Published in final edited form as:

Am J Phys Anthropol. 2014 March ; 153(3): 417–434. doi:10.1002/ajpa.22440.

***In vivo* baseline measurements of hip joint range of motion in suspensory and non-suspensory anthropoids**

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Abstract

Hominoids and atelines are known to use suspensory behaviors and are assumed to possess greater hip joint mobility than non-suspensory monkeys, particularly for range of abduction. This assumption has greatly influenced how extant and fossil primate hip joint morphology has been interpreted, despite the fact that there are no data available on hip mobility in hominoids or *Ateles*. This study uses *in vivo* measurements to test the hypothesis that suspensory anthropoids have significantly greater ranges of hip joint mobility than non-suspensory anthropoids. Passive hip joint mobility was measured on a large sample of anesthetized captive anthropoids (non-human hominids=43, hylobatids=6, cercopithecids=43, *Ateles*=6, *Cebus*=6). Angular and linear data were collected using goniometers and tape measures. Range of motion data were analyzed for significant differences by locomotor group using ANOVA and phylogenetic regression. The data demonstrate that suspensory anthropoids are capable of significantly greater hip abduction and external rotation. Degree of flexion and internal rotation were not larger in the suspensory primates, indicating that suspension is not associated with a global increase in hip mobility. Future work should consider the role of external rotation in abduction ability, how the physical position of the distal limb segments are influenced by differences in range of motion proximally, as well as focus on bony and soft tissue differences that enable or restrict abduction and external rotation at the anthropoid hip joint.

Keywords

hip abduction; external rotation; passive joint mobility; orthograde; primates

INTRODUCTION

Forelimb-dominated arboreality, such as that used during antipronograde bridging, brachiation, and vertical climbing, distinguishes hominoids from nearly all cercopithecids, as well as from most anthropoids in general (Keith 1923; Avis 1962; Erikson 1963; Napier 1963). Suspension is a key component to forelimb-dominant locomotor behaviors and is a particularly important adaptation for larger-bodied species, conferring more positional

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stability by allowing the animals to distribute their weight among multiple arboreal supports (Grand 1972; Fleagle and Mittermeier 1980). Even though suspensory behaviors only account for a relatively small percentage of locomotor behaviors in the great apes (e.g., 7% in *Pan troglodytes* (Doran 1996), 5% in *Gorilla gorilla* (Remis 1995), >12% in *Pongo pygmaeus* (Cant 1987); Table 1), the importance of suspensory behaviors is thought to explain the derived morphologies shared among suspensory anthropoids, such as large intermembral indices and relatively large shoulder breadth (review in Larson 1998).

Suspensory behaviors have different biomechanical requirements of both the fore- and hindlimbs than generalized quadrupedalism (Grand 1972). In particular, suspensory behaviors require reaching for discontinuous, variably-oriented arboreal supports with both the hands and feet. Range of hand and foot positions are influenced by angular excursions at the proximal shoulder and hip joints, making mobility at these joints an important determinant of the range of supports within reach of the hand and foot. Larger abduction abilities at the shoulder and hip joint are frequently cited as relating to climbing, suspensory, and/or less cursorial behaviors (Jenkins 1974; Walker 1974; Fleagle 1976; Jenkins and Camazine 1977; Grand 1984; Cartmill 1985; Larson 1993; Ward 1993; 2007; Crompton et al. 2008; Schmidt and Krause 2011). However, it is possible that non-suspensory anthropoids have an equally high level of joint mobility but more extreme hip postures are not elicited by their locomotor behaviors. This possibility has been highlighted by recent work on passive mobility in the glenohumeral joint, which found few differences between suspensory hominoids and non-suspensory cercopithecids (Chan 2008).

The hypothesis that arboreal versatility is associated with an increased range of hip joint mobility has influenced functional inferences made about hip morphology when reconstructing the behavior of fossil primates (Walker 1974; e.g., Fleagle 1983; Rose 1983; Ruff 1988; Ward 1993; Ward et al. 1993; MacLachy 1995; 1996; MacLachy and Bossert 1996; MacLachy 1998; Köhler et al. 2002; Hogervorst et al. 2009). MacLachy (1995; 1996; MacLachy and Bossert 1996) evaluated the hypothesis *in silico* by modeling hip joint abduction in four non-human anthropoids (*Macaca fascicularis*, *Mandrillus sphinx*, *Pan troglodytes*, *Pongo pygmaeus*). *Pongo pygmaeus* was found to have a significantly greater range of abduction than *Pan* and the cercopithecids, although non-significant differences were observed between *Pan* and *Macaca* (MacLachy 1996). Given the limited taxonomic sample, it is unclear if differences in degree of abduction reflect locomotor behavior *per se* or result from phylogenetic and/or allometric trends.

To date, it has never been shown empirically that suspensory anthropoids have higher levels of hip joint mobility than in non-suspensory anthropoids. Limited data on passive hip joint mobility are available for macaques (DeRousseau et al. 1983; Turnquist and Kessler 1989) and patas monkeys (Turnquist 1983; 1985) but there are no data from suspensory anthropoid taxa for comparison. Hip abduction was not characterized in any of these studies except that of DeRousseau et al. (1983), although detailed descriptive statistics for range of abduction were not provided. A study by MacLachy (1995; 1998) quantified abduction throughout the flexion-extension range in anesthetized strepsirrhines and found differences that seem to correspond to arboreal versatility, although these data do not directly address questions pertaining to hip mobility in suspensory anthropoids. Quantifying range of possible hip joint

motion in suspensory and non-suspensory anthropoids would provide empirical data with which to test the hypothesis that suspensory anthropoids have higher levels of hip joint mobility. The goal of this work is to evaluate whether suspensory primates actually do have a greater range of motion in the hip joint than non-suspensory primates, evaluate the influence of body size on the data, and to report baseline measures for hip mobility in a large sample of anthropoids.

MATERIALS AND METHODS

The handling and use of animals described herein was approved by the University of Missouri Animal Care and Use Committee (protocol #6862) and by the animal care committees of the participating zoos and research centers (Table 1). *In vivo* measurements were collected during primate immobilizations for routine veterinary procedures. The use of captive animals is not ideal but, because captive animals can be measured in a controlled setting with experienced veterinary professionals in attendance, the use of captive animals was the only realistic and safe method of collecting range of motion (ROM) data. Measurements were collected on live animals rather than cadaveric specimens to avoid changes in soft tissue compliance from decay (e.g., rigor mortis) or chemical embalming (Viidik and Lewin 1966; Tolhurst and Hart 1990; Wilke et al. 1996). All institutions visited during this study are fully-accredited with the Aquarium and Zoological Association (AZA), the Zoological Association of America (ZAA), and/or the Council on Accreditation of the Assessment and Accreditation of Laboratory Animal Care International (AAALAC). Some great apes were measured in facilities funded by the National Institutes of Health (NIH) after the great ape research moratorium, although none of these animals were owned by the NIH. Every effort was made to adhere to NIH recommendations and policies during the course of this study.

The subjects used in this study are listed in Table 1. Primates categorized as “suspensory” are those species reported to use suspensory behaviors in the wild (*Hylobates*, *Symphalangus*, *Pongo*, *Gorilla*, *Pan*, *Ateles*), whereas “non-suspensory” taxa are those with no reported use of suspension (*Colobus*, *Trachypitecus*, *Macaca*, *Papio*, *Cebus*) (see references in Table 1). It is worth noting that these are broad locomotor categorizations, and that “suspensory” species can differ by an order of magnitude in the frequency and type of suspensory behaviors.

All animals were selected in consultation with the veterinary staff. All animals were weaned and considered adults by the attending veterinarians. However, based on the age of some of the animals (sex-specific means presented in Table 2), it is unlikely that they were all skeletally mature at the time of study. Any age effects are considered to be unlikely, as range of motion in cercopithecoids has been shown to be relatively stable and only changing significantly during young (first 18 months) and advanced ages (Turnquist 1983; Turnquist and Kessler 1989). Veterinary records indicate that four of the *Ateles* included in this study are hybrids of *Ateles fusciceps-geoffroyi-robustus* and that all *Papio* are hybrids of *Papio hamadryas-anubis-cynocephalus*. Animals with a known history of arthritis, lameness, or hindlimb injury were excluded from the study.

The handling and sedation of all subjects was done by licensed veterinarians or veterinary technicians in compliance with the Institutional Animal Care and Use Committee protocols for each research location. Most institutions use an anesthetic-sedative combination during animal immobilizations. Excluding *Cebus apella*, all animals were in a deep anesthetic plane at time of study and muscle tone was fully passive. *Cebus apella* individuals were immobilized using only an oral sedative and ketamine, resulting in some muscle tension during manipulation. Muscle resistance only noticeably occurred in *Cebus* during measures of hip extension.

Direct measures of (1) flexion, (2) extension, (3) adduction, (4) abduction, (5) internal rotation, and (6) external rotation were measured with each subject laying supine on an examination table. All measurements were collected by the author. In the case of male great apes, it became physically necessary to recruit the assistance of the veterinary staff during some manipulations of the hindlimb. Data were collected using disposable double-armed goniometers and measuring tapes. Measures are based on standard goniometric techniques used in humans (Cole 1971; Norkin and White 1995).

Hip extension and flexion were measured in a parasagittal plane from a lateral view, measuring the angle formed between the femoral diaphysis and the iliac blade (Figure 1). Total range of movement from flexion to extension was calculated for each individual by subtracting the value for flexion from the extension value.

