

## Extreme leg action and hip-joint dynamics in wild primates

We measure how leg actions of cadaver monkeys are transferred within the hip-joint, and we compare physical femoral mobility of wild and captive monkeys in Panama, Costa Rica, and in zoological parks of California. We acquire leg movement data of howler, capuchin and spider monkeys with random 1 second digital photography during 4 months in Central America, and weekly visits for 2 months in California zoos (n=47 wild primates, 1879 focal events; 24 captive primates, 959 focal events). We employ computer software to objectively assess leg angle in regards to flexion, neutral and extension postures of the femur, relative to the hip socket. We apply leg action data to cadaver pelvises in primate bone collections at University of California, Davis, University of Oregon Osteology Lab, and the Denver Museum. Our study reveals that extreme femoral action translates as high diversity of articular contacts within the primate hip joint, and that captive monkeys in artificial habitats have less femoral movements than wild monkeys, with statistical comparisons being: Full leg flexion  $P = 0.0012$ ; Flexion  $P = 0.023$ ; Ambulatory as in walking  $P = 0.075$ ; Extension  $P = 0.002$ ; and Full extension with leg in line with body  $P = 0.00011$ . We speculate that the primate body is built to move in extreme but non-traumatic, wide-ranging appendicular actions. Such movements may help to simulate peripheral articular cartilage, contributing to the longevity of joints, and perhaps extending the life of primates who move in this manner.

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**Extreme leg action and hip-joint dynamics in wild primates**

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## 1 INTRODUCTION

2 Extreme body movements are central to primates. Regardless of ancestral landscape, or whether  
3 the primate is human, ape or monkey, this is a long-lived group that is built to move through  
4 specific biomechanical action at resilient appendicular joints (*De Rousseau, 1985; Jurmain,*  
5 *2000; Maclatchy, 1996*). Wide-ranging appendicular action is one of the core characteristic of  
6 primate mobility, as evidenced by anthropological studies on this group, and by the extensive,  
7 specialized tissues of the body that are dedicated to some extent on extreme physical mobility  
8 (*Bloomsmith & Lambeth, 1995; Dunbar et al., 2004; Madden et al., 2010; Malina & Little,*  
9 *2008*). Leg action in primates is more than the initiation of nervous impulses, muscular  
10 contractions, and leverage of the skeleton during movement. Also involved in movement of the  
11 leg are specific interactions between the head of the femur and the hip socket (or femoro-  
12 acetabular joint). Specific action of the femur is probably translated in this inner joint space of  
13 the hip as precise contacts between adjacent articular surfaces. Exploration of a possible  
14 association between extreme leg movement and the femur-hip socket interface is the focus of  
15 this study.

16 It is within the intra-joint space, between articulating bones, where much of the compressional  
17 and tensional force of physical movements focus on a small area of cartilage (*Jones, Bennell &*  
18 *Cucuttini, 2003; Macirowski, Tepic & Mann, 1994*). This resilient tissue is compressed but  
19 often unharmed from concussive forces derived from abrupt and intense movement (*Roos &*  
20 *Dahlberg, 2005; Salter et al., 1980*). This hardness is due in part to the specific nature of  
21 cartilage; a tissue with relatively few blood vessels and other tissues that would succumb to  
22 massive compression. With limited connection to the body's vascular system, cartilage must  
23 absorb some of its nutrients directly from fluids pumped into the joint space during physical  
24 activity (*Jones et al., 2003; Salter et al., 1980*). Rather than being worn, tattered and useless

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1 after traumatic physical events, articular cartilage has the potential to respond and adapt to  
2 tremendous load differences being exerted within joints (*Macirowski et al., 1994; Roos &*  
3 *Dahlberg, 2005*).

4 A general assumption regarding the rare incidence of chronic osteoarthritis in wild primates is  
5 that natural death occurs before the onset of advanced joint disease. Physical mobility and  
6 performance are linked to longevity, and low levels of these capabilities are associated with  
7 declining health and increased rates of mortality (*Branikowski et al., 2011; Shively et al., 2012*).

8 Etiology of osteoarthritis in primates is often uncertain, and may be the result of injury, disease,  
9 biochemistry, gender, and developmental abnormality; however, advanced age is perhaps the  
10 most prevalent condition associated with this disease (*Chi et al., 2014; Duncan, Colman &*  
11 *Kramer, 2012; Ganz, 2003; Uno, 1997*). Unlike most other mammals, primates have wide-  
12 ranging appendicular capabilities associated with a highly active lifestyle and an exceptionally  
13 long potential life-span (*Larson et al., 2001*). This extreme appendicular mobility may be one of  
14 the foundations of primate longevity; due to the stimulating effect movement has on growth and  
15 maintenance of articular cartilage.

