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Rain forests and movement ecology of neotropical primates

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Abstract

Movement ecology of arboreal monkeys in Central America involves the action of diverse body postures to address challenges in rainforests, where scattered resources and complex habitat structure demand that a primate frequently employ extreme physical finesse to survive. What is not clearly understood about this area of study is the connection between primate body postures as responses to specific types of forest architecture and how forest structure may influence a monkey's continued capacity for wide-ranging mobility over time. We studied tree canopy structure and branch connectivity associated with the movement ecology of black-handed spider monkeys (*Ateles geoffroyi*), mantled howling monkeys (*Alouatta palliata*), Geoffroy's tamarins (*Saguinus geoffroyi*), and white-faced capuchins (*Cebus capucinus*) in Panama and Costa Rica. Laboratory study of primate cadaver pelvises was done at UC Davis, Oregon Osteology Lab, and the Denver Museum. Rain forests appear to induce wide-ranging leg movements in wild neotropical monkeys that were not observed in the same species of monkeys inhabiting artificial environments. We also found that a wild primate employs frequent wide-ranging leg movement that result in widely dispersed contacts between the articulating surfaces within the hip, potentially maintaining cartilage and contributing to the longevity of that joint. Thus, a connection may exist between rain forests, the leg action of wild monkeys, and the continued capacity to move over time in this group of long-lived animals.

Introduction

Describing the movement ecology of an animal often involves appropriate assessment of the habitat, a study of the organism's context within its living space, and an attempt to understand ecological and evolutionary consequences of that organism's movements throughout its lifetime. Movement is a basic trait of nearly all animals, and may range from large-scale migration and widely dispersed foraging to limited activities such as postural adjustments, temporal excursions and station-keeping actions (Bell 1991, de Knegt 2007, Turchin 1991). Animal movements can have far-reaching effects beyond the transient interactions between an organism and its immediate environment, with animal movements influencing other populations and entire ecosystems (Dingle 1996, Madden et al. 2008, Nathan et al. 2008). For example, monkeys comprise a small fraction of the species and biomass in neotropical forests; however, their dispersed defecation of seeds supports diverse populations of animals, and is associated with rain forest regeneration (Andresen 2002, Estrada & Coates-Estrada 1991). Monkeys frequently move in response to local differences in the abundance of resources and the structural aspects of the environment, with disparities in these qualities resulting in variation in the speed, route of travel, and rapid decision-making (Beisner & Isbell 2009, Garber 2000, Hunt et al. 1996). Primate movement often addresses the need to acquire resources, optimize routes of travel, exploit patches of safety, and expand territory, while simultaneously minimizing risk of mortality (Bartoń 2012, Delgado 2011). With movement being central to a monkey's survival in the wild, the continued capacity to move is a key aspect of an organism's movement ecology, especially for animals such as primates that maintain a high degree of mobility throughout their potentially long life.

Many of the common species of monkeys in Central American rain forests typically travel through structurally complex canopy runways, which present frequent obstacles, requiring

extreme body actions, and subtle postural adjustments such as when repositioning a foot to avoid a spiny branch (Cant 1986, Garber 2000, Gebo 1992). An arboreal primate's canopy runway often passes through and across tangled branches tilted at all angles, twisting lianas, abrupt gaps, rotten cavities, prickly stems, and other potential obstacles to locomotion. Canopy structural complexity provides connections between neighboring vegetation that constitute locomotion corridors for primates; however, this connectivity is highly discontinuous due to tree fall gaps, topography, and human activities (Peres 1993, Sandford, Braker, Hartshorn 1986, Schnitzer & Carson 1991). While such breaks in forest canopies disrupt navigation through arboreal habitats, foraging for food is often optimal in fragmented patches of rainforest where ecological edge habitats typically foster patchy, high concentrations of food for primates (Arroyo-Rodríguez 2007, Emmons & Gentry 1983, Worman & Chapman 2006). Canopy complexity and the scattered resources typical of a neotropical primate's niche favors individuals that employ extreme finesse and wide-ranging appendicular mobility as they forage for food, maintain contact with their social troop, and escape from arboreal and aerial predators (Bezanson 2009, Garber 1992, Madden et al. 2010, Smith 2000).

