Patterns of Quadrupedal Locomotion in a Vertical Clinging and Leaping Primate (*Propithecus coquereli*) with Implications for Understanding the Functional Demands of Primate Quadrupedal Locomotion

Michael C. Granatosky,* Cameron H. Tripp, Anne-Claire Fabre, and Daniel Schmitt

Department of Evolutionary Anthropology, Duke University, Durham, NC

ABSTRACT

Objectives: Many primates exhibit a suite of characteristics that distinguish their quadrupedal gaits from non-primate mammals including the use of a diagonal sequence gait, a relatively protracted humerus at touchdown, and relatively high peak vertical forces on the hindlimbs compared to the forelimbs. These characteristics are thought to have evolved together in early, small-bodied primates possibly in response to the mechanical demands of navigating and foraging in a complex arboreal environment. It remains unclear, however, whether primates that employ quadrupedalism only rarely demonstrate the common primate pattern of quadrupedalism or instead use the common non-primate pattern or an entirely different mechanical pattern from either group.
Materials and Methods: This study compared the kinematics and kinetics of two habitually quadrupedal primates (*Lemur catta* and *Varecia variegata*) to those of a dedicated vertical clinger and leaper (*Propithecus coquereli*) during bouts of quadrupedal walking.
Results: All three species employed diagonal sequence gaits almost exclusively, displayed similar degrees of humeral protraction, and exhibited lower vertical peak forces in the forelimbs compared to the hindlimb.
Discussion: From the data in this study, it is possible to reject the idea that *P. coquereli* uses a non-primate pattern of quadrupedal walking mechanics. Nor do they use an entirely different mechanical pattern from either most primates or most non-primates during quadrupedal locomotion. These findings provide support for the idea that this suite of characteristics is adaptive for the challenges of arboreal locomotion in primates and that these features of primate locomotion may be basal to the order or evolved independently in multiple lineages including indriids. Am J Phys Anthropol 160:644–652, 2016.   © 2016 Wiley Periodicals, Inc.

Primates exhibit a remarkable diversity in locomotor capabilities, including a wide range of quadrupedal gaits both on arboreal and terrestrial supports, horizontal leaping and bounding, leaping between vertical supports, and arm-swinging (Napier, 1967; Napier and Napier, 1967; Hunt et al., 1996; Fleagle, 2013). Quadrupedalism, however, remains the most common form of locomotion among primates and is often considered the basal form of locomotion for the order (Rose, 1973; Hunt et al., 1996). All members of the order, with the exception of gibbons (Vereecke et al., 2006), are capable of moving quadrupedally for some distance (Napier and Napier, 1967; Fleagle, 2013). The mechanical characteristics of quadrupedal walking are well-characterized for those primates that are considered habitual quadrupeds (Hildebrand, 1967; Kimura et al., 1979; Vilensky and Larson, 1989; Demes et al., 1994; Schmitt, 1999; Larson et al., 2000; Franz et al., 2005). However, little is known about the mechanics of non-habitual quadrupeds engaging in quadrupedalism, and whether those species that engage in quadrupedalism rarely retain characteristics that define primate quadrupedal walking, or whether these animals use a modified form of quadrupedal walking not seen in other primates.

Compared to most mammals, primate quadrupedal walking gaits are differentiated by a suite of at least three features (Kimura et al., 1979; Reynolds, 1985a,b;

Demes et al., 1994; Schmitt, 1999, 2003a; Schmitt and Lemelin, 2002, 2004; Lemelin and Schmitt, 2004; Hanna et al., 2006). First, primates tend to utilize diagonal-sequence (DS) footfall patterns (i.e., each hindlimb footfall is followed by a contralateral forelimb footfall),

Fig. 1. Three locomotor characteristics that distinguish primates many primates from other non-primate mammals. Primates (right) use **(A)** diagonal-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of left forefoot). In comparison, most non-primate mammals (left) use lateral-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of right forefoot). Primates also tend to have **(B)** protracted humeral positions at forelimb touchdown (i.e., humeral angles greater than 90° relative to horizontal body axis), in comparison to most non-primate mammals that have more retracted humeral positions at forelimb touchdown (i.e., humeral angle less than 90° relative to horizontal body axis). Finally, when the limb makes contact with the substrate, **(C)** forelimbs of primates experience lower peak vertical substrate reaction forces than do hindlimbs. The reverse is true for most other non-primate mammals. Reproduced with permission from Schmitt and Lemelin, Am J Phys Anthropol, 2002, 118:231-238.

