

THE EVOLUTION OF VERTICAL CLIMBING IN PRIMATES: EVIDENCE FROM REACTION FORCES

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SUMMARY STATEMENT

The article describes the force profiles of climbing in a broad array of primates and compares these data to the unusual walking forces exhibited by the same species.

ABSTRACT

Vertical climbing is an essential behavior for arboreal animals, yet limb mechanics during climbing are poorly understood and rarely compared to 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 to 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 hindlimb produced greater propulsive forces than the forelimb during climbing. During climbing, the hindlimb tends 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 forelimb versus the compressive loading of the hindlimb 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.

INTRODUCTION

Climbing, often on vertical supports, is a critical 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, 3-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 forelimb and hindlimb, 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 would drive the evolution of this pattern. It is possible that some features that define the walking gaits of the Order 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, on the other hand, 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 if 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 et al (2008; 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 to the cost of horizontal movement. This result was consistent with an earlier seminal study by Taylor and colleagues (1972) with chimpanzees. Hanna et al. (2008; 2011b) proposed that this difference in cost of movement was explained by the fact that during horizontal locomotion, the primary determinant of energetic costs is the rate at which work is accomplished (i.e. Joules per second, 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 horizontal movement, though this differentiation does not necessarily parallel the pattern seen during walking since 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; Wang et al., 2015b). In comparison, during horizontal locomotion, the forelimb and hindlimb of lizards propel the body forward to the same degree, but the forelimb bears more weight than the hindlimb (Krause and Fischer, 2013; Wang et al., 2015a; Wang et al., 2015b). 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 degrees (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 hindlimb contributed relatively greater upward propulsion than did the forelimb, 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 (Fleagle, 2013) used hindlimbs for propulsion more than the forelimbs when compared to the more terrestrial Japanese macaque (Fleagle, 2013) 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 influences 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 a 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 to horizontal locomotion in which the hindlimb will be net propulsive and the forelimb net braking.
2. while climbing up a vertical support that 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 to horizontal locomotion where both limbs will exert a tangential “push” on, the substrate. These tangential forces during climbing will be higher on the hindlimb than on the forelimb for all primates except lorises.

MATERIALS AND METHODS

Subjects

Adult *Loris tardigradus*, *Nycticebus pygmaeus*, *Cheirogaleus medius*, *Eulemur mongoz*, *Daubentonia madagascariensis*, *Saimiri sciureus*, *Macaca fascicularis*, *Aotus nancymae*, and *Aotus nyanze* were used in this study (Table 1). All data were attained from animals housed at the Duke Lemur Center & Duke University Vivarium (Durham, NC), Monkey Jungle (Miami, FL), Stony Brook University (Stony Brook, NY), and Michale E. Keeling Center (Bastrop, TX).

Procedures

All procedures were approved by the appropriate institutional IACUCs (WVSOM: 2007-1, 2008-1, 2009-4; Duke: A104-09-03; A130-07-05, A270-11-10; SUNY: 91-94-0131). The data collection procedures have been described extensively elsewhere (Demes et al., 1994; Schmitt and Lemelin, 2002; Schmitt and Hanna, 2004; Schmitt and Lemelin, 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 cm-3.81 cm (Table 1). The middle section of the pole was instrumented to a force transducer (MC3A-6[®]; AMTI, Watertown, MA), or force transducers (9317B; Kistler, Amherst, NY), 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 120 frames per second [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; 2016b), 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 ± 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 1/2 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 (Figure 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, 2 way Butterworth or Fourier filter with a 60 Hz cutoff. 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) was used for all analyses. *Aotus nancymae* and *A. nyanze* 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 Leven'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 FL and HL forces were compared across speed or contact time with ANCOVA (Vickers, 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 by 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 Figure 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 (Table 2). Speed and contact time were highly correlated with one another (Table 2). Thus, we used speed for our analysis with forces. Thus, log-transformed ANCOVAs were calculated for the former, and non-parametric tests were calculated for latter, pairwise comparisons.

Climbing Peak forces

Propulsive (along long axis of substrate)

Peak propulsive forces (along the long axis of the pole) of the FL during climbing were significantly correlated with speed in *Eulemur mongoz*, *Saimiri sciureus*, *Cheirogaleus medius*, and *Loris tardigradus* (range $p < 0.0001$ to $p = 0.047$); in contrast, peak propulsive forces of the HL during climbing were significantly correlated with speed only in *E. mongoz* and *S. sciureus* ($p = < 0.0001$ & $p = 0.029$, respectively) (Table 2).

All species except *Daubentonia madagascariensis* exhibited significant differentiation between limbs in terms of peak propulsive forces during climbing (range: $p < 0.0001$ to $p = 0.030$), with HL typically contributing the greatest propulsive forces downwards, which propels the animal upwards (Table 3; Figure 3). The two exceptions to this pattern are the lorisid species (*Loris tardigradus* and *Nycticebus pygmaeus*) in which the FLs contributed to greater peak propulsion forces to ascend ($p = 0.030$ & $p = 0.0017$, 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, *Loris tardigradus* and *Aotus nancymae* showed a correlation between peak pull force and speed for the HL, but not the FL, while *Macaca fascicularis* exhibited the opposite pattern (Table 2). In contrast, *Nycticebus pygmaeus*, *Eulemur mongoz*, and *Daubentonia madagascariensis* showed correlations between peak push force and speed for the HLs but a correlation between speed and peak pull forces for the FL (Table 2). *Cheirogaleus medius* and *Saimiri sciureus* showed no correlations with speed for either limb in terms of tangential forces (Table 2). All species use both FL and HL to both push into the pole and pull away from the pole (Table 3; Figure 4). However, it is most typical for the HLs to have the highest count of event in which the animal pushed into the substrate, while the FLs have the highest count of number of events in which the animal pulls away from the substrate; for example, in peak tangential forces during climbing, *C. medius* FLs exhibited 33 pulls and only 14 pushes, while the HLs exhibited 47 pushes and only 12 pulls (Table 3). In most cases, the magnitude of peak pushing force by the HLs is significantly greater than the peak pushing force by the FLs (range: $p < 0.0001$ to 0.0137) (Table 3). The exception to this pattern is *N. pygmaeus*, which exhibits significantly larger pushing forces by the FLs than by the HLs 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 FL peak pulling force in half the species is significantly larger in magnitude than the HL peak pulling force (range: $p < 0.0001$ to 0.0011) (Table 3). The other four species, *Loris tardigradus*, *Nycticebus pygmaeus*, *Saimiri sciureus*, and *Aotus 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 FL and very few pulls by the HL (Table 2; Figure 4).