16 Many biomechanical factors influence the development and maintenance of articular  
17 morphology (*De Rousseau, 1985; MacLatchy, 1996; Turnquist, 1985*). Physical activity appears  
18 to stimulate articular cartilage growth in mammals and protects injured joints from becoming  
19 arthritic, which is why exercise, rather than rest, is one effective treatment for degenerative joint  
20 disease in the hind limbs (*Lapvetelainen et al., 2001; Uno, 1997*). Joint mobility may decrease  
21 25° in the first 20 years of a monkey's life; however life expectancy in the wild is typically  
22 several years beyond the typical age at which osteoarthritis may influence movement (*Nakai,*  
23 *2003; Waite, Bushnitz & Honess, 2010*). Based on the stimulatory effect of physical activity on  
24 cartilage, it is possible that primates survive low levels of joint disease by maintaining high

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1 levels of physical activity in the wild. Joint disease in wild primates is considered rare, but has  
2 been observed in wild populations of apes (Chimpanzee and *Gorilla*). Although there are reports  
3 of wild primates with arthritis, this situation is far less pronounced than the degree found in  
4 captive members who move less than their wild counterparts (*Rothschild & Woods, 1992*).  
5 Advanced age may account for much of the arthritis reported for captive primates; however,  
6 there are places in the world with highly active elderly wild primates (*Froehlich, Thorington &*  
7 *Otis, 1981*).

8 It is possible that action arising at the primate pelvis is associated with longevity of the hip  
9 joint, where femur joins the pelvic bone (*Jurmain, 2000*). We explore this idea by recording leg  
10 action of primates of different age classes in captivity and in the wild, and by transferring this  
11 data to the laboratory study of monkey cadaver bones (*Fig 1*). We then test whether range of  
12 motion is associated with habitat structural complexity, and whether increased range of motion  
13 influences the distribution of articular contacts within the primate hip joint. We assume that a  
14 primate's wide-ranging appendicular mobility is an adaptive feature involved with survival in an  
15 immediate sense, but are there long-range benefits of an active lifestyle that might be tied to  
16 joint longevity in this group of long-lived animals?

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## METHODS

### Field study

We studied wild populations of black-handed spider monkey (*Ateles geoffroyi*), mantled howling monkey (*Alouatta palliata*), and white-faced capuchin (*Cebus capucinus*) at Isla Barro Colorado (spring 2010), and Estacion Biologica La Suerte (summer, 2013). La Suerte is a lowland tropical forest preserve in Costa Rica, at 10°N, 83°W, acquired in 1987 by the Molina family. Isla Barro Colorado (BCI), at 9°N, 79°W in Panama, is a tropical rainforest preserve that has existed in a protected state since 1923. Adult primate lifespans at both sites are long, with many of the howling monkeys on BCI surviving for over 20 years ([Froehlich, Thorington & Otis, 1981](#)).

We adhered to Animal Care and Use in Research and Education protocols (IACUC # 2957815) and permit to conduct our study was approved by the Smithsonian Tropical Research Institute, Ancon, Panama. Field research began 1 hour before sunrise along forest trails where we listened for calls and movements of primates. We quietly followed a primate troop for an hour, allowing them to habituate to our presence, at which time we employed observational instantaneous sampling of 30 second intervals ([Madden et al., 2010](#)). Based on visible anatomy and behavior, individual monkeys were identified as being either juvenile or adult ([Froehlich, Thorington & Otis, 1981](#)). Age class was determined by coat condition, dentition, feeding habits, anatomical differences between sexes, and other features as per [Balcells & Baró \(2009\)](#). Each sample session progressed as follows: 1) primate observed, and researchers agree to commence (this decision was based on visibility, light levels and other factors that might distort data sampling), 2) scribe initiates stopwatch and enters grid location, time, species, and activity, 3) five photographs are taken at the end of the 30-s interval when the scribe whispers ‘now,’ 4)

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notes, sketches, and camera frame number were written on a clipboard. We experimented with video recordings (Larson et al., 2001), and reverted to a Nikon D5200 with a 75-205 lens) for acquisition of a series of snapshots, much like a CT scan is a series of X-ray images. Low light levels in the forest were managed with an infrared flash, producing monochrome infrared images, as per Huang et al (2014).

