

## RESEARCH ARTICLE

# The evolution of vertical climbing in primates: evidence from reaction forces

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## ABSTRACT

Vertical climbing is an essential behavior for arboreal animals, yet limb mechanics during climbing are poorly understood and rarely compared with those observed during horizontal walking. Primates commonly engage in both arboreal walking and vertical climbing, and this makes them an ideal taxa in which to compare these locomotor forms. Additionally, primates exhibit unusual limb mechanics compared with most other quadrupeds, with weight distribution biased towards the hindlimbs, a pattern that is argued to have evolved in response to the challenges of arboreal walking. Here we test an alternative hypothesis that functional differentiation between the limbs evolved initially as a response to climbing. Eight primate species were recorded locomoting on instrumented vertical and horizontal simulated arboreal runways. Forces along the axis of, and normal to, the support were recorded. During walking, all primates displayed forelimbs that were net braking, and hindlimbs that were net propulsive. In contrast, both limbs served a propulsive role during climbing. In all species, except the lorises, the hindlimbs produced greater propulsive forces than the forelimbs during climbing. During climbing, the hindlimbs tend to support compressive loads, while the forelimb forces tend to be primarily tensile. This functional disparity appears to be body-size dependent. The tensile loading of the forelimbs versus the compressive loading of the hindlimbs observed during climbing may have important evolutionary implications for primates, and it may be the case that hindlimb-biased weight support exhibited during quadrupedal walking in primates may be derived from their basal condition of climbing thin branches.

**KEY WORDS:** Hindlimb, Forelimb, Peak force, Impulse force, Kinetics

## INTRODUCTION

Climbing, often on vertical supports, is a crucial and fundamental form of locomotion for arboreal animals during foraging, travel, escape or finding a safe resting place. Climbing has long been recognized as playing an important role in the evolution of primates (see Jones, 1916; Cartmill, 1985; Hirasaki et al., 1993; Isler, 2005; Hanna et al., 2008), and has been considered by some (Stern, 1976; Fleagle et al., 1981) to be integral to the origins of bipedalism. In order to move and forage in a complex, three-dimensional environment, primates must engage in frequent bouts of climbing, much of it on vertical supports (Preuschoft, 2002). Moreover, they

do so without aid of claws (Cartmill, 1972) and at relatively large body sizes that increase both mechanical challenges and relative energetic costs at least at body sizes above 1 kg (Hanna et al., 2008). Primates are well known to show significant functional differentiation of the mechanical roles of the forelimbs and hindlimbs, both during static loading (e.g. Vilensky and Larson, 1989; Young et al., 2007; Larson and Demes, 2011; Young, 2012) and during horizontal locomotion (see Kimura et al., 1979; Demes et al., 1994; Schmitt, 2012), with the hindlimbs of most primates experiencing higher values of vertical force and playing the primary propulsive role in locomotion on horizontal supports. The origins of this functional differentiation in limb role is poorly understood and remains an area of intense discussion and debate (Raichlen et al., 2009; Shapiro and Young, 2010; O'Neill and Schmitt, 2012; Schmitt, 2012; Young, 2012; Granatosky et al., 2016a). Although much has been made of the idea that primate limb mechanics are associated with arboreal locomotion (Kimura et al., 1979; Demes et al., 1994; Schmitt and Lemelin, 2002; Schmitt, 2003; Schmitt and Hanna, 2004; Wallace and Demes, 2008; Hanna and Schmitt, 2011a), little is known about the specific aspects of arboreal locomotion that would drive the evolution of this pattern. It is possible that some features that define the walking gaits of the order Primates evolved in association with vertical movement. Cartmill (1972) proposed that clawed animals are able to engage with the substrate during climbing by insert claws into the surface, which reduces the reliance on frictional forces for maintaining contact with the substrate. Nailed animals, in contrast, must grasp around the substrate, either with their hands and feet or with their limbs, and use frictional forces to maintain contact with the substrate (Cartmill, 1972). This raises the possibility that the mechanical requirement of vertical climbing in an animal without claws was an important selective factor in the evolution of primate locomotor mechanics. It is not known whether the pattern observed during walking in most primates (i.e. higher loading on the hindlimbs than the forelimbs) is present also during climbing. More radically, it is unknown whether this functional differentiation originated with climbing and is conserved during walking.

Although several studies have examined climbing mechanics in some primates, few have described the kinetics of vertical climbing in primates with a broad sample that includes a range of sizes and phylogenetic groups, and how climbing differs from horizontal quadrupedalism over a wide range of primates. Some studies have looked at the cost of climbing in comparison to quadrupedalism. For example, Hanna and colleagues (Hanna et al., 2008; Hanna and Schmitt, 2011b) found that the mass-specific energy cost of moving upwards is constant across body size, but relatively more expensive in large animals when compared with the cost of horizontal movement. This result was consistent with an earlier seminal study by Taylor and colleagues (1972) with chimpanzees. Hanna and colleagues (Hanna et al., 2008; Hanna and Schmitt, 2011b) proposed that this difference in cost of movement was explained by the fact that during horizontal

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locomotion, the primary determinant of energetic costs is the rate at which work is accomplished (i.e.  $J s^{-1}$ , or power) (e.g. Cavagna and Kaneko, 1977; Heglund et al., 1982; Kram and Taylor, 1990; Willems et al., 1995), whereas in climbing the primary determinant is thought to be related to the magnitude of work accomplished (i.e. the force used to move a meter) (Hanna and Schmitt, 2011b) to move the animal upwards (Pontzer, 2016).

Although the available values for energy used during climbing are consistent with theoretical predictions about work accomplished, little is actually known about the distribution of forces exerted by the forelimbs and the hindlimbs during climbing to accomplish this work. Theoretical models of the equivalent of vertical forces during walking (normal load in or out of the support) during clinging and climbing suggest that in order to ensure the body is appropriately angled to be propelled upwards, the forelimbs must ‘pull’ away from the support (a negative force normal to the support) while the hindlimbs must ‘push’ onto the support (a positive force normal to the support) (e.g. Cartmill, 1985; Zaaf et al., 2001; Preuschoft, 2002; Johnson et al., 2015). In these simple models, the limbs are predicted to have fundamentally different functions during climbing compared with horizontal movement, though this differentiation does not necessarily parallel the pattern seen during walking because the limbs will have effective opposite roles. In models of climbing that describe how limbs should function, forces along the long axis of the support (the equivalent of braking and propulsive forces during walking) should also differ from that of walking in that the forelimbs and hindlimbs should both be propulsive (move the animal up the support). Researchers have found that lizards exhibit strong functional limb differentiation with respect to ‘pushing’ and ‘pulling’ (normal load in and out of the plane of support), and that both limbs function to propel the body upwards to the same degree during purely vertical movement and highly inclined movement (Autumn et al., 2006; Krause and Fischer, 2013; Wang et al., 2015a, b). In comparison, during horizontal locomotion, the forelimbs and hindlimbs of lizards propel the body forward to the same degree, but the forelimbs bear more weight than the hindlimbs (Krause and Fischer, 2013; Wang et al., 2015a,b). This latter pattern of vertical force distribution is typical of walking in most mammals with the exception of most primates, who show the reverse pattern (e.g. Kimura et al., 1979; Vilensky and Larson, 1989; Demes et al., 1994; Larson, 1998; Schmitt, 1999; Schmitt and Lemelin, 2002). Results similar to those of Krause and Fischer (2013) have been reported for *Monodelphis domestica* on inclines of 30 deg (Lammers et al., 2006). Taken together, these studies suggest that in nonprimate animals, the propulsive aspects of force distribution and limb function during climbing are similar to that recorded during walking, but that the pattern of normal forces applied to the substrate are not the same for vertical and horizontal locomotion.

Some force data exist for primates during climbing, which supports the idea that differentiation in limb function is present during both climbing and horizontal movement. Hirasaki and colleagues (1993, 2000) presented kinetic data during climbing by two primate species, the spider monkey and Japanese macaques, which indicate that the forelimbs pull on the substrate while the hindlimbs push on the substrate. However, the two primate species exhibited different upward propulsive forces between the limbs. The spider monkey hindlimbs contributed relatively greater upward propulsion than did the forelimbs, while the Japanese macaque limbs exhibited statistically similar propulsion (Hirasaki et al., 1993). This pattern of role differentiation is consistent with patterns of vertical force production by forelimbs and hindlimbs in these species. Hanna and Schmitt (2011a) showed that the highly arboreal long-tailed macaque used

hindlimbs for propulsion more than the forelimbs when compared with the more terrestrial Japanese macaque studied by Hirasaki and colleagues (1993). This result suggested, as has been argued for other studies of primates, that increases in habitual use of arboreal substrates increases the functional differentiation of the forelimbs and hindlimbs. However, at present we lack data on a wider group of primates with a range of body size and habitual locomotor behaviors. As a result, the question of how horizontal and vertical movement influence limb mechanics in mammals remains underexplored. Primates represent a model that provides an opportunity to fill that gap.

Here, we examine whether the force patterns across limbs differ between vertical climbing and horizontal locomotion and whether the patterns vary as a function of phylogeny, body size or behavioral/morphological characteristics in primate grasp-type climbers. We examined primates walking on an instrumented horizontal pole and climbing an instrumented vertical pole. Here we test the hypotheses that in a wide range of arboreal strepsirrhine and haplorrhine primates: (1) both limbs contribute equally to propulsion while climbing up a vertical support (the null hypothesis) as compared with horizontal locomotion, in which the hindlimbs will be net propulsive and the forelimbs net braking; and (2) while climbing up a vertical support, the hindlimbs exhibit a tangential reaction force directed into the substrate (a ‘push’, or positive force, into the support) and the forelimbs exhibit a tangential reaction force that is away from the support (a ‘pull’, or negative force, on the support) as compared with horizontal locomotion, where both limbs will exert a tangential ‘push’ on the substrate; these tangential forces during climbing will be higher on the hindlimbs than on the forelimbs for all primates except lorises.