Climbing impulse forces

Propulsive (along long axis of substrate)

Impulse propulsive forces during climbing were significantly correlated with speed in all species but *Macaca fascicularis*, *Saimiri sciureus*, and *Loris tardigradus* FL (Table 2). *Cheirogaleus medius* and *Eulemur mongoz* exhibited a significant interaction between speed and limbs ($p < 0.0001$ & $p = 0.0055$, respectively) and were subsequently analyzed with Kruskal-Wallis test. All species exhibit positive propulsive forces in both limbs at all times and all species except *Daubentonia 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 HL typically contributes the

greatest impulse propulsive forces upwards (Figure 3). The lorises utilized their FLs more than their HLs to propel upwards.

Tangential (Push/Pull) (normal to substrate)

Tangential impulse forces during climbing were not correlated with speed in most cases, except *Eulemur mongoz* exhibited a significant correlation with speed in impulse push for the HL ($p=0.001$), whereas *Cheirogaleus medius* exhibited a significant correlation with speed only in the pull direction and only for the FL ($p=0.0056$) (Table 2). Limb comparisons reveal that the impulses of push and pull forces are typically not significantly different between the limbs, except in the larger species (Table 3). That is, *E. mongoz* and *Macaca fascicularis* show significantly larger pushes by the HL than the FL ($p=0.0015$ & 0.0002 , respectively), and the opposite with pulls ($p=0.0002$ & 0.0004 , respectively). Although *Daubentonia madagascariensis* does 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 FL and only one pull by the HL.

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 *Loris tardigradus* and *Saimiri sciureus* (Table 3; Figure 4). Most species exhibit a push by the HL and a pull by the FL, although this pattern is variable at small body masses. At body masses of 1kg and larger, the average net impulse tangential force is positive (push) for the HLs and negative (pull) for the FLs.

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 HL during walking, but the slope of this correlation is less than 1, whereas *Daubentonia 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 FL slope almost twice in magnitude as the HL.

Almost all species exhibited significant functional differences in the role of the limbs in terms of braking and propulsion. In all cases except *Eulemur mongoz*, the FL contributes significantly higher braking force than the HL (range: $p<0.0001$ to 0.0208). In contrast, the HL contributes significantly higher propulsive forces than the FL (range: $p<0.0001$ to 0.0441), except in *Loris tardigradus* and *E. mongoz*, which do not exhibit a functional differentiation of the limbs during propulsion (Table 3).

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

All species exhibited significant differences between the FL and HL in terms of peak weight bearing (range: $p < 0.0001$ to 0.0045) (Table 3). All species except the lorids bear more peak weight on the HLs than the FLs, with the lorids exhibiting the opposite pattern. No species exhibited pull forces during walking (Table 3).

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 HL, while *Nycticebus pygmaeus* and *Daubentonia madagascariensis* exhibited this same correlation for impulse propulsive force (Table 2). Additionally, *N. pygmaeus* exhibited significant correlations for both the FL and HL in the braking direction.

All species but *Loris tardigradus* and *Cheirogaleus 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 3). This differentiation suggests that the HLs are net propulsive and the FLs are net braking. Examination of the net impulse braking/propulsive forces generally reveals 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 *Loris tardigradus* and *Cheirogaleus medius* (Table 3; Figure 4). Most species exhibit net propulsive forces by the HL and net braking forces by the FL, although this pattern is variable at small body masses (Figure 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.* exhibit significant correlations in the push direction by the FLs, while *Saimiri sciureus*, *Aotus spp.*, *Eulemur mongoz*, and *Macaca fascicularis* exhibit the same by the HLs (Table 2). As there were no pull forces by the limbs during walking, no correlations were exhibited with speed for this comparison. All species except *Cheirogaleus medius* and *M. fascicularis* exhibit a functional differentiation between the limbs for the impulse tangential force (range: $p < 0.0001$ to 0.0304) (Table 3). As with the peak tangential force, the HL bear more weight than the FL, except by *Loris tardigradus*, in which the opposite pattern is observed.

DISCUSSION

Hypothesis: Equal propulsion by FL/HL during climbing

Contrary to predictions, all species except the aye-aye exhibit a significant difference between the limbs in peak propulsion during vertical climbing. In most species the hindlimb is the primary limb used to drive the animal upward. Only lorises rely more heavily on their FLs 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 hindlimb 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 HL (in most cases), the HLs are also used mainly in compression during propulsion, while the FLs 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 HLs to and overcome gravity and propel upwards may have facilitated the primary compressive weight-bearing role of the hindlimb during walking.

Hypothesis: FL Pull on the substrate while HL 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 FL mainly in tension (tangential force="Pull") and the HLs mainly in compression (tangential force="Push"). This pattern is predicted by Preuschoft (2002) as in his figure 2, options a and b, describing that during climbing the gravitational force is by the forelimbs as they are used in tension and the hindlimbs as they are used in compression. On the other hand, smaller primates appear able to use their limbs, particularly their HL, to both Push and Pull. This result approximates the "statically undetermined" situation described by Preuschoft (2002; pg. 181), in which the both limbs can change tensile and compressive roles depending on muscle contraction and limb placement, with less rotational moments away from the substrate than in the former situation. This statically undetermined situation is in contrast to data during climbing by other animals at small sizes. For example, geckos use their FLs primarily in tension during climbing, and although peak HL tangential forces indicate they both push and pull with their HLs, impulse forces indicate a net compressive force by the HLs (Autumn et al., 2006; Wang et al., 2015a; Wang et al., 2015b). 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 FLs as incline increases, in that FL 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 fore- 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 1kg 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 (2005). The results of this study further support his proposal that climbing should be more difficult for larger animals, in that at body masses greater than 1kg, 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; Granatosky et al., 2016b). Our data on horizontal walking concur with these studies, and add to the literature by presenting the ground reaction force data during walking on *Aotus* species and *Daubentonia madagascariensis*. Both of these previously unexamined species follow the standard mammalian pattern of anterior/posterior forces, with a greater reliance on the FL for (peak and impulse) braking forces and the HL for (peak and impulse) propulsive forces. Additionally, they both follow the standard primate-like pattern of body weight support, with greater reliance on the HLs 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 3-dimensional environments (e.g. *Monodelphis domestica* [(Lammers et al., 2006)], *Gecko gecko* [(Wang et al., 2015a; Wang et al., 2015b)], *Hemidactylus garnotti* [(Autumn et al., 2006)] & *Chameleo calyptratus* [(Krause and Fischer, 2013)]). Not only do large primates conserve their limb