Photographs were converted into quantitative data by uploading images into Photoshop, and using the software protractor tool to measure leg angles. Consistency and repeatability of leg angle assessment was achieved by aligning all measurements from a baseline, which was the sagittal aspect of the primate's torso, regardless of its pitch and yaw planes (as per Dunbar et al., 2004). Photo shots of legs that could not be accurately assessed were omitted. Protocols to address potential extraneous errors included: 1) pilot studies at study sites in Costa Rica and Panama that established inter-rater reliability > 92%) photographer and scribe duty rotation, 3) use of clinometers (rather than visual estimates), 4) three-way redundant data acquisition, involving data score entries, photographs, and quick field sketches, and 5) photography and data acquisition in elevated position whenever possible (Bezanson, 2012; Garber & Paciulli, 1997; Watts & Jobin, 2012).

1 Each location was noted on the data sheet, marked with colored tape, and sampled later in the  
2 day. We laid out a tape measure 5 m from the base of each flagged tree to establish four corners  
3 of a 100-m<sup>2</sup> quadrat, with a focal landmark situated at the center of each plot (Madden et al.,  
4 2008). We recorded lowest inter-canopy contact (distance from ground surface to where  
5 adjacent tree canopies first made contact), and nearest adjacent canopy (shortest distance to  
6 branch tips of the nearest adjacent tree) as per Madden et al (2010). These assessments  
7 measured habitat complexity that might influence a primate's leg movement as it travels. We  
8 repeated these methods to the best of our ability in California primate facilities (San Francisco,  
9 Mickie grove near Stockton, and San Diego Zoo). Full replication of the Panama and Costa

1 Rica field study was not possible due to crowds of people, and restricted hours of operations  
2 and access.

#### 4 **Laboratory study**

5 We examined pelvic bones and femurs of deceased primates (n=39) at University of  
6 California, Davis' Anthropology department, University of Oregon Osteology Laboratory  
7 (n=12), and the Denver Museum of Science (n=7). Age class of monkey cadaver material was  
8 determined by collection tags that accompanied each specimen, and was confirmed with an  
9 examination of tooth wear, as per *Dennis et al. (2004)*. Consistent placement of disarticulated  
10 monkey pelvic bones in a manner that inferred gross anatomical movement was achieved with  
11 a 3-dimensional system of homologous landmarks, modified from the work of *Bonneau et al.*  
12 *(2014)*. We placed a 1 mm layer of clay within the hip socket, to simulate cartilage mass and to  
13 help to hold the femoral head in place. Positioning the femur so that lateral and medial angles  
14 were consistent among the samples was achieved by placing the head into the socket, making  
15 firm contact with the clay, and then setting the pelvis and femur into a large block of clay so  
16 that the joint was immobile. Once firmly in place, the distance from the lesser trochanter to the  
17 closest point on the rim of the socket was determined by the formula:

18 *Sum of distance (mm) greater & lesser trochanter to nearest point of socket rim/2 • 0.85 (Fig.2)*

19 Once the pelvis was adjusted for the lesser trochanter to socket rim distance, we used calipers  
20 to measure the distance (mm) perpendicular from the hip socket rim to the edge of the articular  
21 surface of the femoral head (Fig. 2). We recorded these measurements by starting at the top of  
22 head of femur, and taking sequential measurements around the femoral head. We repeated  
23 these procedures when the femur was moved into another position along a sagittal plane to  
24 simulate what happens within the hip joint when the leg is moved into different positions. We



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1 obtained bone textures and configurations with photographs and Autodesk 123 Catch software,  
2 and with dental impression clay that was examined for irregularities, bony spurs and other  
3 features of the socket and femoral head.

4 At the conclusion of 4 months of field study in wet and dry seasons of Panama and Costa  
5 Rica, and 2 months of weekly visits to zoological parks of California, we had acquired  
6 observational data on 47 wild primates (1879 focal events) and 24 captive primates (959 focal  
7 events). For statistical analyses, we used one-way ANOVA, with alpha threshold ( $\alpha$ ) at 0.01 to  
8 reduce type II statistical errors. We applied Bayes' theorem of conditional probability for  
9 estimating the likelihood of an event, given a set of data. Pearson's correlation was conducted  
10 on the cadaver pelvis measurements. We pooled the La Suerte and BCI field data after finding  
11 a lack of significant difference in postural data between these sites. Similar compilation was  
12 done with primate data from zoos.

