

Captive Orangutan Locomotion and Its Relation to the Origin of Human Bipedalism

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One of the prominent questions in paleoanthropological studies is the origin of bipedalism. There have been several hypotheses presented on the ancestral type of locomotion that predated bipedalism. These hypotheses include a terrestrial knuckle-walking quadrupedal ape, a brachiating hylobatid-like ancestor, a palmigrade terrestrial ape, and a climbing arboreal ape. Thorpe et al. present an extension to the climbing hypothesis with the data that they gathered from wild orangutans of the Gunung Leuser National Park in Sumatra, Indonesia (2006, 2007). They present the hypothesis that bipedalism originated with an arboreal ape similar to extant orangutans, and they provide that the orangutan locomotor data that they gathered supports this claim. This paper includes locomotor data that I collected from captive orangutans in the Fort Wayne Children's Zoo. The two data sets are not correlative, but my observations of assisted and unassisted bipedalism in the captive orangutans lend some support to the climbing hypothesis. When considering the functional anatomy of the wrist and ankle of extant primates and extinct hominins, the answer still remains inconclusive.

INTRODUCTION

The question of what makes one human may have multiple answers. In the past, it was often assumed that large brains separate us from the apes. Others said it was our tool-making ability. These two opinions have been proven false, since human ancestors had much smaller brains than modern humans, and we have also observed the tool-making abilities of chimpanzees. It is our mode of locomotion, our bipedalism that separates humans and recent human ancestors from the apes, but at one point in time there was a selective advantage for an ape ancestor to stand up on its hind limbs and walk bipedally. The hypotheses for this selective advantage are an entirely separate topic. In this paper I will go more in depth on the type of ape ancestor that was the precursor to the evolution of bipedalism. The four hypotheses that I will consider are a brachiating hylobatid, a digitigrade or palmigrade terrestrial quadrupedal ape, a terrestrial knuckle-walking quadrupedal ape, and a climbing arboreal ape. The former two have little anatomical and paleontological evidence to support them, so I will focus the majority of this discussion on the latter two.

The brachiating hylobatid ancestor hypothesis was proposed by Morton (1926) and furthered by Tuttle (1974, 1975, 1981). The ancestor was believed to be a small-bodied climber with tendencies to stand bipedally while foraging (Richmond, et al., 2001). Additions to the paleontological record have helped researchers abandon this hypothesis. Early hominin traits such as long curved fingers, a broad thorax, and mobile shoulder and wrist joints, features related to climbing, are the only support for this model (Richmond, et al., 2001). Overall, hominin body size is too large for the small-bodied hylobatid ancestor hypothesis to be considered (Jungers, 1988; McHenry, 1992; White et al., 1994, Senut et al., 2001; Haile-Selassie, 2001; Richmond, et al., 2001), and there would have had to be a rapid body size increase for this hypothesis to be plausible (Richmond, et al., 2001).

The palmigrade terrestrial quadruped model claims that the ancestor of bipeds was a monkey-like anthropoid. This was developed by Straus (1949), based on his research on the distinct anatomical differences between the hand of a human and an ape (Richmond, et al. 2001). This hypothesis has been abandoned due to more recent molecular evidence that humans are closely related to extant apes. Expectations for this ancestor are robust phalanges with little to no curve and carpals and tarsals with increased joint areas in order to reduce the stress from proximodistally directed forces (Richmond, et al., 2001). The level of curvature in hominin manual and pedal phalanges suggests that they were using these features for climbing (Tuttle, 1981; Susman et al., 1984), ruling out a purely terrestrial plantigrade ancestor.

The current two most accepted hypotheses are the knuckle-walking ape ancestor and arboreal climbing ape ancestor. These have the most paleontological and anatomical evidence. The knuckle-walking hypothesis suggests that the last common ancestor to humans, chimpanzees, and gorillas had the adaptation of knuckle-walking. The arboreal climbing hypothesis argues for an ancestor adapted to life in the trees that utilized a wide variety of locomotion, including suspensory, pronograde, orthograde, and vertical climbing positions. Proponents of this hypothesis argue that this arboreal ancestor did not knuckle-walk (Richmond, et al., 2001). I will discuss anatomical and paleontological evidence later in this paper.