differentiation in the tangential (normal to the substrate) direction between walking and climbing, by relying on the HLs more in compression, the hindlimb also plays a primary role in propulsion. To analogize these two orthogonal forms of locomotion, it appears that the hindlimb plays 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 overall more force in most primate species than it does during walking. In this context, we propose these results suggest that the unusual FL/HL 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 HLs.

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 change 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. On the other hand, their tangential forces during climbing show a greater reliance on the HLs. Since 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 FLs 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 lorise 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 Lemelin and Schmitt (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 COM 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., forelimb primarily tensile loading, and hindlimb 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 trio 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 due 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 fore- 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 to 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 Carrier 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 1kg 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 species of less than 1kg than are not as derived as lorises, such as *Microcebus* or more *Cheirogaleus*. Despite these limitations, the data presented here provide a general overview of the force pattern of limb use during climbing, and provide for a comparable 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 to what is observed during quadrupedal locomotion. Our data on quadrupedal walking in primates supports the tendency of hindlimb-biased weight support in all species except the lorises. Additionally, all species demonstrate the quadruped pattern of a net braking forelimb and a net propulsive hindlimb. During climbing, however, both the forelimb and the hindlimb serve a propulsive function, although the hindlimb tends to provide most of the gravity-resisting propulsive forces. Similar to level quadrupedal walking, the hindlimb tends 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 forelimb versus the compressive loading of the hindlimb 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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Table 1. Summary characteristics of sample

Species	Individual	Type of locomotion (substrate diameter in cm)		Body mass (kg)	Sex	Date of Birth (DD/MM/YYYY)	Location
<i>L. 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>C. 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>N. pygmaeus</i>	1	Climb (1.27)	Walk (1.27)	0.64	Male	1/6/2006	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	4/3/2002	Duke Lemur Center
<i>S. 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>A. nancymae/nyanze</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>E. 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>D. 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	6/1/1998	Duke Lemur Center
	4		Walk (3.18)	2.86	Male	5/6/1994	Duke Lemur Center
	5		Walk (3.18)	3.02	Female	15/04/1996	Duke Lemur Center
<i>M. 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

Table 2. Least-squares regressions of speed and contact time* and peak forces (BW) or impulse forces (BWS).

			Peak braking			Peak propulsive			Peak push			Peak pull		
			Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value
<i>L. tardigradus</i>	Walking	FL	- (5)	-	0.9444	- (5)	-	0.6036	- (5)	-	0.6027			
		HL	- (7)	-	0.6431	- (7)	-	0.2408	- (7)	-	0.3521			
	Climbing	FL				0.366 (27)	0.166	0.0349	- (16)	-	0.968	- (10)	-	0.8624
		HL				- (33)	-	0.9943	- (17)	-	0.9815	-0.351 (18)	0.321	0.0142
<i>C. medius</i>	Walking	FL	- (7)	-	0.9291	- (7)	-	0.753	- (7)	-	0.6752			
		HL	-0.071 (6)	0.683	0.0425	- (6)	-	0.8883	0.142 (6)	0.81	0.0145			
	Climbing	FL				0.385 (46)	0.343	<0.0001	- (14)	-	0.6574	- (33)	-	0.0645
		HL				- (56)	-	0.4457	- (47)	-	0.0502	- (12)	-	0.7176
<i>N. pygmaeus</i>	Walking	FL	- (14)	-	0.4886	- (14)	-	0.4201	- (14)	-	0.1366			
		HL	- (8)	-	0.4323	0.076 (8)	0.667	0.0134	0.195 (8)	0.557	0.0335			
	Climbing	FL				- (50)	-	0.1669	- (28)	-	0.3974	-0.318 (33)	0.186	0.0123
		HL				- (50)	-	0.0582	0.365 (47)	0.228	0.0007	- (8)	-	0.9109
<i>S. sciureus</i>	Walking	FL	- (51)	-	0.8377	- (51)	-	0.4105	0.175 (51)	0.113	0.0159			
		HL	- (27)	-	0.156	- (27)	-	0.9041	- (27)	-	0.3436			
	Climbing	FL				0.530 (12)	0.339	0.0471	- (7)	-	0.6162	- (7)	-	0.7364
		HL				0.607 (18)	0.264	0.029	- (14)	-	0.0649	- (6)	-	0.4113
<i>A. nancymae/nyanze</i>	Walking	FL	-0.333 (12)	0.518	0.0083	- (12)	-	0.2903	- (17)	-	0.1509			
		HL	-0.135 (16)	0.389	0.0099	- (16)	-	0.9489	- (19)	-	0.3069			
	Climbing	FL				- (16)	-	0.1748	- (4)	-	0.2897	- (13)	-	0.8816
		HL				- (16)	-	0.1581	- (16)	-	0.9497	0.617 (3)	0.995	0.0432
<i>E. mongoz</i>	Walking	FL	- (11)	-	0.8034	- (11)	-	0.8306	- (19)	-	0.0769			
		HL	- (7)	-	0.572	- (7)	-	0.1075	- (13)	-	0.1817			
	Climbing	FL				0.288 (61)	0.553	<0.0001	- (11)	-	0.2798	-0.222 (56)	0.189	0.0008
		HL				0.312 (74)	0.309	<0.0001	0.305 (68)	0.369	<0.0001	- (9)	-	0.3094
<i>D. madagascariensis</i>	Walking	FL	- (46)	-	0.6942	- (46)	-	0.3893	- (46)	-	0.1911			
		HL	- (28)	-	0.0853	-0.162 (28)	0.256	0.006	- (28)	-	0.8501			
	Climbing	FL				- (8)	-	0.6096	- (2)	-	-	-0.216 (7)	0.864	0.0024
		HL				- (28)	-	0.6072	0.403 (28)	0.261	0.0055	- (2)	-	-
<i>M. fascicularis</i>	Walking	FL	- (19)	-	0.8361	- (19)	-	0.8712	- (19)	-	0.1841			
		HL	- (14)	-	0.0903	- (14)	-	0.1952	- (14)	-	0.2413			
	Climbing	FL				- (22)	-	0.2357	0.104 (7)	0.69	0.0206	- (22)	-	0.7936
		HL				- (34)	-	0.726	- (33)	-	0.4516	- (9)	-	0.0863

Table 2 continued.