A “horizontal” femur posture was then identified for each individual, defined as when the femur approximated a 90° orientation (perpendicular) to the horizontal surface of the examination table. Although defined based on perpendicular thigh orientation relative to the examination table, this position is termed “horizontal” here because abduction from the horizontal posture matches the “horizontal abduction” described by Stern and Larson (1993). Measures of adduction, abduction, internal rotation, and external rotation were all measured starting at the “horizontal” posture, which acted as a neutral position to begin measurements across taxa.

The femoral diaphysis was positioned in the horizontal posture and subsequently moved into the maximum positions of adduction and abduction. Abduction and adduction were calculated by measuring the angle formed between the femoral diaphysis and a horizontal plane parallel to the examination table (Figure 1) and then adjusting the measures to reflect angles from the midline. In a few overweight apes, it was necessary to measure and convert the inverse angle due to the large amount of abdominal fat that obstructed the placement of the goniometer over the abdomen. Total range of movement from adduction to abduction was calculated for each individual by adding the adduction and abduction values.

Internal and external rotation were measured following the technique used in humans (Cole 1971; Norkin and White 1995), where femoral rotation is calculated based on tibial movement relative to the observer (Figure 1). Accordingly, hip rotation measures could be partially influenced by interspecific differences in mediolateral rotation of the tibia on the femoral condyles. Published data on primate range of motion at the knee are lacking, and so this must remain an untested possibility. Internal and external rotation of the femur were

measured with the femur oriented in the “horizontal” posture. Total range of movement from internal to external rotation was calculated for each individual by adding the two values together.

Mass (kg) and four linear measures of body size were collected using a digital scale and soft tape measure. All linear measures were rounded to the nearest centimeter (cm) and include overlying soft tissues, making these measures less precise. Linear measures were (1) pelvic breadth measured across the pelvis at the fold between thigh and abdomen, which was identified by flexing the legs, (2) thigh circumference at the level of mid-thigh, (3) thigh length approximated from the anterior hip joint to the anterior center of the patella, and (4) femoral bi-epicondylar breadth measured across the posterior aspect of the knee.

Several additional measures were collected, including (1) maximum hip abduction during flexion, (2) maximum hip abduction during extension, and the (3) distance spanned between the knees during abduction (“abducted knee position”, cm). Abduction during flexion was measured by positioning the leg into the maximally flexed position and then maximally abducting the thigh. Likewise, abduction during extension was measured by positioning the leg into the maximally extended position and then maximally abducting the thigh. Abducted knee position was measured by positioning both the thighs into the abducted posture and then measuring the distances between the centers of the palpable patellae. Because the animals sampled in this study were not anesthetized specifically for this project and there were strict time limits for data collection, these three additional measurements could not be collected for all animals and were only measured on a subset of the animals (*Pan*, *Gorilla*, *Pongo*, *Symphalangus*, *Macaca*).

Quantitative Analyses

Quantitative analyses were performed in R (version 3.0.1, R Core Team 2012). Cleveland dot plots were used to visually inspect for differences between groups (Figure 2). Descriptive statistics (mean, standard deviation, and maximum and minimum values) were calculated for both ROM variables and body size variables. Significant differences in ROM between suspensory and non-suspensory anthropoids were tested by means of one-way analysis of variance (ANOVA), with significance assessed at $p = 0.05$.

In order to provide a finer resolution of the significant ANOVA results, post-hoc Tukey’s honestly significant difference test (Tukey’s HSD) was used as a conservative method of multiple comparisons between species. This study did not directly compare percent of time in suspension with range of motion, in part because of difficulties comparing frequency data and locomotor criteria between different authors. However, pairwise comparisons between species should generally convey frequency, with suspensory and non-suspensory species expected to have more significant differences between groups than within locomotor group. Additionally, pairwise comparisons are particularly useful here when ANOVA detected significant differences in ROM between locomotor groups but the descriptive plots suggested substantial overlap between the broad locomotor groups (e.g., maximum flexion). Tukey’s p -values do not need to be adjusted for multiple comparisons and so significance was assessed at $p = 0.05$. Male and female data were grouped for ANOVA and Tukey’s HSD comparisons due to the small sample sizes for some species.

Allometric Effects

Range of motion variables were tested for a significant relationship with log-transformed body mass (kg) using non-parametric Spearman's rank correlations. A significant correlation ($p < 0.05$) indicates a relationship with body mass.

The ROM variables were then examined versus log-transformed body mass between locomotor groups, with slopes and intercepts of the locomotor-specific regressions tested for significant differences. Allometric slopes were estimated using a phylogenetic generalized least squares (PGLS) and an ordinary least squares (OLS)¹ approach. PGLS models are preferred for this study because the comparative data violate the assumption of non-independence of data points in OLS (review in Nunn 2011). PGLS weights the regression by incorporating phylogenetic distances between taxa, calculated from branch lengths of a phylogeny, into the variance-covariance matrix. The variance-covariance matrix is then scaled by Pagel's lambda (λ) parameter (Pagel 1999; Freckleton et al. 2002), a measure of the dependence of a trait on a specified tree, which was estimated from the data via a maximum likelihood approach. Pagel's λ typically ranges from 0–1, with data showing increasing phylogenetic dependence as λ approaches 1.

The PGLS regressions were implemented in the *caper* package of R (Orme et al. 2012). The phylogenetic tree used for PGLS analyses was a consensus tree downloaded from the 10k Tree Project (Arnold et al. 2010). *Papio cynocephalus* and *Ateles geoffroyi* were used for *Papio hamadryas-anubis-cynocephalus* and *Ateles fusciceps-geoffroyi-robustus* hybrids. PGLS requires a single value for each tip in the phylogeny and, because averaging male and female data can result in unrealistic values for sexually dimorphic species, only female data points were used. It should therefore be emphasized that the PGLS linear modeling used here differs from traditional OLS in two key ways. First, OLS regression by default assumes no phylogenetic relationship between the data points (e.g., independent data points) whereas PGLS incorporates information about phylogenetic distances. Second, because PGLS regression requires that a single value is assigned to each terminal tip in the tree, the PGLS (female means only) regressions have half the number of data points of OLS (male and female means).

RESULTS

Sex-specific descriptive statistics for range of motion are provided in Tables 3–5, with additional size measures from the sample reported in Table 6. Descriptive plots of the data are provided in Figures 2–3. This study found significantly larger ranges of motion in suspensory taxa for maximum measures extension ($p < 0.001$), abduction ($p < 0.001$), external rotation ($p < 0.001$), range of abduction-adduction ($p < 0.001$), and range of internal-external rotation ($p < 0.001$). Non-suspensory taxa had significantly higher mobility in flexion ($p < 0.001$) and internal rotation ($p = 0.03$). Adduction ($p = 0.73$) and range of flexion-extension ($p = 0.63$) were not significantly different between suspensory and non-suspensory taxa.

¹OLS was appropriate over standardized major axis regression (SMA) because ROM values were regressed on body size, which was measured using a digital scale and should therefore introduce virtually no error on the x-axis.

Although there are statistically significant differences by locomotor group, there is substantial overlap between the two groups in degree of flexion, extension, and internal rotation (Figure 2). Tukey's HSD pairwise comparisons provide a finer resolution of the significant differences detected with ANOVA by identifying which pairs of species are significantly different from one another (Tables 7–9). Tukey's HSD comparisons found more comparisons between suspensory and non-suspensory taxa to be significant at ($p < 0.05$) than within a single locomotor group (e.g., suspensory vs. suspensory, non-suspensory vs. non-suspensory). However, many comparisons within the same locomotor group were also significant.

Descriptive statistics for additional measures of abduction for a subset of the taxa are presented in Table 11. Suspensory anthropoids have significantly larger abduction during flexion ($p < 0.001$), abduction during extension ($p < 0.001$), and abducted knee positions ($p < 0.001$). Tukey's HSD pairwise comparisons found significant differences (Table 11) in the majority of species comparisons.

Flexion, range of flexion-extension, and external rotation were found to have significant Spearman rank correlations with body mass (Table 12). External rotation increases with increasing body size, although flexion and range of flexion-extension decrease with increasing body size. It is important to note that, although flexion has a significant positive Spearman rank correlation value ($\rho = 0.68$, $p = 0.02$) indicating a positive scaling relationship between numerical values for flexion and body size, higher numerical values for flexion indicate a reduced range of motion (refer to Figure 1). The result therefore indicates that range of motion in flexion is decreasing with body size, which is clarified by the significant negative relationship between range of flexion-extension and body mass.

Female suspensory and non-suspensory ROM data were regressed against body size using phylogenetic regression (Table 13). The slopes and intercepts were not significantly different between locomotor groups for any variable except internal rotation (p_{slope} and $p_{\text{intercept}}$, Table 13). Flexion and range of flexion-extension, had non-significant differences in slopes and intercepts between the two locomotor groups. This result suggests that, although flexion and range of flexion-extension have a significant correlation with body size, the scaling properties are not different between locomotor groups. Interestingly, the slopes for suspensory and non-suspensory primates denotes opposite scaling relationships for internal and external rotation. With increasing mass in suspensory primates, internal rotation *decreases* and external rotation *increases*, whereas internal rotation *increases* and external rotation *decreases* with increasing mass in non-suspensory primates. However, the differences in external rotation are not statistically different between locomotor groups. The lambda values used in the phylogenetic regressions were estimated to be zero using a maximum-likelihood approach, suggesting little phylogenetic signal in the data. The allometric patterns found using female-specific data in phylogenetic regression are similar to those produced using male and female data in OLS (see Table 12).

