

Understanding Hind Limb Weight Support in Chimpanzees With Implications for the Evolution of Primate Locomotion

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ABSTRACT Most quadrupedal mammals support a larger amount of body weight on their forelimbs compared with their hind limbs during locomotion, whereas most primates support more of their body weight on their hind limbs. Increased hind limb weight support is generally interpreted as an adaptation that reduces stress on primates' highly mobile forelimb joints. Thus, increased hind limb weight support was likely vital for the evolution of primate arboreality. Despite its evolutionary importance, the mechanism used by primates to achieve this important kinetic pattern remains unclear. Here, we examine weight support patterns in a sample of chimpanzees (*Pan troglodytes*) to test the hypothesis that limb position, combined with whole body center of mass position (COM), explains increased hind limb weight support in this taxon. Chimpanzees have a COM

midway between their shoulders and hips and walk with a relatively protracted hind limb and a relatively vertical forelimb, averaged over a step. Thus, the limb kinematics of chimpanzees brings their feet closer to the COM than their hands, generating greater hind limb weight support. Comparative data suggest that these same factors likely explain weight support patterns for a broader sample of primates. It remains unclear whether primates use these limb kinematics to increase hind limb weight support, or whether they are byproducts of other gait characteristics. The latter hypothesis raises the intriguing possibility that primate weight support patterns actually evolved as byproducts of other traits, or spandrels, rather than as adaptations to increase forelimb mobility. *Am J Phys Anthropol* 138:395–402, 2009. © 2008 Wiley-Liss, Inc.

Primates generally support more body weight on their hind limbs than their forelimbs during both terrestrial and arboreal quadrupedalism (Kimura et al., 1979; Demes et al., 1994; Schmitt, 2003; Schmitt and Hanna, 2004). In contrast, non-primate quadrupeds support more weight on their forelimbs than their hind limbs (Demes et al., 1994; Schmitt and Lemelin, 2002). Increased hind limb weight support is generally thought to spare forelimb joints from high ground reaction forces (GRF) during locomotion, permitting primates the greater forelimb joint mobility necessary for arboreal locomotion (Reynolds, 1985a; Larson, 1998). Therefore, increased hind limb weight support is often linked to primates' enhanced arboreal performance (Reynolds, 1985a; Larson, 1998). Despite the possible evolutionary importance of primate kinetic characteristics, the underlying mechanisms that determine primate weight support patterns remain unclear. The goal of this study is to examine the mechanisms that increase hind limb weight support in order to better understand the evolution of primate quadrupedalism.

Two measures are used to compare forelimb and hind limb forces: overall weight support and peak vertical forces. Weight support (e.g., for the forelimb) is generally measured as the ratio of forelimb vertical impulse to the sum of forelimb and hind limb vertical impulse (where impulse is force \times time and is calculated as the area under the vertical GRF curve; see Reynolds, 1985a; Bertram et al., 1997; Lee et al., 2004; Young et al.,

2007).¹ Many authors also discuss the importance of peak vertical GRFs in primate evolution (Demes et al., 1994; Schmitt and Lemelin, 2002; Hanna et al., 2006). Vertical impulse and peak GRF are related because each depends on the duration of stance phase (Reynolds, 1985a). So, as contact time (the duration of stance phase) decreases with increasing speed, the peak vertical force increases and vertical impulse decreases (Bertram et al., 1997; Khumasap et al., 2001; Dutton et al., 2004). However, the ratio of peak forelimb and hind limb force remains similar to the ratio of forelimb and hind limb

¹Note that the vertical impulse for each limb differs from the vertical impulse applied by all limbs over the stride (i.e., average vertical force), which is the summed vertical impulse of all limbs divided by stride duration and is equal to body weight (see Bertram et al., 1997).

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impulse (see Reynolds, 1985a; Bertram et al., 2000). Thus, hypotheses that explain weight support patterns should also explain the relationship between forelimb and hind limb peak vertical GRFs.

Researchers have proposed several hypotheses to explain primates' distinctive kinetic patterns (see Reynolds, 1985b; Schmitt, 1999; Schmitt and Hanna, 2004). These hypotheses are generally based on either active models or passive models. In active models, primates alter their weight support patterns through either kinematic actions or muscle activity to shift weight support from their forelimbs to their hind limbs (see Reynolds, 1985b; Schmitt, 1999; Schmitt and Hanna, 2004). In passive models, weight support patterns are byproducts of other kinematic or anatomical features (see Gray, 1944), and primates do not actively alter their locomotion to achieve increased hind limb weight support.