Movement ecology in a traditional sense tends to focus on major drivers for movement, such as the external motivators (e.g. hunger, safety, reproduction, sociability) that influence population movements over space and time (Bell 1991, Nathan et al. 2008). Also important in this area of study is an understanding of the internal mechanisms that make an organism's movement possible over time or distance (Bartoń 2012, Dingle 1996). For example, leg movements may sustain joints in ways that make similar body action possible over time (De Rousseau 1985, Lapvetelainen et al. 2001, Roos & Dahlberg 2005, Salter et al. 1980). As a primate maneuvers its body to address immediate challenges in the wild, stimulation of joint cartilage occurs in these tissues that adapt to tremendous loads without being damaged (Jurmain 2000,

Macirowski et al. 1994, MacLatchy 1996). Thus, a primate may leap, sprint, tumble, and occasionally fall from heights without injury to joints where much of the compressional and tensional forces are focused. Primates have wide-ranging mobility capabilities that help contribute to a highly active lifestyle and an exceptionally long potential life span (Okada 1996, Larson et al. 2001). Extreme physical mobility may contribute to primate longevity in the wild by increasing the possibility of continued wide-ranging movement and territorial expansion.

A primate's movement ecology includes numerous factors inherent in the niche of a species, and may also encompass internal processes that foster long-term mobility. With movement being central to the immediate survival of a neotropical primate, it follows that continued capacity for movement is also central for these animals with potentially long life-spans. Wide-ranging body postures are typical of primate mobility in the wild, and probably resulted from environmental situations that select for highly mobile and agile individuals (Garber 2000, Larson et al. 2001, Jurmain 2000). A large body of literature describes physical aspects of primate body movement in the wild (e.g. Demes, Fleagle, Jungers 1999, Dunbar et al. 2004, Jurmain 2000, Larson et al. 2001, Malina & Little 2008, Maclatchy 1996), and decades of study have explored links between forest resources and the movements of common primates in Central American rain forests (e.g. Bezanson 2009, Estrada & Coates-Estrada, 1991, Garber 2000, Gebo 1992, Hunt et al. 1996). Beyond addressing many of the immediate aspects of a primate's dietary, social, and safety requirements, it is possible that wide-ranging physical movement through the structural matrix of tropical canopies is associated with long-term survival of arboreal primates, through a continuance of the capacity to move. In this context, our study has three aims: 1) record basic leg postures of primates traveling through different types of rain forest canopies, 2) transfer this information in a laboratory study of articulated hip joints of the species being studied in the field, and 3) compare these data with control groups of captive monkeys. From these data, we may test the hypotheses that 1) rain forests are setting that induce wide-ranging

postures in arboreal monkey populations, 2) that these habitats influence the internal environment of the primate hip, and that 3) the extent of this physical mobility does not occur in controlled environments. It is possible that rain forests provide a specific necessary aspect of a primate's movement ecology that deals with the capacity for wide-ranging movements over time. Alternatively, movements made by wild and captive primates may have similar potential to foster continued physical mobility, and rain forests may not be an important selective force in the movement ecology of wild arboreal primates.

Methods

Field study

We studied wild populations of black-handed spider monkey (*Ateles geoffroyi*), mantled howling monkey (*Alouatta palliata*), Panamanian population of Geoffroy's tamarin (*Saguinus geoffroyi*), 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 (Milton & Hopkins 2006).

We followed Animal Care and Use in Research and Education protocols (IACUC # 2957815), and the research protocols that we submitted to 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, Suen & Ary 1984). Based

on visible anatomy and behavior, individual monkeys were identified as being either juvenile or adult. Age class was determined by coat condition, dentition, feeding habits, anatomical differences between sexes, and other features (Milton & Hopkins 2006, Peres 1993).