DISCUSSION

This study finds significantly larger abduction and external rotation in suspensory taxa (Figure 2). It has previously been hypothesized that limb abduction is a critical movement during climbing and suspensory behaviors (Grand 1972; Jenkins 1974; Grand 1984; Cartmill 1985; Larson 1993; Crompton et al. 2008; Schmidt and Krause 2011), and these results support an association between hip abduction and suspensory behaviors. Not surprisingly, the increased levels of abduction and external rotation result in increased ranges of adduction-abduction and internal-external rotation in suspensory taxa (Figure 3). However, not all measures of joint mobility are necessarily increased in suspensory species relative to the non-suspensory species. Levels of adduction are not significantly different, and non-suspensory primates are actually capable of larger amounts of flexion and internal rotation. Despite the larger range of flexion in non-suspensory taxa, the range of flexion-extension overlaps between suspensory and non-suspensory species (Figure 3).

Because hip mobility shows differences in mobility that track locomotor behavior, hip joint mobility seems to be a better indicator of habitual limb postures used during locomotion than glenohumeral joint mobility. Recent work has shown that the hominoid glenohumeral joint does not actually produce a greater range of circumduction than other primates (Chan 2007a; b), with few differences in passive range of motion observed between suspensory hominoids and non-suspensory cercopithecids (Chan 2008). One potential reason that Chan's work may not have detected significant differences between locomotor groups relates to the structure of the anthropoid shoulder itself. The humeral head is surrounded by soft tissues with only a small receiving articular glenoid on the scapula, whereas the femoral head is more deeply received by the cup-like acetabulum and surrounding soft tissues. Moreover, the humerus is indirectly attached to the trunk by the scapula via the clavicle, with movements possible at the acromioclavicular and sternoclavicular articulations. These secondary articulations might provide some additional shoulder mobility that cannot be strictly differentiated from glenohumeral joint movements in a goniometric study. In contrast, the femoral head directly articulates with the trunk (i.e., in the acetabulum of the bony pelvis) and femoral movements are therefore more easy to isolate.

Some differences detected between suspensory and non-suspensory taxa using ANOVA are potentially influenced by the values for *Pan* and *Macaca*, necessitating pairwise comparisons between all species. Overall, pairwise comparisons between suspensory and non-suspensory taxa yielded a higher number of significant differences than within a single locomotor group. Not surprisingly, highly suspensory *Pongo* was found to have significantly larger abduction and external rotation than all non-suspensory taxa. However, it is not apparent from the multiple comparisons that the broad locomotor groups (suspensory vs. non-suspensory) could be clearly broken into more specific categories (e.g., brachiators, orthograde clambering, vertical climbers). For instance, *Pan* is not significantly different from *Pongo* in any range of motion except for adduction and external rotation (Tables 8–9) despite different frequencies and types of suspensory locomotion. There is probably substantial overlap in hindlimb postures used for different behaviors within anthropoids which makes refined locomotor categories difficult or impossible to distinguish using ROM alone.

Because males and females were grouped together for the (species-specific) pairwise comparisons due to small sample sizes, some male and female differences within a species might be obscured by the pairwise comparisons. In particular, the *Gorilla* intraspecific means for maximum flexion and ranges of flexion-extension differ by more than 30° (Tables 3–5). Therefore some caution should be used when interpreting the results for *Gorilla*, as there may actually be significant sex-specific differences in degree of flexion or range of flexion-extension that are not detected when using the species mean value. A larger sample of gorillas might clarify whether significant inter- and intraspecific differences exist, but this cannot currently be determined with the sample size in this study.

Body size does not influence range of hip mobility overall (Table 13, supplemented by OLS in Table 12). There is a significant correlation (p_{rho}) between mass and flexion but the PGLS slopes and intercepts for flexion do not differ significantly by locomotor group. Descriptive plots of the data (Figure 2) show that all taxa except *Pongo* and some *Gorilla* have similar ranges of flexion. Thus, for flexion, it seems that grouping taxa into “suspensory” and “non-suspensory” categories for regression might mask some of the allometric differences. Moreover, although there is a non-significant correlation (p_{rho}) between body mass and internal rotation, the suspensory and non-suspensory locomotor groups have significantly different scaling relationships. However, when the raw values for internal rotation are examined in the descriptive plots (Figure 2), it is apparent that there is substantial overlap between locomotor groups. Because there is little evidence for a relationship between range of motion variables and body mass, this supports the hypothesis that differences in mobility are related to locomotor behavior and are not strictly a consequence of allometry.

Large body size is often cited as being integral to below-branch locomotion because large-bodied animals are more stable when moving below-branch rather than on top of a similarly-sized branch (Fleagle and Mittermeier 1980; Cartmill 1985; Sarmiento 1995; Almécija et al. 2007; Ward 2007), but it is also worth noting that large body size itself facilitates below-branch locomotion. That is, with increasing body size the physical reach of the animal increases relative to the center of mass, which opens up a greater range of arboreal supports within the animal’s reach. The concept of the spatial “envelope” (e.g., Stevens and Parrish 1999), whereby the range of distal segment positions show the potential for overall abilities, has been considered in a limited capacity within primates (Grand 1972). For this reason, distance between the knees during abduction (Table 10) was evaluated as a potential metric of locomotor adaptation within anthropoids. Although the abducted knee position is largely a consequence of body size, it is also a factor of hip mobility. For instance, *Symphalangus syndactylus* has a span at the knee that is approximately double similarly-sized male *Macaca mulatta*. Interestingly, *Gorilla* has a significantly smaller range of angular abduction than *Pan* and *Pongo* yet has an equivalent distance between the knees during abduction (Tables 10–11), suggesting that the functional outcome of hip mobility (i.e., abducted knee position) is influenced by both body size and hip morphology. The relationship between range of motion, morphological variation in the hip, and the spatial envelope warrants further consideration.

Additionally, the influence of external rotation in locomotor abilities should be considered. According to Stern and Larson (1993), when the hip is flexed, external rotation of the hip

simultaneously occurs in order to achieve an abducted thigh posture. Specifically, Stern and Larson (1993) state that when the femur is flexed to 90° and then abducted (as in this study), 90° of lateral femoral rotation simultaneously occurs. The abducted position measured here, which begins at the “horizontal” posture (defined in Materials and Methods), is near the middle of the flexion-extension range for most species and some conjunct external rotation would therefore be expected to accompany abduction. Because external rotation occurred in unison with abduction, it was not possible here to quantify how much external rotation contributed to abduction ability. However, this study confirmed that non-suspensory taxa achieved abducted femur positions primarily by lateral excursions relative to the midline, whereas abducted femoral postures in suspensory taxa were accompanied by a high level of conjunct external rotation (Figure 4). Thus, lateral rotational ability at the hip appears to be a key determinant of abduction ability which has been largely neglected. Because this study suggests that an ability to highly abduct the thigh in suspensory primates is conferred with a concomitant ability to externally rotate the femur, hypotheses regarding the evolution of hominoid locomotor behaviors should consider the use of laterally rotated hip postures in addition to abduction.

The joint modeling work by MacLachy (1995; 1996; 1998) predicted that range of abduction would discriminate locomotor adaptation, specifically that “differences in abduction during extension may be an indicator of differential ability to assume versatile climbing postures, while abduction during flexion may be a more general indicator of arboreality” (MacLachy 1996, p. 471–472). In this study, mean abduction in flexed and extended postures was found to be within 10° of the mean for abduction from the horizontal posture in all hominoids except male gorillas (Tables 4 and 10). With the exception of male gorillas, which displayed a substantially reduced degree of abduction in an extended posture (mean 48° from horizontal vs. 9° in extension), range of abduction in hominoids is similar throughout the flexion-extension range. As hypothesized by MacLachy (1996), the ability to abduct the thigh in extended positions is associated with high levels of arboreal versatility (e.g., suspension), although large abduction ability in *any* position appears to be associated with arboreal versatility. However, these data show that hip abduction during flexion is probably not a strong indicator of arboreality in general, as *Macaca fascicularis* is a skilled arboreal quadruped (Rodman 1979) with a low range of abduction possible during flexed hip postures.

There are certain considerations for the baseline values reported here. First, this study relies on an opportunistic sample of captive primates. The animals sampled almost certainly did not use their hindlimbs exactly as they would in the wild, and may potentially have ranges of motion, morphologies, and body masses that are different from wild counterparts. Past studies have typically found captive animals to have a greater range of motion rather than free-ranging individuals (Turnquist 1983; 1985). Relying on captive animals may increase the variation of the sample, potentially reducing the likelihood of detecting significant differences between groups. However, significant differences were detected between locomotor groups, and the range of motion data collected for cercopithecids is consistent with all other published ROM data (DeRousseau et al. 1983; Turnquist 1983; 1985; Turnquist and Kessler 1989). The degree of hip abduction in this study is consistent with

DeRousseau et al. (1983)'s findings for *Macaca mulatta* (mean ~30° to midline, versus 25° here), and the mean values for adduction are identical in both studies (mean 36°). The range of hip flexion documented here in cercopithecids is also consistent with previous measures of hip flexion provided by Turnquist and Kessler (1989), who reported low maximum hip flexion values in *M. mulatta* (approximately 11–49° versus 28–41° here).

Second, passive range of motion is the maximum range of motion allowed at the joint, and it is worth noting that a passive range might differ substantially from the range normally employed by a living animal. Unfortunately, there are few data available to compare the key measures of passive abduction and external rotation due to difficulties measuring these with traditional kinematic techniques. The passive data presented here are consistent with Isler's (2005) data on hominoid active hip abduction and range of adduction-abduction during vertical climbing. Isler's (2005) values for *Hylobates* indicate that they use a substantially lower range of abducted hip postures during vertical climbing than they are capable of passively. Isler (2005) also finds a single male gorilla showing an increased ROM relative to a single female gorilla, which is a pattern opposite of what was observed in this study. It remains unknown whether the *Hylobates* and *Gorilla* values differ due to sampling or perhaps real differences in active ROM.

