

THE SHORT LEGS OF GREAT APES: EVIDENCE FOR AGGRESSIVE BEHAVIOR IN AUSTRALOPITHS

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Early hominins, australopiths, were similar to most large primates in having relatively short hindlimbs for their body size. The short legs of large primates are thought to represent specialization for vertical climbing and quadrupedal stability on branches. Although this may be true, there are reasons to suspect that the evolution of short legs may also represent specialization for physical aggression. Fighting in apes is a behavior in which short legs are expected to improve performance by lowering the center of mass during bipedal stance and by increasing the leverage through which muscle forces can be applied to the ground. Among anthropoid primates, body size sexual dimorphism (SSD) and canine height sexual dimorphism (CSD) are strongly correlated with levels of male–male competition, allowing SSD and CSD to be used as indices of male–male aggression. Here I show that the evolution of hindlimb length in apes is inversely correlated with the evolution of SSD ($R^2 = 0.683$, P -value = 0.006) and the evolution of CSD ($R^2 = 0.630$, P -value = 0.013). In contrast, a significant correlation was not observed for the relationship between the evolution of hindlimb and forelimb lengths. These observations are consistent with the suggestion that selection for fighting performance has maintained relatively short hindlimbs in species of Hominoidea with high levels of male–male competition. Although australopiths were highly derived for striding bipedalism when traveling on the ground, they retained short legs compared to those of *Homo* for over two million years, approximately 100,000 generations. Their short legs may be indicative of persistent selection for high levels of aggression.

KEY WORDS: Fighting, hominins, hominoids, male–male competition, sexual dimorphism.

Australopiths, including *Paranthropus*, had short legs compared to humans (Johanson et al. 1982; Susman et al. 1985; Jungers 1988; McHenry 1991; McHenry and Berger 1998; Richmond et al. 2002). Recent analyses suggest that, relative to the length of the humerus, *Australopithecus afarensis* had legs that were intermediate in length between chimpanzees and humans, whereas the legs of *A. africanus* and *Homo (A.) habilis* were similar in length to those of modern chimpanzees (McHenry and Berger 1998; Richmond et al. 2002). In this respect, australopiths were similar to most large-bodied extant primates. Relative limb length decreases with body size in catarrhine primates, and the trend is most pronounced in the hominoids (Jungers 1984). The relatively short legs of larger primates are thought to represent spe-

cialization for climbing. Short legs improve balance when walking quadrupedally above branches by lowering the center of mass (Cartmill 1985; Doran 1993). Short legs also facilitate climbing broad tree trunks by allowing the body to be held close to the trunk, thereby lowering the tensile forces required from the forelimbs (Cartmill 1974; Jungers 1978; Susman et al. 1985). Thus, it is generally assumed that short legs were retained in australopiths because the arboreal habitat remained important to their life history (Susman et al. 1985). Short limbs, however, must limit the ability to bridge gaps between possible sites of support when climbing and traveling through the canopy. Indeed, the most arboreal apes, gibbons, have relatively long hindlimbs for catarrhines of their size (Jungers 1984). Short limbs, therefore,

may facilitate some types of arboreal locomotion but limit others.

Physical aggression associated with male–male competition is prevalent in all extant species of great apes (Wrangham and Peterson 1996) and is a behavior in which short hindlimbs are expected to improve performance. Although teeth are a primary weapon in the Hominoidea, great apes also fight with their forelimbs from a bipedal stance on the ground (Livingstone 1962; deWaal 1982, 1986; Fossey 1983; Goodall 1986; Kano 1992; Wrangham and Peterson 1996; Furuichi 1997). Characters that improve strength and stability in a bipedal stance should enhance fighting performance. Short hindlimbs lower the center of mass in a bipedal stance, increasing postural stability. Short limb elements, all else being equal, also increase the horizontal (i.e., shearing) forces that can be applied to the substrate, by reducing the length of the ground reaction force moment arm at the hip joint (Smith and Savage 1956). Thus, shorter legs may improve the fighting performance of apes.

Fighting behavior of apes has been most thoroughly described in chimpanzees (Nishida et al. 1985; de Waal 1986; Goodall 1986; Nishida et al. 1990; Wrangham 1999). Interindividual attacks consist of “hitting, kicking, stamping on, dragging, slamming, biting, scratching, and grappling” (Goodall 1986). During an attack, a male may jump onto the victim’s back and stamp with his feet. A smaller individual may be lifted into the air and slammed to the ground. Goodall (1986) classified the intensity of fights between individuals in three levels, with level 3 representing a fight that involved a violent attack, lasting more than 30 sec, and during which serious wounds may be inflicted. During the four-year period 1976–1979, 15.4% of the interindividual fights her team observed were level 3.