whereas most other quadrupedal mammals use primarily lateral-sequence (LS) footfall patterns (i.e., each hindlimb footfall is followed by an ipsilateral forelimb footfall) (Muybridge, 1887; Magne de la Croix, 1936; Hildebrand, 1967; Tomita, 1967; Rollinson and Martin, 1981; Vilensky and Larson, 1989; Meldrum, 1991; Cartmill et al., 2002; Lemelin et al., 2003). Second, quadrupedal primates exhibit a relatively more protracted position of the humerus at touchdown (Schmitt, 1998; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002), whereas other quadrupedal mammals display relatively retracted humeral positions at forelimb touchdown. Finally, most quadrupedal primates experience higher peak vertical forces on the hindlimbs relative to the forelimbs, resulting in a relatively lower forelimb to hindlimb peak vertical (Vpk) force ratio (Kimura et al., 1979; Reynolds, 1985a,b; Ishida et al., 1990; Demes et al., 1994; Schmitt and Lemelin, 2002). In contrast most other quadrupedal mammals are characterized by a relatively higher forelimb to hindlimb Vpk force ratios (Kimura et al., 1979; Reynolds, 1985a,b; Demes et al., 1994; Schmitt and Lemelin, 2002) (Fig. 1).

Diagonal-sequence footfall patterns, increased humeral protraction, and relatively low forelimb Vpk forces are often described as a functional suite of features that likely evolved when our early primate ancestors specialized for life in a spatially complex arboreal niche (Kimura et al., 1979; Rollinson and Martin, 1981; Reynolds, 1985a,b; Demes et al., 1994; Larson, 1998; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Wallace and Demes, 2008; Larson and Demes, 2011). The use of DS footfall patterns is thought to be adopted by primates to ensure that a grasping hindfoot is placed on a tested support when the contralateral forefoot touches down on an untested support (Cartmill et al., 2002, 2007; Lemelin

et al., 2003; Schmitt, 2010). Although there has been some debate on this issue, particularly whether DS gaits are necessary for arboreal locomotion (Shapiro and Raichlen, 2005, 2007; Shapiro and Young, 2010), the presence of DS footfall patterns in other highly arboreal non-primate mammals (Schmitt and Lemelin, 2002; Karantanis et al., 2015), the increased frequency of DS footfall patterns on arboreal supports in capuchin monkeys (Wallace and Demes, 2008), and the increase in DS gaits on arboreal supports in sugar gliders [who also use LS and DS gaits on arboreal supports, but rarely use DS on the ground (Shapiro and Young, 2010)] further strengthens the association of the DS footfall pattern with locomotion and foraging on thin branches.

Similar reasoning has been used to explain increased degree of humeral protraction at touchdown in primates. It has been argued that early primates, having first evolved flattened nails, required long limbs with large excursions to reach above their head or around a trunk during climbing and to use long smooth, strides that would not oscillate thin branches (Larson, 1998; Larson et al., 2000, 2001; Schmitt and Hanna, 2004; Schmitt and Lemelin, 2004). Humeral protraction is affected by substrate (Schmitt, 2003a) and is often most extreme in highly arboreal primates like *Loris* and *Alouatta*. In general, higher degrees of humeral protraction are observed in arboreal primates and marsupials compared to closely related terrestrial taxa (Lemelin and Schmitt, 2007).

Finally, the difference in Vpk on the forelimbs versus the hindlimbs between most primates and most non-primate mammals may also represent an adaptation to arboreal locomotion and foraging (Demes et al., 1994; Larson, 1998; Schmitt and Lemelin, 2002, 2004; Schmitt, 2003b, 2010; Larney and Larson, 2004; Franz et al., 2005; Hanna et al., 2006). Successful arboreal locomotion and foraging would have required early primates to exploit food sources placed off the path of locomotion, as well as rapidly make changes of direction along branches, both of which require a highly responsive forelimb. In those cases, a highly mobile forelimb that was not responsible for bearing a majority of the animal's body weight would provide a distinct advantage, as it would allow the animal to test supports prior to committing a majority of body-weight, and free the forelimb from its locomotor function permitting the forelimb to evolve as a highly manipulative organ (Jones, 1916; Kimura et al., 1979; Reynolds, 1985a,b; Demes et al., 1994; Schmitt and Lemelin, 2002, 2004; Lemelin and Schmitt, 2004; Schmitt and Hanna, 2004; Franz et al., 2005; Hanna et al., 2006; Schmitt, 2010).

While DS footfall patterns, increased humeral protraction, and relatively low forelimb Vpk forces are often described as a functional suite of locomotor features, relatively few studies have addressed the legitimacy of this claim (Schmitt and Lemelin, 2002, 2004; Schmitt, 2003b; Wallace and Demes, 2008). Evidence for this functional suite comes from the ubiquity of these features across primates, the complete absence of all features at once in *Callithrix jacchus* (Schmitt, 2003b) and also their presence in *Caluromys philander* (Schmitt and Lemelin, 2002; Lemelin et al., 2003). The latter finding suggests the possibility that the same functional pattern associated with primate locomotion has evolved convergently arisen in *C. philander*, a highly arboreal marsupial (Schmitt, 2010). Wallace and Demes (2008) demonstrated a clear connection between arboreality and DS footfall patterns based on the almost exclusive of use DS

gaits in *Cebus apella* during arboreal locomotion, but much more variable footfall patterns during terrestrial locomotion. Additionally, Wallace and Demes (2008) determined that during arboreal locomotion there appeared to be a link between the use DS footfall patterns and relatively lower Vpk forces on both the forelimbs and the hindlimbs.