ACTIVE MODELS

Two common models suggest that primates might actively shift weight to their hind limbs in some way (Reynolds, 1985b; Schmitt, 1999; Schmitt and Hanna, 2004). Reynolds (1985b) hypothesized that primates increase hind limb weight support using an active mechanism. He suggested that primates accomplish this weight shift by activating hind limb retractor muscles when the hind limb is protracted (Reynolds, 1985b). Activating hind limb retractors will apply a pitching moment to the trunk, shifting weight to the hind limbs (Reynolds, 1985b). Although this hypothesis is appealing, it has one important caveat: shifting weight to the hind limbs using hind limb retractor activity will also alter horizontal GRFs at the feet (Reynolds, 1985b; Lee et al., 2004). When the limb is protracted, hind limb retractor activity will increase propulsive forces on the feet, while the increased weight support brought about by this same muscle action will increase braking forces on the feet (Reynolds, 1985b). During steady-state locomotion, however, the horizontal forces on all the feet must sum to zero (i.e., there can be no net acceleration or deceleration over a stride), so any alterations in horizontal forces caused by retractor activity must be balanced in some way. Reynolds (1985b) suggested that alterations of the horizontal force will cancel each other (i.e., propulsive force due to action on the limb cancels the braking force due to increased weight support), leading to no net change in the horizontal GRF. However, as Reynolds indicates (see Fig. 4 in Reynolds, 1985b), these alterations cannot fully cancel each other; at any limb angle the change in horizontal acceleration is never equal to zero, and a small propulsive acceleration remains.

If activation of hind limb retractors leads to an increase in the net change in hind limb propulsive force, an increase in the net forelimb braking force is needed to maintain steady-state speed. Following this logic, the weight shifted to the hind limbs must be shifted back to the forelimbs to negate the increase in hind limb propulsive force. Thus, increased retractor muscle activity cannot fully explain primate weight support patterns at steady-state speeds. In fact, Yu (2000) suggested that hind limb retractors are active for other reasons, acting as anti-gravity muscles for the hind limb when it is highly protracted and therefore, increased retractor activity would be expected in any quadruped with a highly protracted hind limb.

Recently, Schmitt (1999; see also Schmitt and Hanna, 2004) suggested that primates can actively alter weight

support by using differential limb compliance. Deeply yielding the elbow or knee during stance phase (i.e., flexing the joint from touchdown to mid-stance) and using long contact times should decrease the peak vertical forces acting on the limb (Schmitt, 1999). Thus, large amounts of forelimb yield, combined with little to no hind limb yield, would result in a shift of weight to the hind limbs. Recent studies show that primates do in fact use greater joint yield than most other quadrupeds (Larney and Larson, 2004), and that elbow yield is greater than knee yield in most primate groups. There is evidence, though, that some primates (e.g., lorises) use greater elbow compared to knee yield yet have higher forelimb compared to hind limb forces (see Schmitt and Lemelin, 2004). In addition, rodents, in general, have more compliant forelimbs than hind limbs (Larney and Larson, 2004), but the available evidence suggests that they have greater forelimb compared to hind limb forces (e.g., squirrels and chipmunks; see Biewener, 1983; Demes et al., 1994). Conflicting data do not reject the compliant gait hypothesis, but they do suggest that other mechanisms may act to alter weight support patterns in some taxa.

PASSIVE MODEL

Although active weight shift may account for primates' large hind limb forces, it is possible that weight support is determined simply by the position of the whole body center of mass (COM) relative to the hands and feet (Gray, 1944; Rollinson and Martin, 1981). If the COM is closer to the feet than to the hands, the individual will support more body weight on its hind limbs without needing to alter kinematics or muscle activity (Gray, 1944). Conversely, if the COM is nearer to the hands, the animal will support more body weight on its forelimbs (Gray, 1944). Note that weight support is affected by both the position of the COM, and by the positions of the hands and feet relative to the COM (Gray, 1944; Yu, 2000). Thus, weight support patterns in primates could be a result of relatively protracted hind limbs and forelimbs, which would place the feet closer to the COM compared to the hands. Alternatively, increased hind limb weight support in primates may be driven by a relatively caudal location of the COM compared to other mammals (Rollinson and Martin, 1981). However, several researchers have suggested that COM position does not differ in primates compared to generalized quadrupedal mammals (e.g., Reynolds, 1985b; Vilenky and Larson, 1989), and Reynolds (1985b) suggested that primates do not place their hind limbs close enough to their COM to fully account for their kinetic pattern. Still, despite the straightforward nature of this hypothesis, no study to date has explicitly tested it in primates.