## MATERIALS AND METHODS

### Subjects

Adult *Loris tardigradus* (Linnaeus 1758), *Nycticebus pygmaeus* Bonhote 1907, *Cheirogaleus medius* Geoffroy 1812, *Eulemur mongoz* Linnaeus 1766, *Daubentonia madagascariensis* Gmelin 1788, *Saimiri sciureus* (Linnaeus 1758), *Macaca fascicularis* Raffles 1821, *Aotus nancymae* Hershkovitz 1983 and *Aotus azarae* Hershkovitz 1983 were used in this study (Table 1). All data were attained from animals housed at the Duke Lemur Center & Duke University Vivarium (Durham, NC, USA), Monkey Jungle (Miami, FL, USA), Stony Brook University (Stony Brook, NY, USA) and the Michale E. Keeling Center (Bastrop, TX, USA).

### Procedures

All procedures were approved by the appropriate institutional IACUCs (West Virginia School of Osteopathic Medicine: 2007-1, 2008-1, 2009-4; Duke University: A104-09-03, A130-07-05, A270-11-10; State University of New York: 91-94-0131). The data collection procedures have been described extensively elsewhere (Demes et al., 1994; Schmitt and Lemelin, 2002, 2004; Schmitt and Hanna, 2004; Granatosky et al., 2016a) and will be simply summarized here. Subjects were encouraged by food reward to climb a pole attached to a wall (climbing trials) or the ground (walking trials). The pole varied in diameter between 1.27 and 3.81 cm (Table 1). The middle section of the pole was instrumented to a force transducer (MC3A-6®; AMTI, Watertown, MA, USA), or force transducers (9317B; Kistler, Amherst, NY, USA), following Schoonaert et al. (2006), Hanna and Schmitt (2011a) and Granatosky et al. (2016a), which recorded ground reaction forces in three orthogonal directions. As the animals moved up/across the pole, they were video recorded using cameras (A601f; Basler AG, Ahrensburg, Germany, Sony Handycam, or GoPro Hero3+) at 60 to

**Table 1. Summary characteristics of samples from the study species**

Species	Individual	Type of locomotion (substrate diameter in cm)		Body mass (kg)	Sex	Date of birth (dd/mm/yyyy)	Location
<i>Loris tardigradus</i>	1	Climb (1.27)	Walk (1.27)	0.18	Female	10/10/1997	Duke Lemur Center
	2	Climb (1.27)	Walk (1.27)	0.2	Male	17/10/1992	Duke Lemur Center
<i>Cheirogaleus medius</i>	1	Climb (1.27)	Walk (1.27)	0.225	Female	15/07/2005	Duke Lemur Center
	2	Climb (1.27)	Walk (1.27)	0.25	Female	15/07/2005	Duke Lemur Center
	3	Climb (1.27)	Walk (1.27)	0.23	Male	15/07/2006	Duke Lemur Center
<i>Nycticebus pygmaeus</i>	1	Climb (1.27)	Walk (1.27)	0.64	Male	01/06/2006	Duke Lemur Center
	2	Climb (1.27)	Walk (1.27)	0.4	Female	15/03/1994	Duke Lemur Center
	3	Climb (1.27)	Walk (1.27)	0.48	Male	04/03/2002	Duke Lemur Center
<i>Saimiri sciureus</i>	1	Climb (3.18)		0.855	Male	NA/06/2005	Duke Vivarium
	2	Climb (3.18)		0.85	Male	NA/06/2005	Duke Vivarium
	3		Walk (2.54)	0.571	Male	Unknown	Monkey Jungle
	4		Walk (2.54)	0.64	Male	Unknown	Monkey Jungle
	5		Walk (2.54)	0.701	Male	Unknown	Monkey Jungle
	6		Walk (2.54)	0.798	Female	Unknown	Monkey Jungle
	7		Walk (2.54)	0.932	Male	Unknown	Monkey Jungle
	8		Walk (2.54)	0.958	Female	Unknown	Monkey Jungle
<i>Aotus nancymae/azarae</i>	1	Climb (3.18)	Walk (3.18)	1.104	Female	22/12/2000	Michale E. Keeling Center
	2	Climb (3.18)	Walk (3.18)	0.98	Male	Unknown	Michale E. Keeling Center
	3		Walk (2.54)	1.002	Male	Unknown	Monkey Jungle
	4		Walk (2.54)	0.862	Female	Unknown	Monkey Jungle
	5		Walk (2.54)	0.89	Female	Unknown	Monkey Jungle
<i>Eulemur mongoz</i>	1	Climb (3.18)	Walk (3.18)	1.44	Male	17/06/1990	Duke Lemur Center
	2	Climb (3.18)	Walk (3.18)	1.49	Female	26/05/1995	Duke Lemur Center
	3	Climb (3.18)	Walk (3.18)	1.34	Male	23/04/1988	Duke Lemur Center
<i>Daubentonia madagascariensis</i>	1	Climb (3.81)		2.89	Female	30/07/2001	Duke Lemur Center
	2	Climb (3.81)		2.45	Male	22/02/2005	Duke Lemur Center
	3	Climb (3.81)	Walk (3.18)	3	Female	06/01/1998	Duke Lemur Center
	4		Walk (3.18)	2.86	Male	05/06/1994	Duke Lemur Center
	5		Walk (3.18)	3.02	Female	15/04/1996	Duke Lemur Center
<i>Macaca fascicularis</i>	1	Climb (3.81)		8.00	Male	Circa 2002	Duke Vivarium
	2	Climb (3.81)		6.90	Male	Circa 2002	Duke Vivarium
	3		Walk (3.18)	9.77	Male	Circa 1988	Stony Brook
	4		Walk (3.18)	4.65	Female	Circa 1988	Stony Brook

120 frames  $s^{-1}$  (see Granatosky et al. 2016a for information on data collection with GoPro cameras). Only trials in which the animal was traveling in a straight path and not accelerating or decelerating (i.e. steady-state locomotion) throughout the climbing or walking trial, in which a full forelimb and/or hindlimb contacted the instrumented pole, and which exhibited a symmetric footfall sequence were retained for analysis. For all data, steady-state locomotion was determined by a combination of video, force and symmetry data following the methods of Granatosky et al. (2016a,b), Schmitt and Lemelin (2002) and Hanna and Schmitt (2011a). For all trials, symmetry was determined using the methods of Cartmill et al. (2002), with a  $\pm 10$  criterion such that the timing of opposite limb touchdown could vary between 40 and 60% of the stride cycle (50% indicates the timing of opposing limbs is exactly half of the cycle). In cases where both a forelimb and hindlimb contacted the instrumented pole, we only analyzed the force peaks of this step, and force impulses were not analyzed. Video recordings were consulted in these cases to ensure that a second limb was not in contact with the instrumented pole at the time of the force peak. Peak forces for propulsive (along the long axis of the support) and tangential (into the plane of the support) were determined for these trials (Fig. 1). Force impulses for each of these directions were also determined when a single footfall was available.

### Data processing

Force data were converted from raw voltage data to Newtons for each transducer. The force transducers were calibrated daily using a known mass before or after data collection. Forces were then filtered

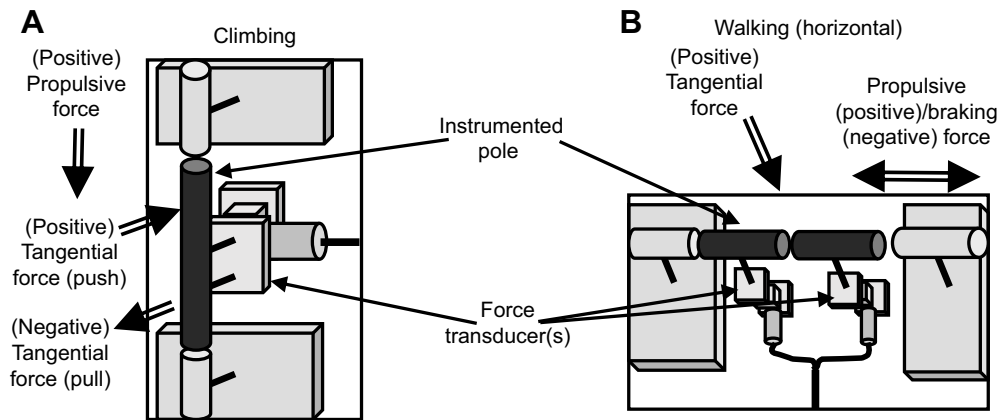
using a low-pass, two-way Butterworth or Fourier filter with a 60 Hz cut-off. Both force peaks and impulses were normalized to subject body weight in Newtons and are expressed as a ratio of body weight (BW) in all text, figures and tables. For all cases in which force traces fluctuated in direction (as in push then pull, or braking and then propulsive) the positive and negative values were recorded.

Cameras were calibrated for distance using a known length in the view of the camera in the same plane as the animal was moving. Speed was determined from this calibration as the average velocity of the animal over the view of the camera, by the position of the head marker from the initial view in the cameras to the last view in the camera. Contact time was determined as the time each hand or foot was in contact with the instrumented pole.