The nature of this link is unclear. One might argue that there are mechanical connections between humeral protraction and peak forces via limb yield or that DS gaits lead to low vertical forces. However, there are no strong theoretical models or empirical data to support (or reject) those links [but see Tomita (1967) and Yamazaki (1976)]. Alternatively, it is possible to argue that the unusual features of primate gait are basal and linked to the neural control of primate locomotion (Vilensky and Larson, 1989; Schmitt, 2010). For most nonprimate mammals, locomotion is thought to be controlled by central pattern generators (CPGs), which are neural networks that produce rhythmic outputs without significant cortical feedback (MacKay-Lyons, 2002; Drew et al., 2004; Ijspeert, 2008) and produce the basic action of stepping without higher commands from the cortex (Mori, 1987; Mori et al., 1996; Golubitsky et al., 1999; MacKay-Lyons, 2002; Drew et al., 2004). Evidence for such circuits in higher order primates, including humans, is tenuous, and studies suggest that supraspinal inputs, and likely cortical inputs, have a more important role in the generation of primate locomotion (Mori, 1987; Vilensky and Larson, 1989; Mori et al., 1996; Schmitt, 2010). Vilensky and Larson (1989) argued that the supraspinal control led to flexibility in footfall pattern and the presence of DS gaits in primates, an argument that can be extended to other aspects of primate gait.

It is important to note that while there are many examples demonstrating a link between DS footfall patterns, increased humeral protraction, and relatively lower forelimb Vpk forces, there are primate species that violate this assumed functional linkage. The lorisids, for example, are typified by unusual locomotor mechanics including the variable use of DS and LS footfall patterns (Hildebrand, 1967; Tomita, 1967; Glassman and Wells, 1984; Jouffroy, 1989; Ishida et al., 1990; Jouffroy and Petter, 1990; Schmitt and Lemelin, 2004), increased humeral protraction at touchdown, and a higher forelimb to hindlimb Vpk force ratio compared with other primates (Ishida et al., 1990; Schmitt and Lemelin, 2004).

One question that remains open and relevant is whether those primates that rarely use quadrupedal walking gaits also exhibit all three features thought to define most primate quadrupedal gaits. Schmitt (2003b) found that, although the walking gaits of *C. jacchus* were rare in his study, when they did occur the animals displayed retracted humeral position at touchdown, LS gaits, and higher forelimb forces. However, one salient criticism of Schmitt (2003b) is that *C. jacchus* rarely use quadrupedal walking gaits at all - choosing to bound, gallop, and leap more often [also see (Young, 2009)]. Schmitt (2003b) argued that the loss of typical primate walking gait characteristics in *C. jacchus* was related to movement on large branches. However, it is equally plausible that primates that rarely quadrupedal walking gaits simply do so in a pattern typical of most non-primates.

The present study addresses this possibility by analyzing gait mechanics of arboreal quadrupedal locomotion
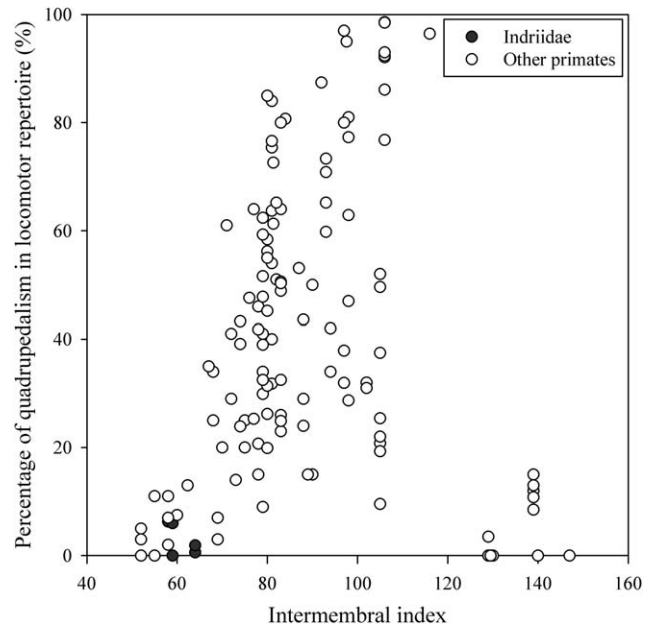
Fig. 2. The effect of intermebral index on the proportion of quadrupedal locomotion observed in the locomotor repertoires of primate species. Indriids display generally low proportions of quadrupedal locomotion. Primate species with high intermembral indices also display low proportions of quadrupedal locomotion. Data collected from literature review of wild and captive studies of primate locomotor and postural diversity (Supporting Information Table S1).