			Impulse braking			Impulse propulsive			Net braking/propulsive			Impulse push			Impulse pull			Net impulse push/pull		
			Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value	Slope (n)	R ²	P-value
<i>L. tardigradus</i>	Walking	FL	- (3)	-	0.3041	- (3)	-	0.1279	- (3)	-	0.4632	- (3)	-	0.0811						
		HL	- (7)	-	0.2434	- (6)	-	0.3908	- (7)	-	0.1942	- (7)	-	0.0717						
	Climbing	FL				- (4)	-	0.2887				- (2)	-	-	- (2)	-	-	- (4)	-	0.4419
		HL				-1.419 (11)	0.697	0.0014				- (5)	-	0.4886	- (6)	-	0.9527	- (11)	-	0.3217
<i>C. medius</i>	Walking	FL	- (2)	-	-	- (0)	-	-	- (2)	-	-	- (2)	-	-						
		HL	- (1)	-	-	- (1)	-	-	- (1)	-	-	- (1)	-	-						
	Climbing	FL				-0.100 (32)	0.236	0.0048				- (10)	-	0.2172	-0.085 (22)	0.325	0.0056	- (32)	-	0.9318
		HL				-0.351 (40)	0.643	<0.0001				- (32)	-	0.1946	- (9)	-	0.2661	- (39)	-	0.4989
<i>N. pygmaeus</i>	Walking	FL	0.037 (11)	0.577	0.0067	- (11)	-	0.6933	- (11)	-	0.0578	-0.274 (11)	0.644	0.0029						
		HL	-0.002 (7)	0.577	0.0475	-0.014 (7)	0.66	0.0264	-0.016 (7)	0.764	0.0101	- (7)	-	0.0573						
	Climbing	FL				-0.985 (27)	0.615	<0.0001				- (15)	-	0.3573	- (18)	-	0.2166	- (27)	-	0.714
		HL				-0.758 (23)	0.54	<0.0001				- (21)	-	0.1584	- (6)	-	0.3388	- (23)	-	0.4901
<i>S. sciureus</i>	Walking	FL	- (51)	-	0.1875	- (51)	-	0.073	- (51)	-	0.489	- (51)	-	0.238						
		HL	0.005 (27)	0.157	0.041	- (27)	-	0.612	- (27)	-	0.8825	-0.096 (27)	0.18	0.0272						
	Climbing	FL				- (10)	-	0.5492				- (5)	-	0.4574	- (6)	-	0.2807	- (10)	-	0.5356
		HL				-0.141 (17)	0.513	0.0012				- (13)	-	0.8587	- (6)	-	0.1837	- (17)	-	0.2053
<i>A. nancymae/nyanze</i>	Walking	FL	- (12)	-	0.5169	- (12)	-	0.1098	- (12)	-	0.8599	- (12)	-	0.0515						
		HL	- (16)	-	0.4334	- (16)	-	0.8211	- (16)	-	0.7574	-0.477 (16)	0.248	0.0498						
	Climbing	FL					0.891 578	<0.0001				- (3)	-	0.1003	- (12)	-	0.1094	- (13)	-	0.7056
		HL				-0.330 (12)	0.552	0.0056				- (12)	-	0.329	- (1)	-	-	- (12)	-	0.4277
<i>E. mongoz</i>	Walking	FL	- (11)	-	0.086	- (11)	-	0.2031	- (11)	-	0.1421	-0.055 (11)	0.401	0.0365						
		HL	- (7)	-	0.8434	- (7)	-	0.162	- (7)	-	0.1765	-0.108 (7)	0.672	0.024						
	Climbing	FL				-0.045 (51)	0.324	<0.0001				- (6)	-	0.0553	- (47)	-	0.0711	- (51)	-	0.2549
		HL				-0.092 (62)	0.447	<0.0001				-0.051 (56)	0.182	0.001	- (8)	-	0.488	- (62)	-	0.69
<i>D. madagascariensis</i>	Walking	FL	- (46)	-	0.7306	- (46)	-	0.3909	- (46)	-	0.8925	- (46)	-	0.5355						
		HL	- (28)	-	0.2856	-0.046 (28)	0.152	0.0404	-0.051 (28)	0.161	0.0343	- (28)	-	0.5683						
	Climbing	FL				-0.190 (6)	0.92	0.0025				- (0)	-	-	- (6)	-	0.1092	- (6)	-	0.1092
		HL				-0.256 (23)	0.348	0.003				- (23)	-	0.1895	- (1)	-	-	- (23)	-	0.1875
<i>M. fascicularis</i>	Walking	FL	- (19)	-	0.102	- (19)	-	0.4176	- (19)	-	0.3938	- (19)	-	0.0517						
		HL	- (14)	-	0.33	- (14)	-	0.1597	- (14)	-	0.1552	-0.088 (14)	0.445	0.0092						
	Climbing	FL				- (20)	-	0.3269				- (6)	-	0.0861	- (20)	-	0.7679	- (20)	-	0.7723
		HL				-0.078 (31)	0.138	0.0394				- (31)	-	0.2225	- (7)	-	0.6174	- (31)	-	0.2188

Table 3. Mean forces (BW) plus or minus 1 standard deviation.