### Statistical analysis

All force data, peak and impulse, were normalized to body weight and analyzed as dimensionless values. Data for all individuals in a species were pooled and JMP Pro (SAS, Cary, NC, USA) was used for all analyses. *Aotus nancymae* and *A. azarae* both participated in walking trials; these data were pooled for analyses, as well. Data were tested for normality and homogeneity of variance with Shapiro–Wilk and Levene’s tests (Sokal and Rohlf, 1995). Speed and contact time were compared to determine correlation with each other. Subsequently, least-squares regressions were calculated to examine whether force data were correlated with speed or with contact time on a per-species, per-limb basis. In cases for which force varied significantly by speed or by contact time, log-transformed forelimb and hindlimb forces were compared across speed or contact time with ANCOVA (Vickers,





**Fig. 1. Schematic depicting instrumented pole setups for climbing and walking trials.** (A) Climbing trials; MC3A AMTI force transducer setup. (B) Walking trials; Kistler 9317B force transducer setup. Both types were used during walking trials, but only the AMTI transducer was used during climbing trials. In terms of the forces, propulsive forces are directed along the long axis of the pole. During climbing, they are always positive. During walking, these forces are positive, termed propulsive, or negative, termed braking. Tangential forces are analogous to the vertical forces. During walking, these forces are always positive (directed into the pole). During climbing, the tangential forces can be positive or negative. Positive tangential forces are termed the 'push' force, because the animal is pushing into the pole, and negative forces are termed 'pull' forces, because the animal is pulling away from the pole.

2005). In cases for which speed or contact time were not significant predictors of force, or if there was an interaction effect between speed or contact time and limbs, limb forces were compared using the Kruskal–Wallis test.

## RESULTS

A total of 860 trials for which single limb forces were available were analyzed. Representative force traces during climbing and walking are illustrated in Fig. 2. While most data did not differ significantly from a normal distribution, some departed from normality and some limb data exhibited heteroscedasticity. In some cases, a significant relationship between speed and force was exhibited; in others, no relationship was exhibited (Tables 2 and 3). Speed and contact time were highly correlated with one another (Tables 2 and 3). Thus, we used speed for our analysis with forces. Thus, log-transformed ANCOVAs were calculated for the former pair-wise comparisons, and non-parametric tests were calculated for the latter.

### Climbing peak forces

#### Propulsive (along long axis of substrate)

Peak propulsive forces (along the long axis of the pole) of the forelimbs during climbing were significantly correlated with speed in *E. mongoz*, *S. sciureus*, *C. medius* and *L. tardigradus* (range  $P < 0.0001$  to  $P = 0.047$ ); in contrast, peak propulsive forces of the hindlimbs during climbing were significantly correlated with speed only in *E. mongoz* and *S. sciureus* ( $P \leq 0.0001$  and  $P = 0.029$ , respectively; Tables 2 and 3).

All species except *D. madagascariensis* exhibited significant differentiation between limbs in terms of peak propulsive forces during climbing (range:  $P < 0.0001$  to  $P = 0.030$ ), with the hindlimbs typically contributing the greatest propulsive forces downwards, which propels the animal upwards (Table 4, Fig. 3). The two exceptions to this pattern are the lorid species (*L. tardigradus* and *N. pygmaeus*), in which the forelimbs contributed to greater peak propulsion forces to ascend ( $P = 0.030$  and  $P = 0.0017$ , respectively). There were no braking forces exhibited by the limbs during climbing.

#### Tangential (push/pull) (normal to substrate)

During climbing, no clear pattern of correlation between speed and peak push or pull forces was observed. For example, *L. tardigradus*

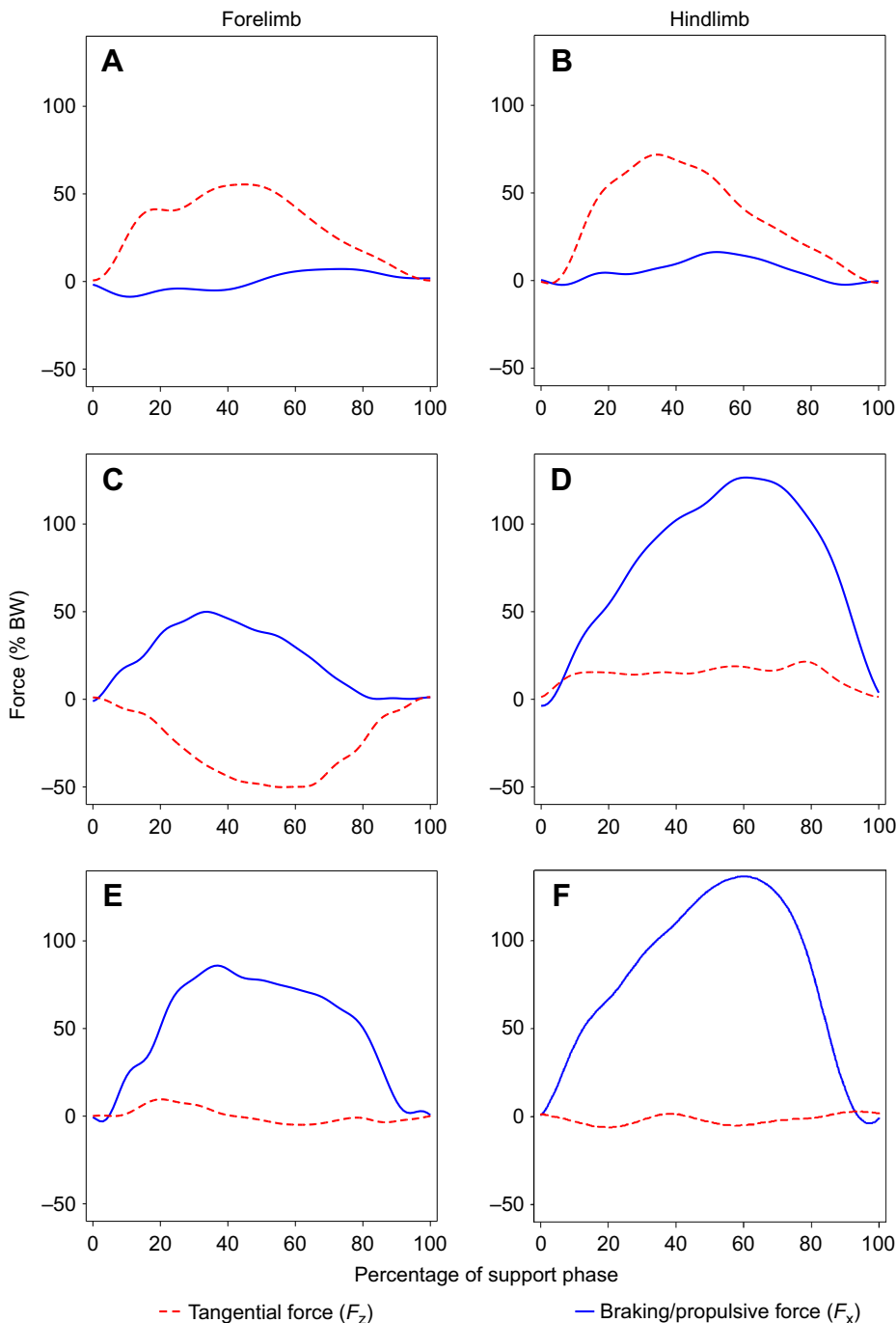
and *A. nancymae* showed a correlation between peak pull force and speed for the hindlimbs, but not the forelimbs, while *M. fascicularis* exhibited the opposite pattern (Table 2). In contrast, *N. pygmaeus*, *E. mongoz* and *D. madagascariensis* showed correlations between peak push force and speed for the hindlimbs but a correlation between speed and peak pull forces for the forelimbs (Table 2). *Cheirogaleus medius* and *S. sciureus* showed no correlations with speed for either limb in terms of tangential forces (Table 2). All species use both forelimbs and hindlimbs to both push into the pole and pull away from the pole (Table 4, Fig. 4). However, it is most typical for the hindlimbs to have the highest number of events in which the animal pushed into the substrate, while the forelimbs have the highest number of events in which the animal pulls away from the substrate; for example, in peak tangential forces during climbing, *C. medius* forelimbs exhibited 33 pulls and only 14 pushes, while the hindlimbs exhibited 47 pushes and only 12 pulls (Table 4). In most cases, the magnitude of peak pushing force by the hindlimbs is significantly greater than the peak pushing force by the forelimbs (range  $P < 0.0001$  to  $0.0137$ ; Table 4). The exceptions to this pattern are *N. pygmaeus*, which exhibits significantly larger pushing forces by the forelimbs than by the hindlimbs during climbing ( $P = 0.0010$ ), and *L. tardigradus*, *S. sciureus* and *A. nancymae*, which show no significant difference between the limbs in this direction during climbing.

Conversely, the peak pulling forces of the hindlimbs in five of the species is significantly larger in magnitude than the peak pulling forces of the hindlimbs (range  $P < 0.0001$  to  $0.0011$ ; Table 4). The other four species, *L. tardigradus*, *N. pygmaeus*, *S. sciureus* and *A. nancymae*, exhibit no significant differentiation in limb pull forces. There is a profound size effect in this pattern. Peak push/pull limb differentiation becomes more prominent as species weight increases, to the point that large species exhibited very few pushes by the forelimbs and very few pulls by the hindlimbs (Table 2, Fig. 4).