in *Propithecus coquereli*, a dedicated vertical-clinging and leaping (VCL) primate. Vertical-clinging and leaping is a type of arboreal locomotion in which primates adopt orthograde postures at rest on vertically-orientated substrates, and movement is initiated through powerful hindlimb extension resulting in animals leaping from one vertical substrate to another (Napier and Walker, 1967; Stern and Oxnard, 1973; Demes et al., 1991; Crompton et al., 1993, 2010; Fleagle, 2013). Vertical-clinging and leaping is common among strepsirrhine primates, and is also observed in the tarsiids and callithricids (Napier and Walker, 1967; Crompton and Andau, 1986; Gebo, 1987, 2011; Demes et al., 1991, 1999; Garber, 1992; Crompton et al., 1993, 2010; Warren and Crompton, 1997; Dagosto et al., 2001; Off and Gebo, 2005). The anatomy of VCL primates is characterized by relatively long hindlimbs in comparison with the forelimbs (Hall-Craggs, 1965; Oxnard et al., 1981a,b; Burr et al., 1982; Gebo and Dagosto, 1988; Ravosa et al., 1993; Demes et al., 1996; Connour et al., 2000; Schaefer and Nash, 2007). This anatomical pattern is thought to make quadrupedal locomotion ungainly and inefficient (Wunderlich et al., 2011, 2014), but despite this, arboreal quadrupedal locomotion has been witnessed in a number of VCL primates, albeit rarely (Fig. 2). The ecological context in which VCL primates use quadrupedal locomotion is poorly known because the studies that have reported such incidences rarely include substrate characteristics associated with locomotor modes. It is likely that quadrupedal locomotion in VCL primates is observed during travel in areas with thin, horizontal substrates in high density where leaping between supports would be more cumbersome. The presence of quadrupedal gaits in these species raises the question of

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

Species	Subject	Sex	Body mass (kg)	Date of birth (mm/dd/yyyy)	Limb*	Number of steps analyzed
Varecia variegata	Individual 1	Male	3.3	05/24/2010	Forelimb	12
					Hindlimb	10
	Individual 2	Female	3.76	04/17/2005	Forelimb	12
					Hindlimb	15
	Individual 3	Female	3.7	05/31/2001	Forelimb	21
					Hindlimb	13
Lemur catta	Individual 1	Male	2.58	05/03/2010	Forelimb	9
					Hindlimb	7
	Individual 2	Female	2.1	05/16/2011	Forelimb	9
					Hindlimb	8
	Individual 3	Female	2.34	04/09/2012	Forelimb	7
					Hindlimb	9
Propithecus coquereli	Individual 1	Male	4.12	02/03/2010	Forelimb	5
					Hindlimb	6
	Individual 2	Female	4.38	02/22/1998	Forelimb	6
					Hindlimb	6
	Individual 3	Female	5.09	02/04/2009	Forelimb	1
					Hindlimb	3

when VCL primates adopt quadrupedal locomotion: (1) do they demonstrate the common primate pattern of quadrupedalism (i.e., DS footfall patterns, increased humeral protraction, and relatively lower forelimb forces); (2) the common non-primate pattern; or (3) an entirely different mechanical pattern from either most primates or most non-primates?

MATERIALS AND METHODS

We collected kinematic and kinetic data from *P. coquereli* (a dedicated VCL primate), *V. variegata*, and *L. catta* (generalized arboreal quadrupeds) at the Duke Lemur Center (Durham, NC) following the protocols approved by the Duke Lemur Center (DLC Research Project #MO-10-11-3) and Duke's Institutional Animal Care and Use Committee (IACUC protocol # A270-11-10). All animals were adults and were clear of any pathologies or gait abnormalities (Table 1). The methods used here have been described extensively elsewhere (Schmitt, 1994, 1999, 2003a; Schmitt and Lemelin, 2002; Hanna et al., 2006; Granatosky et al., 2016), and will only be summarized below.

Forelimb and hindlimb forces were collected while animals walked above an instrumented pole measuring 3.66 m in length and 3.1 cm in diameter. The instrumented portion of the runway consisted of two Kistler force plates (model 9317B) that have been used in previous studies (Bishop et al., 2008; Granatosky et al., 2016). A small section of dowel was secured on one end of each force plate measuring the same diameter as the rest of the runway and large enough to accommodate an entire hand or foot (∼10 cm). These instrumented sections were mounted in the middle of the runway flush with, but separated by a small gap from, the rest of the runway. Force plate output was sampled at 12,000 Hz, and imported, summed, and processed using BioWare™ v.5.1 software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB. From these data, Vpk force was calculated for each limb.

Prior to all trials, animals were weighed. Forces for each day of trials were normalized to the weight recorded for that day. The animals were videotaped during trials within a clear plastic enclosure from a lateral view using a GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA) modified with a Back-Bone Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera (Granatosky et al., 2016). Our previous test of parallax effects using these specific cameras showed that we can record undistorted data over three meters of viewing space with the camera three meters from the line of travel (Granatosky et al., 2016). All videos were recorded at 120 fields/second. For each step, the subject's speed was calculated by digitizing a point on the subject's head at each field over the entire stride and calculating instantaneous velocity at each interval based on known distance marked on the runway used to calibrate the image space. Only walking steps (i.e., duty factor over 50%) in which the animal was traveling in a straight path and not accelerating or decelerating (i.e., steady-state locomotion) were selected for analysis. Steady-state locomotion was determined by calculating the instantaneous speed between subsequent video frames throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride (Bishop et al., 2008; Granatosky, 2015; Granatosky et al. 2016). Only strides in which no change in speed (i.e., slope not significantly different than zero) was detected were used for subsequent analyses. Additionally, only steps with single-limb contacts on the plate or those steps in which the forelimb and hindlimb forces were clearly differentiated were analyzed.