Thorpe et al. (2007) argue that the ancestral ape was most likely exclusively arboreal and adapted bipedalism as a safer way to locomote across supports that are too flexible for other forms of locomotion. When early hominins became terrestrial they retained long grasping forelimbs. Thorpe et al. looked at the locomotion of the only extant great ape that is fully arboreal, the Sumatran orangutan, as an example of what the prebipedal ancestor may have resembled.

METHODS

Study

I conducted the field study at the Fort Wayne Children's Zoo in Fort Wayne, Indiana from July 18, 2008 to August 8, 2008 for a total of ten hours spent at the zoo and additional hours poring over the recorded videos. I observed two orangutans in their captive environment, a twenty-two year old male and a twenty-four year old female. By following the example of Thorpe and Crompton (2006) and using the same positional terminology, I recorded the stationary and locomotor positional types of the two orangutans by using both hand-written notes and a Canon NTSC 2R40 Digital Video Camcorder. I recorded the stationary positions by hand and the locomotion by the video camera. The camera was set up on a tripod, which I picked up and carried to film the orangutans as they moved from one side of the room to the other.

During the day, the two orangutans are kept in a large room so that the public can watch them. This room is one of the larger artificial habitats in the zoo but still relatively small considering the distances wild orangutans travel in a day. The habitat resembles a rainforest in that there are four large, leafless trees made of concrete that extend from the floor to the ceiling. Large branches extend from the trunks, and vines made of wire and rope, covered in plastic, twist their way around the room and descend to the floor. The floor and walls are made of concrete. The floor is covered with shallow water that drains out slowly while more water from a fountain in the tree pours out. The walls have painted scenes of trees, but one wall is made of thick glass to separate the orangutans from the people. The observer is unable to see the entirety of the room because of the high ceiling and an overhang of concrete that blocks the view of the ceiling. One wall has two doors covered by grates that lead to the pens where the orangutans

sleep at night. It is through these grates that they are also fed, but they cannot leave the large room to go to their pens until after 5:00 in the afternoon. There is natural light that enters from glass windows in the ceiling, which are also covered by metal grates. Usually there are blankets hanging off branches, and toys, such as plastic hats, in the habitat.

Locomotor behavior classification

As the orangutans traveled around their habitat, I recorded each stationary and locomotive position. The main locomotion categories I used were quadrupedal walk, tripedal walk, bipedal walk, vertical climb, vertical descent, torso-orthograde suspensory locomotion, torso-pronograde suspensory locomotion, forelimb-hindlimb swing, and bridge, each with its own subcategories. (See Appendix B for subcategories and frequencies.) The quadrupedal walk occurs when the ape is in a compressive, pronograde position and uses all four limbs while traveling. The tripedal walk is similar, but usually one limb is being used to carry something. The bipedal walk is when the ape is in a compressive, orthograde position and only uses its hindlimbs for traveling. The vertical climb and vertical descent are traveling vertically at an angle above 45°. Torso-orthograde suspensory locomotion happens when the ape suspends itself by its forelimbs only and travels in an orthograde position. Torso-pronograde suspensory locomotion takes place when the ape suspends itself by three or four limbs and travels in a pronograde position. The forelimb-hindlimb swing is neither fully orthograde nor pronograde, but rather uses forelimbs and hindlimbs in sequence as the ape travels suspended. The bridge describes when the ape crosses a gap between trees or branches in any manner. There are certain locomotor behaviors that Thorpe and Crompton (2006) note, which have relatively high frequencies that I was unable to witness, such as sway, which is locomoting from tree to tree by rocking a vertical branch back and forth until the animal is propelled forward enough to grab hold of the next tree. Obviously the orangutans I observed were incapable of performing sway because the trees are made of concrete. For a full discussion on the positional terms used in this study, refer to Thorpe and Crompton's "Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea" (2006), which in turn was borrowed from Hunt et al. (1996) and made more specific for orangutans.