		<i>L. tardigradus</i>		<i>C. medius</i>		<i>N. pygmaeus</i>		<i>S. sciureus</i>	
		Walking	Climbing	Walking	Climbing	Walking	Climbing	Walking	Climbing
Peak braking	FL	-0.126±0.040*		-0.134±0.037*		-0.103±0.042*		-0.113±0.047***	
	HL	-0.037±0.024		-0.065±0.049		-0.034±0.020		-0.050±0.029	
Peak propulsive	FL	0.046±0.037	0.654±0.106*	0.036±0.023*	0.427±0.104***	0.080±0.053*	0.609±0.086*	0.029±0.024***	0.504±0.192***
	HL	0.136±0.138	0.593±0.094	0.105±0.011	0.754±0.119	0.112±0.026	0.536±0.122	0.138±0.068	1.020±0.243
Peak push	FL	0.787±0.043*	0.236±0.105	0.600±0.038*	0.173±0.071*	0.759±0.085*	0.092±0.044*	0.476±0.067***	0.195±0.131
	HL	0.504±0.078	0.241±0.112	0.756±0.089	0.273±0.120	0.602±0.073	0.165±0.109	0.665±0.076	0.280±0.198
Peak pull	FL		-0.151±0.090		-0.254±0.105**		-0.146±0.104		-0.154±0.125
	HL		-0.113±0.067		-0.120±0.045		-0.086±0.033		-0.145±0.119
Impulse braking	FL	-0.024±0.012		-0.010±0.002		-0.025±0.017*		-0.009±0.005***	
	HL	-0.011±0.019		-		-0.002±0.001		-0.001±0.002	
Impulse propulsive	FL	0.005±0.004	0.515±0.295*	-	0.072±0.033***	0.008±0.008	0.270±0.170*	0.001±0.002***	0.078±0.039***
	HL	0.008±0.007	0.382±0.206	-	0.186±0.074	0.020±0.005	0.225±0.149	0.015±0.009	0.140±0.041
Net braking/propulsive impulse	FL	-0.019±0.009		-0.010±0.003		-0.017±0.020*		-0.008±0.005***	
	HL	-0.004±0.024		-		0.018±0.005		0.013±0.009	
Impulse push	FL	0.184±0.058*	0.397±0.094	0.090±0.009	0.041±0.023	0.242±0.122*	0.046±0.060	0.055±0.020***	0.043±0.031
	HL	0.072±0.064	0.155±0.118	-	0.045±0.029	0.142±0.045	0.069±0.079	0.088±0.026	0.035±0.026
Impulse pull	FL		-0.165±0.051*		-0.050±0.026***		-0.055±0.054		-0.024±0.018
	HL		-0.044±0.026		-0.020±0.028		-0.037±0.034		-0.020±0.023
Net impulse push/pull	FL		0.116±0.330		-0.022±0.050***		-0.011±0.084*		0.007±0.044
	HL		0.046±0.129		0.032±0.039		0.054±0.088		0.020±0.037
Speed (m/sec)	FL	0.784 (0.294)	0.215 (0.116)	0.636 (0.223)****	0.324 (0.159)****	0.748 (0.338)	0.267 (0.135)	0.588 (0.129)	0.490 (0.211)
	HL	0.931 (0.318)	0.243 (0.112)	0.769 (0.566)****	0.362 (0.167)****	0.712 (0.278)	0.266 (0.142)	0.593 (0.116)	0.654 (0.206)
Contact time (1/sec)	FL	0.380 (0.113)	1.088 (0.761)	0.241 (0.066)****	0.323 (0.154)****	0.411 (0.2304)	0.792 (0.465)	0.211 (0.074)	0.320 (0.119)
	HL	0.307 (0.096)	1.006 (0.653)	0.219 (0.035)****	0.329 (0.154)****	0.448 (0.165)	0.753 (0.365)	0.237 (0.062)	0.243 (0.071)

Table 3 continued. Mean forces (BW) plus or minus 1 standard deviation.

		<i>A. nancymae/nyanze</i>		<i>E. mongoz</i>		<i>D. madagascariensis</i>		<i>M. fascicularis</i>	
		Walking	Climbing	Walking	Climbing	Walking	Climbing	Walking	Climbing
Peak braking	FL	-0.113±0.046*		-0.078±0.058		-0.137±0.064***		-0.135±0.027**	
	HL	-0.066±0.037		-0.091±0.055		-0.039±0.028		-0.064±0.051	
Peak propulsive	FL	0.038±0.027***	0.511±0.074**	0.146±0.093	0.629±0.110**	0.044±0.037***	0.568±0.030	0.086±0.037**	0.499±0.054***
	HL	0.107±0.045	0.614±0.060	0.107±0.078	0.703±0.148	0.153±0.061	0.573±0.093	0.136±0.015	0.591±0.100
Peak push	FL	0.485±0.161***	0.211±0.089	0.592±0.112***	0.122±0.058***	0.535±0.091***	0.058±0.016***	0.579±0.076**	0.038±0.019**
	HL	0.744±0.078	0.261±0.135	0.888±0.112	0.363±0.130	0.736±0.082	0.310±0.113	0.672±0.049	0.184±0.121
Peak pull	FL		-0.314±0.155		-0.352±0.138***		-0.245±0.116**		-0.223±0.146*
	HL		-0.063±0.028		-0.093±0.052		-0.020±0.002		-0.033±0.027
Impulse braking	FL	-0.022±0.011*		-0.021±0.009**		-0.031±0.017***		-0.026±0.008***	
	HL	-0.009±0.009		-0.002±0.001		-0.003±0.004		-0.004±0.005	
Impulse propulsive	FL	0.004±0.006***	0.120±0.051**	0.002±0.001**	0.098±0.023***	0.003±0.004***	0.249±0.105	0.008±0.005***	0.168±0.036***
	HL	0.028±0.014	0.194±0.056	0.017±0.007	0.157±0.038	0.042±0.023	0.319±0.070	0.021±0.008	0.260±0.054
Net braking/propulsive impulse	FL	-0.019±0.012***		-0.019±0.009**		-0.028±0.016***		-0.078±0.009***	
	HL	0.019±0.013		0.015±0.007		0.040±0.024		0.017±0.011	
Impulse push	FL	0.137±0.062***	0.025±0.038	0.102±0.027***	0.033±0.023*	0.149±0.047***	-	0.155±0.032	0.002±0.001**
	HL	0.364±0.165	0.084±0.048	0.172±0.059	0.076±0.032	0.225±0.067	0.160±0.048	0.153±0.045	0.062±0.045
Impulse pull	FL		-0.071±0.044		-0.060±0.025**		-0.104±0.035		-0.086±0.053**
	HL		-		-0.020±0.014		-		-0.003±0.003
Net impulse push/pull	FL		-0.060±0.058***		-0.051±0.038***		-0.104±0.035**		-0.085±0.054***
	HL		0.082±0.051		0.066±0.044		0.160±0.048		0.062±0.046
Speed (m/sec)	FL	0.692 (0.155)	0.431 (0.147)	0.856 (0.271)	0.931 (0.283)	0.611 (0.247)*****	0.562 (0.465)****	1.123 (0.171)	0.703 (0.220)
	HL	0.583 (0.183)	0.351 (0.110)	1.077 (0.342)	0.906 (0.263)	0.610 (0.192)****	0.512 (0.143)	1.181 (0.342)	0.741 (0.266)
Contact time (1/sec)	FL	0.583 (0.233)	0.388 (0.124)	0.308 (0.094)	0.275 (0.088)	0.473 (0.093)*****	0.831 (0.284)****	0.512 (0.080)	0.538 (0.131)
	HL	0.744 (0.252)	0.521 (0.130)	0.309 (0.113)	0.308 (0.099)	0.587 (0.163)****	0.867 (0.183)	0.416 (0.096)	0.631 (0.132)