Here, we re-examine the COM hypothesis by measuring the relative distance of the hands and feet from the COM during chimpanzee locomotion. We predict that increased hind limb weight support in chimpanzees will be due to a COM position that is closer to the average position of the feet than the hands over a stride. We then explore the possibility that this hypothesis may explain primate weight support patterns more generally.

METHODS

Gray's model

As outlined above, the COM hypothesis is based on Gray's (1944) model of quadrupedal weight support

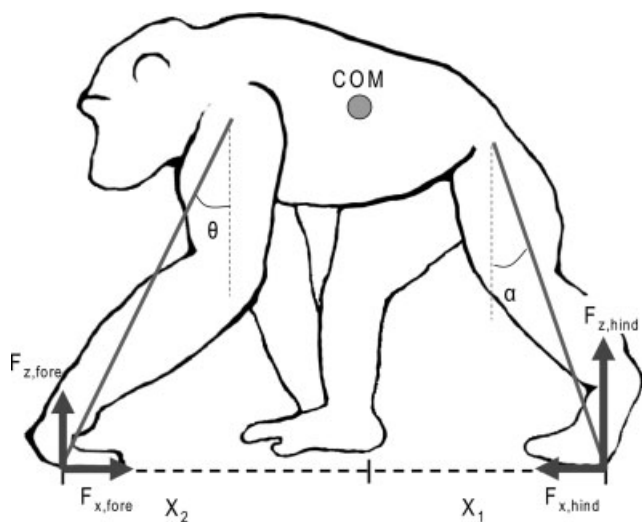


Fig. 1. Gray's (1944) model of weight support in quadrupedal mammals. The model shows average positions of the forelimb and hind limb that are determined by their average limb angle (θ and α respectively) over a step. At a steady state speed, horizontal forces will sum to zero and weight support will be due to the position of the COM relative to the fore- and hindfeet (X_2 and X_1 respectively). F_x and F_z are the horizontal and vertical forces at the forelimbs and hind limbs.

which considers averaged kinematics and kinetics over an entire stride. Averaged over a stride, the summed vertical force exerted by the four limbs on the ground must equal body weight (during steady speed locomotion, horizontal forces sum to zero [braking = propulsion] and are therefore ignored in this model). A simple model of a quadruped (see Fig. 1) suggests that the average position of the hands and feet, relative to the COM, will determine how much weight each limb supports. On the basis of this model, and assuming a symmetrical gait, forelimb weight support (R) is predicted using the following equation

$$R = \frac{X_1}{X_1 + X_2} \tag{1}$$

where R is the percentage of weight supported by the forelimb, X_1 (m) is the average horizontal distance from the center of the foot to the body COM, and X_2 (m) is the average horizontal distance from the center of the hand to the body COM. Note that all values in the equation above are averages for a single step. If the limbs oscillate perfectly about a vertical line from the hip or shoulder to the ground (dotted vertical lines in Fig. 1), then weight support patterns are determined solely by the position of the COM relative to the hip and shoulder. However, if the limbs oscillate about any other position (e.g. their average position over a step is either protracted or retracted), then weight support is determined by a combination of COM position and average limb position.

SAMPLE

To test the hypothesis that primate weight support patterns are explained by whole body COM positions relative to the hands and feet, we modeled weight support in a sample of chimpanzees (*Pan troglodytes*; $n = 3$;

TABLE 1. Segment inertial properties for each chimpanzee

Variable	Segment	Subject 1	Subject 2	Subject 3
Length (m)	Arm	0.30	0.20	0.25
	Forearm	0.30	0.22	0.28
	Hand	0.15	0.24	0.25
	Thigh	0.30	0.23	0.25
	Leg	0.28	0.23	0.30
	Foot	0.23	0.22	0.24
Mass (kg)	Trunk + head	0.56	0.53	0.60
	Arm	2.96	1.32	2.44
	Forearm	1.72	1.16	1.92
	Hand	0.56	0.80	1.01
	Thigh	5.75	2.45	3.65
	Leg	1.98	1.15	2.25
COM position (m) ^a	Foot	0.92	0.92	1.25
	Trunk + head	35.41	20.72	31.08
	Arm	0.16	0.10	0.13
	Forearm	0.18	0.12	0.16
	Hand	0.08	0.12	0.12
	Thigh	0.17	0.13	0.14
	Leg	0.14	0.12	0.16
	Foot	0.13	0.11	0.13
	Trunk + head	0.29	0.29	0.32

^a COM positions are from proximal end of segment.

mean body mass [SD] = 49.4 [14.6] kg). To compare the model to observed weight support patterns, we measured kinematics, kinetics, and calculated whole body COM positions during overground locomotion in this sample (see below). All methods were approved by Harvard University and University of California at Davis IACUC.