There are five study sites in which chimpanzees have neighbors such that intercommunity interactions have been observed (Wrangham 1999). Coalitional killings have been reported from four of these five sites, and the deaths can represent a significant part of the population (Wrangham 1999). In Gombe, for example, the proportion of adult male mortality from intraspecific coalitional aggression was 30–40% during the 1970s. Detailed, eyewitness accounts of lethal fighting are provided by Goodall (1986). In these cases, groups of three to six adult males attacked isolated individuals, usually males, from the adjacent community. The attacks began by grappling and pulling the victim to the ground, in some cases from out of a tree the victim had attempted to flee into. The victim was held, pinned to the ground by one member of the group while other members attacked by biting, hitting with fists, and kicking and stomping on. The victims were often dragged for distances on the ground, lifted and slammed back to the ground, and attempts were made to break arms and legs by twisting. In one case (Sniff), the victim’s leg was broken. In these lethal attacks, a bipedal stance was used as a base for striking with the fore-

limbs, as well as lifting, dragging, and twisting the victim. The hindlimbs were also used as primary weapons to kick and stomp on the victim.

Male–male aggression among bonobos appears similar in many ways to that of chimpanzees, but of a lower intensity. The vast majority of aggressive interactions in bonobos are between adult males (Kano 1992; Furuichi 1997). Kano’s (1992) analysis found that male–male aggressive interactions were twice as common as instances of male–female aggression, and 18-times more common than female–female aggressive interactions. Most aggressive interactions do not involve physical contact (Furuichi 1997). Nevertheless, when aggression escalates to physical attacks, bonobos bite, hit, kick, slap, grab, drag, shove aside, and pin down.

The frequency and intensity of fighting in orangutans and gorillas is poorly understood and has received relatively little attention in published literature. Mature male orangutans are reported to be totally intolerant of each other (Galdikas 1985). Of two observed encounters between adult males in the presence of adult females, both “entailed considerable physical violence” (Galdikas 1985). One of these fights lasted for over half an hour and involved “bouts of grappling in the canopy and on the ground with the males biting each other’s hands, head and shoulders.” In gorillas, male–male aggression during intergroup encounters is common. Harcourt (1978) reported that violent displays occur during 80% of these encounters and fights between males occur during 50% of the encounters.

The bipedal threat displays used by gorillas, chimpanzees, and bonobos are also consistent with a fighting strategy in which striking with the forelimbs from a bipedal posture is important. Game theory modeling of aggressive encounters suggests that threat displays should provide a maximal but accurate indication of one’s fighting ability (Maynard Smith and Price 1973; Parker 1974; Enquist and Leimar 1990; Szamado 2003). Stags display the size of their antlers and body (Clutton-Brock et al. 1979). Wolves (Zimen 1978), hippos (Kingdon 1979), honey badgers (i.e., ratsels), baboons (Estes 1991), and many other species display the size of their canines. In this context, it is interesting that the most dramatic threat performed by chimpanzees and bonobos is the charging display. This display includes running along the ground, often bipedally; dragging or flailing branches; throwing rocks or other loose material; slapping the ground with the hands and stomping with feet, or both alternately; and leaping up to hit and stomp on a tree (deWaal 1982; Goodall 1986; Kano 1992). These displays emphasize strength and agility in a bipedal stance and the power with which an individual can hit with his forelimbs and stomp with his hindlimbs. Jablonski and Chaplin (1993) provided a scenario for the evolution of threat displays in Catarrhini and suggested that display–appeasement behavior was important in the evolution of habitual terrestrial bipedalism

in proto-hominins. Terrestrial bipedal threat displays appear to be basal to the *Gorilla*, *Pan*, *Homo* clade and are indicative of a fighting strategy in which the limbs are important weapons used to punch, slap, kick, stomp, and twist.

Analysis of skeletal trauma also provides an indication of the severity of aggressive behavior among apes and of the importance of weapons other than teeth (i.e., canines) as the cause of injury. Jurmain (1997) analyzed museum collections of "wildshot" adult specimen of chimpanzees (crania, 127; postcrania, 92), bonobos (crania, 71; postcrania, 15), and gorillas (crania, 136; postcrania, 62). He also studied 14 crania and 13 postcrania of chimpanzees that died of natural causes at the Gombe study site. The case for many of the injuries being caused by interindividual aggression is strong. Among the wildshot chimpanzees, 5.5% exhibited cranial trauma: four healed fractures (one of the vault, three of the face) and three probably bite wounds. Only 2.8% of the bonobo crania showed signs of trauma (two healed zygomatic fractures). Gorillas displayed twice the prevalence of cranial trauma (11%) as that observed in the chimpanzees; five vault fractures, five face fractures, and one bite wound. In the combined sample for all groups, including that from Gombe, a total of 21 facial lesions were observed. Most significantly, of these 21 facial lesions, 20 (95%) occurred in males. Jurmain (1997) concluded that although many of the injuries were likely caused by falls, an equal or greater proportion were likely the result of interindividual aggression. Lovell (1990) analyzed skeletal trauma in orangutans. Of 16 crania from adult males, one (6.2%) exhibited a healed fracture (frontal bone), whereas no trauma was observed in 17 crania of adult females.