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) notes, sketches, and camera frame number were written on a clipboard. We experimented with video recordings, and reverted to a Nikon D5200 and 205 lenses; generating a sequence of snapshots, much like a CT scan is a series of X-ray images.

Video vs. snap-shot capture is debated among scientist, and many favor video (e.g. Larson et al. 2001). However, we found that snap-shot photography reduced the time and potential bias involved with making decisions about which frame in a video recording to use for a data sample. Also, we preferred the high resolution shots that resulted from individual photographs when compared to video recordings. In addition, snap-shot battery life reduced the need to change batteries in what were often misty-wet conditions during long days in the field. 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 (as per methods described by [Bezanson et al. 2012](#)).

Each location was noted on the data sheet, marked in the field 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](#)). For each flagged plant, the following data were recorded: trunk diameter at breast height (dbh), lowest inter-canopy contact (distance from ground surface to where adjacent tree canopies first made contact), nearest adjacent canopy (shortest distance to branch tips of the nearest adjacent tree), growth form of nearest woody vegetation (liana, palm, woody dicot, other) and light penetration through the overhead canopy, converted to percent from a hand-held densiometer. For mid to high level canopy assessment, we used the following equipment to work above ground surfaces: 10.5mm climbing ropes, Petzl ascenders, climbing harness, locking carabiners, and webbing slings. With a sling shot, we projected a thin lead-line across a major lower branch, tied our 10.5 mm main-line to the lead-line, and pulled the main-line over the major branch. A secondary line provided redundant safety, with rope feed to the climber being controlled at the base of the tree via a figure-8 belay plate attached to the harness of another researcher ([Laman 1995](#)).

At each 100-m² plot, a SLR camera braced and leveled on a tripod was used to photograph the area around each flagged tree. White sheets of 1.5 × 3 m were draped vertically like a wall on one side of each plot, about 5 m from the base of each flagged tree. In this manner, the

flagged tree and nearest adjacent tree canopy was photographed and illustrated. This drape made it possible to illustrate cross-sections of the forest to characterize habitats (Fig. 1). Flagged vegetation was identified to species according to Croat (1978), and confirmed later with herbarium samples on BCI. Tape measures were used to determine mean distance to nearest forest clearing ($\geq 75\%$ light penetration determined by densiometer), which were typically gaps in the overhead canopy caused by treefalls, physical processes such as stream action or human activity (Madden et al. 2010; Sanford et al. 1986, Schnitzer & Carson 1991). These assessments measured habitat complexity that might influence a primate's leg movement as it travels. For a control group, we repeated field methods to the best of our ability in California primate facilities (San Francisco Zoo, Mickie Grove Zoo near Stockton, and San Diego Zoo). Advanced permits were approved at these facilities that extended our study sessions; however, full replication of the Panama and Costa Rica field study was not possible in zoos due to restricted hours of operations and access.

Laboratory study

A laboratory phase of study was used in conjunction of the field study to estimate how actions in different habitats, and as done by juveniles and adults, might be translated within a monkey's hip (Figs. 1A, B). We contacted managers of facilities with cadaver bone collections of the primate species we studied in the field. After receiving advanced clearance for our visit, we used surgical gloves, calipers, plasticine modeling clay that does not leave pieces of clay on bone specimens, artists' triangles, protractors, a camera and tripod to carefully examine pelvic bones and femurs of deceased primates. We conducted this work on howler, capuchin, and spider monkey skeletons at the University of California, Davis Anthropology department (n=20), 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:

