the hypothesis that primates actively shift weight (have higher forces) to the hindlimbs, two biomechanical models have been proposed to explain how primates maintain relatively higher $f_{V,peak}$ on their hindlimbs. The first model, proposed by Reynolds (1985a,b, 1987) and supported by Larson and Stern (2009), suggests that primates actively shift weight caudally on their relatively protracted hindlimbs using powerful muscular retractors of the hindlimb. The second model, proposed by Schmitt (1998, 1999) and tested by Larney and Larson (2004), argues that primates change vertical stiffness of their limbs by increasing limb yield, contact time and angular excursion. These models are not mutually exclusive and both provide important mechanisms by which

locomotor forces on the limbs can be moderated (Schmitt and Hanna, 2004; Young, 2012).

While the aforementioned hypotheses may apply during above-branch quadrupedal locomotion, it is unlikely that these mechanisms are in play when walking below branches. Models of limb yield used to explain above-branch locomotor loading (Schmitt, 1999) may not apply in this context. Nor would Reynolds' (1985a,b, 1987) argument for the advantages of actively shifting weight caudally during above-branch quadrupedalism apply to below-branch quadrupedal locomotion because activation of hindlimb retractors as a mechanism to reduce $f_{V,peak}$ forces on the forelimbs would have the added effect of applying a braking force during the downward swing of the COM and pull the forequarters away from the support.

An additional mechanism to explain the higher $f_{V,peak}$ forces in the forelimbs compared with the hindlimbs may be found in kinematic movements during below-branch quadrupedalism.

Fig. 6. Mean (±s.d.) net horizontal impulse (HI) in the forelimbs and hindlimbs. (A) *Lemur catta* (N=3 individuals and 141 steps). (B) *Varecia variegata* (N=3 individuals and 162 steps). All data are presented as a percentage of body weight seconds (%bws). Asterisks indicate a significant difference (***$P \leq 0.001$). ns, no significant difference was observed. Positive values indicate a net propulsive limb while negative values indicate a net braking limb.
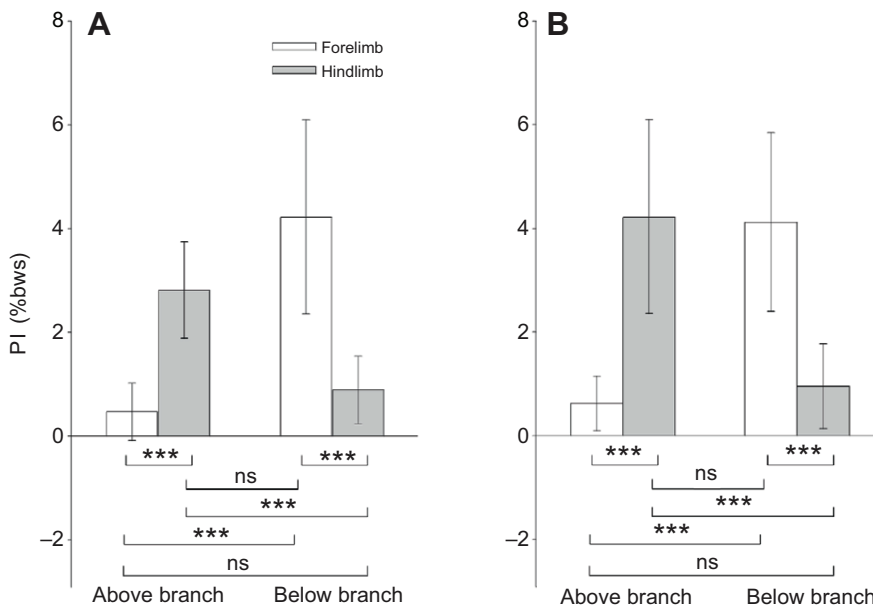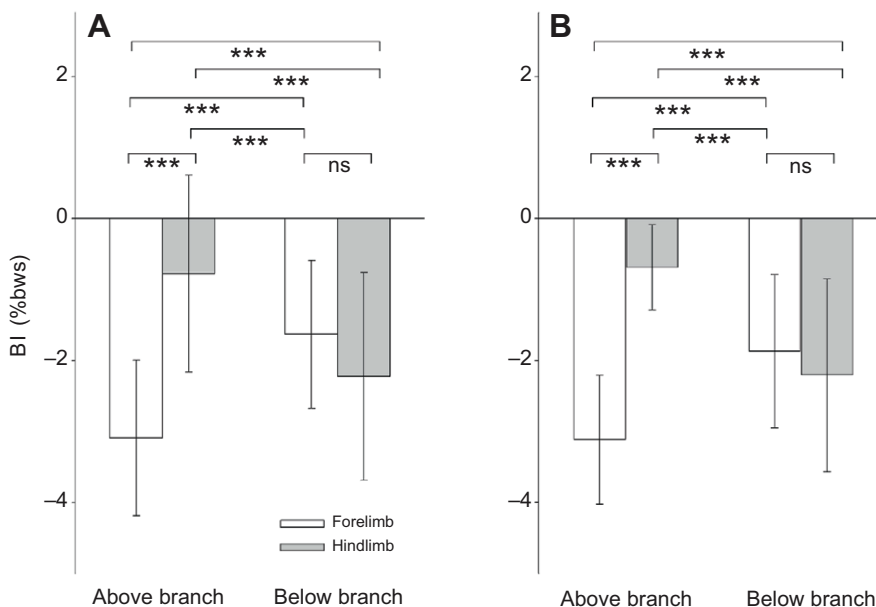
Fig. 7. Mean (±s.d.) propulsive impulse (PI) in the forelimbs and hindlimbs. (A) *Lemur catta* (*N*=3 individuals and 141 steps). (B) *Varecia variegata* (*N*=3 individuals and 162 steps). All data are presented as a percentage of body weight seconds (%bws). Asterisks indicate a significant difference (***$P \leq 0.001$). ns, no significant difference was observed.