### Climbing impulse forces

#### Propulsive (along long axis of substrate)

Impulse propulsive forces in forelimbs during climbing were significantly correlated with speed in all species but *M. fascicularis*, *S. sciureus* and *L. tardigradus* (Table 3). *Cheirogaleus medius* and *Eulemur mongoz* exhibited a significant interaction between speed



**Fig. 2. Representative single-limb force traces during walking and climbing by *Saimiri sciureus*.** All force data are presented as a percent of body weight (BW) and time as a percentage of contact time. The red, dashed line is the tangential force, whereas the blue, solid line is the braking/propulsive force. Positive and negative forces are as illustrated in Fig. 1, in which negative braking/propulsive forces are braking, positive braking/propulsive forces are propulsive, positive tangential forces are 'push' or compressive forces and negative tangential forces are 'pull' or tensile forces. (A,B) Typical force traces during walking for the forelimbs (A) and hindlimbs (B). (C) A typical force trace for the forelimbs during climbing where the tangential force is only a 'pull' (the forelimbs are used only in tension). (D) A typical force trace for the hindlimbs during climbing where the tangential force is only a 'push' (the hindlimbs are used only in compression). (E,F) Typical force traces in which the forelimbs (E) and hindlimbs (F) are used both in tension and compression during climbing.

and limbs ( $P < 0.0001$  and  $P = 0.0055$ , respectively) and were subsequently analyzed with a Kruskal–Wallis test. All species exhibited positive propulsive forces in both limbs at all times and all species except *D. madagascariensis* exhibited a significant differentiation between limbs in terms of impulse propulsive forces during climbing (range  $P < 0.0001$  to  $P = 0.048$ ). In these cases, the hindlimbs typically contribute the greatest impulse propulsive forces upwards (Fig. 3). The lorises utilized their forelimbs more than their hindlimbs to propel upwards.

#### Tangential (push/pull) (normal to substrate)

Tangential impulse forces during climbing were not correlated with speed in most cases, except *E. mongoz* exhibited a significant

correlation with speed in impulse push for the hindlimbs ( $P = 0.001$ ), whereas *C. medius* exhibited a significant correlation with speed only in the pull direction and only for the forelimbs ( $P = 0.0056$ ; Table 3). Limb comparisons revealed that the impulses of push and pull forces were typically not significantly different between the limbs, except in the larger species (Table 4). That is, *E. mongoz* and *M. fascicularis* showed significantly larger pushes by the hindlimbs than the forelimbs ( $P = 0.0015$  and  $0.0002$ , respectively), and the opposite with pulls ( $P = 0.0002$  and  $0.0004$ , respectively). Although *D. madagascariensis* did not show these same significant differentiations between the limbs, this may be partly due to the fact that this species exhibited no pushes by the forelimbs and only one pull by the hindlimbs.

**Table 2. Least-squares regressions of speed and peak forces (BW)**

		Peak braking			Peak propulsive			Peak push			Peak pull			
		Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	
<i>L. tardigradus</i>	Walking	FL	– (5)	0.9444	–	– (5)	0.6036	–	– (5)	0.6027	–	– (5)	0.6027	
		HL	– (7)	0.6431	–	– (7)	0.2408	–	– (7)	0.3521	–	– (7)	0.3521	
<i>C. medius</i>	Climbing	FL	– (7)	<b>0.0349</b>	<b>0.166</b>	<b>0.366 (27)</b>	<b>0.0349</b>	–	– (16)	0.968	–	– (10)	0.8624	
		HL	– (33)	0.9943	–	– (33)	0.9943	–	– (17)	0.9815	<b>0.321</b>	<b>–0.351 (18)</b>	<b>0.0142</b>	
	Walking	FL	– (7)	0.9291	–	– (7)	0.753	–	– (7)	0.6752	–	– (7)	0.6752	
		HL	<b>–0.071 (6)</b>	<b>0.683</b>	<b>0.0425</b>	<b>– (6)</b>	0.8883	<b>0.142 (6)</b>	<b>0.81</b>	<b>0.0145</b>	–	– (33)	0.0645	
<i>N. pygmaeus</i>	Climbing	FL	– (14)	0.4886	–	<b>0.385 (46)</b>	<b>0.343</b>	–	– (14)	0.6574	–	– (12)	0.7176	
		HL	– (8)	0.4323	–	– (56)	0.4457	–	– (47)	0.0502	–	– (12)	0.7176	
	Walking	FL	– (14)	0.4886	–	– (14)	0.4201	–	– (14)	0.1366	–	– (12)	0.7176	
		HL	– (8)	0.4323	–	<b>0.076 (8)</b>	<b>0.667</b>	<b>0.134</b>	<b>0.195 (8)</b>	<b>0.557</b>	–	– (12)	0.7176	
<i>S. sciureus</i>	Climbing	FL	– (51)	0.8377	–	– (50)	0.1669	–	– (28)	0.3974	–	– (8)	0.0123	
		HL	– (27)	0.156	–	– (51)	0.4105	–	<b>0.175 (51)</b>	<b>0.113</b>	–	– (8)	0.0123	
	Walking	FL	– (51)	0.8377	–	– (27)	0.9041	–	– (27)	0.3436	–	– (7)	0.7364	
		HL	– (27)	0.156	–	<b>0.530 (12)</b>	<b>0.339</b>	<b>0.0471</b>	–	– (7)	0.6162	–	– (7)	0.7364
<i>A. nancymaelazarae</i>	Climbing	FL	– (12)	<b>0.518</b>	<b>0.264</b>	<b>0.607 (18)</b>	<b>0.264</b>	<b>0.029</b>	–	– (14)	0.0649	–	– (6)	0.4113
		HL	<b>–0.333 (12)</b>	<b>0.389</b>	<b>0.0099</b>	– (12)	0.2903	–	– (17)	0.1509	–	– (6)	0.4113	
	Walking	FL	– (11)	0.8034	–	– (16)	0.9489	–	– (19)	0.3069	–	– (13)	0.8816	
		HL	– (7)	0.572	–	– (16)	0.1748	–	– (4)	0.2897	–	<b>0.617 (3)</b>	<b>0.0432</b>	
<i>E. mongoz</i>	Climbing	FL	– (11)	0.8034	–	– (16)	0.1581	–	– (16)	0.9497	–	– (13)	0.8816	
		HL	– (7)	0.572	–	– (11)	0.8306	–	– (19)	0.0769	–	<b>0.617 (3)</b>	<b>0.0432</b>	
	Walking	FL	– (46)	0.6942	–	<b>0.288 (61)</b>	<b>0.553</b>	<b>0.0001</b>	–	– (11)	0.2798	–	– (9)	0.3094
		HL	– (28)	0.0853	–	<b>0.312 (74)</b>	<b>0.309</b>	<b>0.0001</b>	<b>0.305 (68)</b>	<b>0.369</b>	<b>0.189</b>	<b>–0.222 (56)</b>	<b>0.0008</b>	
<i>D. madagascariensis</i>	Climbing	FL	– (46)	0.6942	–	– (46)	0.3893	–	– (46)	0.1911	–	– (9)	0.3094	
		HL	– (28)	0.0853	–	<b>–0.162 (28)</b>	<b>0.256</b>	<b>0.006</b>	–	– (28)	0.8501	–	– (9)	0.3094
	Walking	FL	– (46)	0.6942	–	– (8)	0.6096	–	– (2)	–	–	<b>–0.216 (7)</b>	<b>0.0024</b>	
		HL	– (28)	0.0853	–	– (28)	0.6072	–	<b>0.403 (28)</b>	<b>0.261</b>	<b>0.0055</b>	–	–	
<i>M. fascicularis</i>	Climbing	FL	– (19)	0.8361	–	– (19)	0.8712	–	– (19)	0.1841	–	– (2)	–	
		HL	– (14)	0.0903	–	– (14)	0.1952	–	– (14)	0.2413	–	– (2)	–	
	Walking	FL	– (14)	0.0903	–	– (22)	0.2357	–	<b>0.104 (7)</b>	<b>0.69</b>	<b>0.0206</b>	–	0.7936	
		HL	– (14)	0.0903	–	– (34)	0.726	–	– (33)	–	–	–	0.0863	

BW, body weight; FL, forelimb; HL, hindlimb. Bold indicates a significant correlation between speed and peak force as a ratio to body weight at the 0.05 level.