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## 1 RESULTS AND DISCUSSION

### 2 Results

3 Femoral flexion and extension observed while monkeys were traveling was not significantly  
4 different between open and closed tree canopies ( $P = 0.083$ ), nor between different types of  
5 artificial habitats ( $P > 0.14$ ) (Row 1 vs. 2 in Table 1). Significant differences were observed  
6 when comparing femoral action of captive vs. wild monkeys. These data represent frequency of  
7 the angle of the leg, relative to the sagittal plane of the torso (Fig. 3), and are separated into the  
8 following categories describing leg position: Full leg flexion ( $<30^\circ$ )  $P = 0.0012$ ; Flexion ( $30^\circ$  to  
9  $45^\circ$ )  $P = 0.023$ ; Ambulatory as in walking ( $45-110^\circ$ )  $P = 0.075$ ; Extension ( $110$  to  $145^\circ$ )  $P =$   
10  $0.002$ ; and Full extension with leg in line with body ( $145$  to  $180^\circ$ )  $P = 0.0001$ . Individual  
11 capuchins at San Diego Zoo displayed sporadic episodes of frequent wide ranging leg  
12 movements that resembled data from wild capuchins; however, these data were offset by long  
13 periods of leg flexion while resting, and frequent short-step ambulatory movements. Bayesian  
14 conditional probability indicated that femoral excursion was similar among wild adults and  
15 juveniles (Last row in Table 1).

16 Laboratory study of cadaver material revealed placement of the femur in flexion, extension,  
17 and neutral positions to result in different parts of the the head of the femur being exposed  
18 outside of the hip socket, while other articular surfaces of the head were in contact with  
19 surfaces within the hip. Wild and captive primate hip posture analyses that were pooled,  
20 making data independent of habitat structure, revealed a positive correlation ( $r^2 = 0.79$ ) in the  
21 comparison of exposed femoral articular surface of small-bodied primate species (*Saimiri*  
22 *sciureus* and *Sequinus oedipus*) and medium-sized primate primates (*Ateles geoffroyi* and  
23 *Alouatta palliata*), but these patterns of femoral head-hip socket contacts did not correlate ( $r^2 =$   
24  $0.28$ ) with human cadaver bones (Fig. 4). Dental impression clay and Autodesk computer

1 images indicated 23.2% greater incident of captive monkey material with bony spurs  
 2 (osteophytes), deformity of the neck and femoral head, and femoral head erosion; all indicative  
 3 of advanced osteoarthritis. However, the small sample size and condition of some bones limited  
 4 confidence (e.g. one arthritic specimen could drastically skew data). Serial photography and  
 5 conversion through Autodesk software indicated significant increase ( $P < 0.001$ ) of erosion at  
 6 tagged sites of captive monkeys when compared to wild sources of primate cadaver bones.

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8 **Discussion**

9 Wild primates frequently moved with wide-range femoral action, regardless of the variable  
 10 structural complexities in rainforest canopies they navigated, which is indicated by data in  
 11 [Table 1](#). These data indicate that primates are built to employ finesse and extreme postures as  
 12 they address a wide range of simple and complex obstacles in their routes of travel, which is  
 13 also supported by the work of [Beisner & Isbell, \(2009\)](#), [Dunbar et al. \(2004\)](#), [Demes, Fleagle  
 14 and Jungers \(1999\)](#). Wide ranging motions were observed throughout various habitat  
 15 complexities; in open habitats monkeys twisted, reached, and conducted long and wide femoral  
 16 excursions in similar fashion as was done in complex habitats characterized by wickers of  
 17 overlapping branches, thorny stems, and crowded canopies. It appears that diverse body  
 18 movements are central to the locomotion of wild monkeys in nature, which also appears to be  
 19 the case for early humans, as suggested by [Malina and Little \(2008\)](#). Unlike their wild  
 20 counterparts, captive primates spent extensive time in hip flexion postures, with knee toward  
 21 chest or in a rotational splay of the legs. Also, captive primates were rarely observed in extreme  
 22 femoral extension, in which the legs were aligned with the sagittal plane of the torso, as  
 23 supported by data in [Figure 3](#). Hip flexion is common in artificial habitats where primates have  
 24 little motivation to forage, maintain contact with a social troop, or to avoid hazards ([Turnquist,](#)

1 *1985; Jurmain, 2000; Waitt, Bushnitz & Honess, 2010*). Thus, leg excursion differences we  
 2 observed between captive and wild populations make sense when considering the architectural  
 3 and motivational dissimilarities between wild and artificial habitats.

