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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INTRODUCTION

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

It is within the intra-joint space, between articulating bones, where much of the compressional and tensional force of physical movements focus on a small area of cartilage (Jones, Bennell & Cucuttini, 2003; Macirowski, Tepic & Mann, 1994). This resilient tissue is compressed but often unharmed from concussive forces derived from abrupt and intense movement (Roos & Dahlberg, 2005; Salter et al., 1980). This hardiness is due in part to the specific nature of cartilage; a tissue with relatively few blood vessels and other tissues that would succumb to massive compression. With limited connection to the body’s vascular system, cartilage must absorb some of its nutrients directly from fluids pumped into the joint space during physical activity (Jones et al., 2003; Salter et al., 1980). Rather than being worn, tattered and useless
after traumatic physical events, articular cartilage has the potential to respond and adapt to
tremendous load differences being exerted within joints (Macirowski et al., 1994; Roos &
Dahlberg, 2005).

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

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

Many biomechanical factors influence the development and maintenance of articular
morphology (De Rousseau, 1985; MacLatchy, 1996; Turnquist, 1985). Physical activity appears
to stimulate articular cartilage growth in mammals and protects injured joints from becoming
arthritic, which is why exercise, rather than rest, is one effective treatment for degenerative joint
disease in the hind limbs (Lapvetelainen et al., 2001; Uno, 1997). Joint mobility may decrease
25° in the first 20 years of a monkey’s life; however life expectancy in the wild is typically
several years beyond the typical age at which osteoarthritis may influence movement (Nakai,
2003; Waitt, Bushnitz & Honess, 2010). Based on the stimulatory effect of physical activity on
cartilage, it is possible that primates survive low levels of joint disease by maintaining high
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levels of physical activity in the wild. Joint disease in wild primates is considered rare, but has been observed in wild populations of apes (Chimpanzee and Gorilla). Although there are reports of wild primates with arthritis, this situation is far less pronounced than the degree found in captive members who move less than their wild counterparts (Rothschild & Woods, 1992). Advanced age may account for much of the arthritis reported for captive primates; however, there are places in the world with highly active elderly wild primates (Froehlich, Thorington & Otis, 1981).

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

Each location was noted on the data sheet, marked with colored tape, and sampled later in the day. We laid out a tape measure 5 m from the base of each flagged tree to establish four corners of a 100-m² quadrat, with a focal landmark situated at the center of each plot (Madden et al., 2008). We recorded lowest inter-canopy contact (distance from ground surface to where adjacent tree canopies first made contact), and nearest adjacent canopy (shortest distance to branch tips of the nearest adjacent tree) as per Madden et al (2010). These assessments measured habitat complexity that might influence a primate’s leg movement as it travels. We repeated these methods to the best of our ability in California primate facilities (San Francisco, Mickie grove near Stockton, and San Diego Zoo). Full replication of the Panama and Costa
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Rica field study was not possible due to crowds of people, and restricted hours of operations and access.

Laboratory study

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

\[ \text{Sum of distance (mm) greater & lesser trochanter to nearest point of socket rim/2 } \times 0.85 \] (Fig. 2)

Once the pelvis was adjusted for the lesser trochanter to socket rim distance, we used calipers to measure the distance (mm) perpendicular from the hip socket rim to the edge of the articular surface of the femoral head (Fig. 2). We recorded these measurements by starting at the top of head of femur, and taking sequential measurements around the femoral head. We repeated these procedures when the femur was moved into another position along a sagittal plane to simulate what happens within the hip joint when the leg is moved into different positions. We
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obtained bone textures and configurations with photographs and Autodesk 123 Catch software, and with dental impression clay that was examined for irregularities, bony spurs and other features of the socket and femoral head.

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

Results

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

Laboratory study of cadaver material revealed placement of the femur in flexion, extension, and neutral positions to result in different parts of the the head of the femur being exposed outside of the hip socket, while other articular surfaces of the head were in contact with surfaces within the hip. Wild and captive primate hip posture analyses that were pooled, making data independent of habitat structure, revealed a positive correlation ($r^2 = 0.79$) in the comparison of exposed femoral articular surface of small-bodied primate species ($Saimiri sciureus$ and $Seguinus oedipus$) and medium-sized primate primates ($Ateles geoffroyi$ and $Alouatta palliata$), but these patterns of femoral head-hip socket contacts did not correlate ($r^2 = 0.28$) with human cadaver bones (Fig. 4). Dental impression clay and Autodesk computer
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images indicated 23.2% greater incident of captive monkey material with bony spurs (osteophytes), deformity of the neck and femoral head, and femoral head erosion; all indicative of advanced osteoarthritis. However, the small sample size and condition of some bones limited confidence (e.g. one arthritic specimen could drastically skew data). Serial photography and conversion through Autodesk software indicated significant increase (P < 0.001) of erosion at tagged sites of captive monkeys when compared to wild sources of primate cadaver bones.