COM POSITION

To calculate whole body COM position, body segment circumferences and lengths (for the trunk, head, arm, forearm, hand, thigh, leg, and foot) were measured using measuring tape to the nearest millimeter. Chimpanzees were trained to stand quietly during data collection and measurements were taken when the individual was still. These measurements were used to calculate body segment masses and COM positions using a geometric model (Table 1; see Crompton et al., 1996; Raichlen, 2004, 2005a,b). Whole body COM position was calculated as the average of all segment COM positions, weighted by segment mass, relative to the shoulder. COM positions were calculated with the chimpanzees standing in a static quadrupedal position (limbs perpendicular to the ground) as well as with limb positions matching their average positions over stance phase (see below). Values for our chimpanzee sample are similar to those reported by Schoonaert et al. (2007).

KINEMATICS AND KINETICS

Ground forces were measured using a portable forceplate (Kistler[®]) built into a short (10 m) trackway, recording at 4 kHz. Chimpanzees walked over the forceplate at a range of self-selected speeds. Trials were used if either a forelimb ($n = 19$) or hind limb ($n = 16$) contacted the force plate with no other limb contacts (Table 2). Simultaneously, the positions of joint centers (shoulder, elbow, wrist, head of fifth metacarpal, hip [greater trochanter], knee, and ankle, heel, head of fifth metatarsal), marked with non-toxic water-based white paint, were tracked using high-speed digital video (Redlake[®], 125 frames per second). Frame-by-frame coordinates of joint centers were calculated using a Matlab

TABLE 2. Description of kinematic and kinetic trials for each subject

Subject	Body mass (kg)	Hind limb v (ms ⁻¹)	Forelimb v (ms ⁻¹)	Hind limb trials	Forelimb trials
Subject 1	63.9	1.13 (0.08)	1.10 (0.12)	8	10
Subject 2	33.9	1.32 (0.09)	1.15 (0.13)	4	3
Subject 3	51.6	1.22 (0.07)	1.12 (0.11)	4	6

Velocity (v) data are means (SEM) for all fore- or hind limb strides.

image analysis program. Force plate and video data were synchronized using a custom built trigger that initiated data recording for each instrument simultaneously. Force plate trials were accepted if only one limb contacted the force plate cleanly and trials were excluded if the individuals were clearly accelerating or decelerating (determined from visual inspection of video).

TESTING THE MODEL

To test the model for weight support, we combined whole body COM positions (calculated using average limb positions over each limb's stance phase) with kinematics, and predicted weight support values using Gray's (1944) model. Average hind limb angle during stance was calculated as the average of (1) the angle between the vertical and a line connecting the hip and heel markers at touchdown, and (2) the angle between the vertical and a line connecting the hip and fifth metatarsal markers at lift off. Average forelimb angle during stance was calculated as the average of the angles between the vertical and the lines connecting the markers at the shoulder and the fifth metacarpal head at touchdown and lift off. We combined forelimb and hind limb data from different trials at similar speeds for each individual. Error estimates for the model were calculated by modeling subjects with their hind limb and forelimb angles calculated as their average angles plus one standard deviation. Chimpanzees generally overstride when walking, placing a hind foot either inside or outside of the ipsilateral hand in ground contact (Reynolds, 1985a) and force profiles differ depending on whether a given limb is being used as an inside or outside limb (Reynolds, 1985a; Demes et al., 1994). In this study, subjects consistently placed their hind limbs inside their forelimbs for all trials, allowing us to combine forelimb and hind limb steps from different trials. We then compared predicted and observed weight support values in this sample. To determine actual weight support patterns, vertical impulses (J_{fore} and J_{hind}) were calculated as the area under the vertical ground reaction force/time curve. The percentage of body weight carried by the forelimb ($R_{observed}$) was calculated as the forelimb vertical impulse as a fraction of the sum of the forelimb and hind limb vertical impulse after Lee et al. (2004):

$$R_{observed} = \frac{J_{fore}}{J_{fore} + J_{hind}} \quad (2)$$

RESULTS

Weight support

Averaged over a step, chimpanzee hind limbs are relatively protracted, while their forelimbs are more variable (Fig. 2A). For two individuals, the forelimbs are protracted, on average, which will bring the feet closer to their COM than their hands. In one subject, the forelimb