In summary, there are three types of observations that are consistent with life-threatening male–male fighting in which individuals fight by striking an opponent with the fore and hindlimbs from a bipedal stance: (1) observed aggressive interactions, (2) posture and behavior during threat displays, and (3) cranial trauma that is strongly male biased and appears not to have resulted from biting. Although most of these observations are from chimpanzees, the patterns are similar in many respects to the fighting behavior of humans and are consistent with what is known about fighting in orangutans, gorillas, and bonobos.

To address the possibility that the short legs of great apes are associated with selection for improved fighting performance, I looked at the relationship between limb length and sexual dimorphism in body size and sexual dimorphism in canine height in Hominoidea (i.e., Hylobatidae and Hominidae). Although other factors may lead to sexual dimorphism in which males are larger than females (Andersson 1994; Blanckenhorn 2005), this type of dimorphism tends to occur in mammalian species that have polygynous mating systems in which males compete physically for reproductive access to females (reviewed in Andersson 1994). Among anthropoid primates, size sexual dimorphism (SSD) is

strongly associated with both male–male competition levels and operational sex ratio (Plavcan and van Schaik 1997a; Plavcan 1999, 2004). Canine height sexual dimorphism (CSD) is more pronounced in polygynous species (Leutenegger 1982) and is strongly correlated with male–male competition levels when species values are compared, but not when phylogenetic independent contrast values are compared (Plavcan 2004). A recent analysis suggests that canine size is more important in male–male competition among haplorhine primates than is body size (Thoren et al. 2006). Thus, in this study, both SSD and CSD were used as indices of male–male aggression. The expectation was that species with relatively high SSD and CSD would have relatively short legs.

Methods

To determine whether or not relative limb length was negatively correlated with SSD and CSD, records of male limb length, body mass for both males and females, body mass sexual dimorphism, and maxillary CSD were acquired from the literature (Table 1) for seven species of apes (Hominoidea) and two species of monkey (Cercopithecinae). Average limb lengths for *Hylobates* and the great apes were taken from Jungers (1984). Average limb lengths for *Miopithecus* and *Papio* are from Jungers (1985). Values of average body mass and SSD (male mass / female mass) are from studies of wild populations and include only specimens that were reported to be adult. With the exceptions of *Homo* and *Gorilla*, the references used are those recommended by Plavcan and van Schaik (1997a). Average limb lengths, body mass, and SSD for *Homo* are from a sample of Australian Aborigines (Macho and Freedman 1987), consisting of adult males ($N = 60$) and females ($N = 83$) between the ages of 20 and 30 years. Average body mass data for *Gorilla* are from Smith and Jungers (1997). This study was used because the values listed in Plavcan and van Schaik (1997a) for *Gorilla* were derived from low sample sizes. Values of maxillary canine height dimorphism are from Plavcan (2004) with the exception of values for *Homo sapiens*, which are from Thoren et al. (2006).

Three approaches were used to investigate the relationships between limb length and indices of sexual dimorphism. First, log-transformed species values of relative limb length ($\text{length} \times \text{male body mass}^{-0.333}$) were regressed against log-transformed SSD (male mass \times female mass $^{-1}$) or log-transformed CSD (male canine height \times female canine height $^{-1}$). Second, because sexual dimorphism in body size and canine height are positively correlated with body size (Leutenegger 1982; Smith and Cheverud 2002) and relative limb length is negatively correlated with body size (Jungers 1984) in hominoids, I removed the effect of body size with residual analysis. Residuals for limb length, SSD, and CSD were derived from least-squares regressions of species values of

Table 1. Species, limb lengths, male body masses, and body size sexual dimorphism (SSD) and canine height sexual dimorphism (CSD) used in this analysis.