RESULTS

I observed 377 locomotive and stationary bouts for the male, 230 for the female, for a total of 607 bouts. The main focus of this study is on the locomotion, however. The most frequent locomotor behavior of the two captive orangutans (14.8% of the locomotor bouts) is the symmetrical gait walk, which is a quadrupedal walk with a slow, regular gait. Surprisingly, the hand-assisted flexed bipedal walk was the second most frequent locomotion, tied with the forelimb swing (11.9%). The bipedal walk category occurred much more frequently than expected. Overall, the bipedal walk category (including extended and flexed bipedal walk and hand-assisted extended and flexed-bipedal walk) counts for 24.6% of the locomotion, 93% of which is hand assisted. Other high frequencies of locomotion include brachiation (11.1%), ipsilateral swing (9.4%), and flexed-elbow vertical climb (6.6%). From what I observed, the habitat extremely restricted locomotion, and there were also differences between the sexes. The female was far less active than the male, and in general, most locomotion that I witnessed was slow because the room did not permit scrambling. The male performed the same routine day after day, assumedly out of boredom. This may account for abnormally high frequencies of locomotive behaviors such as the ipsilateral swing. Normally, we would expect a much lower

frequency for this behavior, according to the more extensive data gathered by Thorpe and Crompton (2006).

DISCUSSION

Comparisons with Thorpe and Crompton's study (2006)

From the data gathered by Thorpe and Crompton (2006), Thorpe et al. (2007) concluded that a) bipedal locomotion can have selective advantages on arboreal apes, b) their data contradict predictions that suspensory locomotor modes or quadrupedalism are always used for unstable supports, and c) bipedalism evolved not from a quadrupedal knuckle-walking ancestor but rather the African apes innovated a new type of locomotion from an arboreal ancestor while hominins were the conservative ones by evolving terrestrial bipedalism from an adaptation of locomoting on flexible branches. Begun et al. (2007) in their response to these conclusions stated that knuckle-walking characters in some early hominins that were fully bipedal imply that this was an adaptation in a prior ancestor and that the hypothesis of Thorpe et al. would require knuckle-walking features to evolve independently within three different lineages (chimpanzees, gorillas, and humans). Within the human lineage, knuckle-walking would have had to evolve in the absence of knuckle-walking behavior, which is very improbable.

Overall, the data that I collected at the Fort Wayne Children's Zoo do not compare to the data collected by Thorpe and Crompton (2006) at Gunung Leuser National Park in Sumatra, Indonesia. The results of a contingency table X^2 statistical test show that there is a significant difference between the two, with a probability of less than 0.001%.

Table 1: Data Contingency Table

	Thorpe/Crompton (2006)	Current Study	TOTAL
Quadrupedal and Tripedal Walk	271	39	310
Vertical Climb and Descent	376	44	420
Bipedal Walk	105	60	165
Orthograde Clamber	316	0	316
Brachiation and Swing	211	80	291
Drop and Leap	30	0	30
Torso-Pronograde Suspensory	60	9	69
Bridge	45	12	57
TOTAL	1414	244	1658

Table 2: Expected Contingency Table

	Thorpe/Crompton (2006)	Current Study
Quadrupedal and Tripedal Walk	264.0	45.6
Vertical Climb and Descent	368.0	61.8
Bipedal Walk	141.0	24.3
Orthograde Clamber	269.0	46.5
Brachiation and Swing	248.0	42.8
Drop and Leap	25.6	4.41
Torso-Pronograde Suspensory	58.8	10.2
Bridge	48.6	8.39

Inspection of the expected frequencies reveals that vertical climb and descent, orthograde clamber, and drop and leap are all less frequent than expected, while bipedal walk is more frequent than expected among the orangutans at the Fort Wayne Children's Zoo. There may be several reasons for these differences: 1) the fact that the orangutans I observed live in a small room compared to the freedom that the Sumatran orangutans experience; 2) I spent only ten hours at the zoo observing their locomotion where Thorpe and Crompton spent a full year at Gunung Leuser National Park; 3) I encountered some problems with observer error and poor visibility due to zoogoers in addition to the concrete overhang obstructing the view; and 4) the artificial environment may not compare to the natural rainforests of Gunung Leuser. It is clear from the data that I have collected that the orangutans at the Fort Wayne Children's Zoo are restricted in their locomotion due to the structure of their environment. It makes some forms of locomotion, such as sway and ride impossible, while the overall rigidity of the support branches may make it easier for the orangutans to travel bipedally than may otherwise be the case for wild orangutans. There are no branches snapping under their weight, and there is no movement in the trees.