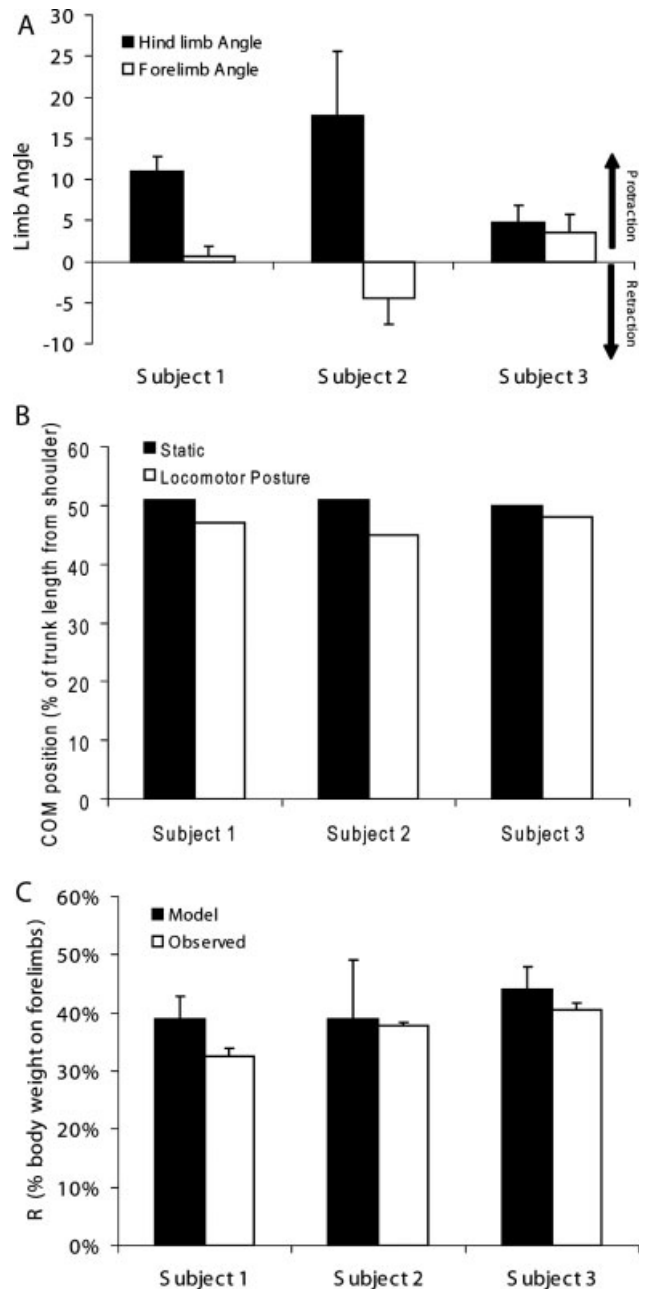


Fig. 2. Weight support model of chimpanzee kinetics. **A:** Fore- (white bars) and hind limb (black bars) angles, averaged over a step relative to the vertical. Positive values are protracted and negative values are retracted. **B:** Whole body COM positions relative to the shoulder (positions greater than 50% [dotted line] are posterior to the trunk midline). Black bars are COM positions calculated with limbs perpendicular to the ground and white bars and COM positions calculated with limbs in their average positions shown in A. **C:** Modeled (black bars) vs. observed (white bars) forelimb weight support.