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

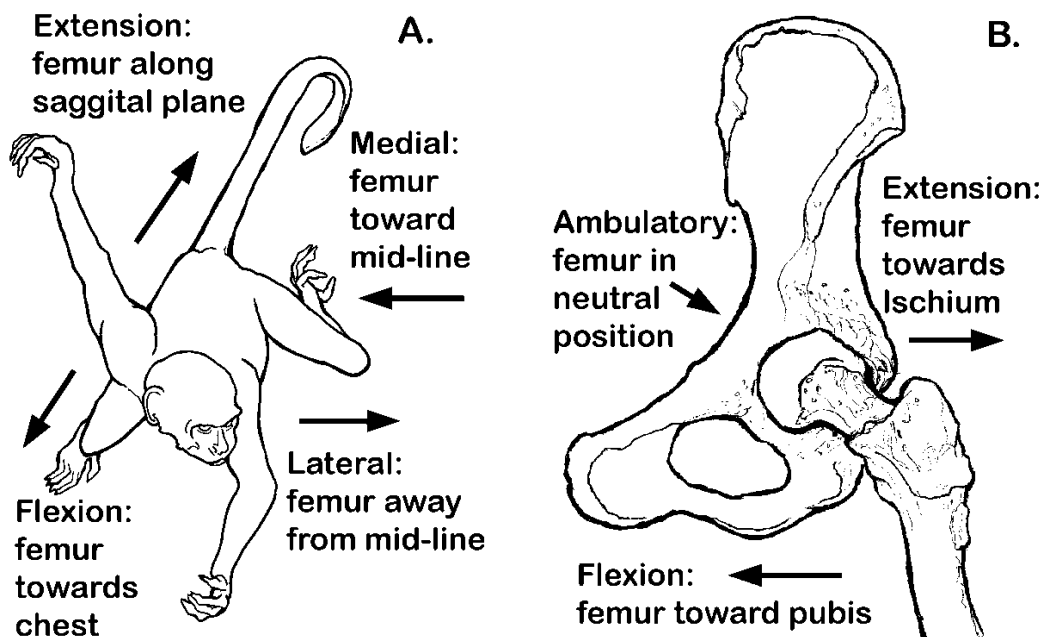


Figure 1.

Leg positions acquired by digital photography and analyzed with computer software were used for positioning the pelvis and femur of primate cadavers. Shown here is A. basic appendage movements illustrated at La Suerte, Costa Rica, and B. Basic leg positions radiating out from a primate pelvis.

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. 2A). In an effort to reduce time-consuming, trial-and-error when we visited primate collections to acquire data, we first conducted a series of pilot studies on small human skeletons in Modesto JC's collection. We recorded these measurements by starting at the top of head of femur, and taking sequential measurements around the femoral head (Fig. 2B). 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 by a live monkey. We frequently referred to our field photographs and sketches when positioning the pelvis for measurement, and omitted data that was based on suspect images. We 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.

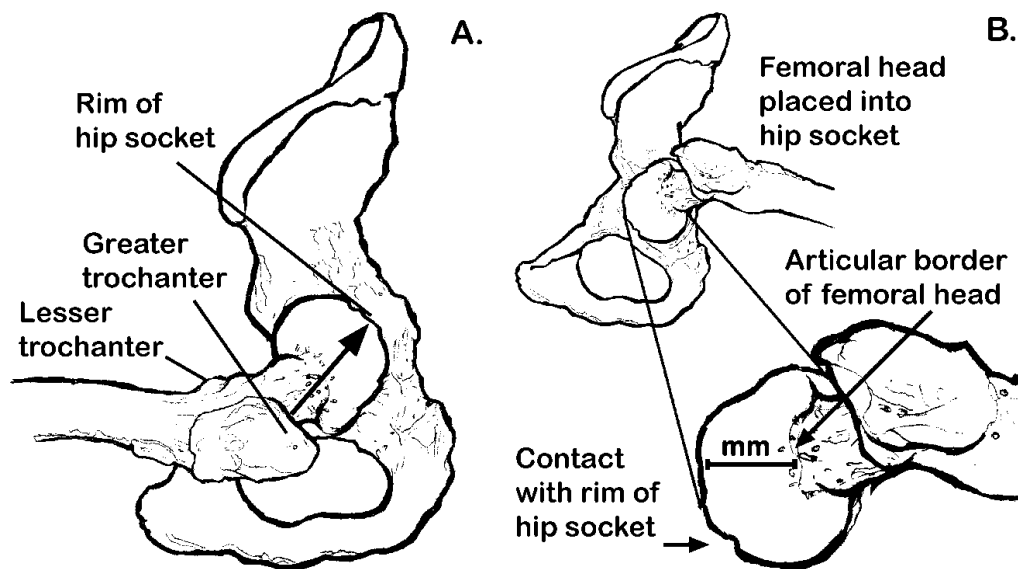


Figure 2.