Third, questions remain as to what determines hip joint range of motion. Multiple morphologies of the pelvis and femur have been related to hip mobility (e.g., Napier and Walker 1967; Schultz 1969; Walker 1974; Stern and Susman 1983; Fleagle and Anapol 1992; Ward 1993; Ward et al. 1993; MacLachy 1995; 1996; MacLachy and Bossert 1996; MacLachy 1998). For instance, a longer femoral neck length has been related to mobility at the primate hip joint by increasing the distance between the bony pelvis and the greater trochanter, allowing for more abduction potential (Fleagle and Meldrum 1988). A lower greater trochanter should enable more abduction before impingement of bony or soft tissues occurs (MacLachy 1995; 1996), and this effect could even be amplified by having a high neck-shaft angle, which would further position the femoral head above the greater trochanter. The distribution of the subchondral bone on the femoral head (Jenkins 1972; Fleagle 1976; Jenkins and Camazine 1977; Ward et al. 1993; MacLachy 1996; MacLachy and Bossert 1996) and potentially femoral head size (Ruff 1988) are hypothesized to relate to hip mobility. The geometry of the femur itself might be especially influential in measuring abduction-adduction, as higher neck-shaft angles will increase the angle of the thigh relative to the midline for any given hip position². In order to test the relationship between morphologies and ROM, future studies should attempt to directly quantify morphologies using x-ray or CT data from the same individuals that ROM data is collected from.

Joint pathologies such as osteoarthritis reduce joint mobility (e.g., Steultjens et al. 2000), limiting normal joint gliding movements by atypical bone growth, fusions, or joint erosions. Naturally-occurring osteoarthritis and other inflammatory diseases of the joints are observed

²Similarly, the bi-condylar angle would also play an inverse role in angular measures of abduction and adduction in humans. The bicondylar angle orients the thigh towards the midline (i.e., at a negative angle). Angular measures relative to the midline are inherently influenced by the bi-condylar angle and, thus, human measures of abduction and adduction may not be directly comparable to the same measures on nonhuman primates.

in catarrhines (DeRousseau 1988; Rothschild and Woods 1989; 1992b; 1996; Rothschild 2005; Rothschild and Ruhli 2005), although incidences of arthritis specifically at the anthropoid hip joint are either rare or under-reported (Schultz 1944; Bramblett 1967; Rothschild and Woods 1992a; 1996; DeGusta and Milton 1998; Nakai 2003). In healthy joints, such as those sampled in this study, species-specific differences in observed ranges of motion are likely to originate from bony or soft tissue features.

However, in normally functioning joints, range of motion is determined primarily by soft tissue structures surrounding the joint itself, such as ligament, tendon and passive muscle tension (Kapandji 1970; Wright and Radin 1993; Levangie and Norkin 2005; McGinnis 2005; Standing and Gray 2008; Safran et al. 2012). A number of soft tissues probably influence the movements at the hip joint, including the ligamentum teres femoris, the acetabular labrum, the hip joint capsule and associated ligaments, and surrounding (passive) hip musculature. Interspecific variation in soft tissue attachments and/or size can contribute to differences in mobility observed between species, limiting movement by differences in length, orientation, and even by physical obstruction.

Little is known about the composition, material properties, variation, size/strength of the deep hip joint soft tissue structures in nonhuman anthropoids (Sonntag 1923; 1924; Howell and Straus 1933; Raven 1950; von Klaus Uhlmann 1968; Sigmon 1969; 1974; Payne 2001; Payne et al. 2006a; b). The joint capsule, particularly in reference to the three capsular ligaments, is thought to be one of the strongest soft tissue limits on femoral head movement within the acetabulum (Myers et al. 2011; Smith et al. 2011; Smith et al. 2012). The capsule surrounds the neck of the femur, attaching along the intertrochanteric line anteriorly and at the base of the neck posteriorly, and along the border of the acetabular labrum on the pelvis. In humans, the capsular ligaments (ischiofemoral, pubofemoral, iliofemoral), each have discrete functions to resist femoral head translation as the hip moves through its ROM (Martin et al. 2008; Smith et al. 2012). The iliofemoral ligament is the strongest of the three, and functions to resist extension and external rotation in humans (Myers et al. 2011), with the inferior band limiting extension and the superior band primarily responsible for limiting external rotation (Wagner et al. 2012). The ischiofemoral ligament attaches along the caudal acetabular border and the superior aspect of the femoral neck and intertrochanteric line, limiting internal rotation in humans (Wagner et al. 2012). The pubofemoral ligament originates along the obturator crest and superior pubic ramus and blends with the iliofemoral ligament distally to insert near the lesser trochanter, acting to limit abduction in humans (Wagner et al. 2012).

The limited data on hip capsular structure in non-human primates suggest that the chimpanzee and orangutan capsule is lax with indistinct capsular ligaments (Sonntag 1923; 1924), allowing more mobility than that of cercopithecids, which have a broad, thick iliofemoral ligament (Keith 1894; Howell and Straus 1933; Walji 1988). The only microstructural descriptions of capsular composition is for the vervet monkey (Walji 1988) and macaque (He et al. 1998). The vervet monkey is described as having strong, structural collagen fibers on the anterior and superior portions of the capsule but with a more irregular collagenous structure in the inferior and posterior portions of the capsule (Walji 1988). The distribution of nerve endings in the *Macaca fascicularis* hip joint capsule is most dense on

the medial side of the capsule, and has been argued to “...prevent abnormal hip joint movement, especially extreme lateral rotation and abduction” during active movement (He et al. 1998, p. 85). Although this may be a mechanosensory check to extreme postures, reduced ROM in this study must relate to physical limitations of soft tissues because the animals measured were unconscious.

Several studies have found a link between mammalian adult joint stability and ligamentum teres integrity, although whether the intra-articular ligament confers joint stability via proprioceptive (Leunig et al. 2000; Sarban et al. 2007) or biomechanical functions (Chen et al. 1996; Demange et al. 2007; Wenger et al. 2007; Dodds et al. 2008; Bardakos and Villar 2009; Martin et al. 2011) is uncertain. If the ligamentum teres is mechanically limiting joint movements, it appears to do so when the femur is in a position of combined adduction, flexion, and external rotation (Dodds et al. 2008). The ligamentum teres insertion varies in different mammalian species, and work on carnivores suggests that a more centrally-positioned ligamentum teres insertion on the femoral head might reduce the potential for impinging the ligament during abducted limb postures (Jenkins and Camazine 1977). Interestingly, orangutans (Crelin 1988), “sloth-like” subfossil paleopropithecids (Godfrey et al. 2010), and both genera of extant sloths (personal observation) lack a subchondral ligamentum teres insertion altogether. However, it must be noted that lacking a subchondral ligamentum teres insertion cannot be exclusively attributed to high joint mobility related to suspension because some non-suspensory species, such as the Indian elephant (Crelin 1988), also lack a subchondral ligamentum teres insertion.

The acetabular labrum, a fibrocartilaginous ring around the border of the acetabulum, limits movements of the femoral head within the acetabulum by deepening the acetabular socket and by increasing the negative intra-articular joint pressure (Crawford et al. 2007; Myers et al. 2011; Smith et al. 2011; Safran et al. 2012). A large acetabular labrum in humans is implicated in certain types of femoroacetabular impingement, with patients having a decrease in joint mobility associated with labral overcoverage of the femoral head (Tannast et al. 2007). Unfortunately, no data are published on labrum size or structure in nonhuman anthropoids.

Muscular structure can also limit active (voluntary) range of motion through mechanoreceptor feedback, as well as limit motion passively by physically obstructing movement at the joint or through tension in the antagonistic muscles and associated tendons (Brinckmann et al. 2002; Levangie and Norkin 2005). Although anthropoid hip muscle attachments are generally similar (Anapol and Barry 1996; Thorpe et al. 1999; Payne et al. 2006a; b; Myatt et al. 2011), the mechanical arrangement of the muscles around the joint differs due to skeletal structure. For instance, great ape and hylobatid gluteal, hip adductor, quadriceps, and hamstring muscles have smaller physiological cross section areas and longer fascicles compared to *Homo sapiens* (Payne 2001; Payne et al. 2006b; a; Channon et al. 2009), which would allow a higher range of motion at the hip joint (Payne 2001). Interspecific differences in muscle attachments, orientations, size, extensibility and tone could therefore affect range of passive movement at the hip joint.

It is difficult to speculate as to what soft tissue structures specifically restricted or enabled the different ranges of motion observed in this study. As was previously noted, hip rotation as measured here could potentially be increased by a more mobile knee joint, and so this may have factored into the results. However, manual manipulations of the hip joint through its range of circumduction implicated strong, deep ligamentous hip structures in limiting both abduction and external rotation in the non-suspensory taxa. This inference is made by the author because the limits were not bony and there was no observable muscle tension during maximum positions of the limb, except perhaps in hip extension. As previously mentioned, there is some evidence that cercopithecids have stronger, more distinct ligaments in the hip joint capsule compared to orangutans and chimpanzees (Sonntag 1923; 1924; Howell and Straus 1933). Given that the superior band of the iliofemoral on the anterior aspect of the capsule limits external rotation in humans, it is possible that the iliofemoral ligament plays an important role in limiting external rotation (and in turn, abduction) in cercopithecids. This is supported by the histological findings on the vervet hip joint capsule by Walji (1988) described the anterior and superior portions of the capsule as having a strong collagenous structure which would limit excessive range of motion. Detailed comparative dissection and histological work is necessary to evaluate how interspecific differences in size, strength, and/or configuration of soft tissue structures relate to hip joint mobility.