Video sequences were used to identify humeral protraction angle and footfall sequence (beginning with the contact of the right hindfoot). Humeral protraction angle was collected at forelimb touchdown and was measured as the angle of the humerus relative to a horizontal line passing through the shoulder joint. Limb angles were digitized using MaxTRAQ and analyzed using Max-MATE (Innovision Systems Inc., Columbiaville, MI).

All angular measurements were measured in degrees (°), and an analysis of variance (ANOVA) was used to determine whether there are statistically significant differences in humeral protraction angle between species. The relative frequency of DS footfall patterns was calculated for each species and a Pearson's Chi-square was used to determine whether there were statistically significant differences in the frequency of DS footfall patterns between species. In order to make statistical comparisons between subjects of differing body masses,
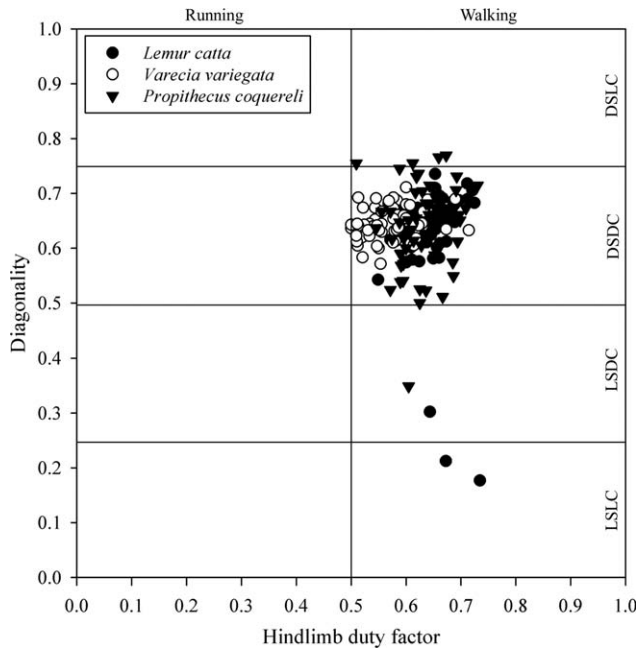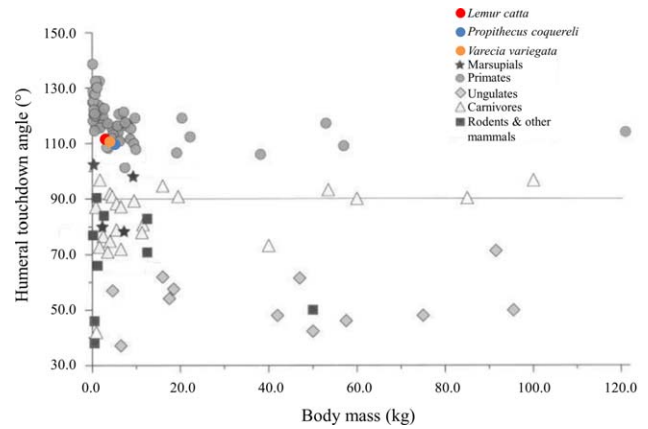
Fig. 3. A "Hildebrand" plot displaying diagonality for multiple strides of each of the study species against hindlimb duty factor. All three species in this study primarily used diagonal sequence diagonal couplets (DSDC) gaits most often. Limited strides demonstrated diagonal sequence lateral couplets (DSLC), lateral sequence lateral couplets (LSLC), and lateral sequence diagonal couplets (LSDC).

Fig. 4. Mean humeral touchdown angle plotted against mean body size for each species. Angles are described relative to a horizontal line passing through the shoulder to the substrate. Values greater than 90° denote a protracted humeral position. Values less than 90° denote a protracted humeral position. All species in this study display similar levels of humeral protraction to each other and closely match other primate species. Figure reprinted with permission from Larson et al., Am J Phys Anthropol, 2000, 112, 87-101.