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 **** indicates no significant correlation. ***** Indicates a significant, positive correlation.

Figures

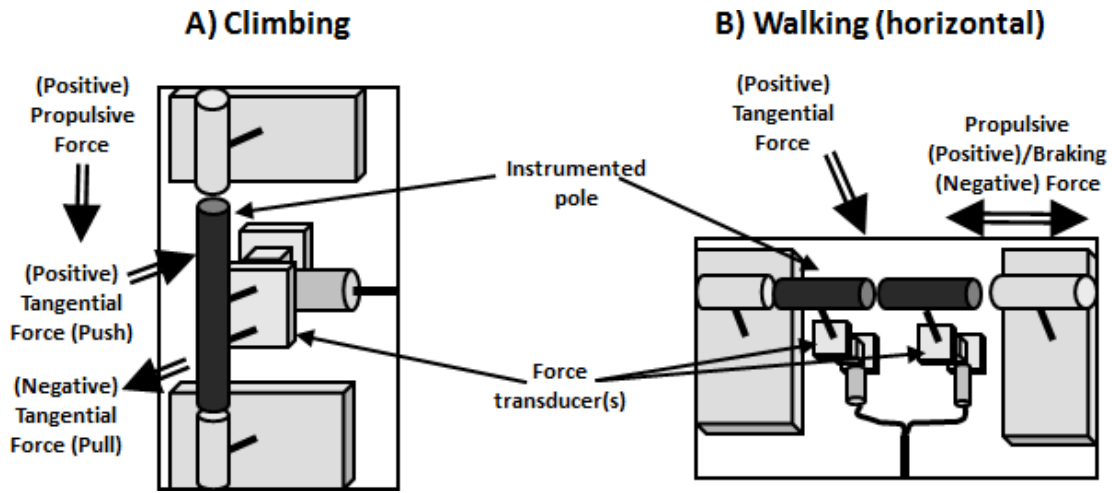


Figure 1. Schematic depicting instrumented pole setups for A) climbing and B) walking trials. A) Depicts a MC3A AMTI force transducer setup, whereas B) depicts a Kistler 9317B force transducer setup. Both types were used during walking trials, but only the AMTI transducer was used during climbing trials. 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.