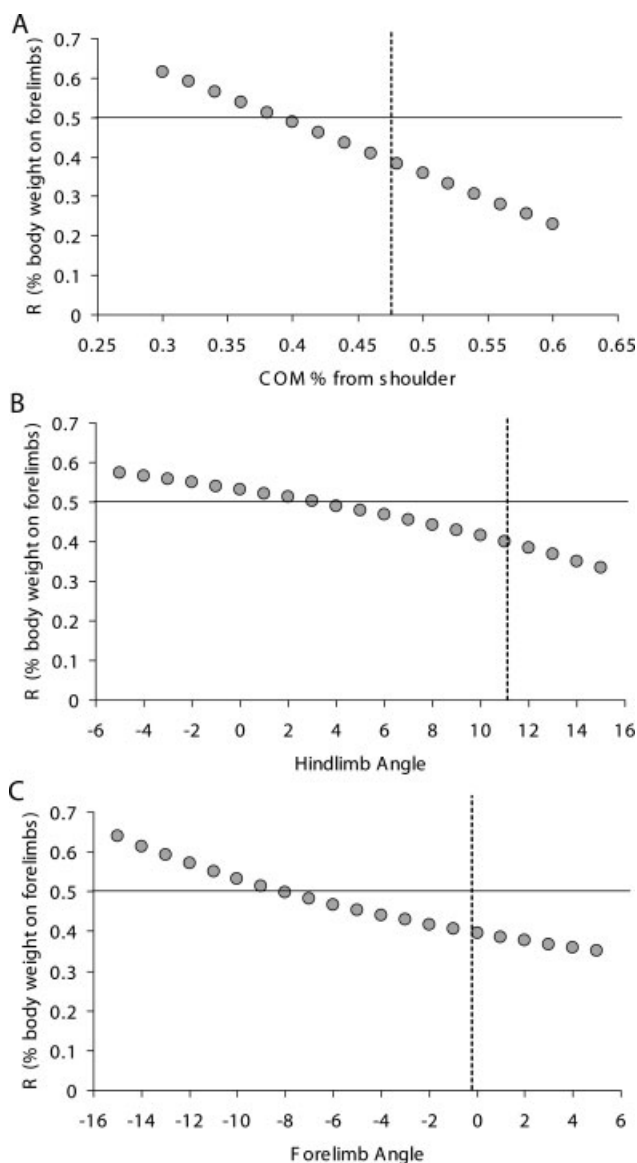


Fig. 3. Sensitivity analysis. Solid horizontal line indicates equal forelimb and hind limb weight support and values above the line indicate the non-primate pattern of greater overall forelimb weight support. Broken vertical line indicates observed mean values for chimpanzees in this sample. **A:** Effects of changing COM position on weight support patterns. Average hind limb and forelimb angles were calculated from the chimpanzee sample and are held static as COM position varies. **B:** Effects of changing average hind limb angle while holding COM position and forelimb angle static. **C:** Effects of changing average forelimb angle, while holding COM position and hind limb angle static.

is retracted, when averaged over a step, but the hind limb is more protracted than the forelimb is retracted. Chimpanzees have whole body COMs that are nearly midway between the hip and shoulder when calculated with each subject in a static position with limbs perpendicular to the ground (mean [SEM] = 50.67 [0.003]; Fig. 2B). When the COM is calculated with limbs in their average position over a step (i.e., using average limb angles for each subject), COM positions shift cranially slightly (mean [SEM] = 47.0 [0.01]). Notably, weight support

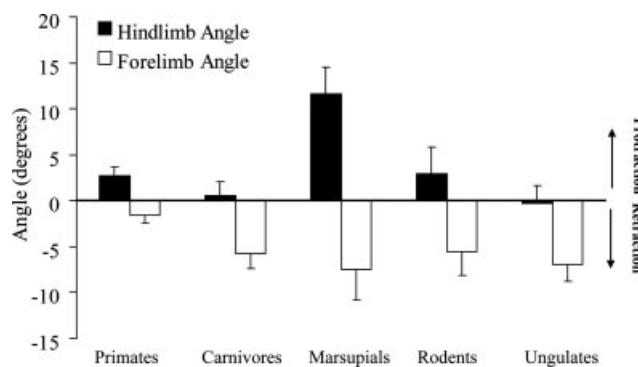


Fig. 4. Average limb angles in mammalian quadrupeds (data from Larson et al., 2000, 2001). All values are relative to the vertical and are averages for a step. Positive values are protracted, negative values are retracted.

patterns predicted by Gray's model corresponded very well with observed weight support patterns. The model predicted that the forelimbs would support 39% ($\pm 3.9\%$), 39% ($\pm 10.1\%$), and 44% ($\pm 3.8\%$) of body weight in subjects 1–3 respectively (Fig. 2C). Actual weight support values are very similar with subjects 1–3 supporting 32% ($\pm 1.2\%$), 38% ($\pm 1.1\%$), and 41% ($\pm 0.05\%$) of body weight on their forelimbs (Fig. 2C). In all cases, error in model predictions due to stride-to-stride variation in average limb angles encompass actual weight support values calculated from force plate data.

We performed sensitivity analyses on the chimpanzee model (average of all three subjects; COM = 47% of trunk length from the shoulder; forelimb angle = -0.14° ; hind limb angle = 11.19°) to determine the effects of different average limb angles and COM positions on forelimb weight support. First, we varied COM position while keeping forelimb and hind limb average angles static and equal to the average for the three individuals in this study. In this case, chimpanzees would bear more weight on their forelimbs than their hind limbs if the COM were less than 40% of trunk length from the shoulder (Fig. 3A). We then varied average hind limb angle keeping COM position and forelimb angle static. In this case, chimpanzees would need an average hind limb position of $\sim 2^\circ$ before the forelimbs would support more body weight overall (Fig. 3B). Finally, we held hind limb angle and COM position constant and varied average forelimb angle (Fig. 3C). Chimpanzee forelimbs would support more body weight than their hind limbs if their average forelimb angle was $\sim -9^\circ$.