I did not observe a direct correlation between the size of the branches and hand assisted bipedalism as Thorpe and Crompton found. The orangutans walked bipedally on both large branches and thin ropes, and they did not exclusively walk bipedally on the vines. If it was too thin or if there were not enough hand supports for the symmetrical gait walk, they would employ the inverted quadrupedal walk. They also concluded that their observations show more compressive locomotion than suspensory, which suggests that orthograde positional behavior characterizes hominoid positional behavior, not suspensory. I found that 45% of the Fort Wayne orangutans' locomotion is compressive, and 55% is suspensory. From this data, it is not safe to say that compressive locomotion dominates orangutan locomotion. Suspensory behavior is associated with feeding more than other behaviors (Thorpe, Crompton, 2006), and they found that only 24% of behaviors were suspensory during feeding compared to 47% in Cant's study of Bornean female orangutans (1987). One day when I observed at the zoo, one of the keepers tossed coleslaw into the habitat from the ceiling, and the two orangutans spent the rest of the hour collecting it. I was only able to observe the female during this hour and found that suspensory behavior accounted for 36% of her positional behavior. This is roughly in the middle of the frequencies that Thorpe and Crompton and Cant found, though it may not be comparable since coleslaw normally does not rain from the sky in the wild. However, my assumption is that they can be compared since the orangutans traveled from tree to tree to collect the coleslaw like wild orangutans might travel to collect fruit. There may also be a difference between the sexes when it comes to feeding. Even though I did not record the positions of the male, I watched him and compared him to the female during the feeding, and he preferred compressive positions over suspensory to collect the food on the floor while the female suspended herself from the lowest branches to collect what was within reach. In fact, I witnessed the male perform more unassisted extended bipedal walking in this hour than I did in any of the other hours that I observed him. Thorpe and Crompton (2006) also note that 7.3% of the locomotion they observed was a bipedal walk, 75% of which was hand assisted. As noted earlier, the percentage of bipedal walk that I observed was a quarter of all locomotion. This lends support to an arboreal hypothesis for the origin of bipedalism.

Evidence for a knuckle-walking ancestor

If the last common ancestor of humans and chimpanzees was a knuckle-walker, we would expect hominins to have strongly flexed proximal interphalangeal joints and extended metacarpophalangeal joints in order to bear the weight distribution on the middle phalanges (Richmond, et al., 2001) as retentions of a knuckle-walking past. There is ample evidence to support a knuckle-walking ancestor by looking at features on the entire body, but for our purposes, I will concentrate on the wrist and hand. Derived features in knuckle-walkers include the transverse ridge on the metacarpal head, the distally projecting dorsal ridge of the radius, and the elongated intermediate phalanges. If the last common ancestor was a knuckle-walker, we would expect to see these features in human ancestors.

Knuckle-walkers are characterized by the limited amount of dorsiflexion that they are capable of doing with their wrist, which is a result of the distal edge of the radius abutting against the dorsal ridge of the scaphoid, as well as the transverse ridge on the head of the metacarpal. While knuckle-walking, these bony ridges prevent collapse from the weight that is placed on these joints (Aiello, Dean, 2002; Richmond, et al., 2001; Richmond, Strait, 2000). Though transverse ridges are absent on the metacarpals of *Australopithecus anamensis* and *Australopithecus afarensis*, the distal projection of the radius is present, suggesting a knuckle-walking past (Richmond, Strait, 2000). The absence of features such as transverse ridges is not enough to rule out a knuckle-walking ancestry because these features are absent in many extant African apes as well (Richmond, et al., 2001; Richmond, Strait, 2000). It has also been suggested (Gebo, 1996; Marzke, 1971; Richmond et al., 2001; Richmond, Strait, 2000) that the fusion of the os centrale to the scaphoid in African apes and humans is an adaptation to strengthen the wrist in an area that receives extreme amounts of stress during the act of knuckle-walking. This could be a retention in humans from a knuckle-walking ancestor because these two bones are not fused in the Asian apes. *Pongo* occasionally fuse the os centrale (Schultz, 1936), but this occurs later in life due to loading in adult locomotion, whereas humans and African apes begin the fusion in utero, meaning that this is genetically programmed and not a response to loading (Richmond et al., 2001).