Discussion

Wild primates frequently moved with wide-range femoral action, regardless of the variable structural complexities in rainforest canopies they navigated, which is indicated by data in Table 1. These data indicate that primates are built to employ finesse and extreme postures as they address a wide range of simple and complex obstacles in their routes of travel, which is also supported by the work of Beisner & Isbell, (2009), Dunbar et al. (2004), Demes, Fleagle and Jungers (1999). Wide ranging motions were observed throughout various habitat complexities; in open habitats monkeys twisted, reached, and conducted long and wide femoral excursions in similar fashion as was done in complex habitats characterized by wickers of overlapping branches, thorny stems, and crowded canopies. It appears that diverse body movements are central to the locomotion of wild monkeys in nature, which also appears to be the case for early humans, as suggested by Malina and Little (2008). Unlike their wild counterparts, captive primates spent extensive time in hip flexion postures, with knee toward chest or in a rotational splay of the legs. Also, captive primates were rarely observed in extreme femoral extension, in which the legs were aligned with the sagittal plane of the torso, as supported by data in Figure 3. Hip flexion is common in artificial habitats where primates have little motivation to forage, maintain contact with a social troop, or to avoid hazards (Turnquist,
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1985; Jurmain, 2000; Waitt, Bushnitz & Honess, 2010). Thus, leg excursion differences we
observed between captive and wild populations make sense when considering the architectural
and motivational dissimilarities between wild and artificial habitats.

In regards to juvenile and adult movements observed in our field study, we assumed that
experience and/or physical limitations of adult primates might cause them to move in ways
slightly different than those of juveniles. We expected adults to be selective in their locomotion
strategies, perhaps by opting for alternate routes to avoid risky leaps, awkward postures,
precarious perches, and other cliff-hanging situations that were common among juveniles.

However, this was not the case in our study (Table 1), nor was it observed by Bezanson,
(2009), who reported similarities between juvenile and adult primate movements. These results
made sense when considering the energetic constraints of a primate’s niche. In addition, similar
body movements among different age classes was probably common for early human social
groups, in which much of the daily routine centralized on physical activity and mobility
(Malina & Little, 2008). One can speculate that the primate body is shaped by environmental
forces, and regardless of whether it is monkey or human, potential exists in the adult body for
wide ranging mobility and vigorous physical activity that resembles the movements typically of
a young, vital primate’s physique.

Variations in specific types of femoral action in wild primates are probably responses to
moment-to-moment challenges that are rooted in forces dictating survival (Madden et al., 2010).
A side benefit to wide-ranging physical mobility may be to foster articular wellness. Primate
locomotion through wild habitats demands different sets of body movements than those required
for artificial environments, where there are limited prospects for diverse physical activity (De
Rousseau 1985; Rothschild & Woods, 1993; Waitt, Bushnitz & Honess, 2010). As a primate
maneuvers its body to address immediate challenges, a compression and stimulation of sparsely
vascularized, dense and durable articular cartilage occurs. Thus, a primate may leap, collide with
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objects, sprint, tumble, and occasionally fall from heights without suffering extensive trauma to joints where much of the compressional and tensional forces are focused. Indeed, certain forces experienced within joints may foster cartilage health, when nourishing fluids within articular sites are absorbed by this spongy tissue (De Rousseau, 1985; Lapvetelainen et al., 2001).

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

Our research indicates that an association exists between frequent wide-range movement of the leg and a diversity of contacts between articular surfaces within the hip-joint. We also present a case that the primate body is naturally built to move in an extreme range of appendicular motion, with supportive literature suggesting that such action may help maintain articular cartilage on peripheral areas of the joint, which are not fostered by small-range motion. Further study is recommended, as our cadaver pelvis work does not account for fluid pressure and living tissues that manage load and pressure distribution within joints, as suggested by Macirowski, Tepic & Mann (1994), and Nagura et al. (2006). If wide-range leg action translates as increased variety of articular contacts within the hip joint, as our study
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suggests, then health and longevity of this joint may be linked to more than simple, short
excursions of the leg. We can speculate that non-traumatic, extreme leg movements are a
natural action for the healthy hip-joint of a primate’s body. Such physical mobility may help to
foster articular cartilage mass by providing wide range stimulation to articular surfaces, and
may feasibly increase the overall life expectancy of the hip joint, and ultimately the longevity
of the primate.

ACKNOWLEDGEMENTS

We are grateful for assistance from Paul Garber, Michele Bezanson, Elizabeth Mallott, Natasha
Mazumdar, David Quesada, and Renee Molina of Maderas Rainforest Conservancy. Primate
bone work was made possible through Timothy Weaver and Teresa Steele of UC Davis
Anthropology Department, Andrea Eller at the University of Oregon Osteology lab, and Jeff
Stephenson of the Denver Museum. James Street was our editor. Grant funding came from
Yosemite Community College District and the US Department of Education, STEM grant #
PO31C110107 (B. Sanders & J. Abbot).
REFERENCES


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

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*Bayes theorem, given an observed posture, what is the likelihood that it is a juvenile?*
Fig. 4: Amount of exposed femoral articular surface measured outside of the hip socket, as a result of femur extension (knee in line with body), flexion (knee toward chest), and neutral as in walking without extreme excursion, in primate pelvises that were a) Small: 3 Saimiri and 1 Seguinus, b) Mid-sized: 12 Cebus, 3 Ateles, and 1 Aotus, and c) Large: 7 human cadavers and 24 sets of human bones. Numerical values at 0.0 indicate sites on the head of the femur that were completely covered by the hip socket.