Species	Hindlimb length ¹ (mm)	Forelimb length ¹ (mm)	Mass of males ² (g)	SSD ² (male/female)	CSD ⁴ (male/female)	Reference for body masses and SSD
<i>Miopithecus talapoin</i>	189	160	1,380	1.23	1.69	Gautier-Hion (1975)
<i>Papio anubis</i>	471	458	25,100	1.78	2.22	Dechow (1983)
<i>Hylobates concolor</i>	361	514	5,600	0.96	1.15	Schultz (1973)
<i>Hylobates syndactylus</i>	399	581	10,850	1.02	1.18	Schultz (1973)
<i>Pongo pygmaeus</i>	557	739	86,300	2.23	1.69	Markham and Groves (1990)
<i>Pan paniscus</i>	553	553	45,000	1.36	1.38	Jungers (1985)
<i>Pan troglodytes</i>	574	614	43,000	1.3	1.42	Jungers and Susman (1984)
<i>Homo sapiens</i> ³	857	595	56,590	1.17	1.09	Macho and Freedman (1987)
<i>Gorilla gorilla</i>	698	762	170,400	2.38	1.73	Smith and Jungers (1997)

¹Average male limb lengths for *Hylobates* and Pongidae are from Jungers (1984). Average male limb lengths for *Miopithecus* and *Papio* are from Jungers (1985).

²Average body mass and size sexual dimorphism (SSD; male mass / female mass) were taken from the sources listed. The choices are consistent with those of Plavcan and van Schaik (1997a), with the exceptions of *Homo* and *Gorilla*.

³Data for *Homo* are from a sample of Australian Aborigines (Macho and Freedman 1987). Average limb lengths, body mass, and SSD were calculated from adult males ($N = 60$) and females ($N = 83$) between the ages of 20 and 30 years.

⁴Values of maxillary canine height dimorphism are from Plavcan (2004) with the exception of values for *Homo sapiens*, which are from Thoren et al. (2006).

limb length, SSD, and CSD on male body mass. Then the body mass residuals of limb length were regressed against body mass residuals of SSD and CSD. Lastly, because the closely related species in this study are not statistically independent entities, independent contrast analysis was done to compare the evolution of limb length and SSD and CSD.

Independent contrast analysis was done following the methods of Garland et al. (1992). Two species of cercopithecine monkey were used to represent the outgroup of Hominoidea. Data were log transformed. Mesquite PDTREE (mesquiteproject.org) was used to calculate contrast values for male forelimb length, male hindlimb length, SSD, CSD, and male body mass. Phylogeny and branch lengths used in the analysis (Fig. 1) were taken from Purvis (1995). To correct for the effect of body size, residual contrast values were calculated by regressing contrast values of SSD, CSD, and limb length on contrast values of male body mass. Then residual contrast values of limb length were regressed against residual contrast values of SSD and CSD. In all cases, lines of the regressions were restricted to an intercept of zero.

Results

Among the species used in this analysis (two species of cercopithecine monkeys and seven species of Hominoidea), sexual dimorphism in canine height was positively correlated with sexual dimorphism in body mass. This was true for species values ($R^2 = 0.548$, P -value = 0.022), male body mass residuals of species values ($R^2 = 0.797$, P -value = 0.001), and independent contrast values ($R^2 = 0.650$, P -value = 0.011).

Hindlimb length, normalized to body mass ($\text{mm} \times \text{g}^{-0.333}$), was inversely correlated with SSD and CSD (Fig. 2; Table 2). Species of apes with the highest levels of SSD and CSD tended to have relatively short legs. In contrast, the relationships between normalized forelimb length and SSD and CSD were not significant (Table 2), and the trends were largely functions of the long forelimbs and low SSD and CSD of gibbons (Fig. 2). Additionally,

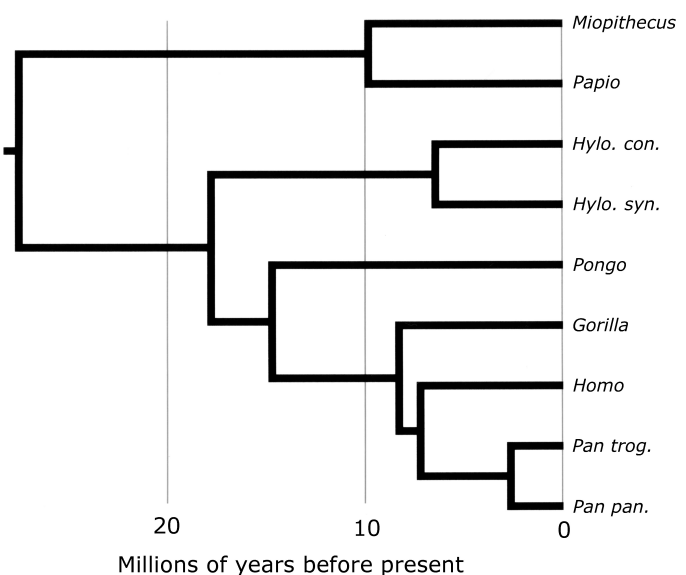


Figure 1. Phylogeny used in the analysis of independent contrasts (compiled from Purvis 1995).