Vpk forces are given in multiples of body weight (bw). A Shapiro–Wilk and Levene's test was used to determine normality and equal variance within the data (Sokal and Rohlf, 2012). Prior to any statistical comparisons, body weight normalized Vpk for above branch walking was compared with speed using a regression analysis to determine if this variable was influenced by variation in speed within the sample. The magnitude of substrate reaction forces are generally influenced by speed (Demes et al., 1994). In order to account for the effect of speed, all data were examined using a non-parametric analysis of covariance with average speed during support phase as the covariate to compare across limbs (Olejnik and Algina, 1984; Vickers, 2005). All P-values were adjusted for multiple comparisons by the Bonferroni method to account for type I error resulting from multiple comparisons. Although has been considerable discussion recently concerning the possibility that adjustments for multiple comparisons like the Bonferroni method are too conservative (Nakagawa, 2004), this study retains their use in order to make the most robust argument possible, while acknowledging that our significance may be a conservative estimate. All statistical tests were conducted using JMP Pro ver. 11 (SAS Institute Inc., Cary, NC).

RESULTS

Footfall pattern

In all species DS footfall patterns were by far the most common representing 100% of strides in *V. variegata* (n = 60), 97.75% of strides in *L. catta* (n = 89), and 98.27% of strides in *P. coquereli* (n = 58) (Fig. 3). The frequencies of DS footfall patterns were not significantly (P = 0.52) different between any of the species within this study.

Humeral protraction angle

The angle of the humerus of the subjects in this study was consistently in a protracted position at touchdown (i.e., above 90° relative to a horizontal line passing through the shoulder). No significant difference (P = 0.38) in humeral protraction angle at touchdown was observed between *V. variegata* (110.49 ± 10.17; n = 30), *L. catta* (112.74 ± 9.32; n = 29), and *P. coquereli* (109.44 ± 6.72; n = 25) (Fig. 4).

Limb-loading

In total, 159 single limb forces were collected and analyzed. Table 2 summarizes the number of steps collected per limb for each species, and data for speed and Vpk. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant (P ≤ 0.001) positive association was observed between Vpk and speed.

All species displayed significantly different (P ≤ 0.001) Vpk forces between the forelimb and hindlimb during quadrupedal locomotion. Forelimb Vpk forces were lower than hindlimb Vpk forces during quadrupedal locomotion for all species. While we observed the same pattern of limb-loading in all species, we did detect differences in Vpk force magnitude between species. In regards to the forelimb, *L. catta* exerted statistically (P ≤ 0.001) lower Vpk forces than either *V. variegata* or *P. coquereli* (Figs. 5 and 6).

DISCUSSION

Our data demonstrate that during arboreal quadrupedal locomotion, *P. coquereli* display the almost exclusive use of DS footfall patterns, protracted humeral angles at touchdown, and lower Vpk forces in the forelimb compared to the hindlimb (Fig. 7). The locomotor data collected from *P. coquereli* was very similar in footfall pattern, humeral angle at touchdown, and kinetics to what we observed in more generalized arboreal quadrupeds (i.e., *V. variegata*

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

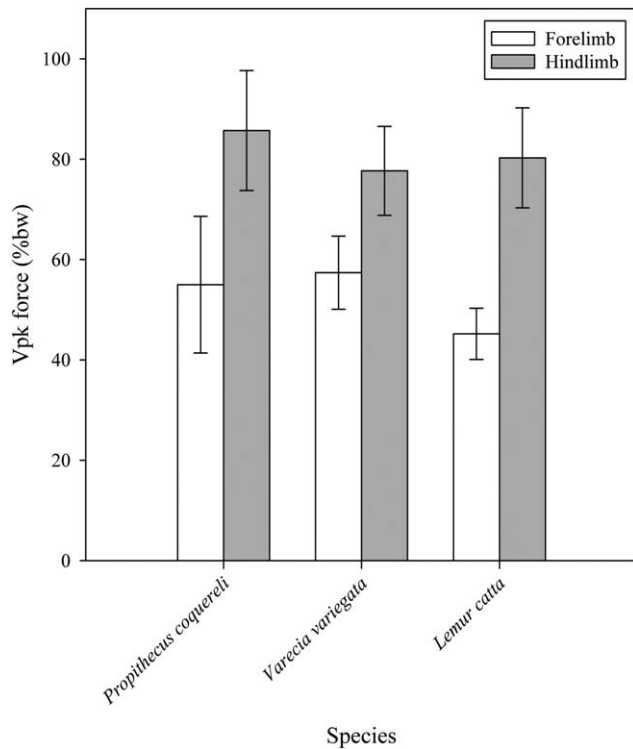| Species	Velocity (m/s)	Limb	N	Vertical peak (%bw)
Varecia variegata	0.81 ± 0.17	Forelimb	45	57.38 ± 7.30
		Hindlimb	38	77.68 ± 8.85
Lemur catta	0.57 ± 0.15	Forelimb	25	45.19 ± 5.11
		Hindlimb	24	80.26 ± 9.97
Propithecus coquereli	0.65 ± 0.19	Forelimb	12	54.99 ± 13.61
		Hindlimb	15	85.70 ± 11.94

Fig. 5. Mean and s.d. of peak vertical (Vpk) forces in the forelimbs and hindlimbs of *Propithecus coquereli*, *Varecia variegata*, and *Lemur catta*. All data presented as a percentage of the animal's body weight (%bw).