When knuckle-walking, *Pan* and *Gorilla* place their weight on their medial phalanges, unlike *Pongo*, which place their weight on their proximal phalanges when fist-walking. There are no clear knuckle-walking adaptations in phalanges (Richmond et al., 2001), but one adaptation may be the elongation of the intermediate phalanx. The metacarpal and proximal phalanges are shorter with less curvature among humans and the African apes (Begun, 1988, 1993, 2004; Inouye, 1992; Susman, 1979) in contrast to Asian apes, which have long curved proximal phalanges. African apes and humans have long intermediate phalanges relative to the length of their proximal phalanges. The reason for having a long intermediate shaft and a reduced proximal shaft may be to provide a larger area for supporting body mass during knuckle-walking (Begun, 2004).

Evidence for an arboreal climbing ancestor

There are many features in hominins to suggest an arboreal ancestor. An ape with an adaptation for life in the trees, as we see in orangutans, has phalanges that are long with a greater degree of curvature than that in the African apes. This increases the length of the hand, which allows for gripping branches with a relatively large diameter (Aiello, Dean, 2002). When orangutans and chimpanzees walk bipedally, they use some muscles, such as the gluteus minimus, for the same function as humans do when walking (Richmond et al., 2001; Stern and

Susman, 1981). There are many arboreal traits in the early hominin skeleton, such as long, curved fingers and toes, pronounced ridges for the insertion points of forearm flexor muscles, and aspects of the shape of the metatarsal heads, that are related to arboreal mobility (Richmond, et al., 2001; McHenry, 1991; Stern, 2000). These retentions suggest an arboreal climbing ancestor. The fact that early hominins retain long grasping forelimbs adapted to an arboreal environment and evidence that hominins inhabited woodland environments 2 to 3 mya and not open or bush-savannah environments discredits the knuckle-walking hypothesis (Thorpe, et al. 2007). The OH7 (*Homo habilis*) hand has curved proximal phalanges, an ape-like scaphoid, and a well-developed flexor digitorum superficialis, a muscle that is inactive during knuckle-walking but active during climbing and suspensory locomotion, which suggests that OH7 was very adapted to life in the trees (Aiello, Dean, 2002).

Along with arboreal adaptations that early hominins retain, *Australopithecus afarensis* (Bush, et al., 1982; Tuttle, 1981; Stern, Susman, 1983; Ward, et al., 1999), *Australopithecus africanus* (Ricklan, 1988), and *Homo habilis* (Susman, Stern, 1979) also lack features related to a knuckle-walking adaptation. A transverse ridge is a well-defined dorsal ridge on the heads of the metacarpals that limits dorsiflexion of the wrist in a knuckle-walking posture. It is present in *Gorilla* and *Pan*, though it may be absent in the pygmy chimpanzee (*Pan paniscus*). *Pongo* lacks a transverse ridge on the heads of its metacarpals because it does not knuckle-walk and spends the majority of its time in the trees. *Australopithecus afarensis* also lacks transverse ridges (Aiello, Dean, 2002; Tuttle, 1981; Stern, Susman, 1983), which suggests that *A. afarensis* was neither knuckle-walking nor evolved from a knuckle-walking ancestor. There are no other indications of knuckle-walking adaptations in *A. afarensis*.