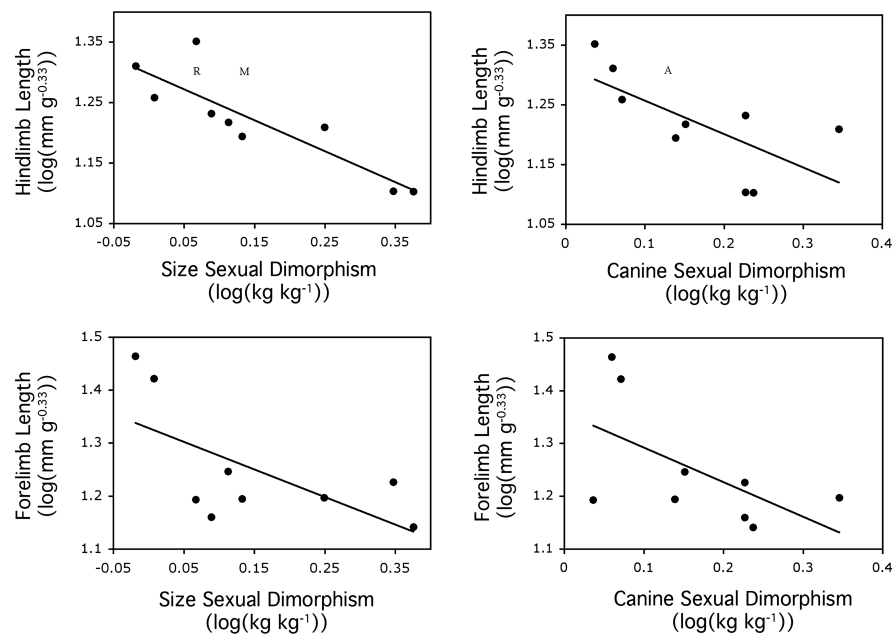


Figure 2. Regressions of mass specific hind and forelimb length on size sexual dimorphism (SSD) and canine sexual dimorphism (CSD) for seven species of apes (Hominoidea) and two species of anthropoid monkey (Cercopithecinae). SSD is male mass divided by female mass. CSD is male canine height divided by female canine height. For comparison, estimated values for *Australopithecus africanus* are noted in the hindlimb graphs and are marked by the letters “M” and “R” for hindlimb length versus SSD and by “A” for hindlimb length versus CSD. These estimates were not used in the analysis, but are shown on the graphs to illustrate where australopiths would likely fall relative to the extant hominoids. The estimate of hindlimb length of *A. africanus* is based on the femur length estimate of McHenry (1991) and a tibia length of $0.85 \times$ femur length (Steudel-Numbers and Tilkens 2004). Estimates of size sexual dimorphism of *A. africanus* are from McHenry (1992) for “M” and a value similar to that of modern humans, as suggested by Reno et al. (2003) for “R.” Canine sexual dimorphism for *A. africanus* is from Plavcan (2000).

there was not a significant correlation between normalized forelimb and hindlimb length (Fig. 3; Table 2).

There are at least two factors that could make the inverse correlations between normalized hindlimb length and sexual dimorphism spurious: the effect of body size and that of phylogeny. The concern about body size is that relative hindlimb length is negatively correlated with body size in apes, whereas SSD and CSD are positively correlated with body size. If the reasons for these relationships with body size are not both related to selection

for aggression, then the observed correlations between hindlimb length and sexual dimorphism would be false. Thus, to remove the effect of body size, I regressed male body mass residuals of limb length against male body mass residuals of SSD and CSD. When this was done, the inverse correlations between hindlimb length and SSD and between hindlimb length and CSD remained strong (Table 2). Ape species with relatively high levels of SSD or CSD for their body size tend to have relatively short hindlimbs. In contrast, significant relationships were not observed when body

Table 2. Analysis of species values and independent contrasts for the relationships between hind or fore limb lengths and body size (i.e., body mass) sexual dimorphism (SSD) or canine height sexual dimorphism (CSD).

	Species values		Species values body mass residuals		Contrast values	
	R^2	P -value	R^2	P -value	R^2	P -value
Hindlimb versus SSD	0.764	0.002*	0.714	0.004*	0.683	0.008*
Hindlimb versus CSD	0.468	0.042*	0.520	0.028*	0.630	0.013*
Forelimb versus SSD	0.416	0.061	0.321	0.111	0.475	0.045*
Forelimb versus CSD	0.340	0.099	0.343	0.097	0.324	0.117
Hindlimb versus forelimb	0.210	0.214	0.115	0.372	0.403	0.073

*Slope of regression significant at $P < 0.05$.