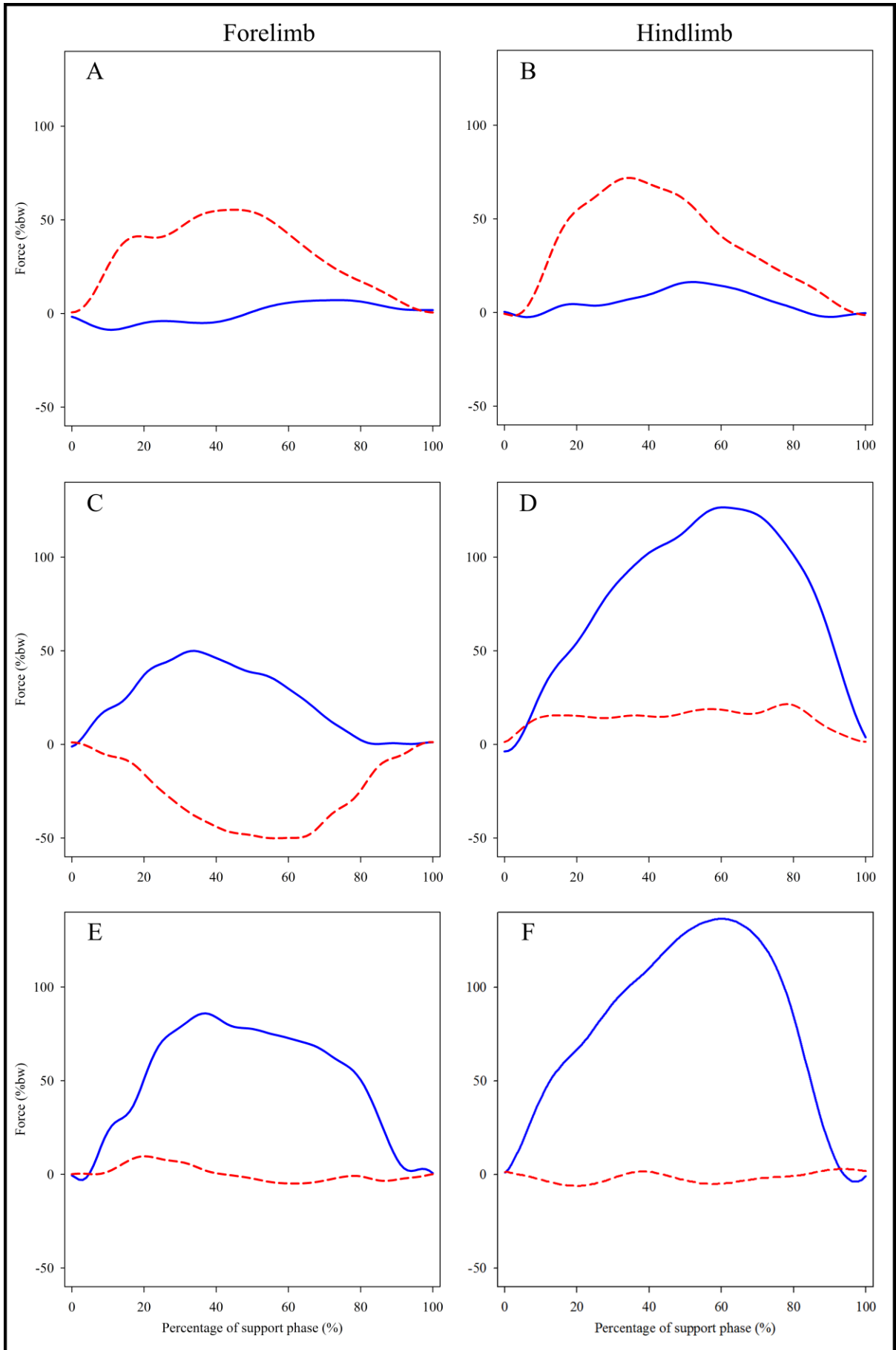


Figure 2. Representative single-limb force traces during walking and climbing by *Saimiri sciureus*. All force data are presented as a percent of body weight and time as a percentage of contact time. The red, dashed line is the tangential force, whereas the blue, solid line is the braking/propulsive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

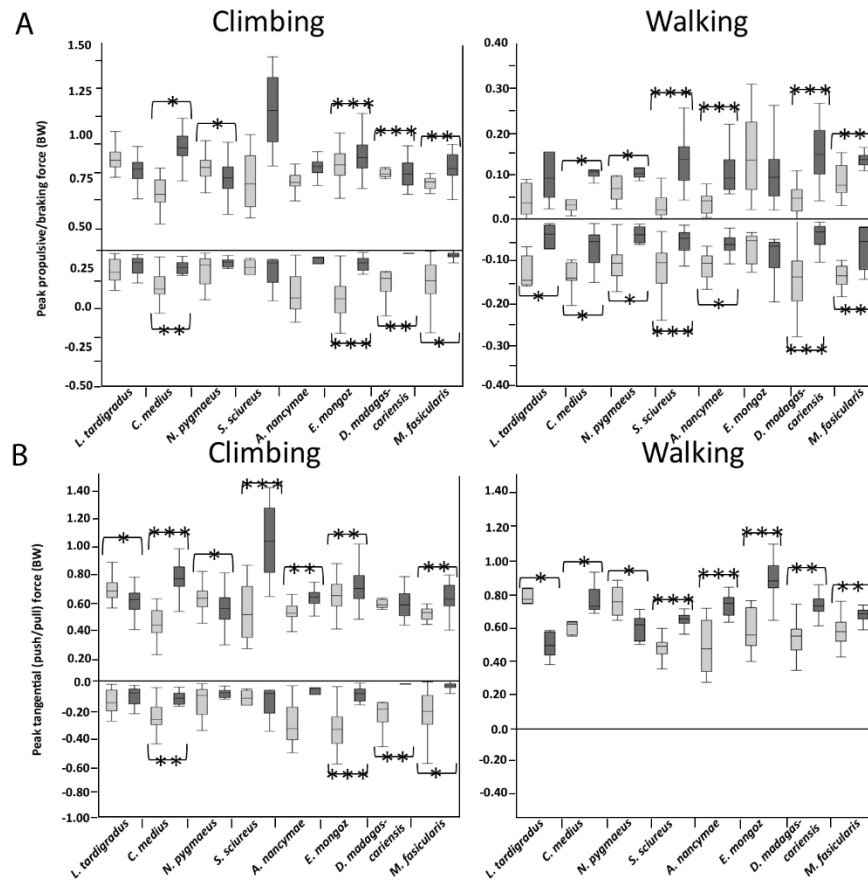


Figure 3. Box and whisker plots of the peak forces within species across limbs. The light grey boxes represent the forelimb, the dark grey represent the hindlimb. A) The peak of braking/propulsive force (BW), where positive is propulsive force, and negative is braking force. B) The peak of tangential 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 methods and Table 2). * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$. For detailed means and standard deviations, see Table 3. For Sample sizes see Table S1.