Although the quantification of kinematic patterns during below-branch quadrupedal locomotion is beyond the scope of this study, other studies that have quantified patterns of kinematic movement during below-branch quadrupedal locomotion (Fujiwara et al., 2011; Ishida et al., 1990; Nyakatura et al., 2010; Turnquist, 1975) and brachiation (Bertram, 2004; Michilsens et al., 2011) provide compelling evidence for a potential mechanism that may explain the higher $f_{V,peak}$ in the forelimbs. Consistent across all kinematic studies of below-branch quadrupedal locomotion (Fujiwara et al., 2011; Ishida et al., 1990; Nyakatura et al., 2010; Turnquist, 1975), and some studies on brachiation (Bertram, 2004; Michilsens et al., 2011) is a tendency for animals to actively flex the forelimbs during the support phase. Data for hindlimbs during inverted quadrupedalism in sloths (Nyakatura et al., 2010) show that the hindlimbs maintain more extended positions throughout the stride. This forelimb flexion suggests that as the animals activate flexor musculature to 'pull-up' the COM toward the support during these

suspensory forms of locomotion, they subsequently create higher $f_{V,peak}$ forces on the substrate.

The capacity for animals to change between locomotor modes – altering gait, limb posture or body position – fluidly and efficiently is key to locomotor success in multiple settings. This ability seems especially important in a complex arboreal milieu occupied by many mammalian species (Blanchard and Crompton, 2011; Fleagle, 2013). In the trees, some animals have the ability to switch between above- and below-branch movement, and primates seem particularly adept at this behavior compared with other mammals (Table S1; but see Fujiwara et al., 2011). The idea that primates have a well-developed capacity for adjusting aspects of gait in order to effectively adjust to particular environmental circumstances is not new (Nyakatura et al., 2008; Schmitt, 1999; Vilensky and Larson, 1989), and this mechanical flexibility (Iriarte-Diaz et al., 2012; Wainwright et al., 2008) has been seen as reflecting underlying neuromuscular

Fig. 8. Mean (±s.d.) braking impulse (BI) in the forelimbs and hindlimbs. (A) *Lemur catta* (*N*=3 individuals and 141 steps). (B) *Varecia variegata* (*N*=3 individuals and 162 steps). All data are presented as a percentage of body weight seconds (%bws). Asterisks indicate a significant difference (***$P \leq 0.001$). ns, no significant difference was observed.

mechanisms that may have allowed for the great amount of locomotor diversity within the primate order (Schmitt, 2010; Vilensky and Larson, 1989).

The finding that our animals have adapted the forelimb to be the primary propulsive and weight-bearing limb is reminiscent of bimanual suspension observed in brachiating and arm-swinging species, and may reflect the best possible biomechanical solution for primates to effectively move below branches. This supports ideas proposed by Cartmill and Milton (1977), and later substantiated by Mendel (1979) that many of the anatomical features of slow-moving species that commonly adopt below-branch quadrupedal locomotion (i.e. lorises, howling monkeys and sloths) are similar to those of arm-swinging primates. As proposed by these authors, a possible scenario to explain the acquisition of arm swinging is that as relatively large-bodied, anatomically unspecialized arboreal primates began to adopt a relatively greater proportion of below-branch quadrupedal locomotion, the mechanical challenges associated with suspensory locomotion would have driven certain anatomical features (e.g. changes in the wrist, elbow and shoulder, and increased finger and forelimb length) to be selectively favored (Cartmill and Milton, 1977; Fujiwara et al., 2011; Jungers et al., 1997; Mendel, 1979; Michilsens et al., 2010; Rein et al., 2015; Turnquist, 1975). These features would in turn be beneficial for the subsequent acquisition of arm swinging. Eventually, brachiation and/or arm swinging would have replaced below-branch quadrupedal locomotion as the primary mode of suspensory locomotion observed in primates.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.120840/-/DC1

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