CONCLUSION

For the first time, *in vivo* data on hip joint range of motion in hominoids and *Ateles* are presented and quantitatively compared to cercopithecids and *Cebus*. The data for cercopithecids is comparable to other studies. The null hypothesis that there are no significant differences in hip joint mobility between suspensory and non-suspensory taxa can be rejected, with significant increases in suspensory anthropoids in range of external hip rotation and hip abduction. It is hypothesized here that the ability to differentially abduct the thigh is facilitated by an increased range of external rotation at the hip joint. The analyses show that range of motion is not strictly a consequence of body size but does indicate that higher joint mobility increases the “spatial envelope” for a given body size. Limits on external rotation and abduction in non-suspensory taxa are a combination of bony and soft-tissue constraints and it is proposed here that range of motion was probably primarily constrained by strong capsular ligaments of the hip joint. Formal characterization of soft tissue structures in anthropoids is needed to clarify why non-suspensory species have a reduced range of abduction and external rotation. Future work should also seek to identify how differences in range of motion relate to bony morphologies so that we have a clearer framework for assessing functional abilities in fossil anthropoids.

Acknowledgments

Doug Armstrong, Julie Napier, Chris Hanley, Kathleen Brasky, Beth Hammond, Nancy Schultz-Darken, Kimberley A. Phillips, Robert Baker, Melissa De La Garza, Elizabeth Strobert, and all veterinary and IACUC staff at zoos and national primate research centers are thanked for their dedication and commitment to facilitating this research. Ray Craigshead is thanked for assistance creating illustrations. Kevin Middleton provided extensive statistical advice and useful discussions, which significantly improved this manuscript. Carol Ward, William Hylander, William Jungers, Gregory Blomquist, Michael Plavcan, Casey Holliday, Scott Maddux, Kristina Aldridge, and Matthew Ravosa are thanked for constructive input at different stages of this work. Two anonymous reviewers, the Associate

Editor, and Peter Ellison are thanked for constructive feedback as well. Several National Institutes of Health grants indirectly supported this research, including P51OD011133 to the Southwest National Primate Research Center, R15NS070717-01 to Kimberly A. Phillips, P51OD011132 to Yerkes National Primate Research Center, P51OD011106 to the Wisconsin National Primate Research Center.

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Figure 1.

Adduction, abduction, internal rotation and external rotation were measured from the “horizontal” posture, which was defined as when the femur was 90° (perpendicular) to the examination table. Adduction and abduction were measured relative to the horizontal surface of the examination table for accuracy but the angles were then adjusted to the midline (indicated in grey). Although best illustrated from a caudal view (shown above), adduction and abduction were measured cranially between the abdomen and thigh.

Figure 2.

Mean and interquartile ranges are indicated by the boxplots. All angles shown, except adduction, are significantly different between locomotor groups ($p < 0.05$). Note that smaller values for flexion reflect a higher range of motion (see Figure 1). Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 3.

Ranges of flexion-extension, adduction-abduction, and internal-external rotation are shown. Mean and interquartile ranges are indicated by the boxplots. Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 4.

Examples of passive positions of abduction for (a) *Pongo pygmaeus*, (b) *Gorilla gorilla*, and (c) *Macaca mulatta*. The patella is indicated by blue arrows to highlight the external rotation that accompanies abduction in suspensory species. Note the lateral knee orientation (externally rotated thigh) in *Pongo* and *Gorilla* and the anterior orientation (non-rotated thigh) in *Macaca*.

Table 1

Sample

Species	N	Location	Frequency of suspensory locomotion	Frequency data reference
<i>Pan troglodytes</i>	31	YNPRC, SNPRC	7%	Doran (1996)
<i>Gorilla gorilla</i>	6	OHD	5%	Hunt (2004) from Remis (1995)
<i>Pongo pygmaeus</i>	6	OHD	12%	Cant (1987) for ♀, excludes quadrumanous clambering (51% of locomotion)
<i>Symphalangus syndactylus</i>	4	LCS, OHD	51%	Hunt (2004) calculated from Fleagle (1980)
<i>Hylabates lar</i>	2	LCS	56%	Hunt (2004) calculated from Gittins (1982), Fleagle (1980), and Srikosamatara (1984)
<i>Trachypithecus francoisi</i>	1	TZ	rarely observed/not observed	Zhou et al. (2012)
<i>Colobus guereza</i>	2	TZ	rarely observed/not observed	Gebo and Chapman (1995)
<i>Macaca fascicularis</i>	16	WNPRC	rarely observed/not observed	Cannon and Leighton (1994)
<i>Macaca mulatta</i>	16	WNPRC	rarely observed/not observed	Wells and Turnquist (2001)
<i>Papio</i> sp.*	8	SNPRC	rarely observed/not observed	Hunt (1991)
<i>Ateles</i> sp.*	6	OHD, LCS	31%	Mittermeier (1978) and Fleagle and Mittermeier (1980)
<i>Cebus apella</i>	6	SNPRC	rarely observed/not observed	Gebo (1992)

Abbreviations for institutions: LCS, Lion Country Safari; OHD, Omaha's Henry Doorly Zoo; YNPRC, Yerkes National Primate Research Center; TZ, Toledo Zoo; WNPRC, Wisconsin National Primate Research Center; SNPRC, Southwest National Primate Research Center.

Asterisk (*) indicates species-level hybridization in these subjects.

Table 2

Sex-specific descriptive statistics for age and body size

Species	Sex	n	Age (years)			Mass (kg)		
			Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min
<i>Pan troglodytes</i>	F	13	20.2 $\pm$ 8.4	31.0	5.6	54.1 $\pm$ 14.3	79.5	30.6
	M	18	21.1 $\pm$ 5.3	31.9	14.0	67.4 $\pm$ 7.3	79.3	56.8
<i>Gorilla gorilla</i>	F	2	13.3 $\pm$ 5.6	17.2	9.4	70.8 $\pm$ 5.3	74.5	67.0
	M	4	18.3 $\pm$ 6.6	28.0	13.2	198.8 $\pm$ 19.2	225.0	179.0
<i>Pongo pygmaeus</i>	F	3	10.5 $\pm$ 2.2	12.0	7.9	47.6 $\pm$ 14.5	62.1	33.1
	M	3	12.8 $\pm$ 7.5	20.2	5.1	74.4 $\pm$ 64.9	148.3	27.2
<i>Symphalangus syndactylus</i>	F	2	17.4 $\pm$ 12.1	25.9	8.8	13.6 $\pm$ 6.2	17.9	9.2
	M	2	17.6 $\pm$ 8.1	23.3	11.9	14.3 $\pm$ 4.8	17.7	10.9
<i>Hylobates lar</i>	F	1	23.5	N/A		6.5	N/A	
	M	1	23.9	N/A		10.7	N/A	
<i>Colobus guereza</i>	F	1	2.9	N/A		7.0	N/A	
	M	1	4.5	N/A		13.2	N/A	
<i>Trachypithecus francoisi</i>	M	1	3.0	N/A		7.0	N/A	
<i>Macaca fascicularis</i>	F	8	9.4 $\pm$ 1.4	12.1	7.7	4.8 $\pm$ 0.9	6.0	3.5
	M	8	7.7 $\pm$ 0.5	8.6	7.0	6.9 $\pm$ 1.1	9.2	6.1
<i>Macaca mulatta</i>	F	8	9.1 $\pm$ 0.3	9.5	8.6	8.3 $\pm$ 1.3	9.8	7.0
	M	8	9.0 $\pm$ 0.2	9.3	8.8	12.1 $\pm$ 1.9	14.1	9.1
<i>Papio sp.</i>	F	3	9.6 $\pm$ 0.8	10.4	8.9	17.7 $\pm$ 1.1	18.8	16.6
	M	5	10.5 $\pm$ 0.5	11.4	10.1	28.4 $\pm$ 1.7	31.0	26.5
<i>Ateles sp.</i>	F	3	18.0 $\pm$ 10.5	27.9	7.0	9.3 $\pm$ 1.8	11.2	7.7
	M	3	18.7 $\pm$ 15.8	37.0	9.2	8.2 $\pm$ 0.2	8.3	7.9
<i>Cebus apella</i>	F	4	14.7 $\pm$ 12.5	28.3	3.0	2.6 $\pm$ 0.1	2.7	2.5
	M	2	4.4 $\pm$ 1.3	5.3	3.5	3.2 $\pm$ 0.9	3.8	2.6

Sex-specific samples consisting of n=1 individual are not mean values.

* mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total n listed.
SD= standard deviation, N/A= not applicable.