Whole body COM positions do not exist for a comparative sample of primates and non-primates, making a broader test of this model for weight support difficult. However, Larson et al. (2000, 2001) collected data comparing limb excursions in a large sample of quadrupedal mammals, which we used to examine the average positions of the fore- and hindfeet relative to the trunk midline. Using this dataset, we calculated average limb position over a step by finding the average of touchdown and lift-off angles and assuming that limb angular velocity is constant during stance phase (see Fig. 4). Primates generally walk with a hind limb that is, averaged over a step, more protracted than the forelimb is retracted. These limb positions bring the hind limbs closer to the COM than the forelimbs and therefore contribute to primates' greater hind limb weight support. Marsupials

appear similar to the primate pattern, although overall values are much larger for both the fore- and hind limbs. Interestingly, this sample includes *Caluromys*, the only other taxon known to have greater hind limb compared to forelimb weight support (see Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2007). Other quadrupeds have a forelimb that is retracted more than the hind limb is protracted, which would likely lead to greater forelimb weight support.

DISCUSSION

Chimpanzee weight support patterns are well explained by the average position of the hands and feet relative to the whole body COM. Using Gray's COM model, the position of the COM and protraction of the forelimb and hind limb predict the degree of hind limb support seen in our chimpanzee sample. Although the comparative analysis is very coarse since it does not include information on limb lengths, trunk lengths, or COM positions, a similar explanation may be valid for other primates. Importantly, these results suggest that alternative mechanisms (e.g., active models) are not needed to explain chimpanzee weight support patterns.

Are chimpanzees unique?

Chimpanzees walk with more protracted hind limbs during quadrupedal walking than most other primates (Reynolds, 1987; Larson et al., 2001), raising the possibility that Gray's (1944) model may not generally explain primate patterns. However, chimpanzees also have some of the greatest hind limb weight support values among primates (see Demes et al., 1994), and according to Gray's (1944) model, increased hind limb protraction should be associated with greater hind limb weight support. Chimpanzees would therefore be predicted to fall at the high end of the primate hind limb weight support continuum. It is important to note that there is some variation in the degree of hind limb protraction in our sample of chimpanzees. However, this variation in hind limb positioning within our sample leads to predictable variation in the degree of hind limb weight support, in accordance with Gray's model.

Our sensitivity analysis shows that variation in weight support among primates is also likely explained by variation in COM position, hind limb angle, forelimb angle, or a combination of these parameters (see Fig 3). The lower average values of hind limb protraction for primates in general compared to chimpanzees (Figs. 2 and 4) are still consistent with primates' greater hind limb compared to forelimb weight support. However, primates with less accentuated hind limb protraction should support slightly less weight on their hind limbs compared to primates such as chimpanzees and spider monkeys, which walk with greatly exaggerated hind limb protraction angles (see Reynolds, 1985a).

Evolution of primate weight support patterns

Primate weight support patterns play an important role in our understanding of primate evolution (see Larson, 1998). For example, researchers have argued that decreased forelimb weight support relaxed selection for forelimb stability, and allowed for the evolution of less stable, more mobile forelimb joints in primates (Reynolds, 1985a; Larson, 1998). Reynolds (1985a) went further in describing this increased reliance on hind limb

weight support in suspensory primates as a precursor to the evolution of human bipedalism. Thus, understanding how increased hind limb weight support evolved may clarify explanations of primate morphological and locomotor evolution.

Because weight support patterns are a product of COM position and limb kinematics, increased hind limb weight support patterns may have evolved in primates as a result of changes in either parameter. However, there is little current evidence indicating that primate COM positions differ greatly from those of other mammals (see Vilensky and Larson, 1989). For example, Young et al. (2007) recently showed that Patas monkey COMs were ~43% of trunk length from the shoulder, similar to the assumed COM position of dogs (see Lee et al., 2004). The more caudal COM positions of chimpanzees may play a role in their greater hind limb weight support compared to Patas monkeys (Patas R = 47%; see Young et al., 2007), but it appears that most mammals, including primates, have COMs at, or cranial to the trunk midline (Vilensky and Larson, 1989). A caudal shift in some primate COMs would not be surprising, since Aerts et al. (2003; see also Clemente et al., 2008) suggest that a relatively caudal COM increases maneuverability, which would be advantageous to arboreal primates. Until more data are collected, however, a change in limb kinematics must be considered the most likely evolutionary path for primates' increased hind limb weight support. If so, then understanding why primate limb kinematics differ from those of other mammals may help explain how primate kinetic patterns evolved.