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 rim of the 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) in the years between 2010 and 2014. 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. Bayes' was used in a specific case to determine the likelihood that is a monkey is an adult or juvenile, based on its leg flexion or extension when in a specific patch of habitat. 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

Femoral flexion and extension observed while monkeys were traveling was not significantly different between open and closed tree canopy habitat categories in rain forests of La Suerte and BCI ($P = 0.083$). Similar lack of significant difference ($P > 0.14$) was observed in the comparison of monkey movement in the different types of artificial environments assessed in this study (Row 1 vs. 2 in Table 1). Remarkable differences were observed when comparing femoral action of monkeys in artificial habitats with the movements of monkeys in their native rainforest canopies. 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° to 45°) $P = 0.023$; Ambulatory as in walking (45 - 110°) $P = 0.075$; Extension (110 to 145°) $P = 0.002$; and Full extension with leg in line with body (145 to 180°) $P = 0.0001$. Individual tufted 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).

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).

	Open canopy			Semi-open canopy			Closed canopy			Total
	flexion ^a	extend ^b	neutral ^c	flexion	extend	neutral	flexion	extend	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 ^d	46.2	52.7	58.5	44.7	51.3	62.11	43	59.4	57.5	1879

a Thigh of leg at < 30° angle from torso, with knee towards chest.
 b Thigh at 110 to 145° from torso, with knee mostly aligned with sagittal plane of torso.
 c Thigh at 45-110° angle from torso, as in normal walking and climbing postures.
 d Bayes theorem: Given an observed posture, what is the likelihood that it is a juvenile?

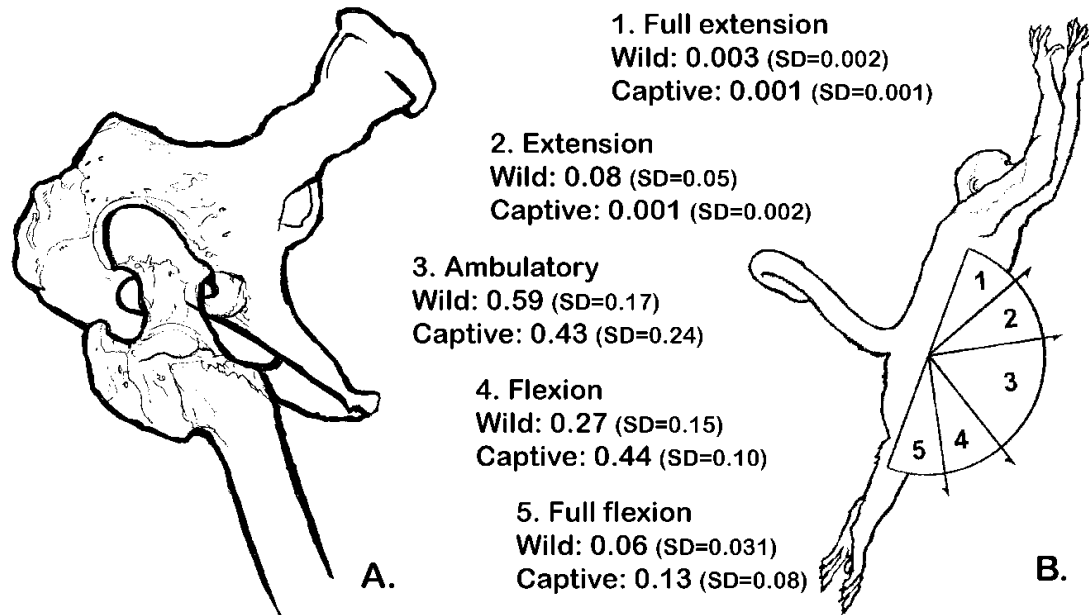


Figure 3.