Fig. 6. Mean ratios of peak vertical substrate reaction forces for forelimb versus hindlimb during walking for various mammals. Ratios have been logged (ln) so that ratios greater or less than zero (i.e., equal forelimb and hindlimb peak vertical substrate reaction forces) are weighted equally and can be directly compared among taxa (Sokal and Rohlf, 2012). Data from this study were compared with non-primate mammals (open bars) and primates (solid bars) collected from other data sources. Figure and data reprinted with permission from Schmitt and Lemelin, Am J Phys Anthropol, 2002, 118:231-238.

and *L. catta*). The finding that *P. coquereli* adopts the characteristic patterns of primate arboreal locomotion provides evidence for the idea that these patterns may represent a functional suite that may be adaptive for arboreal locomotion and is potentially a basal primate gait condition (Schmitt and Lemelin, 2002); although alternatives cannot be rejected.

The common limb-loading pattern observed in primates in which forelimb Vpk forces are subequal or lower than hindlimb forces (Kimura et al. 1979; Reynolds, 1985; Demes et al. 1994; Lemelin and Schmitt, 2002; Schmitt and Hanna, 2004; Schmitt and Lemelin, 2007; Wallace and Demes, 2008; Young, 2012) is thought to be an important mechanism to free the forelimbs from their normal weight-bearing role in locomotion, permitting the forelimbs to become highly manipulative and mobile grasping organs (Jones, 1916; Kimura et al. 1979; Reynolds, 1985a; Demes et al, 1994; Schmitt, 1999; Schmitt and Lemelin, 2002; Schmitt and Hanna, 2004). The mechanism for how this is accomplished is still a matter of inquiry. There remains productive discussion as to whether this altered limb loading pattern is an active
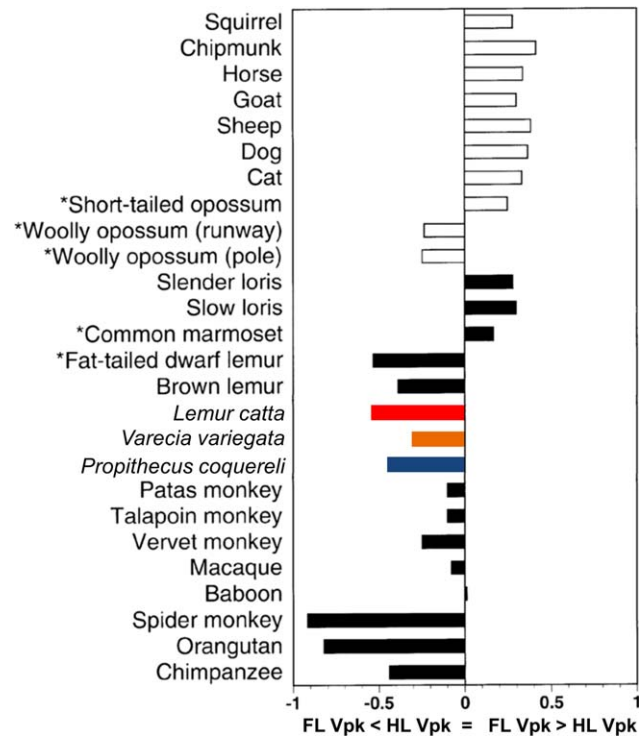
process (Reynolds, 1985a,b, 1987; Schmitt, 1999) or passive process, which is simply an unintentional byproduct of other aspects of normal primate locomotor patterns (Raichlen et al., 2009). The data presented in this study cannot support or refute whether this mechanism is an active or passive process, and it is possible that either scenario may be possible based on the finding of our study. Primates as a group are characterized by a relatively greater amount of limb excursion during above branch quadrupedal locomotion (Larson et al., 2000) that tends to place relatively protracted hindlimbs underneath the center-of-mass for longer periods of time than relatively retracted forelimbs (Raichlen et al., 2009). It has been argued that this pattern is thought to result in relatively greater hindlimb Vpk forces simply because the hindlimb's position in relation to the body's center-of-mass (but see Larson and Demes, 2011).
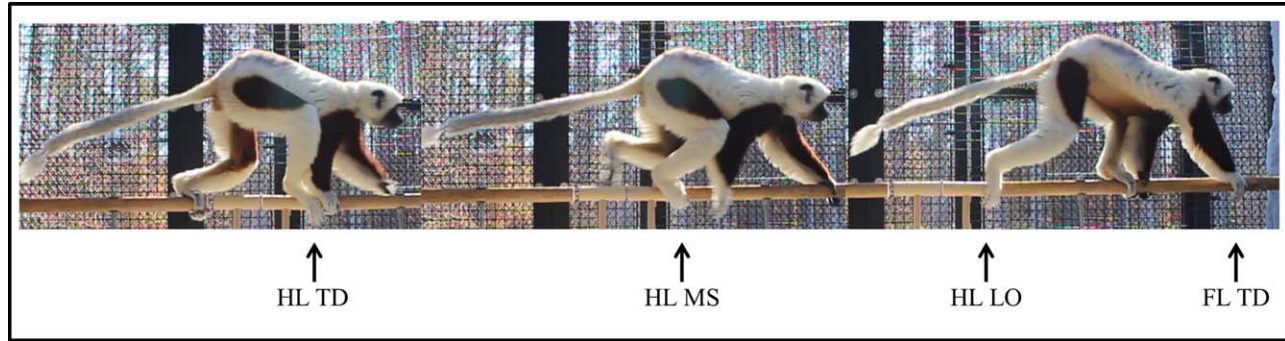
Fig. 7. A representative stride collected from *Propithecus coquereli* during varying portions of the stride [i.e., hindlimb touchdown (HL TD), hindlimb mid-support (HL MS), hindlimb lift-off (HL LO), and forelimb touchdown (FL TD).