Table 3

Sex-specific descriptive statistics for flexion and extension

Species	Sex	n	Flexion			Extension			Flexion-extension range		
			Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Max, Min
<i>Pan troglodytes</i>	F	13	33.2 $\pm$ 10.3	52.0, 21.0	157.5 $\pm$ 6.7	168.0, 148.0	124.4 $\pm$ 11.9	139.0, 102.0			
	M	18	40.4 $\pm$ 11.3	63.0, 20.0	160.5 $\pm$ 9.5	176.0, 138.0	120.1 $\pm$ 11.8	143.0, 99.0			
<i>Gorilla gorilla</i>	F	2	31.5 $\pm$ 3.5	34.0, 29.0	155.5 $\pm$ 3.5	158.0, 153.0	124.0 $\pm$ 0.0	124.0, 124.0			
	M	4	66.5 $\pm$ 4.4	70.0, 60.0	143.5 $\pm$ 11.4	160.0, 136.0	77.0 $\pm$ 10.9	90.0, 68.0			
<i>Pongo pygmaeus</i>	F	3	42.3 $\pm$ 8.6	50.0, 33.0	156.7 $\pm$ 4.9	160.0, 151.0	114.3 $\pm$ 10.2	126.0, 107.0			
	M	3	55.3 $\pm$ 7.1	63.0, 49.0	171.3 $\pm$ 1.5	173.0, 170.0	116.0 $\pm$ 8.5	124.0, 107.0			
<i>Symphalangus syndactylus</i>	F	2	27.5 $\pm$ 3.5	30.0, 25.0	150.5 $\pm$ 10.6	158.0, 143.0	123.0 $\pm$ 14.1	133.0, 113.0			
	M	2	28.0 $\pm$ 2.8	30.0, 26.0	161.0 $\pm$ 12.7	170.0, 152.0	133.0 $\pm$ 9.9	140.0, 126.0			
<i>Hyllobates lar</i>	F	1	23.0	N/A	175.0	N/A	152.0	N/A			
	M	1	26.0	N/A	170.0	N/A	144.0	N/A			
<i>Colobus guereza</i>	F	1	20.0	N/A	148.0	N/A	128.0	N/A			
	M	1	33.0	N/A	168.0	N/A	135.0	N/A			
<i>Trachypithecus francoisi</i>	M	1	22.0	N/A	116.0	N/A	94.0	N/A			
<i>Macaca fascicularis</i>	F	8	29.9 $\pm$ 5.1	34.0, 19.0	155.3 $\pm$ 4.9	163.0, 150.0	125.4 $\pm$ 8.4	142.0, 116.0			
	M	8	26.1 $\pm$ 3.9	30.0, 20.0	142.5 $\pm$ 4.8	149.0, 135.0	116.4 $\pm$ 7.1	129.0, 108.0			
<i>Macaca mulatta</i>	F	8	33.3 $\pm$ 4.7	41.0, 28.0	157.5 $\pm$ 6.1	167.0, 150.0	124.3 $\pm$ 9.1	139.0, 109.0			
	M	8	32.0 $\pm$ 2.2	35.0, 29.0	144.4 $\pm$ 7.6	153.0, 131.0	112.4 $\pm$ 8.5	121.0, 98.0			
<i>Papio sp.</i>	F	3	34.0 $\pm$ 5.3	40.0, 30.0	140.7 $\pm$ 16.7	160.0, 131.0	106.6 $\pm$ 19.1	128.0, 75.0			
	M	5	41.4 $\pm$ 7.3	50.0, 34.0	134.6 $\pm$ 11.4	150.0, 123.0	93.2 $\pm$ 14.7	116.0, 75.0			
<i>Ateles sp.</i>	F	3	26.3* $\pm$ 4.2	31.0, 23.0	139.7 $\pm$ 18.9	161.0, 125.0	113.3 $\pm$ 21.4	138.0, 100.0			
	M	3	31.3 $\pm$ 3.1	34.0, 28.0	152.0 $\pm$ 4.4	157.0, 149.0	120.7 $\pm$ 7.2	129.0, 116.0			
<i>Cebus apella</i>	F	4	28.5 $\pm$ 6.0	34.0, 20.0	155.5 $\pm$ 27.2	180.0, 130.0	127.4 $\pm$ 29.4	158.0, 99.0			
	M	2	26.0 $\pm$ 5.7	30.0, 22.0	159.5 $\pm$ 6.4	164.0, 155.0	133.5 $\pm$ 12.0	142.0, 125.0			

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values. SD= standard deviation, N/A= not applicable.

Table 4

Sex-specific descriptive statistics for adduction and abduction

Species	Sex	n	Adduction			Abduction			Adduction-abduction range		
			Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min
<i>Pan troglodytes</i>	F	13	39.5 $\pm$ 10.7	22.0	58.0	75.4 $\pm$ 4.9	83.0	68.0	114.9 $\pm$ 11.6	132.0	90.0
	M	18	43.6 $\pm$ 7.1	26.0	54.0	70.1 $\pm$ 4.4	80.0	63.0	113.6 $\pm$ 8.2	123.0	91.0
<i>Gorilla gorilla</i>	F	2	41.5 $\pm$ 7.8	36.0	47.0	62.5 $\pm$ 3.5	65.0	60.0	104.0 $\pm$ 4.2	107.0	101.0
	M	4	45.0 $\pm$ 13.9	27.0	61.0	48.0 $\pm$ 4.7	55.0	45.0	93.0 $\pm$ 10.4	107.0	82.0
<i>Pongo pygmaeus</i>	F	3	25.7 $\pm$ 11.6	18.0	39.0	82.3 $\pm$ 3.2	86.0	80.0	108.0 $\pm$ 14.8	125.0	98.0
	M	3	24.3 $\pm$ 18.0	7.0	43.0	81.0 $\pm$ 8.2	88.0	72.0	105.3 $\pm$ 17.9	126.0	95.0
<i>Symphalangus syndactylus</i>	F	2	34.5 $\pm$ 0.7	34.0	35.0	52.0 $\pm$ 5.7	56.0	48.0	86.5 $\pm$ 4.9	90.0	83.0
	M	2	37.5 $\pm$ 12.0	29.0	46.0	67.5 $\pm$ 3.5	70.0	65.0	105.0 $\pm$ 15.6	116.0	94.0
<i>Hylobates lar</i>	F	1	23.0	N/A	N/A	78.0	N/A	N/A	145.0	N/A	N/A
	M	1	31.0	N/A	N/A	69.0	N/A	N/A	128.0	N/A	N/A
<i>Colobus guereza</i>	F	1	34.0	N/A	N/A	30.0	N/A	N/A	86.0	N/A	N/A
	M	1	31.0	N/A	N/A	26.0	N/A	N/A	85.0	N/A	N/A
<i>Trachypithecus francoisi</i>	M	1	50.0	N/A	N/A	41.0	N/A	N/A	81.0	N/A	N/A
<i>Macaca fascicularis</i>	F	8	38.5 $\pm$ 9.9	19.0	49.0	24.8 $\pm$ 3.3	31.0	20.0	63.3 $\pm$ 10.1	80.0	46.0
	M	8	25.4 $\pm$ 10.1	11.0	43.0	26.0 $\pm$ 5.4	36.0	20.0	51.4 $\pm$ 11.0	66.0	31.0
<i>Macaca mulatta</i>	F	8	38.2 $\pm$ 8.7	29.0	54.0	26.9 $\pm$ 9.9	37.0	10.0	65.1 $\pm$ 14.2	86.0	41.0
	M	8	33.2 $\pm$ 7.9	23.0	43.0	23.9 $\pm$ 5.3	35.0	19.0	57.1 $\pm$ 11.1	75.0	44.0
<i>Papio</i> sp.	F	3	41.3 $\pm$ 10.3	30.0	50.0	30.7 $\pm$ 5.0	36.0	26.0	72.0 $\pm$ 7.2	80.0	27.0
	M	5	35.4 $\pm$ 16.1	10.0	49.0	18.4 $\pm$ 2.5	22.0	16.0	53.8 $\pm$ 16.5	69.0	27.0
<i>Ateles</i> sp.	F	3	29.5 $\pm$ 14.8	19.0	40.0	62.3 $\pm$ 3.1	65.0	59.0	90.5* $\pm$ 17.7	103.0	78.0
	M	3	23.3 $\pm$ 15.3	10.0	40.0	70.3 $\pm$ 0.6	71.0	70.0	93.7 $\pm$ 15.8	111.0	80.0
<i>Cebus apella</i>	F	4	54.7 $\pm$ 10.5	43.0	67.0	34.8 $\pm$ 11.7	50.0	22.0	89.5 $\pm$ 18.4	117.0	79.0
	M	2	57.0 $\pm$ 7.1	52.0	62.0	49.0 $\pm$ 1.4	50.0	48.0	106.0 $\pm$ 5.7	110.0	102.0

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values.

* mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total n listed.

SD= standard deviation. N/A= not applicable.