**Table 3. Least-squares regressions of speed and impulse forces (BWS)**

	Impulse braking			Impulse propulsive			Net impulse braking/propulsive			Impulse push			Impulse pull			Net impulse push/pull			
	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	Slope (n)	R <sup>2</sup>	P	
<i>L. fatidigradius</i>	Walking	FL	-(3)	-	0.3041	-	0.1279	-(3)	0.4632	-	0.0811	-	0.0811	-	0.0811	-	0.0811	-	0.0811
		HL	-(7)	-	0.2434	-	0.3908	-(7)	0.1942	-	0.0717	-	0.0717	-	0.0717	-	0.0717	-	0.0717
<i>C. medius</i>	Climbing	FL	-(4)	-	0.2887	-	0.2887	-(4)	0.2887	-	0.4886	-	0.4886	-	0.4886	-	0.4886	-	0.4886
		HL	-(2)	-	0.0014	0.697	0.0014	-(2)	-	-	-	-	-	-	-	-	-	-	-
<i>N. pygmaeus</i>	Walking	FL	-(1)	-	-	-	-	-(1)	-	-	-	-	-	-	-	-	-	-	-
		HL	-(1)	-	-	-	-	-(1)	-	-	-	-	-	-	-	-	-	-	-
<i>S. sciureus</i>	Climbing	FL	0.037 (11)	0.577	0.0067	0.0048	0.0048	0.037 (11)	0.577	0.0067	0.0048	0.0048	0.037 (11)	0.577	0.0067	0.0048	0.0048	0.037 (11)	0.577
		HL	-0.002 (7)	0.577	0.0475	0.643	<0.0001	0.643	-0.002 (7)	0.577	0.0475	0.643	<0.0001	0.643	-0.002 (7)	0.577	0.0475	0.643	<0.0001
<i>A. nancymaelazarae</i>	Walking	FL	-(51)	-	0.1875	-	0.073	-(51)	0.489	-	0.238	-	0.238	-	0.238	-	0.238	-	0.238
		HL	0.005 (27)	0.157	0.041	0.513	0.0012	0.513	0.005 (27)	0.157	0.041	0.513	0.0012	0.513	0.005 (27)	0.157	0.041	0.513	0.0012
<i>E. mongoz</i>	Climbing	FL	-(12)	-	0.5169	-	0.1098	-(12)	0.8599	-	0.0515	-	0.0515	-	0.0515	-	0.0515	-	0.0515
		HL	-(16)	-	0.4334	-	0.8211	-(16)	0.7574	-	0.248	-	0.248	-	0.248	-	0.248	-	0.248
<i>M. fascicularis</i>	Walking	FL	-(11)	-	0.086	-	0.2031	-(11)	0.1421	-	0.1003	-	0.1003	-	0.1003	-	0.1003	-	0.1003
		HL	-(7)	-	0.8434	-	0.162	-(7)	0.1765	-	0.329	-	0.329	-	0.329	-	0.329	-	0.329
<i>D. madagascariensis</i>	Climbing	FL	-(46)	-	0.7306	-	0.3909	-(46)	0.8925	-	0.5355	-	0.5355	-	0.5355	-	0.5355	-	0.5355
		HL	-(28)	-	0.2856	-	0.0025	-(28)	0.0343	-	0.182	-	0.182	-	0.182	-	0.182	-	0.182
<i>M. fascicularis</i>	Walking	FL	-(19)	-	0.102	-	0.4176	-(19)	0.3938	-	0.1895	-	0.1895	-	0.1895	-	0.1895	-	0.1895
		HL	-(14)	-	0.33	-	0.1597	-(14)	0.1552	-	0.0092	-	0.0092	-	0.0092	-	0.0092	-	0.0092
<i>M. fascicularis</i>	Climbing	FL	-(20)	-	-	-	0.3269	-(20)	-	-	-	-	-	-	-	-	-	-	-
		HL	-0.078 (31)	0.138	0.394	0.138	0.394	-0.078 (31)	0.138	0.394	0.138	0.394	-0.078 (31)	0.138	0.394	0.138	0.394	-0.078 (31)	0.138

BWS, body weight seconds; FL, forelimb; HL, hindlimb. Bold indicates a significant relationship between speed and impulse force as a ratio to body weight seconds at a level of 0.05.

Table 4. Mean (±s.d.) forces (BW) for the study species

	<i>L. tardigradus</i>			<i>C. medius</i>			<i>N. pygmaeus</i>			<i>S. scuireus</i>		
	Walking	Climbing		Walking	Climbing		Walking	Climbing		Walking	Climbing	
Peak braking	FL -0.126±0.040*	HL -0.037±0.024		FL -0.134±0.037*	HL -0.065±0.049		FL -0.103±0.042*	HL -0.034±0.020		FL -0.113±0.047***	HL -0.050±0.029	
Peak propulsive	FL 0.046±0.037	HL 0.136±0.138	0.654±0.106*	FL 0.036±0.023*	HL 0.105±0.011	0.427±0.104***	FL 0.080±0.053*	HL 0.112±0.026	0.609±0.086*	FL 0.029±0.024***	HL 0.138±0.068	0.504±0.192***
Peak push	FL 0.787±0.043*	HL 0.504±0.078	0.593±0.094	FL 0.600±0.038*	HL 0.756±0.089	0.754±0.119	FL 0.759±0.085*	HL 0.602±0.073	0.536±0.122	FL 0.476±0.067***	HL 0.665±0.076	1.020±0.243
Peak pull	FL 0.041±0.112	HL -0.151±0.090	0.236±0.105	FL 0.756±0.089	HL -0.113±0.067	0.173±0.071*	FL 0.273±0.120	HL -0.254±0.105**	0.092±0.044*	FL 0.165±0.109	HL -0.146±0.104	0.195±0.131
Impulse braking	FL -0.024±0.012	HL -0.011±0.019	-0.113±0.067	FL -0.010±0.002	HL -0.113±0.067	-0.120±0.045	FL -0.025±0.017*	HL -0.002±0.001	-0.086±0.033	FL -0.009±0.005***	HL -0.001±0.002	-0.154±0.125
Impulse propulsive	FL 0.005±0.004	HL 0.008±0.007	0.155±0.295*	FL -0.010±0.002	HL -0.113±0.067	-0.120±0.045	FL -0.002±0.001	HL -0.008±0.008	0.270±0.170*	FL 0.001±0.002***	HL 0.078±0.039***	0.078±0.039***
Net braking/propulsive impulse	FL -0.019±0.009	HL -0.004±0.024	0.382±0.206	FL -0.010±0.003	HL -0.113±0.067	-0.120±0.045	FL 0.008±0.008	HL 0.020±0.005	0.225±0.149	FL -0.008±0.005***	HL 0.013±0.009	0.140±0.041
Impulse push	FL 0.184±0.058*	HL 0.072±0.064	0.397±0.094	FL 0.090±0.009	HL 0.045±0.029	0.041±0.023	FL 0.018±0.005	HL 0.242±0.122*	0.046±0.060	FL 0.055±0.020***	HL 0.088±0.026	0.043±0.031
Impulse pull	FL 0.184±0.058*	HL 0.072±0.064	0.155±0.118	FL -0.010±0.003	HL -0.113±0.067	-0.120±0.045	FL 0.242±0.122*	HL 0.142±0.045	0.069±0.079	FL 0.088±0.026	HL 0.055±0.026	0.035±0.026
Net impulse push/pull	FL 0.072±0.064	HL 0.072±0.064	-0.165±0.051*	FL -0.010±0.003	HL -0.113±0.067	-0.120±0.045	FL 0.242±0.122*	HL 0.142±0.045	-0.055±0.054	FL -0.037±0.034	HL -0.020±0.023	-0.024±0.018
Speed (m s <sup>-1</sup> )	FL 0.784 (0.294)	HL 0.931 (0.318)	0.215 (0.116)	FL 0.636 (0.223)†	HL 0.769 (0.566)†	0.324 (0.159)†	FL 0.748 (0.338)	HL 0.712 (0.278)	0.267 (0.135)	FL 0.588 (0.129)	HL 0.267 (0.129)	0.490 (0.211)
Contact time (1 s <sup>-1</sup> )	FL 0.380 (0.113)	HL 0.307 (0.096)	1.088 (0.761)	FL 0.241 (0.066)†	HL 0.329 (0.154)†	0.362 (0.167)†	FL 0.411 (0.2304)	HL 0.448 (0.165)	0.792 (0.465)	FL 0.211 (0.074)	HL 0.320 (0.119)	0.654 (0.206)
	FL 1.006 (0.653)†	HL 0.329 (0.154)†	0.329 (0.154)†	FL 0.219 (0.035)†	HL 0.329 (0.154)†	0.329 (0.154)†	FL 0.448 (0.165)	HL 0.448 (0.165)	0.753 (0.365)	FL 0.237 (0.062)	HL 0.243 (0.071)	0.243 (0.071)