CONCLUSIONS

The conclusion by Thorpe et al. stating that there is a selective advantage to orthograde behavior is questionable. Because the orangutans that they observed walked bipedally across unstable supports more often than stable supports and used more compressive behavior than suspensory, they claim that this is a selective advantage for bipedalism in an arboreal setting. The orangutans I studied used bipedalism on unstable and stable supports without any noticeable difference and used more suspensory locomotion than compressive, especially while feeding. My observations, though they do not compare overall to the data of Thorpe and Crompton (2006), lend some support to the arboreal hypothesis because of the excessive amount of bipedalism that the Fort Wayne Children's Zoo orangutans performed. However, even with the increased frequency of bipedal walk relative to Thorpe and Crompton (2006), this kind of locomotion in orangutans is not the same as terrestrial bipedality because it is usually hand-assisted and it is not a striding gait.

There is evidence to support both a knuckle-walking and arboreal ancestor. Early hominins have weight-bearing features in the wrist, such as the fusion of the os centrale, while they retain long, curved phalanges from an arboreal past and lack the weight-bearing character of the transverse ridge on the metacarpals. Facts like these should not be ignored, and that is why neither hypothesis should be ruled out at this point. Gebo (1996) gives an alternative hypothesis to the knuckle-walker and arboreal climber hypotheses for a last common ancestor. He suggests that there were three main stages that our ape ancestors went through. The first stage was arboreal, quadrupedal, and vertical climbing. Brachiation and orthograde posture, such as we see in orangutans, then evolved. From this stage, they entered the last. These were the ancestors to African apes and humans, and they were knuckle-walking, terrestrial quadrupeds capable of

climbing. From this ancestor we get the weight-bearing wrist and other knuckle-walking features. Support for a vertical climber as the direct ancestor to the bipeds is waning, and Gebo's hypothesis provides us with a model that takes into account why humans and human ancestors have both knuckle-walking and arboreal morphological features. In my opinion, this is a more parsimonious model, which molecular evidence as far as we know cannot refute.

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Appendix A. Postural % bouts

	Male	Female	Both sexes	Thorpe/ Crompton results
Sit				
Sit	5.8	5.7	5.8	50.50
Sit/Forelimb-suspend	6.4	4.3	5.6	5.91
Sit/hindlimb suspend	1.3	0.0	0.8	0.22
Sit/forelimb-hindlimb suspend	1.6	0.4	1.2	0.17
Sit/forelimb compression	0.3	0.4	0.3	0.21
Sit/hindlimb compression	1.1	0.9	1.0	0.91
Sit/forelimb-hindlimb compression	0.0	0.9	0.3	0.03
Sit/forelimb suspend/hindlimb compression	0.3	3.0	1.3	0.13
Squat				
squat	4.0	5.2	4.4	0.10
squat/forelimb suspend	4.0	9.1	5.9	0.25
Cling				
bimanual cling	0.3	0.4	0.3	0.01
cling/forelimb suspend	0.3	0.0	0.2	0.08
Pronograde stand				
quadrupedal stand	1.6	0.0	1.0	1.48
tripedal stand	0.3	0.0	0.2	1.26
tripedal stand/forelimb suspend	0.3	0.0	0.2	0.10
tripedal hindlimb crouch	0.0	0.4	0.2	0.07
*ipsilateral compression/hindlimb-forelimb suspend	0.3	0.0	0.2	
Orthograde stand				
extended bipedal stand	0.5	0.4	0.5	1.58
flexed bipedal stand	0.0	0.4	0.2	0.18
flexed bipedal stand/forelimb suspend	1.9	2.2	2.0	0.24
extended bipedal stand/forelimb suspend	2.7	1.7	2.3	1.09
extended bipedal stand/forelimb compression	0.3	0.0	0.2	0.07
bipedal compression	0.3	0.0	0.2	0.06
monopodal stand/forelimb suspend	0.5	0.9	0.7	0.77
monopodal stand/forelimb-hindlimb suspend	3.2	2.6	3.0	0.03
monopodal compression/forelimb suspend	0.5	0.0	0.3	0.06
monopodal compression/tripedal suspend	0.3	0.0	0.2	0.04
monopodal compression/forelimb-hindlimb suspend	1.1	0.0	0.7	0.20
monopodal stand/hindlimb cling	0.3	0.9	0.5	0.01