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*) ($N = 1879$).

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. When primate hip posture data from wild and artificial habitats were pooled, making this set of data independent of habitat structure, revealed was a positive correlation ($r^2 = 0.79$) in the comparison of exposed femoral articular surface of small and mid-sized primate species (Fig. 4).

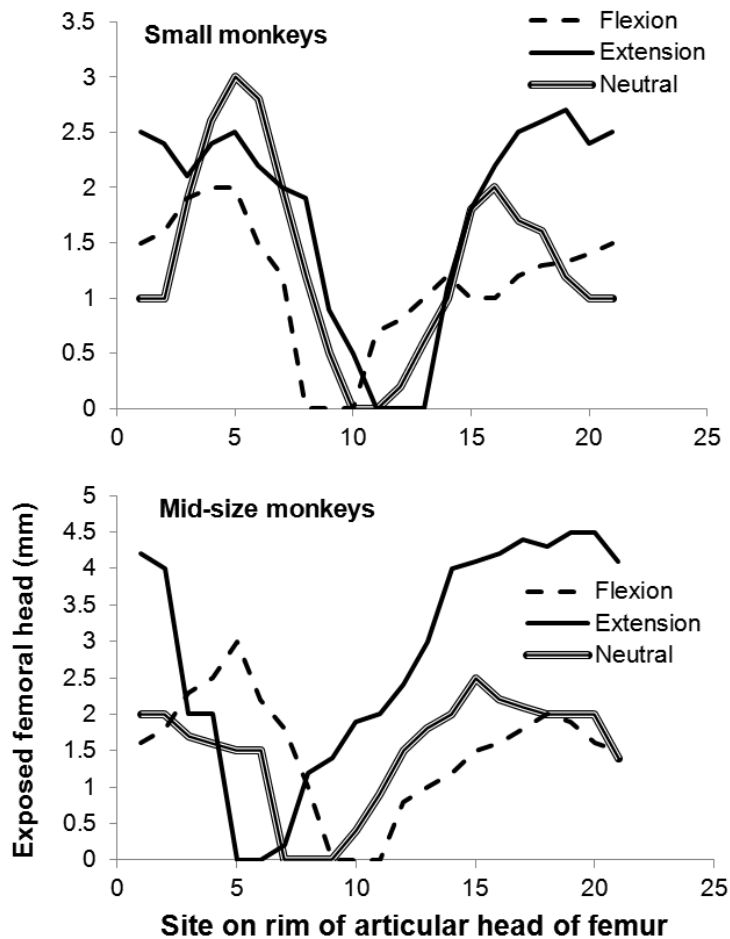


Figure 4.

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: *Sequinus geoffroyi*, and b) Mid-sized: 12 *Cebus capucinus*, 5 *Ateles geoffroyi*, and 4 *Alouatta palliata*. Numerical values at 0.0 indicate sites on the head of the femur that were in complete contact with the hip socket.

Dental impression clay and Autodesk computer 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 were 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

Use of climbing gear enabled us to acquire data on primates and their habitats in ways that few studies on movement ecology have achieved; however, our rigorous approaches may not fully describe events from an arboreal primate's perspective. This is a difficult quality of the forest to accurately assess, according to [Bezanson et al. \(2012\)](#). We are not arboreal primates, thus parameters such as inter-branch space, thorn abundance, stem size, stem angle, and so forth may have little impact on the movements of highly agile and skilled primates. Furthermore, we observed frequent obstacles to travel tended to be unpredictable substrates, in which branches snapped as a monkey was poised to leap, woody walkways abruptly collapsed and tumbled downward, winds swirled canopies in chaotic manners, and other unpredictable events that sent primates into abrupt, chaotic postures. We took note of these actions; however, habitat data that provided the greatest reliability and gave the best sense of the structural character of the arboreal habitat was canopy connectivity, based on descriptions by [Madden et al. \(2010\)](#), and [Raboy et al. \(2004\)](#). By climbing into various tiers of the forest, we found canopy connectivity extending in vertical and horizontal directions, with each calculated category of connectivity (open, semi-open, closed) speeding or slowing down our progress accordingly as we moved through canopies (Fig. [5A](#)).