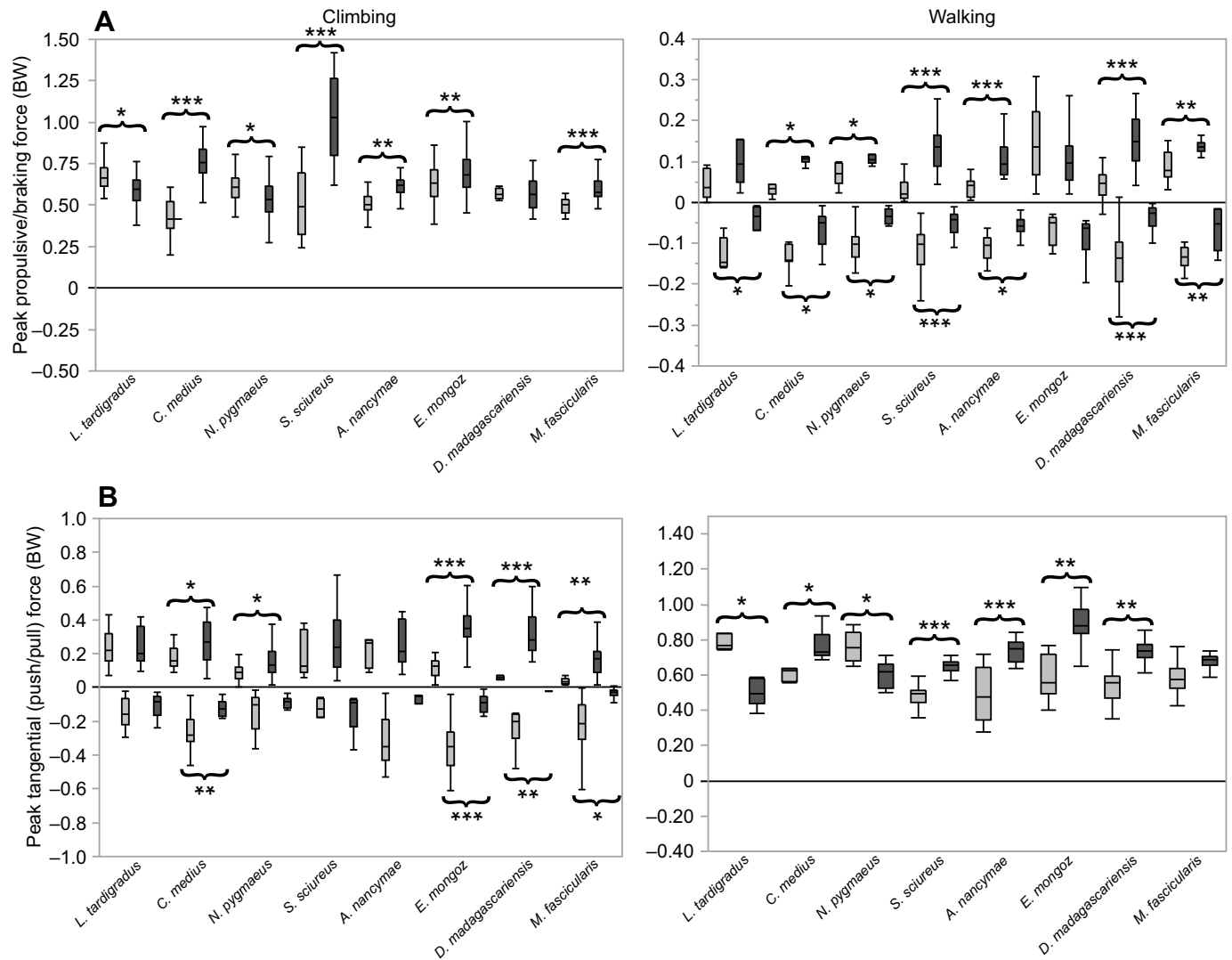
	<i>E. mongoz</i>			<i>D. madagascariensis</i>			<i>M. fascicularis</i>					
	Walking	Climbing		Walking	Climbing		Walking	Climbing				
Peak braking	FL -0.113±0.046*	HL -0.066±0.037		FL -0.078±0.058	HL -0.091±0.055		FL -0.137±0.064***	HL -0.039±0.028		FL -0.135±0.027**	HL -0.064±0.051	
Peak propulsive	FL 0.338±0.027***	HL 0.107±0.045	0.511±0.074**	FL 0.146±0.093	HL 0.107±0.078	0.629±0.110**	FL 0.044±0.037***	HL 0.153±0.061	0.568±0.030	FL 0.136±0.015	HL 0.579±0.076**	0.499±0.054***
Peak push	FL 0.485±0.161***	HL 0.744±0.078	0.614±0.060	FL 0.592±0.112***	HL 0.888±0.112	0.703±0.148	FL 0.535±0.091***	HL 0.736±0.082	0.573±0.093	FL 0.579±0.076**	HL 0.672±0.049	0.591±0.100
Peak pull	FL 0.199±0.013	HL 0.364±0.165	0.261±0.135	FL 0.888±0.112	HL -0.353±0.138***	0.122±0.058***	FL 0.310±0.113	HL -0.245±0.116**	0.058±0.016**	FL 0.672±0.049	HL -0.223±0.146*	0.038±0.019*
Impulse braking	FL -0.022±0.011*	HL -0.009±0.009	-0.314±0.155	FL -0.021±0.009**	HL -0.002±0.001	-0.093±0.052	FL -0.031±0.017***	HL -0.003±0.004	-0.020±0.002	FL -0.026±0.008***	HL -0.004±0.005	-0.033±0.027
Impulse propulsive	FL 0.004±0.006***	HL 0.028±0.014	0.120±0.051**	FL 0.002±0.001**	HL 0.017±0.007	0.098±0.023***	FL 0.003±0.004***	HL 0.042±0.023	0.249±0.105	FL 0.008±0.005***	HL 0.021±0.008	0.166±0.036***
Net braking/propulsive impulse	FL -0.019±0.012***	HL 0.019±0.013	0.194±0.056	FL -0.019±0.009**	HL 0.015±0.007	0.157±0.038	FL -0.028±0.016***	HL 0.040±0.024	0.319±0.070	FL -0.078±0.009***	HL 0.017±0.011	0.260±0.054
Impulse push	FL 0.137±0.062***	HL 0.364±0.165	0.025±0.038	FL 0.102±0.027***	HL 0.172±0.059	0.033±0.023*	FL 0.149±0.047***	HL 0.225±0.067	0.160±0.048	FL 0.155±0.032	HL 0.153±0.045	0.002±0.001**
Impulse pull	FL 0.019±0.013	HL 0.364±0.165	0.084±0.048	FL 0.172±0.059	HL -0.060±0.025**	0.076±0.032	FL 0.225±0.067	HL -0.104±0.035	0.160±0.048	FL 0.153±0.045	HL -0.086±0.053**	0.062±0.045
Net impulse push/pull	FL 0.692 (0.155)	HL 0.583 (0.183)	-0.060±0.058***	FL 0.856 (0.271)	HL 1.077 (0.342)	-0.020±0.014	FL 0.856 (0.271)	HL 1.077 (0.342)	-0.104±0.035	FL 0.153±0.045	HL -0.086±0.053**	0.062±0.045
Speed (m s <sup>-1</sup> )	FL 0.692 (0.155)	HL 0.583 (0.183)	0.082±0.051	FL 0.856 (0.271)	HL 1.077 (0.342)	0.066±0.044	FL 0.856 (0.271)	HL 1.077 (0.342)	0.160±0.048	FL 0.153±0.045	HL -0.086±0.053**	0.062±0.045
Contact time (1 s <sup>-1</sup> )	FL 0.583 (0.233)	HL 0.744 (0.252)	0.431 (0.147)	FL 1.077 (0.342)	HL 0.308 (0.094)	0.931 (0.283)	FL 0.856 (0.271)	HL 1.077 (0.342)	0.562 (0.465)†	FL 1.123 (0.171)	HL 1.181 (0.226)	0.703 (0.220)
	FL 0.583 (0.233)	HL 0.744 (0.252)	0.351 (0.110)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.906 (0.263)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.610 (0.192)†	FL 0.512 (0.143)	HL 0.538 (0.131)	0.741 (0.266)
	FL 0.583 (0.233)	HL 0.744 (0.252)	0.388 (0.124)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.275 (0.088)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.473 (0.093)§	FL 0.512 (0.143)	HL 0.538 (0.131)	0.741 (0.266)
	FL 0.583 (0.233)	HL 0.744 (0.252)	0.521 (0.130)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.308 (0.099)	FL 0.308 (0.094)	HL 0.309 (0.113)	0.587 (0.163)†	FL 0.416 (0.096)	HL 0.416 (0.096)	0.631 (0.132)

BW, body weight; FL, forelimb; HL, hindlimb.

Bold pairs indicate significant difference between limb pairs, tested with an ANCOVA if speed was significantly correlated, or with Kruskal–Wallis tests if speed was not significantly correlated or when there was an interaction between speed and limb. \* $P<0.05$ , \*\* $P<0.001$ , \*\*\* $P<0.0001$ . Means are reported only if there are multiple trials (see Table 2).

There was a significant, negative correlation between speed and contact time in each limb during climbing and walking except for these indicated: † indicates no significant correlation; § indicates a significant, positive correlation.





**Fig. 3. Box and whisker plots of the peak forces within species across limbs.** Light gray boxes represent the forelimb, dark gray boxes represent the hindlimb. (A) Peak braking/propulsive force (BW), where positive is propulsive force and negative is braking force. (B) Peak tangential force (BW), where positive is push force and negative is pull force. Significant differences were tested with an ANCOVA on log-transformed data if the force on any limb was significantly correlated with speed, or with Kruskal–Wallis tests if speed was not significantly correlated or when there was an interaction between speed and limb (see Materials and methods and Tables 2 and 3). \* $P < 0.05$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ . For detailed means and standard deviations, see Table 4. For sample sizes, see Table S1.

Net impulse tangential forces exhibited no correlations with speed for any species or limb (Table 2). Almost all net impulse tangential forces showed a significant differentiation between the limbs (range  $P < 0.0001$  to 0.0079), save for *L. tardigradus* and *S. sciureus* (Table 4, Fig. 4). Most species exhibited pushing by the hindlimbs and pulling by the forelimbs, although this pattern was variable at small body masses. At body masses of 1 kg and larger, the average net impulse tangential force was positive (push) for the hindlimbs and negative (pull) for the forelimbs.

### Walking peak forces

#### Propulsive (fore–aft; braking–propulsive; along long axis of substrate)

There are limited correlations with speed for any limb and species in this sample. *Nycticebus pygmaeus* exhibited a significant correlation with speed by the hindlimbs during walking, but the slope of this correlation is less than 1, whereas *D. madagascariensis* exhibited a significantly negative slope for this variable (Table 2). *Aotus* spp. exhibited significant correlations with speed for both

limbs in the braking direction, with the forelimbs slope almost twice in magnitude as that of the hindlimbs.

Almost all species exhibited significant functional differences in the role of the limbs in terms of braking and propulsion. In all species except *E. mongoz*, the forelimbs contributed significantly higher braking force than the hindlimbs (range:  $P < 0.0001$  to 0.0208). In contrast, the hindlimbs contributed significantly higher propulsive forces than the forelimbs (range:  $P < 0.0001$  to 0.0441), except in *L. tardigradus* and *E. mongoz*, which did not exhibit a functional differentiation of the limbs during propulsion (Table 4).

#### Tangential (push/pull) (vertical force; normal to substrate)

All species exhibited significant differences between the forelimbs and hindlimbs in terms of peak weight bearing (range  $P < 0.0001$  to 0.0045; Table 4). All species except the lorises bore more peak weight on the hindlimbs than on the forelimbs, with the lorises exhibiting the opposite pattern. No species exhibited pull forces during walking (Table 4).