4 In regards to juvenile and adult movements observed in our field study, we assumed that  
 5 experience and/or physical limitations of adult primates might cause them to move in ways  
 6 slightly different than those of juveniles. We expected adults to be selective in their locomotion  
 7 strategies, perhaps by opting for alternate routes to avoid risky leaps, awkward postures,  
 8 precarious perches, and other cliff-hanging situations that were common among juveniles.  
 9 However, this was not the case in our study (*Table 1*), nor was it observed by *Bezanson,*  
 10 *(2009)*, who reported similarities between juvenile and adult primate movements. These results  
 11 made sense when considering the energetic constraints of a primate's niche. In addition, similar  
 12 body movements among different age classes was probably common for early human social  
 13 groups, in which much of the daily routine centralized on physical activity and mobility  
 14 (*Malina & Little, 2008*). One can speculate that the primate body is shaped by environmental  
 15 forces, and regardless of whether it is monkey or human, potential exists in the adult body for  
 16 wide ranging mobility and vigorous physical activity that resembles the movements typically of  
 17 a young, vital primate's physique.

18 Variations in specific types of femoral action in wild primates are probably responses to  
 19 moment-to-moment challenges that are rooted in forces dictating survival (*Madden et al., 2010*).  
 20 A side benefit to wide-ranging physical mobility may be to foster articular wellness. Primate  
 21 locomotion through wild habitats demands different sets of body movements than those required  
 22 for artificial environments, where there are limited prospects for diverse physical activity (*De*  
 23 *Rousseau 1985; Rothschild & Woods, 1993; Waitt, Bushnitz & Honess, 2010*). As a primate  
 24 maneuvers its body to address immediate challenges, a compression and stimulation of sparsely  
 25 vascularized, dense and durable articular cartilage occurs. Thus, a primate may leap, collide with

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1 objects, sprint, tumble, and occasionally fall from heights without suffering extensive trauma to  
2 joints where much of the compressional and tensional forces are focused. Indeed, certain forces  
3 experienced within joints may foster cartilage health, when nourishing fluids within articular  
4 sites are absorbed by this spongy tissue (*De Rousseau, 1985; Lapvetelainen et al., 2001*).

5 Regarding physical mobility in primates, mere simple movement may not foster articular  
6 joint longevity. We observed long and wide strokes of the leg frequently employed by wild  
7 primates, but rarely in captive populations, as indicated in [Figure 3](#). Peripheral joint cartilage is  
8 maintained by extreme excursions of limbs when outer articulating surfaces are compressed,  
9 such as during long strides. Mobility variation may influence the large joints of chimpanzees,  
10 which suffer less joint degradation than gorillas that are frequently in a hip flexion position  
11 (*Jurmain, 2000*). Extreme appendicular strokes of the legs that exert exceptionally high forces  
12 on a primate's skeleton and supportive tissues may be associated with cartilaginous coverage in  
13 large capsular joints, as suggested by *Demes, Fleagle & Jungers (1999)*. Wide-range leg  
14 movements are central to a primate's immediate survival in nature, may be indirectly vital for  
15 joint joint maintenance, with even early humans having more extreme walking gaits than their  
16 contemporaries in East Africa (*Musiba et al., 1998*).

17 Our research indicates that an association exists between frequent wide-range movement of  
18 the leg and a diversity of contacts between articular surfaces within the hip-joint. We also  
19 present a case that the primate body is naturally built to move in an extreme range of  
20 appendicular motion, with supportive literature suggesting that such action may help maintain  
21 articular cartilage on peripheral areas of the joint, which are not fostered by small-range  
22 motion. Further study is recommended, as our cadaver pelvis work does not account for fluid  
23 pressure and living tissues that manage load and pressure distribution within joints, as  
24 suggested by *Macirowski, Tepic & Mann (1994)*, and *Nagura et al. (2006)*. If wide-range leg  
25 action translates as increased variety of articular contacts within the hip joint, as our study

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1 suggests, then health and longevity of this joint may be linked to more than simple, short  
2 excursions of the leg. We can speculate that non-traumatic, extreme leg movements are a  
3 natural action for the healthy hip-joint of a primate's body. Such physical mobility may help to  
4 foster articular cartilage mass by providing wide range stimulation to articular surfaces, and  
5 may feasibly increase the overall life expectancy of the hip joint, and ultimately the longevity  
6 of the primate.