With use of canopy connectivity as a consistent, defining parameter for canopy complexity regarding primate movement ecology, we assumed that leg postures would vary according to the degree of connectivity of the rainforest patch being traversed. However, our data did not support this association. One explanation for this lack of correlation between canopy

connectivity and leg action may be due to improper assessment of posture, since monkeys were often in visually disrupted and dappled canopy habitats. As was done in the study of forest architecture, we strived for accuracy by simplifying data into categories with consistent inter-rater reliability; in this case it became the five basic types of leg postures displayed in Figure 3. Based on our assessment of canopy structural complexity and primate leg postures, it appears likely that the monkeys observed in this study frequently conducted extreme leg action, regardless of structural complexities in rainforest, as revealed in Table 1. These data indicate that primates employ physical finesse and extreme postures as they address a wide range of obstacles in their routes of travel; a concept also supported by the work of many others (e.g. [Beisner & Isbell 2009](#), [Demes et al. 1999](#), [Dunbar et al. 2004](#)).

Canopy architecture and scattered forest resources probably influence the movement ecology of arboreal monkeys in our study; however, a different situation exists for the same species of captive monkeys. 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, as indicated in Figures 3 & 5B. Hip flexion is common in artificial habitats where primates have little motivation to forage, to maintain contact with a social troop, or to avoid hazards ([Jurmain 2000](#), [Shively 2012](#), [Turnquist 1985](#), [Waite et al. 2010](#)). Thus, differences in the movement ecology we observed between captive and wild populations make sense when considering the ecological dissimilarities between wild and artificial habitats. In regards to juvenile and adult movements in our field study, we wondered whether adults would 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). It is likely that a primate's movement ecology is shaped by environmental forces, and that there is similar potential for wide ranging mobility and vigorous physical activity in both adult and juveniles.

Based on results from this study, it appears that wide ranging leg postures are a common aspect of a neotropical primate's movement ecology, and it is likely that such movements play a role in fostering the continued capacity for future mobility. Unlike most other mammals, primates have wide-ranging appendicular capabilities that contribute to an active lifestyle and an exceptionally long potential life-span (Larson et al. 2001, Nakai 2003, Okada 1996, Rothschild & Woods 1992). Even early humans had more extreme walking gaits than their contemporaries in East Africa (Musiba et al. 1998). Our study assessed diverse contacts within the hip of monkey cadavers, but we can only speculate about how this influences movement ecology during a primate's lifetime, since fluid pressure in living tissues helps to manage load and pressure distribution, as suggested by Macirowski et al. (1994), and Nagura et al. (2006).

Conclusion

It is general knowledge that monkeys routinely use diverse body postures to address immediate challenges in rainforests, where scattered resources and complex habitat structure demand that a primate frequently employ extreme physical finesse to survive. Wide-ranging body postures are a core characteristic of a primate's movement ecology; evidenced by ecological and anthropological studies on this group. What is not clearly understood is the connection between body postures as responses to specific types of forest architecture and how forest structure may influence a monkey's continued capacity for wide-ranging mobility

over time. We observed wild monkeys to employ diverse leg postures in a variety of canopy types, regardless of whether forest architecture was relatively open or contained interconnected canopies with abundant potential routes of travel. Rain forests appear to induce wide-ranging leg movements in wild neotropical monkeys; movements which are not matched by the same species of monkeys inhabiting artificial environments with numerous structures for recreational movement. Furthermore, as a wild primate employs frequent wide-ranging leg movement when navigating rain forest canopies, these leg actions result in widely dispersed contacts between the articulating surfaces within the hip, potentially maintaining cartilage and contributing to the longevity of that joint. Thus, a connection may exist between rain forests, the leg action of wild monkeys, and the continued capacity to move over time. This subtle connection, which centers on rain forest complexity, may ultimately translate as increased time to expand territories, mate, and to out-compete those individuals that can not maintain a highly mobile daily regimen in this long-lived group of animals.