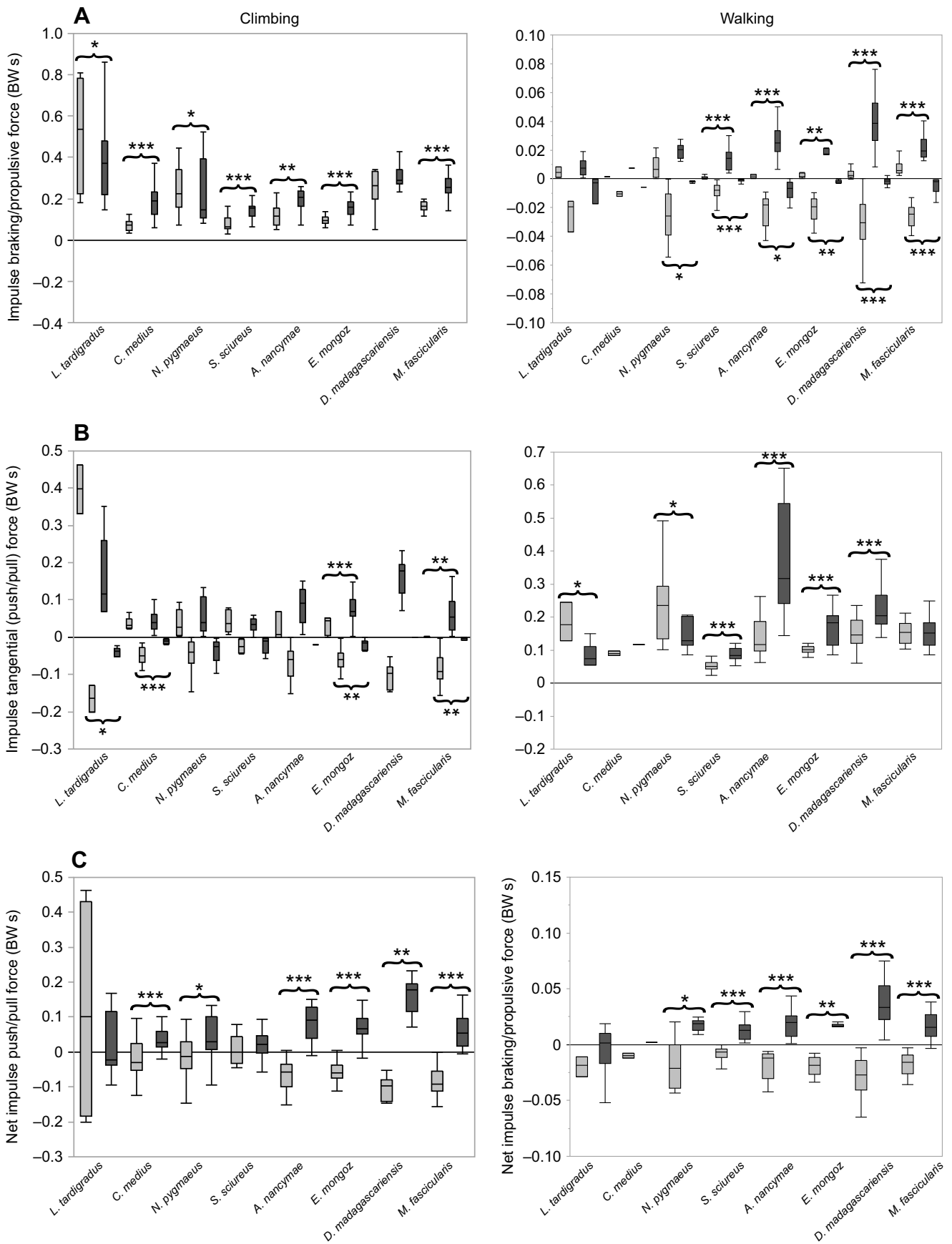


Fig. 4. See next page for legend.

**Fig. 4. Box and whisker plots of the impulse forces within species across limbs.** The light gray boxes represent the forelimb, the dark gray represent the hindlimb. (A) Impulse/propulsive force as a ratio to body weight seconds (BWS), where positive is propulsive force and negative is braking force. (B) Impulse tangential force (BWS), where positive is push force and negative is pull force. (C) Net impulse of forces (BWS) in which positive and negative tangential impulses in the same trial were exhibited, and summed for the net results. Significant differences were tested with an ANCOVA on log-transformed data if the force on any limb was significantly correlated with speed, or with Kruskal–Wallis tests if speed was not significantly correlated or when there was an interaction between speed and limb (see Materials and methods and Tables 2 and 3). \* $P < 0.05$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ . For detailed means and standard deviations, see Table 4. For sample sizes, see Table S1.

### Walking impulse forces

#### Propulsive (along long axis of substrate)

Few species exhibited a significant correlation between speed and impulse propulsive or braking force on the limbs. *Saimiri sciureus* exhibited a significant correlation with speed in the braking direction for the hindlimbs, while *N. pygmaeus* and *D. madagascariensis* exhibited this same correlation for impulse propulsive force (Table 3). Additionally, *N. pygmaeus* exhibited significant correlations for both the forelimbs and hindlimbs in the braking direction.

All species but *L. tardigradus* and *C. medius* exhibited significant functional differentiation of the limbs in terms of both braking and propulsive impulse forces (range:  $P < 0.0001$  to 0.0024; Table 4). This differentiation suggests that the hindlimbs are net propulsive and the forelimbs are net braking. Examination of the net impulse braking/propulsive forces generally revealed no correlations with speed for any species or limb (Table 2). Almost all net impulse braking/propulsive forces showed a significant differentiation between the limbs (range  $P < 0.0001$  to 0.0032), save for *L. tardigradus* and *C. medius* (Table 4, Fig. 4). Most species exhibited net propulsive forces by the hindlimbs and net braking forces by the forelimbs, although this pattern was variable at small body masses (Fig. 4).

#### Tangential (push/pull) (vertical; normal to the substrate)

During walking, there are few significant correlations with speed in terms of the tangential impulse force. *Nycticebus pygmaeus* and *Aotus* spp. exhibited significant correlations in the push direction by the forelimbs, while *S. sciureus*, *Aotus* spp., *E. mongoz* and *M. fascicularis* exhibited the same by the hindlimbs (Table 3). As there were no pull forces by the limbs during walking, no correlations were exhibited with speed for this comparison. All species except *C. medius* and *M. fascicularis* exhibited a functional differentiation between the limbs for the impulse tangential force (range  $P < 0.0001$  to 0.0304; Table 4). As with the peak tangential force, the hindlimbs bore more weight than the forelimbs, except by *L. tardigradus*, in which the opposite pattern was observed.

## DISCUSSION

### Hypothesis: equal propulsion by forelimb/hindlimb during climbing

Contrary to predictions, all species except *Daubentonia madagascariensis* exhibit a significant difference between the limbs in peak propulsion during vertical climbing. In most species, the hindlimbs are the primary limbs used to drive the animal upward. Only lorises rely more heavily on their forelimbs for this peak propulsion effort, but they exhibit no difference in total (impulse) propulsive force between the limbs. Thus, it appears that the propulsive role of the hindlimbs during climbing is similar to the pattern exhibited during walking. Impulse propulsive forces during climbing also show a

similar pattern of significant difference in limb use. In addition to the propulsive role of the hindlimbs (in most cases), the hindlimbs are also used mainly in compression during propulsion, while the forelimbs are used in tension during propulsion, as illustrated by the tangential forces pattern (discussed below). Thus, climbing is a hindlimb-dominated locomotor mode in most primates, and the use of the hindlimbs to overcome gravity and propel the animal upwards may have facilitated the primary compressive weight-bearing role of the hindlimbs during walking.

### Hypothesis: forelimbs pull on the substrate while hindlimbs push during climbing

As predicted, both the peak and impulse climbing data suggest that as primates increase in mass, the limbs become profoundly functionally differentiated in terms of the tangential force. Net impulse tangential data illustrate this pattern even more clearly. Primates larger than 1 kg appear to use the forelimbs mainly in tension (tangential force='pull') and the hindlimbs mainly in compression (tangential force='push'). This pattern is predicted by Preuschoft (2002, fig. 2, options a and b), who described that during climbing, the gravitational force is resisted by the forelimbs as they are used in tension and the hindlimbs as they are used in compression. In contrast, smaller primates appear able to use their limbs, particularly their hindlimbs, to both push and pull. This result approximates the 'statically undetermined' situation described by Preuschoft (2002; p. 181), in which both limbs can change tensile and compressive roles depending on muscle contraction and limb placement, with less rotation away from the substrate than in the former situation. This statically undetermined situation is in contrast to data during climbing from other animals of small size. For example, geckos use their forelimbs primarily in tension during climbing, and although peak tangential forces of the hindlimbs indicate they both push and pull with their hindlimbs, impulse forces indicate a net compressive force by the hindlimbs (Autumn et al., 2006; Wang et al., 2015a,b). Additionally, grasping chameleons (Krause and Fischer, 2013) and *Monodelphis domestica* (Lammers et al., 2006) may follow a similar pattern of increased reliance on tensile force by the forelimbs as incline increases, in that forelimb tangential force decreases with increasing incline.

Our results suggest a greater behavioral flexibility to the arboreal environment by small primates than other animals, perhaps because of their grasping hands and feet and their small size. The primates in our sample, unlike clawed animals and those with adhesive pads, must be able to grip vertical substrates, and in this study, were able to grip almost completely around the substrate. We believe such grasping around a substrate requires greater mechanical flexibility in terms of the use of the forelimbs and hindlimbs during climbing. Claws permit a more consistent interface with the substrate, whereas grasping extremities must adjust their interface every contact period, requiring the limbs to adapt constantly. However, as primates increase in size, they must overcome greater moments about the limbs during climbing, regardless of being able to grip around a substrate. It may be that smaller primates (those 1 kg or less) are able to generate enough force to overcome these rotational moments and climb in the 'statically undetermined' manner described by Preuschoft (2002), whereas larger primates are constrained, even though they have grasping extremities, to resisting gravitational forces by using the forelimbs in tension and the hindlimbs in compression. However, as body size increases, the cross-sectional area of limb muscles does not increase at the same rate (scaling factor of less than 1) (Alexander et al., 1981), whereas the forces

required for climbing are proportional to body mass (Alexander 2005). The results of the present study further support Alexander's proposal that climbing should be more difficult for larger animals, in that at body masses greater than 1 kg, grasping primates appear constrained to rely on the hindlimbs to a greater degree.