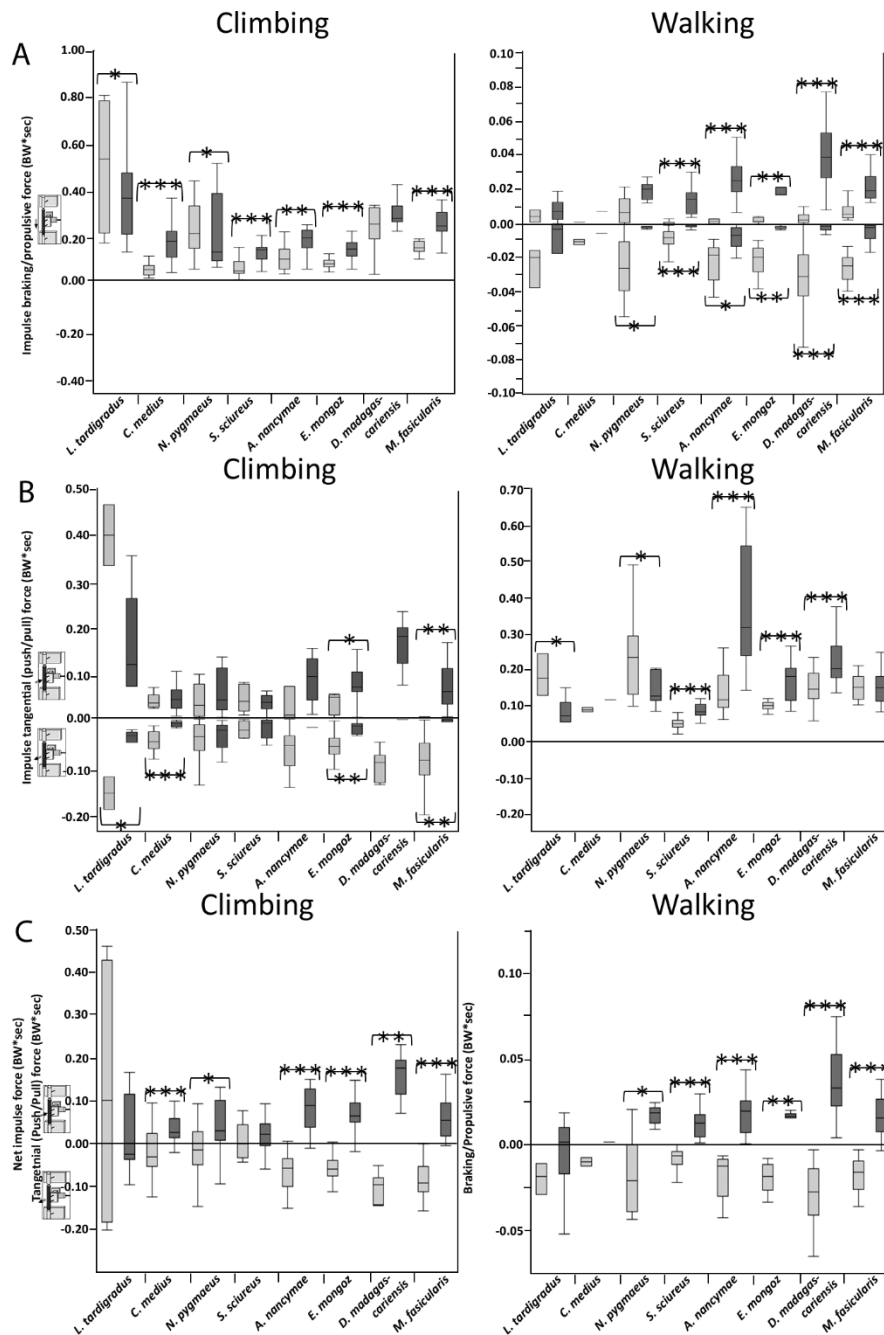


Figure 4. Box and whisker plots of the impulse forces within species across limbs. The light grey boxes represent the forelimb, the dark grey represent the hindlimb. A) The impulse of braking/propulsive force (BW), where positive is propulsive force, and negative is braking force. B) The impulse of tangential force (BW), where positive is push force, and negative is pull force. C) The net impulse of forces (BW) in which positive and negative were exhibited. 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 methods and Table 2). * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$. For detailed means and standard deviations, see Table 3. For Sample sizes see Table S1.

Table S1. Sample sizes for captions of Figures 3 and 4.

Figure 3 Peak Forces	A						B					
	Climbing Propulsive		Walking Propulsive		Walking Braking		Climbing Push		Climbing Pull		Walking Push	
	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL
<i>L. tardigradus</i>	27	33	5	7	5	7	16	17	10	18	5	7
<i>C. medius</i>	46	56	7	6	7	6	14	47	33	12	7	6
<i>N. pygmaeus</i>	50	50	14	8	14	8	28	47	33	8	14	8
<i>S. sciureus</i>	12	18	51	27	51	27	7	14	7	6	51	27
<i>A. nancymae/nyanze</i>	16	16	12	16	12	16	4	16	13	3	17	19
<i>D. madagascariensis</i>	61	74	11	7	11	7	11	68	59	9	19	13
<i>M. fascicularis</i>	8	28	46	28	46	28	2	28	7	2	46	28

Figure 4 Impulse Forces	A						B						C			
	Climbing Propulsive		Walking Propulsive		Walking Braking		Climbing Push		Climbing Pull		Walking Push		Climbing Net Push/Pull		Walking Net Propulsive/Braking	
	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL
<i>L. tardigradus</i>	4	11	3	6	3	7	2	5	2	6	3	7	4	11	3	7
<i>C. medius</i>	32	40	1	1	2	1	10	32	22	9	2	1	32	39	2	1
<i>N. pygmaeus</i>	27	23	11	7	11	7	15	21	18	6	11	7	27	23	11	7
<i>S. sciureus</i>	10	17	51	27	51	27	5	13	6	6	51	27	10	17	51	27
<i>A. nancymae/nyanze</i>	13	12	12	16	12	16	3	12	12	1	12	16	13	12	12	16
<i>D. madagascariensis</i>	51	62	11	7	11	7	6	56	47	8	11	7	51	62	11	7
<i>M. fascicularis</i>	6	23	46	28	46	28	0	23	6	1	46	28	6	23	46	28

Table S1. Sample sizes for captions of Figures 3 and 4.

Figure 3 Peak Forces	A						B					
	Climbing Propulsive		Walking Propulsive		Walking Braking		Climbing Push		Climbing Pull		Walking Push	
	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL
<i>L. tardigradus</i>	27	33	5	7	5	7	16	17	10	18	5	7
<i>C. medius</i>	46	56	7	6	7	6	14	47	33	12	7	6
<i>N. pygmaeus</i>	50	50	14	8	14	8	28	47	33	8	14	8
<i>S. sciureus</i>	12	18	51	27	51	27	7	14	7	6	51	27
<i>A. nancymae/nyanze</i>	16	16	12	16	12	16	4	16	13	3	17	19
<i>D. madagascariensis</i>	61	74	11	7	11	7	11	68	59	9	19	13
<i>M. fascicularis</i>	8	28	46	28	46	28	2	28	7	2	46	28

Figure 4 Impulse Forces	A						B						C			
	Climbing Propulsive		Walking Propulsive		Walking Braking		Climbing Push		Climbing Pull		Walking Push		Climbing Net Push/Pull		Walking Net Propulsive/Braking	
	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL	FL	HL
<i>L. tardigradus</i>	4	11	3	6	3	7	2	5	2	6	3	7	4	11	3	7
<i>C. medius</i>	32	40	1	1	2	1	10	32	22	9	2	1	32	39	2	1
<i>N. pygmaeus</i>	27	23	11	7	11	7	15	21	18	6	11	7	27	23	11	7
<i>S. sciureus</i>	10	17	51	27	51	27	5	13	6	6	51	27	10	17	51	27
<i>A. nancymae/nyanze</i>	13	12	12	16	12	16	3	12	12	1	12	16	13	12	12	16
<i>D. madagascariensis</i>	51	62	11	7	11	7	6	56	47	8	11	7	51	62	11	7
<i>M. fascicularis</i>	6	23	46	28	46	28	0	23	6	1	46	28	6	23	46	28