Orthograde forelimb-suspend

unimanual forelimb suspend	0.3	0.9	0.5	1.17
bimanual forelimb suspend	1.9	2.6	2.1	0.15
forelimb suspend/sit	0.3	0.4	0.3	0.46
forelimb suspend/sit/hindlimb compression	0.3	0.4	0.3	0.01
forelimb suspend/squat	0.5	0.9	0.7	0.07
forelimb suspend/hindlimb compression	2.1	1.7	2.0	1.27
forelimb suspend/tripedal compression	0.5	0.4	0.5	0.01
forelimb suspend/hindlimb cling	0.5	0.0	0.3	0.11
forelimb suspend/lie	0.0	0.4	0.2	0.01

Orthograde quadrumaneous-suspend

trunk-verticle suspend	1.6	0.0	1.0	1.95
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Forelimb-hindlimb suspend

ipsilateral suspend	1.9	1.3	1.6	7.32
ipsilateral suspend/hindlimb compression	0.3	0.0	0.2	0.71
contralateral suspend	0.3	0.4	0.3	0.81

Pronograde suspend

quadrumaneous suspend	0.5	7.0	3.0	3.41
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Lie

lie	0.5	4.8	2.1	10.37
lie/forelimb suspend	0.5	5.2	2.3	0.03
*lie/hindlimb suspend	0.0	0.4	0.2	
sit/lie	0.0	0.4	0.2	1.75
sit/lie/forelimb suspend	0.0	0.4	0.2	0.03
*sit/lie/hindlimb suspend	0.3	0.0	0.2	

Postural bridge

pronograde bridge	1.3	0.0	0.8	0.08
orthograde bridge	0.5	3.0	1.5	0.04

Appendix B. Locomotor % bouts

	Male	Female	Both sexes	Thorpe/ Crompton results
Quadrupedal walk				
symmetrical gait walk	7.7	3.0	5.9	8.00
irregular gait walk (scramble)	0.3	0.0	0.2	9.36
tripedal walk				
tripedal walk	0.3	0.4	0.3	0.22
Bipedal walk				
extended bipedal walk	0.3	0.0	0.2	1.28
flexed bipedal walk	0.3	0.9	0.5	0.36
hand-assisted extended bipedal walk	3.7	5.7	4.4	2.88
hand assisted flexed bipedal walk	4.5	5.2	4.8	0.57
Vertical climb				
flexed-elbow vertical climb	3.2	1.7	2.6	5.59
ladder climb	0.0	0.4	0.2	0.18
vertical scramble	0.3	0.0	0.2	7.08
extended elbow vertical climbing	0.5	0.9	0.7	1.17
bimanual pull-up	1.1	0.9	1.0	1.28
vertical climb forelimbs only	0.3	0.0	0.2	0.18
Vertical descent				
rump-1st symmetrical descent	0.5	0.4	0.5	1.99
rump-1st cascade descent	0.8	0.0	0.5	0.18
rump-1st extended elbow descent	0.0	0.4	0.2	0.28
fire pole slide	1.1	0.0	0.7	0.18
pronograde slide	0.3	0.0	0.2	0.04
sideways vertical descent	0.0	0.4	0.2	1.07
cartwheel descent	0.3	0.4	0.3	0.14
Torso-orthograde suspensory locomotion				
brachiate	6.1	1.7	4.4	6.15
forelimb swing	6.1	2.6	4.8	8.25
flexed-elbow forelimb swing	0.0	0.4	0.2	0.18
Torso-pronograde suspensory locomotion				
inverted quadrupedal walk	1.1	1.7	1.3	2.28
Forelimb-hindlimb swing				
cartwheel swing	0.3	0.0	0.2	0.18
ipsilateral swing	6.1	0.0	3.8	0.07

Bridge

cautious pronograde bridge	0.5	0.0	0.3	2.53
inverted pronograde bridge	1.1	0.9	1.0	0.11
lunging bridge	0.5	0.9	0.7	0.14

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