In respect to hypotheses concerning the mechanism with which primates maintain relatively higher Vpk forces on their hindlimbs, two models have been developed. The first model, proposed by Reynolds (1985a,b, 1987) and supported by Larson and Stern (2009), suggests that primates actively shift weight caudally away from the forelimbs on their relatively protracted hindlimbs using powerful muscular retractors of the hindlimb. The second model, proposed by Schmitt (1998, 1999) and tested by Larney and Larson (2004) argues that primates change vertical stiffness of their limbs by increasing limb yield, contact time, and angular excursion. These models are not mutually exclusive, and some studies suggest that both provide important mechanisms by which locomotor forces on the limbs can be moderated (Schmitt and Hanna, 2004; Young, 2012).

Although *P. coquereli* are anatomically and behaviorally specialized for vertical clinging and leaping, during bouts of quadrupedalism they nonetheless exhibit the same mechanical characteristic of other primate species - a surprising finding, especially considering that other anatomically-specialized primate species (i.e., the lorisids and *C. jacchus*) deviate from the characteristic patterns of primate arboreal quadrupedal locomotion. While our findings support the possibility of that these features represent an adaptive suite that meets the challenges of arboreal locomotion that may be basal for primates (Schmitt and Lemelin, 2002), it is also possible that the locomotor patterns observed in *P. coquereli* may come from a more recent ancestral split. Phylogenetic and molecular reconstructions reveal a close relationship between the extant indriids and a number of the subfossil lemurs of Madagascar (i.e., *Archaeolemur*, *Hadropithecus*, *Palaeopropithecus*, *Archaeoindris*, *Babakotia*, and *Mesopropithecus*) (Gebo and Dagosto, 1988; Godfrey and Jungers, 2003; Karanth et al., 2005) which are thought to have exhibited the broad range of locomotor behaviors (Simons et al., 1992; Jungers et al., 1997; Godfrey and Jungers, 2003). Among the subfossil lemurs are animals that have been described as being arboreal/terrestrial pronograde quadrupeds (*Archaeolemur* and *Hadropithecus*), arboreal inverted quadrupeds (*Palaeopropithecus, Babakotia, Mesopropithecis*), and large-bodied terrestrial quadrupeds (*Archaeoindris*) (Jungers et al., 1997; Godfrey and Jungers, 2003; Granatosky et al., 2014). Based on the position of Indriidae in relation to these sub-fossil species, it is likely that the common ancestor of this group was, in terms of postcranial anatomy and locomotor behavior, more similar to extant lemurids than to any extant indriid; that is to say, it was an arboreal quadruped capable of leaping and climbing, but not as specialized for these activities as are extant indriids (Gebo and Dagosto, 1988; Karanth et al., 2005). It is possible that the presence of the mechanical characteristic of other primate species in living indriids represents a retention from a primitive quadrupedal indriid ancestor, and therefore allow large-bodied VCL primates, or at least *P. coquereli*, to maintain normal patterns of primate locomotion.

From the data presented in this study, it is possible to reject the idea that a primate like *P. coquereli* that uses quadrupedal locomotion rarely will adopt the common non-primate pattern, or an entirely different mechanical pattern from either most primates or most non-primates, during quadrupedal locomotion. The findings that a habitual VCL primate will use primate-like gait mechanics during quadrupedal locomotion provide support for the idea that the suite of characteristics that define primate walking gaits are adaptive for arboreal mammals (especially those without and claws, that have grasping feet and mobile forelimb joints) to meet the challenges of arboreal locomotion in a complex fine-branch environment. In that context, these data may also lend support to the idea that these features are basal to the order or evolved independently at the base of the indriid lineage. While the data presented in this study does provide support for the aforementioned hypotheses, we cannot reject possible alternatives concerning the reason for these mechanisms. For example, it is possible that higher peak vertical forces observed in the hindlimbs of *P. coquereli* does not represent some basal condition conserved across all primates, but instead represents a mechanical consequence predicted by Raichlen et al. (2009) of an animal (*P. coquereli*) with a caudally positioned center-of-mass and a highly protracted hindlimb at touchdown. Additional studies with a greater taxonomic diversity and a broader range of experimental protocols would help illuminate this issue further.

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