Table 5

Sex-specific descriptive statistics for internal and external rotation

Species	Sex	n	Internal rotation			External rotation			Range of rotation		
			Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min
<i>Pan troglodytes</i>	F	13	37.1 $\pm$ 9.2	49.0	21.0	78.3 $\pm$ 8.9	92.0	65.0	115.4 $\pm$ 14.4	132.0	92.0
	M	18	35.4 $\pm$ 9.3	59.0	18.0	76.1 $\pm$ 13.0	97.0	49.0	111.4 $\pm$ 16.3	138.0	72.0
<i>Gorilla gorilla</i>	F	2	29.5 $\pm$ 9.2	36.0	23.0	69.5 $\pm$ 4.9	73.0	66.0	99.0 $\pm$ 14.1	109.0	89.0
	M	4	31.3 $\pm$ 10.7	47.0	24.0	80.5 $\pm$ 12.1	93.0	67.0	111.8 $\pm$ 20.1	140.0	96.0
<i>Pongo pygmaeus</i>	F	3	32.0 $\pm$ 2.0	34.0	30.0	97.0 $\pm$ 10.6	105.0	85.0	129.0 $\pm$ 12.2	137.0	115.0
	M	3	28.7 $\pm$ 7.1	35.0	21.0	94.3 $\pm$ 14.0	108.0	80.0	123.0 $\pm$ 11.3	130.0	110.0
<i>Symphalangus syndactylus</i>	F	2	44.5 $\pm$ 6.4	49.0	40.0	69.5 $\pm$ 12.0	78.0	61.0	114.0 $\pm$ 18.4	127.0	101.0
	M	2	56.0 $\pm$ 8.5	62.0	50.0	67.0 $\pm$ 2.8	69.0	65.0	123.0 $\pm$ 11.3	131.0	115.0
<i>Hylobates lar</i>	F	1	62.0	N/A	N/A	61.0	N/A	N/A	123.0	N/A	N/A
	M	1	50.0	N/A	N/A	70.0	N/A	N/A	120.0	N/A	N/A
<i>Colobus guereza</i>	F	1	40.0	N/A	N/A	50.0	N/A	N/A	90.0	N/A	N/A
	M	1	45.0	N/A	N/A	45.0	N/A	N/A	90.0	N/A	N/A
<i>Trachypithecus francoisi</i>	M	1	50.0	N/A	N/A	32.0	N/A	N/A	82.0	N/A	N/A
<i>Macaca fascicularis</i>	F	8	45.1 $\pm$ 9.6	62.0	30.0	61.9 $\pm$ 9.7	75.7	47.0	107.0 $\pm$ 16.3	130.0	81.0
	M	8	50.0 $\pm$ 5.7	59.0	42.0	52.5 $\pm$ 7.6	67.0	43.0	102.5 $\pm$ 10.6	115.0	89.0
<i>Macaca mulatta</i>	F	8	39.4 $\pm$ 8.1	54.0	29.0	63.0 $\pm$ 8.1	81.0	55.0	102.4 $\pm$ 7.9	114.0	91.0
	M	8	34.8 $\pm$ 4.6	40.0	28.0	48.8 $\pm$ 6.6	59.0	40.0	83.5 $\pm$ 5.7	90.0	72.0
<i>Papio sp.</i>	F	3	47.7 $\pm$ 7.1	54.0	40.0	43.0 $\pm$ 2.6	45.0	40.0	90.7 $\pm$ 9.7	99.0	60.0
	M	5	47.2 $\pm$ 8.2	60.0	40.0	32.0 $\pm$ 9.1	45.0	20.0	79.2 $\pm$ 11.6	90.0	60.0
<i>Ateles sp.</i>	F	3	51.0 $\pm$ 10.1	60.0	40.0	70.7 $\pm$ 3.5	74.0	67.0	121.7 $\pm$ 12.9	131.0	107.0
	M	3	29.0 $\pm$ 1.0	30.0	28.0	86.3 $\pm$ 6.7	92.0	79.0	115.3 $\pm$ 7.0	122.0	108.0
<i>Cebus apella</i>	F	4	28.5 $\pm$ 3.8	31.0	23.0	53.5 $\pm$ 24.2	80.0	23.0	82.0 $\pm$ 21.6	103.0	54.0
	M	2	24.0 $\pm$ 5.7	28.0	20.0	54.5 $\pm$ 0.7	55.0	54.0	78.5 $\pm$ 6.4	83.0	74.0

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values. SD= standard deviation, N/A= not applicable.

Table 6

Sex-specific descriptive statistics for linear dimensions

Species	Sex	n	Pelvic breadth (cm)			Mid-thigh circumference (cm)			Thigh length (cm)			Bi-epicondylar breadth (cm)		
			Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min
<i>Pan troglodytes</i>	F	13	38.8 $\pm$ 8.3	53.0	25.0	46.9 $\pm$ 7.2	62.0	38.0	26.2 $\pm$ 2.2	30.0	24.0	7.0 $\pm$ 2.1	11.0	5.0
	M	18	39.9* $\pm$ 4.9	47.0	31.0	55.5 $\pm$ 4.4	62.0	48.0	27.9 $\pm$ 1.5	31.0	25.0	9.5* $\pm$ 2.2	14.0	7.0
<i>Gorilla gorilla</i>	F	2	43.0 $\pm$ 0.0	43.0	43.0	50.0 $\pm$ 4.2	53.0	47.0	25.0 $\pm$ 0.0	25.0	25.0	7.5 $\pm$ 0.7	8.0	7.0
	M	4	64.8 $\pm$ 14.4	85.0	53.0	81.5 $\pm$ 6.6	90.0	74.0	30.8 $\pm$ 4.8	35.0	24.0	11.5 $\pm$ 2.4	14.0	9.0
<i>Pongo pygmaeus</i>	F	3	35.7 $\pm$ 6.1	41.0	29.0	40.3 $\pm$ 7.0	47.0	33.0	22.7 $\pm$ 0.6	23.0	22.0	6.7 $\pm$ 1.5	8.0	5.0
	M	3	39.0 $\pm$ 16.8	58.0	26.0	44.7 $\pm$ 18.5	65.0	29.0	23.0 $\pm$ 4.6	27.0	18.0	11.3 $\pm$ 3.8	14.0	7.0
<i>Symphalangus syndactylus</i>	F	2	19.5 $\pm$ 0.7	20.0	19.0	19.0* $\pm$ N/A	19.0	19.0	22.5 $\pm$ 3.5	25.0	20.0	4.5 $\pm$ 2.1	6.0	3.0
	M	2	20.5 $\pm$ 0.7	21.0	20.0	30.0* $\pm$ N/A	30.0	30.0	20.5 $\pm$ 0.7	21.0	20.0	5.0 $\pm$ 0.0	5.0	5.0
<i>Hyllobates lar</i>	F	1	18.0	N/A	N/A	15.0	N/A	N/A	21.0	N/A	N/A	4.0	N/A	N/A
	M	1	19.0	N/A	N/A	20.0	N/A	N/A	21.0	N/A	N/A	6.0	N/A	N/A
<i>Colobus guereza</i>	F	1	11.0	N/A	N/A	23.0	N/A	N/A	20.0	N/A	N/A	4.0	N/A	N/A
	M	1	14.0	N/A	N/A	27.0	N/A	N/A	22.0	N/A	N/A	4.5	N/A	N/A
<i>Trachypithecus francoisi</i>	M	1	12.0	N/A	N/A	21.0	N/A	N/A	20.0	N/A	N/A	4.0	N/A	N/A
<i>Macaca fascicularis</i>	F	8	13.8 $\pm$ 2.2	17.0	10.0	17.4 $\pm$ 1.0	18.5	15.5	12.8 $\pm$ 1.6	15.0	10.0	2.3 $\pm$ 0.4	3.0	2.0
	M	8	13.1 $\pm$ 1.8	17.0	11.0	21.3 $\pm$ 1.7	24.0	18.5	14.6 $\pm$ 1.4	17.0	13.0	2.9 $\pm$ 0.6	4.0	2.0
<i>Macaca mulatta</i>	F	8	16.6 $\pm$ 1.8	19.0	14.0	23.9 $\pm$ 1.1	26.0	23.0	17.4 $\pm$ 1.1	18.0	15.0	3.3 $\pm$ 0.5	4.0	3.0
	M	8	17.6 $\pm$ 2.1	20.0	14.0	28.3 $\pm$ 1.7	31.0	26.0	20.5 $\pm$ 1.4	22.0	18.0	3.9 $\pm$ 1.0	6.0	3.0
<i>Papio</i> sp.	F	3	19.7 $\pm$ 0.6	20.0	19.0	29.7 $\pm$ 3.8	34.0	27.0	20.0 $\pm$ 1.0	21.0	19.0	5.7 $\pm$ 0.6	6.0	5.0
	M	5	21.8 $\pm$ 2.3	24.0	19.0	35.4 $\pm$ 3.2	39.0	31.0	25.8 $\pm$ 2.8	30.0	23.0	5.4 $\pm$ 0.9	6.0	4.0
<i>Ateles</i> sp.	F	3	16.3 $\pm$ 4.9	22.0	13.0	20.8 $\pm$ 4.1	25.5	18.0	19.3 $\pm$ 0.6	20.0	19.0	4.7 $\pm$ 1.2	6.0	4.0
	M	3	15.3 $\pm$ 0.6	16.0	15.0	21.7 $\pm$ 1.5	23.0	20.0	19.3 $\pm$ 1.5	21.0	18.0	3.3 $\pm$ 0.6	4.0	3.0
<i>Cebus apella</i>	F	4	8.3 $\pm$ 1.5	9.0	6.0	14.8 $\pm$ 1.0	16.0	14.0	12.3 $\pm$ 0.5	13.0	12.0	1.9 $\pm$ 0.3	2.0	1.5
	M	2	7.5 $\pm$ 0.7	8.0	7.0	17.3 $\pm$ 1.1	18.0	16.5	14.5 $\pm$ 0.7	15.0	14.0	2.5 $\pm$ 0.7	3.0	2.0

Sex-specific samples consisting of 1 individual are not mean values.

* mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total N listed.

SD= standard deviation, N/A= not applicable.

Table 7

Species-specific pairwise comparisons for flexion-extension

	<i>Gorilla</i>	<i>Pongo</i>	<i>Symphalangus</i>	<i>Hylobates</i>	<i>Ateles</i>	<i>Colobus</i>	<i>Trachypithecus</i>	<i>M. fascicularis</i>	<i>M. mulatta</i>	<i>Papio</i>	<i>Cebus</i>
<i>Pan</i>	1,3						2	1		2,3	
<i>Gorilla</i>			1,3	1,3	1	1,3	1	1,3	1,3	1	1,3
<i>Pongo</i>			1		1		2	1	1	2	1
<i>Symphalangus</i>							2			3	
<i>Hylobates</i>							2			2,3	
<i>Ateles</i>											
<i>Colobus</i>											
<i>Trachypithecus</i>											2
<i>M. fascicularis</i>										3	
<i>M. mulatta</i>										3	
<i>Papio</i>											2,3

Significant Tukey HSD pairwise comparisons (p 0.05) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in grey cells represent comparisons between suspensory and non-suspensory species. Stippled cells are redundant species comparisons, and blank cells have no significant comparisons. 1=flexion, 2=extension, 3=range of flexion-extension.