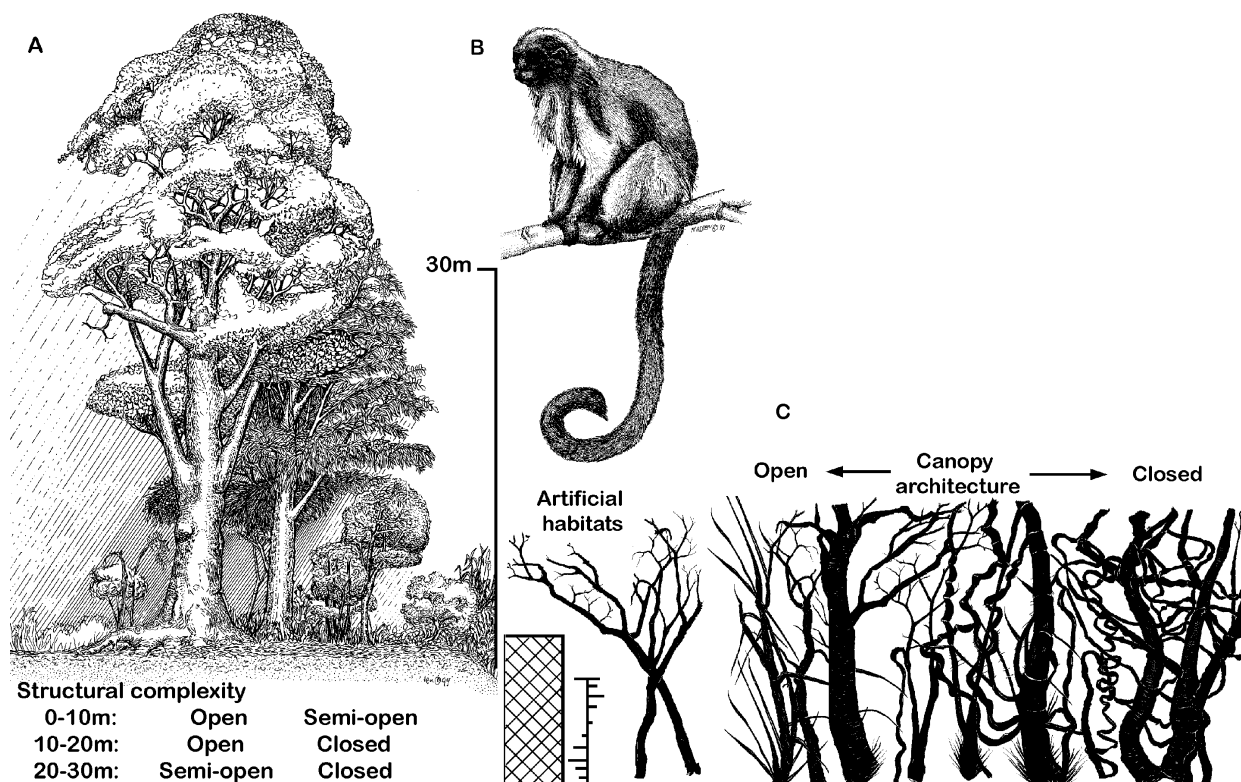


Figure 5.

A. Forest architecture based on measurements of woody growth at ground level, and as assessed through climbing ascenders at 10 m intervals in rainforests up to 30 m on Isla Barro Colorado, Panama and La Suerte, Costa Rica. **B.** Tamarin in hip-flexion. **C.** Profile of structural complexity in different patches of rainforest, and in artificial environments assessed at Mickie Grove, San Francisco, and San Diego Zoo, California (modified from Madden *et al.* 2010).

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