One possible evolutionary explanation is that primates' actively protract average foot positions to increase hind limb weight support. Alternatively, it is possible that primates walk with a relatively protracted hind limb compared to their forelimb for reasons other than actively shifting weight support. Schmidt (2005) suggested a novel explanation for primate limb excursion patterns that supports this view of weight support. Her hypothesis has not been fully tested, but it suggests that primate limb kinematics are associated with footfall sequence. Primates prefer a diagonal sequence, diagonal couplets gait (DSDC), where a forelimb footfall follows the contra-lateral hind limb footfall, and these limbs are related in time as a pair. This footfall sequence differs from the lateral sequence gaits (LS) used by most other mammals, where a forelimb footfall follows an ipsilateral hind limb footfall. In a DSDC gait, a primate's hind foot touches down while the ipsilateral forefoot is still on the substrate. This footfall sequence, combined with primates' relatively long strides (see Alexander and Maloiy, 1984), increases the likelihood of ipsilateral fore- and hind limb interference (see Hildebrand, 1968). Schmidt (2005) suggested that one solution to this interference problem is to walk with a relatively protracted forelimb (e.g. increased forelimb protraction at touchdown and decreased forelimb retraction at lift-off). Increased forelimb protraction allows for a large limb excursion without large forelimb retraction angles at lift-off, reducing overlap of the ipsilateral limbs prior to forelimb lift-off. In addition to reducing the degree of ipsilateral limb interference, walking with a highly protracted forelimb places the average position of the hind foot closer to the whole body COM than the forefoot, and thus incidentally leads to greater hind limb weight support.

If Schmidt's (2005) hypothesis is supported, then morphological variation among primates may explain further

variation in weight support patterns (i.e., greater or lesser degrees of hind limb weight support). Ratios of forelimb to hind limb total angular excursion are correlated with intermembral indices (IMI; ratio of forelimb length to hind limb length; see Larson et al., 2001). If individuals have a high IMI (i.e., relatively long forelimbs), then hind limb excursion angles must be larger than forelimb excursion angles to maintain equivalent forelimb and hind limb step lengths (Larson et al., 2001). Conversely, in animals with low IMIs, forelimb excursion angles must be larger than hind limb excursion angles (Larson et al., 2001). Thus, variation in limb proportions, associated with locomotor behaviors (see Fleagle, 1998) will lead to variation in average limb angles. It is certainly possible that this variation in hind limb excursion is brought about by increased hind limb retraction at lift-off only, which would actually reduce average hind limb protraction angles over a step. However, if variation in limb excursion is brought about by greater degrees of protraction, then variation in IMI may explain variation in weight support patterns. Since suspensory taxa (such as chimpanzees) generally have higher IMIs (Fleagle, 1998), this interpretation may explain why they also use highly protracted hind limbs and have the greatest amount of hind limb weight support.

If increased hind limb weight support evolved as a byproduct of limb kinematics associated with DS gait, then the evolution of more mobile primate forelimb joints would also ultimately be a byproduct of primate footfall sequences. Further variation in the overall degree of hind limb weight support among primates may be a byproduct of variation in IMIs. This explanation suggests that primate weight support patterns may not be adaptations in the strict sense, but may be better characterized as evolutionary byproducts of other traits (i.e., spandrels; see Gould and Lewontin, 1979; Aerts et al., 2003; Raichlen, 2004, 2005a). Viewing increased hind limb weight support as an evolutionary byproduct does not preclude its potential benefits in an arboreal environment, however, it does suggest a novel pathway for the origins of this distinctive trait.

CONCLUSIONS

Chimpanzees support more weight on their hind limbs because they walk with a relatively protracted hind limb, averaged over a step. Chimpanzee limb kinematics bring the feet closer to the COM than the hands, leading to a reduction in forelimb weight support. Comparative data suggest this same mechanism may explain increased hind limb weight support in primates in general, although this hypothesis requires further testing. The evolution of these kinematic characteristics is of particular interest because reduced forces on the forelimb likely allowed for the evolution of more mobile, less stable forelimb joints in primates. If increased hind limb protraction evolved in response to DSDC gait, then the reduction of forelimb forces is a byproduct (or spandrel) of footfall sequence. This intriguing possibility deserves further research since it suggests that forelimb mobility in primates may be tied to their unique footfall sequence.

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