### Hypothesis: similarity of force patterns between climbing and walking

Kinetic data during horizontal walking by primates are available for many species (Demes et al., 1994; Larson, 1998; Schmitt, 2003; Schmitt and Hanna, 2004; Schmitt and Lemelin, 2004; Franz et al., 2005; Larson and Demes, 2011; O'Neill and Schmitt, 2012; Young, 2012; Granatosky et al., 2016a,b). Our data on horizontal walking concur with these studies, and add to the literature by presenting the ground reaction force data during walking in *Aotus* species and *D. madagascariensis*. These previously unexamined species follow the standard mammalian pattern of anterior/posterior forces, with a greater reliance on the forelimbs for (peak and impulse) braking forces and the hindlimbs for (peak and impulse) propulsive forces. Additionally, they follow the standard primate-like pattern of body weight support, with greater reliance on the hindlimbs for support of body weight (both tangential force peak and impulse).

Our data show that limb differentiation is conserved between locomotor modes in the large primates examined, including *Ateles fusciceps* and *Macaca fuscata* from Hirasaki et al. (1993). To our knowledge, no other species examined to date shows a consistent pattern of conservation of tangential limb force patterns between walking and climbing, even other animals that use complex three-dimensional environments [e.g. *Monodelphis domestica* (Lammers et al., 2006), *Gecko gecko* (Wang et al., 2015a,b), *Hemidactylus garnotti* (Autumn et al., 2006) and *Chameleo calyptratus* (Krause and Fischer, 2013)]. Large primates conserve their limb differentiation in the tangential (normal to the substrate) direction between walking and climbing, but by relying on the hindlimbs more in compression, their hindlimbs also play a primary role in propulsion. To analogize these two orthogonal forms of locomotion, it appears that the hindlimbs play the largest role in weight bearing and force production, taking both propulsive and tangential forces into account, during climbing and during horizontal locomotion. It may be the case that during climbing, the hindlimbs produce more force overall in most primate species than they do during walking. In this context, we propose that these results suggest that the unusual forelimb/hindlimb differentiation during walking in primates is a basal pattern derived from their early adoption of thin-branch arborealism that included the need to ascend such small branches through reliance on the hindlimbs.

Most primates in this study, including small (i.e. *Cheirogaleus*) and large-bodied (i.e. *Macaca*) species, show a pattern of hindlimb reliance during both forms of locomotion, possibly leaving the forelimbs more available to adjust to changes in substrate and to acquire food, as was suggested by Jones (1916) and explored by many studies thereafter (Kimura et al., 1979; Reynolds, 1985; Schmitt, 1999; Schmitt and Lemelin, 2002, 2004; Wallace and Demes, 2008; Hanna and Schmitt, 2011a; Granatosky et al., 2016b). Even lorises appear to conserve their limb differentiation between locomotor modes. During climbing, they exhibit propulsive or force differentiation of the limbs similar to the tangential forces during walking. In contrast, their tangential forces during climbing show a greater reliance on the hindlimbs. Because these primates are able to ascend in a 'statically undetermined' (Preuschoft, 2002) manner, we suggest that there is no absolute requirement to always be prepared for using the forelimbs in tension in small primates. Thus, during

walking locomotion, lorises may be able to exhibit the standard mammalian force pattern in terms of weight bearing, because they are able to climb in a more mechanically flexible manner on thin branches. Alternatively, the lorisid pattern of weight bearing during walking may simply be a derived trait that is a result of their relatively long limbs and prehensile abilities, as argued previously by Schmitt and Lemelin (2004). Further speculation for the lorises' odd limb-loading behavior is beyond the scope of this study.

The suggestion that climbing may be responsible for certain aspects of the relatively unusual pattern of primate quadrupedal walking mechanics – diagonal sequence footfall patterns, protracted humeral angles at touchdown and hindlimb-biased weight support (Schmitt, 2003; Schmitt and Lemelin, 2004; Wallace and Demes, 2008; Granatosky et al., 2016a) – is not a new idea. As originally reported by Vilensky and colleagues (1994), and later supported by Nyakatura and colleagues (2008), increasing support inclination also increases the presence of diagonal sequence gaits (each hindlimb footfall is followed by a contralateral forelimb footfall, i.e. the feet touch down in the order of right hindlimb, left forelimb, left hindlimb, right forelimb) over lateral sequence gaits (likely the primitive tetrapod footfall sequence in which hindlimb footfall is followed by an ipsilateral forelimb footfall, i.e. the feet touch down in the order of right hindlimb, right forelimb, left hindlimb, left forelimb). A diagonal sequence gait pattern maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod, and allows the center of mass to be contained within the base of support and reduces the risk of falling off or rotating around the support during climbing (Cartmill et al., 2002). Vilensky et al. (1994) proposed that as climbing became more important to the locomotor repertoire of primitive primates, the frequency of diagonal sequence gait utilization also increased, until animals commonly began using this gait on level as well as vertical surfaces. In the same vein, it seems possible that as climbing behavior became more common in primitive primates, the loading pattern observed during climbing (i.e. forelimbs primarily tensile loading, and hindlimbs primarily compressive and propulsive loading) could have resulted in functional and morphological changes between the limbs. This, in turn, would have made assuring hindlimb weight support bias an important consideration during other forms of locomotion (i.e. level quadrupedal locomotion) as well. Future work exploring forelimb protraction during climbing and quadrupedal walking in primates should be undertaken to assess the possibility that climbing gave rise to the unusual locomotor patterns observed in primates.

### Limitations

Our study does have limitations, which should be explored in further works. First, our data do not permit for an understanding of how the forelimb and hindlimb forces balance each other during a single stride of climbing. This limitation is because only single limb forces were collected owing to equipment limitations and the unusual footfall sequence exhibited by many primates (i.e. diagonal sequence gaits) (Larson et al., 2001; Schmidt, 2005; Cartmill et al., 2007). Some of the variation observed in our data may be due to our inability to capture how forelimb and hindlimb forces balance each other within a single stride during climbing.

Second, these data do not provide much information on how primates control pitching/rotational moments away from or into the substrate during climbing, and whether tangential forces during climbing can be compared with the same during horizontal movement. In the larger primates, pitch appears to be balanced by the tangential forces, but this may not be the case during horizontal locomotion, as pitch is likely mostly balanced by gravity



[although see Walter and Carrier (2009) for models describing how tangential force influences pitch]. However, tangential forces certainly play a role in how limbs are prepared to bear the reaction forces, and hindlimbs prepared to bear greater compressive forces during climbing would certainly prepare them for the same during horizontal walking. Without the kinematics of each limb during a stride, an understanding of the functional differentiation of the limbs is incomplete.

Finally, the 1 kg threshold that our data reveal in terms of a clear differentiation of the roles of the limbs is in contrast to the current understanding about the body size of the earliest primates based on the fossil record (e.g. Bloch et al., 2007; Silcox et al., 2007; Ni et al., 2013; Chester et al., 2015). Future studies ought to include additional primate taxa of less than 1 kg that are not as derived as lorises, such as *Microcebus* or other *Cheirogaleus* species. Despite these limitations, the data presented here provide a general overview of the force pattern of limb use during climbing, and provide a comparison to the multitude of studies on single-limb forces during horizontal walking in primates and other animals. Whether it is appropriate to analogize similar roles of each cardinal force during the different forms of locomotion remains to be seen.

## Conclusions

These data are the largest collection of climbing kinetic data across an order of magnitude in body size in primates. Additionally, this represents one of the few works to compare the kinetics of primate vertical climbing with what is observed during quadrupedal locomotion. Our data on quadrupedal walking in primates support the tendency of hindlimb-biased weight support in all species except the lorises. Additionally, all species demonstrate the quadrupedal pattern of a net braking forelimb and a net propulsive hindlimb. During climbing, however, both the forelimbs and the hindlimbs serve a propulsive function, although the hindlimbs tend to provide most of the gravity-resisting propulsive forces. Similar to level quadrupedal walking, the hindlimbs tend to support highest compressive forces during climbing. In contrast, forelimb forces during climbing tend to be primarily tensile. This functional disparity appears to be greater in larger-bodied animals, which may suggest some level of mechanical flexibility in the limb-loading patterns of smaller-bodied primates. The tensile loading of the forelimbs versus the compressive loading of the hindlimbs observed during climbing may have important evolutionary implications for primates, and it may be the case that hindlimb-biased weight support exhibited during quadrupedal walking in primates may be derived from their basal condition of climbing thin branches.

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## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: J.B.H., M.C.G., D.S.; Methodology: J.B.H., M.C.G.; Validation: J.B.H., D.S.; Formal analysis: J.B.H., P.R., D.S.; Investigation: J.B.H., M.C.G., P.R., D.S.; Resources: J.B.H., D.S.; Data curation: J.B.H., M.C.G., P.R., D.S.; Writing - original draft: J.B.H., M.C.G., D.S.; Writing - review & editing: J.B.H., M.C.G., P.R., D.S.; Visualization: J.B.H.; Supervision: J.B.H., D.S.; Project administration: J.B.H.; Funding acquisition: J.B.H., M.C.G., D.S.

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## Supplementary information

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