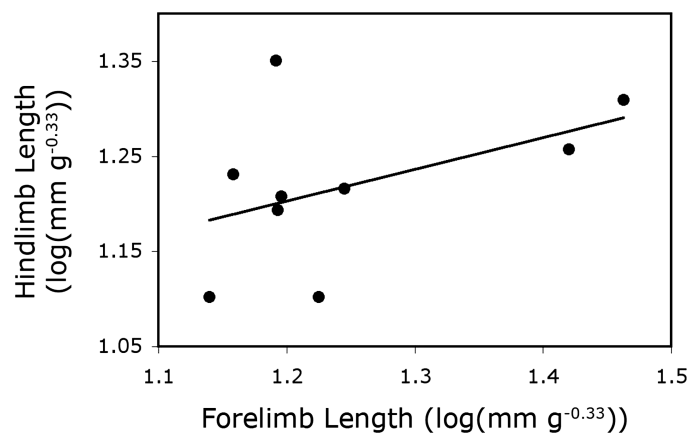


Figure 3. Regression of mass specific hindlimb length on mass specific forelimb length for seven species of apes (Hominoidea) and two species of anthropoid monkey (Cercopithecinae).

mass residuals of forelimb length were regressed against residuals of SSD and CSD (Table 2). The relationship between body mass residuals of hindlimb length and forelimb length was also not significant (Table 2).

The second factor that could lead to false correlations between limb length and SSD and between limb length and CSD is phylogeny. Because the species used in this analysis are not statistically independent entities, independent contrasts of limb length were regressed against independent contrasts of SSD and CSD. The effect of body size was removed with residual analysis, in which contrast values of sexual dimorphism and limb length were regressed on contrast values of male body mass to obtain residual contrast values. Then residual contrast values of limb length were regressed against residual contrast values of size and canine sexual dimorphism. There were strong negative correlations between contrast values of hindlimb length and contrast values of SSD and CSD (Table 2). Among these species, the evolution of increased SSD and CSD was correlated with the evolution of relatively shorter hindlimbs. There was also a significant inverse correlation between contrast values of forelimb length and SSD, but the relationship between contrast values of forelimb length and CSD was not significant (Table 2). The evolution of hindlimb length was not significantly correlated with the evolution of forelimb length (Table 2).

Relative to body mass, females had longer hindlimbs than males in four of the five species of Hominidae analyzed (Table 3). The exception was *Homo*. Nevertheless, as a group, female Hominidae have relatively longer legs than males (P -value = 0.035, paired t -test).

Discussion

In apes, hindlimb length is inversely correlated with both body SSD and CSD. When the effect of body size is removed from

Table 3. Comparison of male and female relative hindlimb length ($\text{mm} \times \text{g}^{-0.333}$).

Species	Male hindlimb length ¹	Female hindlimb length ¹
<i>Pongo pygmaeus</i>	12.6	14.3
<i>Pan paniscus</i>	15.6	17.0
<i>Pan troglodytes</i>	16.4	17.0
<i>Homo sapiens</i>	22.4	22.0
<i>Gorilla gorilla</i>	12.6	14.0

¹Limb length data from Jungers (1984). Body mass data from sources listed in Methods.

species values, 71% of the variation in relative limb length is correlated with SSD and 52% of the variation is correlated with CSD. Size-corrected phylogenetic independent contrasts show a similar pattern; 68% of the evolution of limb length is correlated with evolution of SSD and 63% is correlated with evolution of CSD. Thus, species with the highest levels of male-biased SSD and CSD have relatively short hindlimbs. These results, plus the observation that female great apes have longer hindlimbs for their body size than do males, are consistent with short legs having evolved in response to selection for male–male aggression.

Forelimb length, in contrast, was found not to be strongly associated with sexual dimorphism. Analysis of species values showed that forelimb length is not significantly correlated with either SSD or CSD. Independent contrast values for forelimb length and SSD did exhibit a significant inverse correlation. The relationship between contrast values of forelimb length and CSD, however, was not significant. Thus, the inverse relationship between limb length and sexual dimorphism is much weaker for the forelimb than for the hindlimb. The possibility that different selection pressures govern the evolution of forelimb length than the evolution of hindlimb length is clearly evident from the observation that the evolutions of hindlimb and forelimb lengths are not significantly correlated in hominoids. Why this is the case remains unclear. The forelimbs have different roles and mechanical demands from those of the hindlimbs in both climbing and fighting, as well as in terrestrial locomotion, foraging, feeding, grooming, and mating. In the case of fighting, shorter forelimbs could be expected to increase the leverage, and possibly the power, with which roundhouse and over-the-head blows could be delivered to an opponent. Shorter forelimbs, however, would decrease the reach, which is likely to be disadvantageous in a fight. Additionally, functional trade-offs in limb length between selection for climbing versus selection for fighting (Pasi and Carrier 2003; Carrier 2004; Kemp et al. 2005) might be more pronounced in the forelimb than in the hindlimb, resulting in different evolutionary trends among species for the forelimbs versus hindlimbs. In any case, this analysis suggests that the selective factors

governing limb length are different for the fore and hindlimbs of hominoids.