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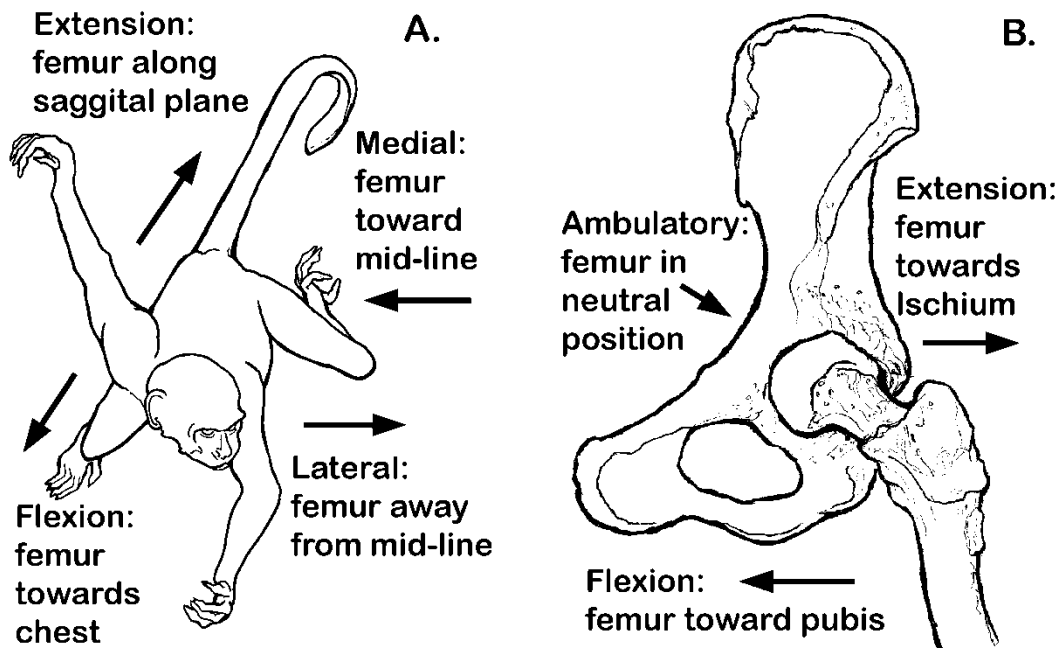
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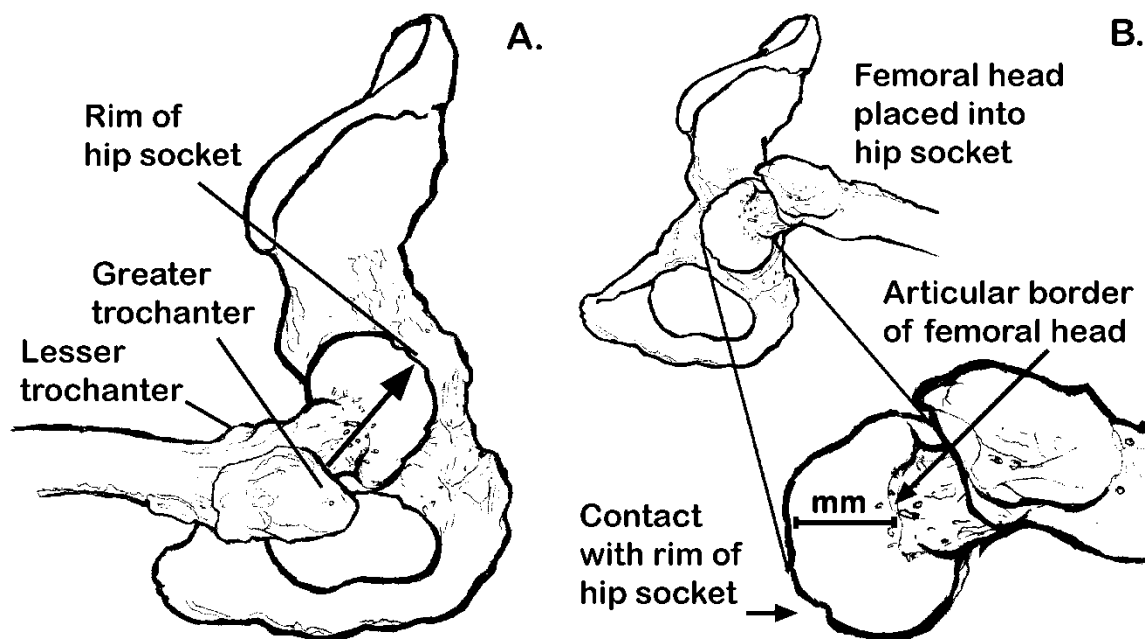
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**Fig. 1** Leg positions acquired by digital photography and analyzed with computer software were used for positioning the pelvis and femur of primate cadavers. Show here is **A.** an illustration of a capuchin monkey foraging at La Suerte, Costa Rica, and **B.** a human pelvis that was used for practicing the positioning and measurement of bones in ways that simulate the acquired primate postures.