Table 8

Species-specific pairwise comparisons for adduction-abduction

	<i>Gorilla</i>	<i>Pongo</i>	<i>Symphalangus</i>	<i>Hyllobates</i>	<i>Ateles</i>	<i>Colobus</i>	<i>Trachypithecus</i>	<i>M. fascicularis</i>	<i>M. mulatta</i>	<i>Papio</i>	<i>Cebus</i>
<i>Pan</i>	2	1	2		3	2	2	2,3	2,3	2,3	2,3
<i>Gorilla</i>		2		2,3	2	2		2,3	2,3	2,3	2
<i>Pongo</i>			2	1	2	2,1	2	2,3	2,3	2,3	1,2
<i>Symphalangus</i>				3		2		2,3	2,3	2,3	2
<i>Hyllobates</i>					1,3	2,3	2,3	1,2,3	1,2,3	2,3	2,3
<i>Ateles</i>						2,1,	2	2,3	2,3	2,3	1,2
<i>Colobus</i>											
<i>Trachypithecus</i>											
<i>M. fascicularis</i>											1,2,3
<i>M. mulatta</i>											1,2,3
<i>Papio</i>											2,3

Significant Tukey HSD pairwise comparisons (p 0.05) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in grey cells represent comparisons between suspensory and non-suspensory species. Stippled cells are redundant species comparisons, and blank cells have no significant comparisons. 1=adduction, 2=neutral abduction, 3=range of abduction-adduction.

Table 9

Species-specific pairwise comparisons for rotation

	<i>Gorilla</i>	<i>Pongo</i>	<i>Symphalangus</i>	<i>Hylobates</i>	<i>Ateles</i>	<i>Colobus</i>	<i>Trachypithecus</i>	<i>M. fascicularis</i>	<i>M. mulatta</i>	<i>Papio</i>	<i>Cebus</i>
<i>Pan</i>		2				2	2	1,2	2,3	1,2	2,3
<i>Gorilla</i>			1	1			2	1,2	2	1,2	2
<i>Pongo</i>			1,2	1,2			2	1,2	2,3	1,2,3	2,3
<i>Symphalangus</i>										2,3	1,3
<i>Hylobates</i>						1				2,3	1,3
<i>Ateles</i>						2	2	2	2,3	2,3	3
<i>Colobus</i>										2	
<i>Trachypithecus</i>											
<i>M. fascicularis</i>									1	2,3	1,3
<i>M. mulatta</i>										2	
<i>Papio</i>											1

Significant Tukey HSD pairwise comparisons (p 0.05) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in grey cells represent comparisons between suspensory and non-suspensory species. Stippled cells are redundant species comparisons, and blank cells have no significant comparisons. 1=internal rotation, 2=external rotation, 3=range of internal-external rotation.

Table 10

Additional measures of abduction

Species	Sex	n	Abduction in extension			Abduction in flexion			Abducted knee position (cm)		
			Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min
<i>Pan troglodytes</i>	F	10	74.8 $\pm$ 5.1	80.0	65.0	75.2 $\pm$ 4.3	84.0	69.0	69.2 $\pm$ 5.4	76.0	58.0
	M	13	70.7 $\pm$ 3.5	79.0	64.0	69.5 $\pm$ 2.6	73.0	65.0	72.1 $\pm$ 4.9	81.0	61.0
<i>Gorilla gorilla</i>	F	2	71.0 $\pm$ 1.4	70.0	72.0	ND	ND	ND	66.5 $\pm$ 5.0	70.0	63.0
	M	4	9.4 $\pm$ 25.2	62.0	6.0	ND	ND	ND	71.5 $\pm$ 3.5	75.0	68.0
<i>Pongo pygmaeus</i>	F	3	82.0 $\pm$ 2.7	85.0	80.0	82.0 $\pm$ 2.7	85.0	80.0	63.0 $\pm$ 4.2	66.0	60.0
	M	3	85.0 $\pm$ 4.2	88.0	82.0	76.7 $\pm$ 5.5	82.0	71.0	65.5 $\pm$ 6.4	70.0	61.0
<i>Symphalangus syndactylus</i>	F	2	59.0 $\pm$ 12.7	68.0	50.0	51.0 $\pm$ 12.7	60.0	42.0	51.0 $\pm$ 5.0	N/A	N/A
	M	2	70.0 $\pm$ 7.1	75.0	65.0	65.0 $\pm$ 0.0	65.0	65.0	55.0 $\pm$ 5.0	N/A	N/A
<i>Macaca fascicularis</i>	F	8	20.4 $\pm$ 3.2	23.0	14.0	20.3 $\pm$ 4.1	26.0	15.0	21.3 $\pm$ 2.8	26.0	18.0
	M	8	18.5 $\pm$ 5.7	26.0	10.0	21.9 $\pm$ 6.4	32.0	11.0	24.1 $\pm$ 3.0	28.0	19.0
<i>Macaca mulatta</i>	F	8	21.5 $\pm$ 6.2	35.0	15.0	24.0 $\pm$ 4.9	32.0	16.0	28.1 $\pm$ 3.4	34.0	24.0
	M	8	18.9 $\pm$ 3.7	21.0	10.0	18.9 $\pm$ 5.2	26.0	10.0	31.3 $\pm$ 3.6	36.0	26.0

Units for abduction in extension and flexion are degrees. No data were collected for *Gorilla* in positions of abduction during flexion as the large abdomen prevented accurate placement of the goniometer.

* mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total N listed.

SD= standard deviation, N/A= not applicable, ND=no data.

Table 11

Species-specific pairwise comparisons for additional measures

	<i>Gorilla</i>	<i>Pongo</i>	<i>Symphalangus</i>	<i>M.fascicularis</i>	<i>M.mulatta</i>
<i>Pan</i>	1		2,3	1,2,3	1,2,3
<i>Gorilla</i>		1	3	1,2,3	1,2,3
<i>Pongo</i>			1,2,3	1,2,3	1,2,3
<i>Symphalangus</i>				1,2,3	1,2,3
<i>M.fascicularis</i>					3

Significant Tukey HSD pairwise comparisons (p 0.05) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in grey cells represent comparisons between suspensory and non-suspensory species. Stippled cells are redundant species comparisons, and blank cells have no significant comparisons. 1=range of abduction in flexion, 2=range of abduction in extension, 3=abducted knee position.

Table 12

Species-specific Spearman correlations and OLS regressions

	rho	p _{rho}	non-suspensory			suspensory			p _{slope}	p _{intercept}
			r ²	slope	intercept	r ²	slope	intercept		
flexion	0.74	<0.01	0.44	16.46	17.87	0.67	19.04	11.55	0.76	0.50
extension	0.06	0.80	0.10	-55.81	196.19	0.08	-31.45	182.30	0.07	0.34
flex-extension range	-0.43	0.04	0.33	-72.27	178.32	0.55	-50.48	170.76	0.16	0.65
adduction	0.16	0.46	0.13	18.34	65.05	0.02	10.79	54.44	0.65	0.57
abduction	0.31	0.15	0.42	-18.53	1.44	0.02	-11.44	38.02	0.58	0.02
add-abduction range	0.24	0.26	0.32	-36.87	66.49	0.05	-22.23	92.46	0.28	0.48
internal rotation	-0.18	0.40	0.36	49.18	-12.75	0.49	15.86	26.59	<0.01	<0.01
external rotation	0.43	0.04	0.35	-62.85	88.73	0.19	-27.12	76.43	<0.01	0.29
rotation range	0.30	0.17	0.01	-13.67	75.98	0.20	-11.27	103.02	0.82	0.03

Three variables (flexion, range of flexion-extension, external rotation) were found to be significantly correlated with body mass (bold p_{rho} value). OLS results are provided as a supplement to phylogenetic regression (PGLS) results. Significant differences in slope (p_{slope}) or intercept (p_{intercept}) between locomotor groups are indicated in bold.

Table 13

Phylogenetic regressions (female-specific data only)

	non-suspensory			suspensory			P _{slope}	P _{intercept}	lambda
	r ²	slope	intercept	r ²	slope	intercept			
flexion	0.12	6.43	23.84	0.58	11.71	14.84	0.63	0.44	0.00
extension	0.54	-16.80	165.18	0.06	11.29	164.53	0.52	0.97	0.00
flex-extension range	0.64	-23.24	141.33	0.33	-17.22	149.69	0.76	0.69	0.00
adduction	0.21	-13.25	56.64	0.18	-14.06	58.72	0.97	0.94	0.00
abduction	0.06	-3.15	32.00	0.04	5.66	60.84	0.67	0.20	0.00
add-abduction range	0.17	-16.40	88.64	0.03	-8.40	119.56	0.84	0.46	0.00
internal rotation	0.62	19.04	24.51	0.91	-29.07	83.10	<0.01	<0.01	0.00
external rotation	0.22	-12.98	64.93	0.32	15.87	53.07	0.19	0.59	0.00
rotation range	0.03	6.06	89.44	0.26	-13.20	136.17	0.40	0.08	0.00

The phylogenetic regressions did not detect significant differences in slope (pslope) or intercept (Pintercept) between locomotor groups for most variables. The Pagel's lambda (λ) values calculated using a maximum likelihood approach are reported for each phylogenetic regression. Although r² values are reported, PGLS r² values are not directly comparable to those in traditional OLS and have less inferential utility (see supplemental materials in Lavin et al. 2008).