The observation that bonobos have relatively shorter hindlimbs than common chimpanzees (Table 3) appears inconsistent with the hypothesis that shorter limbs enhance fighting performance. Although physical fights among both male and female bonobos have been observed (Kano 1992; Furuichi 1997 and reviewed above), there are no known instances of lethal fighting in bonobos. In contrast, fighting that results in fatalities is well documented in several populations of chimpanzees. If fighting is less important in bonobos than chimpanzees, chimpanzees should have relatively shorter hindlimbs than bonobos. One possible explanation is that the data for hindlimb length or body mass used in this analysis are not accurate for one or both of these two species. For example, Zihlman and Cramer (1978) report average hindlimb lengths of 535 mm for bonobos and 529 mm chimpanzees. If the body mass values reported by Jungers and Susman (1984) are used to correct for body size, relative hindlimb lengths are 12% longer in bonobos than chimpanzees (16.46 vs. $14.63 \text{ mm} \times g^{-0.333}$, respectively). Alternatively, given that the hindlimbs of apes are used for a wide variety of behaviors, it is unlikely that selection for performance in one activity, such as fighting, will explain the difference of relative hindlimb length in every species comparison.

The results of this study do not address the possibility that selection for climbing performance results in the evolution of relative short legs in larger primate species, as previously suggested (Cartmill 1974, 1985; Jungers 1978; Susman et al. 1985). The two hypotheses for the evolution of relatively short legs in larger primates, specialization for climbing and specialization for aggression, are not mutually exclusive. Indeed, selection for climbing performance may result in the evolution of a body configuration that improves fighting performance and vice versa (Carrier 2004). Currently, support for each of these hypotheses is limited. Both hypotheses are based on simple biomechanical principles and on correlations. In the case of the climbing hypothesis, relatively short limbs in larger apes are correlated with reduced use of the arboreal habitat. On the other hand, the inverse correlations between relative limb length and body size and between relative limb length and CSD are consistent with the aggression hypothesis. The proposed performance advantages of the two hypotheses, improved arboreal locomotion, and improved fighting performance are yet to be tested empirically.

There is also the question of whether the positional behavior of great apes is consistent with the climbing hypothesis for the evolution of short legs. The argument that relatively short legs help make climbing practical in larger species is hard to reconcile with the limited arboreality of the larger apes. Male gorillas, the largest of the apes, have the shortest legs for their body mass. Although male gorillas are adept climbers (Remis 1995, 1999), they are predominantly terrestrial. In the Virunga mountain goril-

las, terrestrial knuckle-walking accounts for 94% of their travel distance (Tuttle and Watts 1985). Gorillas generally feed on the ground in the herb and shrub stratum of the forest and most of their diurnal resting spots and night nests are located on or very near the ground (Tuttle 1986). Furthermore, large males forage less in trees than do the much smaller females (Remis 1995, 1999). This sex difference is also true for orangutans (Tuttle 1986). Contrary to common perception, orangutans are not strictly arboreal and large adult males are known to travel greater distances walking quadrupedally on the ground than do females (reviewed by Tuttle 1986). For instance, Rodman (1979) observed that an adult male in the Kutai Nature Reserve of Kalimantan Timur, Indonesia, spent 20% of his travel time on the ground. Galdikas (1979) found that among large males that are fully habituated to the presence of human observers almost all of their long distance travel is done on the ground. Adult male and female chimpanzees also differ in their arboreal locomotor behavior, with the larger males using less quadrupedalism and more climbing, scrambling, and aided bipedalism than females (Doran 1993). Although these observations are consistent with a body size constraint on climbing performance, they indicate that the relatively shorter legs of larger species and of male great apes do not adequately compensate for the limits imposed by larger size. Indeed, the positional data are consistent with the possibility that relatively short legs actually limit climbing performance rather than enhance it.

Although this analysis does not test the climbing hypothesis for the evolution of short legs, it does independently address the aggression hypothesis. The climbing hypothesis is based on the mechanical reality that climbing becomes more difficult as body size increases. It argues that the evolution of relatively short legs helps compensate for biomechanical limits on the climbing performance of larger species. Thus, removing the effect of body size in the analysis provides a way to address the aggression hypothesis independently of the climbing hypothesis. Regardless of the extent to which selection for climbing performance leads to the evolution of relatively shorter legs in larger primate species, the finding of size-independent correlations between the evolution of hindlimb length and body size and between relative limb length and CSD suggests that male-male competition in apes selects for relatively shorter legs.