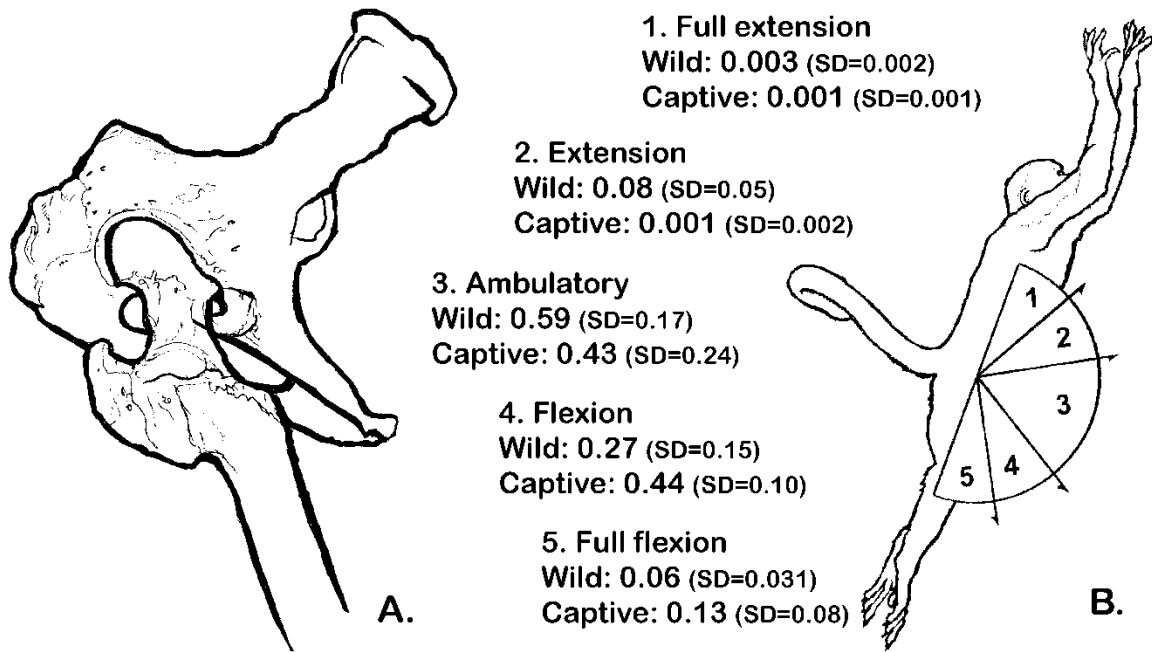
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**Fig. 2** A. Location of the greater and lesser trochanter, relative to the nearest point on the rim of the hip socket, and B. amount of exposed articular surface of the head of the femur, measured from the junction of the femoral head with the hip socket to the articular margin or rim of the femoral head.

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**Fig. 3** A. Femoral categories, measured with digital photography and geometric angle software, were 1. full flexion (knee near chest), 2. flexion, 3. ambulatory as in moderate walking and climbing, 4. extension, and 5. full extension with femur nearly in line with spine. B. Comparison of femur position frequencies during wakeful daytime activities for captive (N = 959) and wild black-handed spider monkey (*Ateles geoffroyi*), mantled howling monkey (*Alouatta palliata*), white-faced capuchin (*Cebus capucinus*) and Tufted capuchin (*Cebus apella*) (N = 1879).

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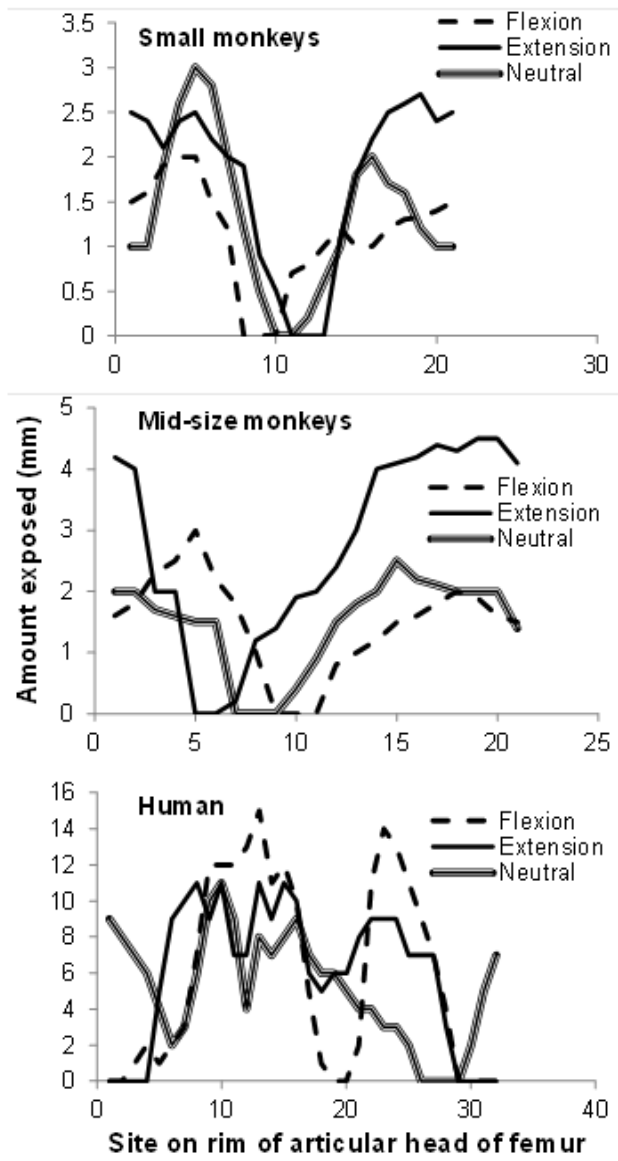
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	Open canopy			Semi-open canopy			Closed canopy			Total
	flexion	extension	neutral	flexion	extension	neutral	flexion	extension	neutral	
Mean wild primate hip position (N):	0.19 (357)	0.053 (99)	0.27 (432)	0.10 (188)	0.013 (24)	0.16 (300)	0.105 (160)	0.004 (8)	0.124 (245)	1879
Mean captive primate hip position (N):	0.30 (285)	0.018 (17)	0.22 (209)	0.27 (256)	0.002 (2)	0.20 (190)	N/A	N/A	N/A	959
Probable position if juvenile*	46.2	52.7	58.5	44.7	51.3	62.11	43	59.4	57.5	1879

\*Bayes theorem, given an observed posture, what is the likelihood that it is a juvenile?

6 **Table 1** Frequency of flexion, extension and neutral femur positions during 1 second random  
 7 focal observations in different canopy habitats (open = no inter-canopy branch connections;  
 8 closed = multiple overlapping canopy branches). Observations were of black-handed spider  
 9 monkey (*Ateles geoffroyi*), mantled howling monkey (*Alouatta palliata*), and white-faced  
 10 capuchin (*Cebus capucinus*) at La Suerte, Costa Rica and BCI, Panama (wild n= 47 different  
 11 individuals, 1879 focal sessions), and zoological parks in California (captive n= 24 individuals,  
 12 959 focal sessions).

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2 **Fig. 4** Amount of exposed femoral articular surface measured outside of the hip socket, as a  
 3 result of femur extension (knee in line with body), flexion (knee toward chest), and neutral as in  
 4 walking without extreme excursion, in primate pelvises that were a) Small: 3 *Saimari* and 1  
 5 *Sequinus*, b) Mid-sized: 12 *Cebus*, 3 *Ateles*, and 1 *Aotus*, and c) Large: 7 human cadavers and 24  
 6 sets of human bones. Numerical values at 0.0 indicate sites on the head of the femur that were  
 7 completely covered by the hip socket.