One prediction of the hypothesis that relatively short hindlimbs represent specialization for aggressive behavior is that gorillas and orangutans should experience higher intensity physical aggression than either chimpanzees or bonobos. Analysis of behavioral reports suggests this is true. Plavcan and van Schaik (1992, 1997a) estimated male-male competition levels for a large number of primates based on observations of the frequency and intensity of aggression. Their analysis placed gibbons in the low-frequency, low-intensity group; chimps and bonobos in the high-frequency, low-intensity group; and orangutans and gorillas in

the low-frequency, high-intensity group. Although the nature and intensity of male–male aggression is well documented in both chimpanzees and bonobos, much less is known about male–male aggression in orangutans and gorillas. The available literature, reviewed above, suggests that fighting among male orangutans and gorillas is intense and is expected to have a significant impact on their reproductive fitness. For example, Jurmain (1997) found that gorillas display twice the prevalence of cranial trauma as that observed in chimpanzees. Nevertheless, more field observations are required before we can have confidence in estimates of male–male aggression levels of orangutans and gorillas.

Relative to their arboreal ancestors, australopiths were highly specialized for terrestrial, bipedal locomotion (Lovejoy 1988; Latimer and Lovejoy 1989, 1990a,b; Wolpoff 1999). Even the forelimb and hand of australopiths appears to have been less specialized for arboreality than is the case in nonhominins (Drapeau et al. 2005). Regardless of the extent to which australopiths used trees in their daily activities (Susman et al. 1985), it is clear that terrestrial locomotion was important to their life history. It is well established that longer limbs reduce the cost of transport in terrestrial species (Kram and Taylor 1990; Steudel-Numbers and Tilkens 2004; Pontzer 2005). Thus, it is something of a paradox that for roughly two million years, approximately 100,000 generations, the relative length of early hominin legs did not increase (McHenry 1991; McHenry and Berger 1998). The lack of increase in limb length, during this period, is consistent with some form of selection acting in opposition to selection for improved locomotor speed and economy.

The anatomical bauplan of australopiths has been suggested to represent specialization for fighting with the forelimbs (Carrier 2004). The observation that, among apes, the evolution of relative hindlimb length is inversely correlated with the evolution of SSD and CSD (proxies for male–male aggression) strengthens the case for fighting specialization in australopiths. The retention of legs that were short compared to those of humans for more than two million years suggests that australopiths were subject to persistent selection for high levels of aggression.

A criticism that is frequently raised against the suggestion that australopiths were anatomically specialized for male–male fighting is the observation that they had relatively small canine teeth. Large canines are generally considered to be the “primary” weapon used by primates to threaten and injure an opponent. Compared to living primates, australopiths had small canines and minimal canine sexual dimorphism (Wolpoff 1971, 1976, 1999; Greenfield 1992; Plavcan and van Schaik 1997b; Plavcan 2001). The canines of *Homo* are smaller still and exhibit even less sexual dimorphism. Greenfield (1992) reviewed the various theories for canine reduction in hominoids and found all of them inadequate at some level. The most popular hypothesis is that hand-held weapons supplanted the use of canines in male–male aggression

(Darwin 1871; Washburn 1960; Brace 1967; Wolpoff 1976). This is a plausible suggestion for the canine reduction associated with the evolution of australopiths (Wolpoff 1976). The hominoid trend of canine reduction, however, begins millions of years before the appearance of stone tools in the fossil record. Alternatively, the limbs of Hominidae may have evolved to be formidable weapons, partially supplanting the use of canines as weapons. The fighting styles and threat displays of extant Hominidae, reviewed above, are certainly consistent with this.

In any case, at least one extant species with small canines does exhibit high levels of aggression. The hominoid species with the smallest canines relative to body mass and the lowest level of canine sexual dimorphism is arguably the most violent vertebrate on the planet. Analysis of the archeological record indicates that high levels of interpersonal violence predate the historical record, state societies, and the invention of agriculture (Keeley 1996; Melbye and Fairgrieve 1994; Walker 2001). Evidence of interpersonal violence is also strikingly apparent in some of the earliest fossils of our species (White 1986; Fernandez-Jalvo et al. 1999). In a scholarly review of the archeological evidence of interpersonal violence Walker (2001) concludes—“as far as we know, there are no forms of social organization, modes of production, or environmental settings that remain free from interpersonal violence for long.” Of direct relevance to this discussion of anatomical specialization for aggression in apes is the suggestion that much of the aggressive behavior observed in modern humans is rooted evolutionarily in male–male competition (Chagnon 1979a,b; Thornhill and Thornhill 1983; Manson and Wrangham 1991; Wilson and Daly 1993, 1998; Wilson et al. 1995; Daly and Wilson 1997; Daly et al. 2001; Thornhill and Palmer 2003). Given the behavior of extant hominids, evidence of high levels of male–male aggression in the fossil taxa that link humans to nonhuman hominids should not come as a surprise.

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